Hydrobiologia (2005) 549:219–237
DOI 10.1007/s10750-005-5443-0

Primary Research Paper

Role of life history strategy in the colonisation of Western Australian aquatic systems by the introduced crayfish *Cherax destructor* Clark, 1936

Stephen Beatty*, David Morgan & Howard Gill
Centre for Fish and Fisheries Research, School of Biological Sciences, Murdoch University, 6150, Murdoch, Western Australia, Australia
*(*Author for correspondence: Tel.: 61-9-360-6322; Fax: 61-9-360-6303; E-mail: sbeatty@murdoch.edu.au)*

Received 22 August 2004; in revised form 16 March 2005; accepted 11 April 2005

Key words: *Cherax destructor*, translocation, life history, ovarian development, spawning period, growth

Abstract

The presence of the yabbie *Cherax destructor* in a number of wild aquatic systems in the Pilbara and Southwest Coast Drainage Divisions of Western Australia is documented. This is of great concern as all native freshwater crayfishes in Western Australia are endemic and restricted to the southwest, while the Pilbara Division has no native species. An introduced population of *C. destructor* was sampled monthly from the Hutt River (Pilbara Drainage Division) for determination of life-history and reproductive biology in a wild aquatic system in Western Australia for the first time. Proliferation in that system was attributed to specific traits including: attaining first maturity at the end of its first year of life; a protracted spawning period (July–January); relatively high mean ovarian fecundity of 210.2 (±9.24 S.E.); and a rapid growth rate (curvature parameter $K = 0.78$ and asymptotic orbital carapace length $OCL_{\infty} = 51.25$ mm ascertained from a seasonal von Bertalanffy growth curve) that was comparable to the larger sympatric marron *Cherax cainii* in this system. The life-history characteristics of *C. destructor* in the Hutt River were typical of many other invasive crayfish species and it has the potential to impact the unique aquatic ecosystems and the endemic freshwater crayfish species of the region.

Introduction

Once established in an aquatic system, the presence of exotic species is often viewed as permanent, with eradication difficult or almost impossible (Horwitz, 1990; Lodge et al., 1998). The omnivorous nature of freshwater crayfishes allows them to occupy many trophic levels, where they contribute to the structuring of ecosystems and may complicate predicted trophic cascades (Lodge et al., 1994; Nyström et al., 1996). Thus, introductions of non-native freshwater crayfishes are likely to alter the ecology of freshwater systems, and in particular the structure of food-webs (e.g., Hanson et al., 1990; Olsen et al., 1991; Momot, 1995; Nyström & Strand, 1996; Nystrom et al., 1999; Stenroth & Nyström, 2003). Furthermore, introductions of non-native crayfishes have been shown to cause a decline of native freshwater crayfish species or sub-species via predation and/or competition (e.g., Butler & Stein, 1985; Horwitz, 1990; Hill et al., 1993), the loss of genetic and morphological variation as a result of hybridisation (Horwitz, 1990), and/or the introduction and spread of disease (Holdich, 1988; Horwitz, 1990). Therefore, the translocation of non-indigenous freshwater crayfishes has often been detrimental to both naturally occurring crayfish species in particular and the receiving aquatic ecosystem in general.

Cherax destructor Clark, 1936 was first introduced into Western Australian farm dams for

aquaculture in 1932 (Austin, 1985; Morrissy & Cassells, 1992). In an attempt to prevent the spread of the species into wild aquatic systems of the naturally forested, higher rainfall region of the Southwest Coast Drainage Division that is home to all 11 endemic freshwater crayfish species of this State (Austin & Knott, 1996; Horwitz & Adams, 2000), the Department of Fisheries, Government of Western Australia only allows the culture of *C. destructor* east of Albany Highway between Perth and Albany (see Fig. 1). Inevitably, and despite this legislative restriction, *C. destructor* was first collected with a native freshwater crayfish species (*Cherax quinquecarinatus* Gray, 1845) in a wild aquatic system in Western Australia in 1982 (Austin, 1985).

Since that first record in a natural system, Morrissy & Cassells (1992) and Jasinska et al. (1993) reported the occurrence of *C. destructor* in natural watercourses of the southern Pilbara, i.e., the Irwin, Chapman, Bowes and Hutt Rivers (Morrissy & Cassells, 1992) and in streams of the Aiyennu and Beekeepers Caves, Hill River catchment (Jasinska et al., 1993) (Fig. 1). Whilst the latter two studies did not record it from the 26 sites that they sampled in natural watercourses throughout the Southwest Coast Drainage Division, they documented a considerable increase in its occurrence in farm dams west of Albany Highway, and suggested that the risk of further escape into natural river systems and coastal wetlands in the region was likely (Fig. 1).

Many biologists (i.e., Austin, 1985; Horwitz, 1990; Morrissy & Cassells, 1992; Jasinska et al., 1993) consider that the invasion of *C. destructor* into natural Western Australian aquatic systems poses a serious threat not only to the endemic freshwater crayfishes, but to the freshwater ecosystems of the

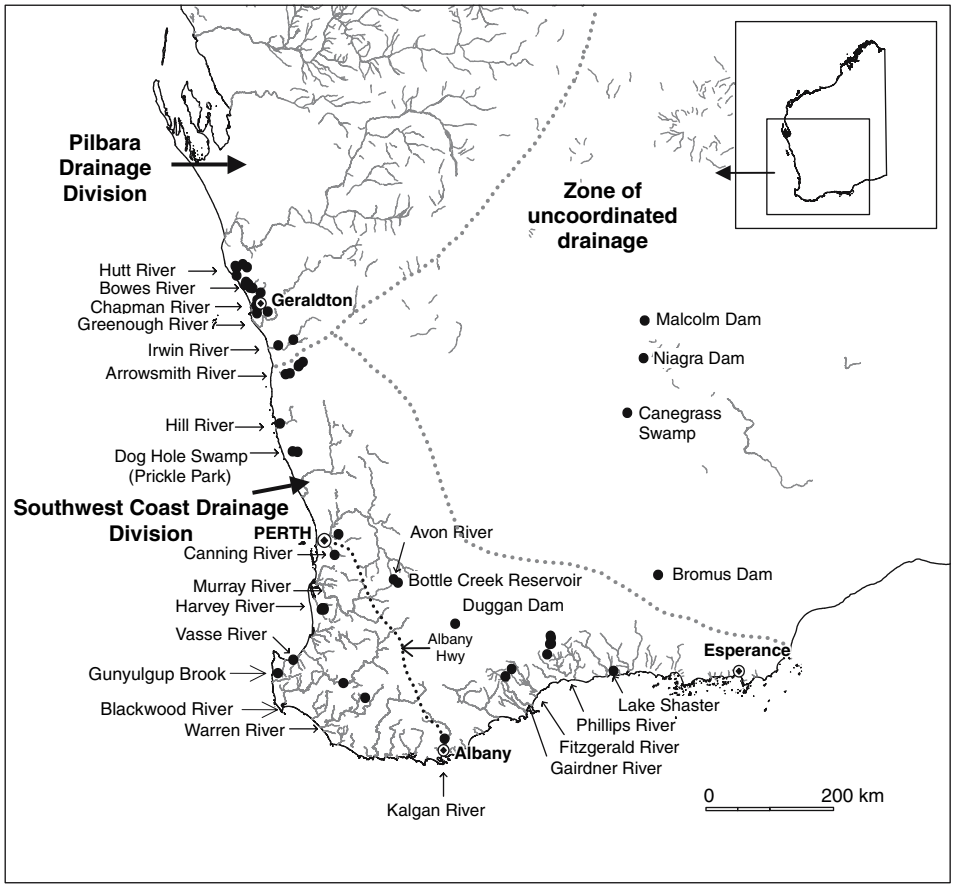

Figure 1. The location of the Hutt River study site and the major rivers (black dots correspond to capture sites) within Western Australia that *Cherax destructor* was captured.

region. Many of these concerns are based on the ability of *C. destructor* to tolerate variable physicochemical conditions thereby allowing it to inhabit a wide range of aquatic habitats, including temporary and permanent systems (Austin, 1985; Jasinska et al., 1993; Horwitz & Knott, 1995). Of particular note is its tolerance of low oxygen levels (Morris & Callaghan, 1998) and ability to burrow and survive in ephemeral aquatic habitats; environmental conditions that are common to many natural aquatic systems and farm dams in Western Australia (Morrissy, 1978). The success of *C. destructor* in colonising the natural systems of the southern Pilbara Drainage Division may also be attributable to it possessing life-history traits that are commonly displayed by other invasive species, e.g., rapid growth rate, young age at first maturity and high fecundity (see, for example, Honan & Mitchell, 1995).

Thus, the present study aimed to document the current distribution of *C. destructor* in aquatic systems in Western Australia and to describe the life-history characteristics of a successful population from the wild. These life-history parameters will be compared with those of endemic congeners, such as *Cherax cainii* Austin and Ryan, 2002; furthering our understanding of the threat, this species poses to sympatric native crayfishes.

Materials and methods

Distribution of Cherax destructor *in Western Australia*

Between 1996 and 2003, over 1300 sites were sampled for fish and decapods in all of the major drainage systems between the Fitzroy River in the north and the Thomas River in the south-east of Western Australia. Freshwater crayfish were captured using a back-pack electro-fisher (*Smith Root* Model 12-A); seine nets of 5 and 10 m lengths (mesh width of 3 mm) that fished to a depth of 1.5 m, manual scoop netting (nets of mesh sizes 250 μm and 10 mm); and box-style crayfish traps baited with poultry pellets. The latitude and longitude of each site as recorded using a hand-held Global Positioning System (GPS) and the *MapInfo*™ programme was used to produce a distribution map for *C. destructor* (see Fig. 1).

Hutt River study site and sampling regime

The Hutt River (Fig. 1) drains a catchment of ca. 1080 km^2 that has been extensively cleared for agriculture. In order to obtain a representative sample from the entire river system, *C. destructor* were captured from both the main channel of the Hutt River (28.2395° S, 114.3654° E) and the tributary Yerina Springs (28.1059° S, 114.3449° E) that were approximately 8 and 25 river km from the coast, respectively (Fig. 1). Between 50 and 182, *C. destructor* were captured from these sites each calendar month between January and December 2001 in the 2 h immediately after dusk. Sampling involved those methods described above. Considerable effort was employed to ensure that all life-stages were captured (see Discussion). Animals were placed immediately in an ice slurry for transport to the laboratory. All crayfish were dissected within 48 h of capture.

Environmental variables

Water temperature was recorded from the bottom of the water column at three locations at each site in the Hutt River. Day-lengths for Geraldton were obtained from the Perth Observatory.

Reproductive biology

The orbital carapace length (OCL, measured from the base of the orbital region to the posterior margin of the branchiostegite) of each individual was measured to the nearest 1 mm. The length at which 50 (OCL_{50}) and 95% (OCL_{95}) of individuals of female and male *C. destructor* matured in the Hutt River was determined by undertaking logistic regression analysis of the percentage contributions made to each length class by individuals that contained developing/mature gonads (stages III–VII and stages III–VI for females and males, respectively, see next section for staging protocol). Data were randomly re-sampled and re-analysed to create 1000 sets of bootstrap estimates. The medians of the bootstrap estimates were used as the point estimates of the parameters and the probability of maturity at each length category. The bootstrap estimates also determined the 95% confidence limits of the parameters. The logistic equation is:

$$P_{\mathrm{OCL}} = 1/[1 + \mathrm{e}^{-\ln 19(\mathrm{OCL}-\mathrm{OCL}_{50})/(\mathrm{OCL}_{95}-\mathrm{OCL}_{50})}] \quad (1)$$

where P_{OCL} is the proportion of *C. destructor* with mature gonads (see below) at length interval OCL. Only those individuals captured between May and January (i.e., immediately prior to and throughout the breeding period, see Results) were used in the analysis.

The gonads of female and male *C. destructor* were initially macroscopically assigned to developmental stages by following the descriptions of Johnson (1979), McRae & Mitchell (1995) and Beatty et al. (2003). As the macroscopic staging of the ovaries of *C. destructor* has not previously been verified histologically, and such an account of ovarian development has recently been used to provide a more comprehensive description of the reproductive biology of a freshwater crayfish (Beatty et al., 2003), the ovaries of up to 22 randomly selected female *C. destructor* in each month, and a sub-sample of up to three of each stage of testicular development, were prepared for histological examination using the protocol of Beatty et al. (2003). Histological sections of female and male gonads and individual eggs were examined under a compound microscope at 100× magnification. The maximum and minimum diameters of up to 30 randomly selected oocytes of each sectioned gonad, and also a number of attached eggs, were measured through the nucleus and the mean diameter calculated. The proportions of oocytes at different stages of development and within the different months were also determined. The ovarian stages were: I, virgin (immature); II, maturing virgin/recovering; III, developing; IV, developed; V, mature (gravid); VI, ripe (spawning) and VII, spent. If larger, orange oocytes were present in stage II ovaries, they were classified as mature as it was indicative of post-spawning resorption (see Results). The testicular stages were: I, virgin (immature); II, maturing virgin; III, mature; IV, gravid; V, spawning and VI, spent. It was deemed appropriate to add an additional male stage (i.e., VI, not described in Beatty et al., 2003) that was typified by swollen, well-developed testes and swollen proximal region of the vas deferens with relatively flattened, clear distal region of the vas deferens largely lacking spermatophore bundles.

The gonads of up to 116 *C. destructor* were removed in each month under a dissecting microscope. The excess moisture was removed and the ovary or testes weighed to the nearest 0.01 g. The GSI was calculated using the equation:

$$\mathrm{GSI} = 100(W_1/W_2) \quad (2)$$

where W_1 is wet weight of the gonad and W_2 is total wet weight of the animal. The GSIs of both mature (stage III–VII for females and III–VI for males) and immature (stages I/II) gonads were plotted separately so as not to bias the trend in the GSI of those that had spawned with those that had not (i.e., with immature gonads).

There was a single ovigerous *C. destructor* captured during the study period. The ovarian fecundity (F_{o}) was determined using ovaries at stages V and VI of 21 female *C. destructor*. Ovaries were removed and fixed in Bouin's fixative (Beatty et al., 2003). Fixed gonads were padded dry, weighed to the nearest 0.01 g, and a sub-sample of oocytes removed and counted under a dissecting microscope. The ovarian fecundity was then determined using the following formula:

$$F_{\mathrm{o}} = N_{\mathrm{s}} \cdot W_{\mathrm{g}}/W_{\mathrm{s}} \quad (3)$$

where F_{o} is the potential fecundity of the individual, N_{s} is the number of oocytes in the sub-sample of the ovary, W_{g} is the weight of the entire ovary and W_{s} is the weight of the sub-sample of oocytes.

The relationship between the F_{o} and OCL of *C. destructor* was determined by testing a number of regression equations, and that which displayed the highest coefficient of determination was used to describe the relationship.

Growth and mortality

The most appropriate description of the growth data for *C. destructor* was initially determined utilising the chi-squared method described in Schnute & Fournier (1980) and using the modification described in de Lestang et al. (2003). Although the Schnute & Fournier (1980) method fitted two or three normal distributions to the monthly length–frequencies, it was decided that age cohorts could only confidently be discerned in the first 12 months of life (see below) as

considerable overlap in the age cohorts of *C. destructor* existed for most months and therefore, a single or two normal distributions were fitted to length–frequency distributions in 2 mm OCL increments in each month.

Peak spawning activity during the extended breeding period of *C. destructor* was found to be July to August (see Results for rationale), however, the most easily followed 0+ length–frequency cohort was recorded for a 12-month-period from January as a result of an apparent spawning event between October and November. Therefore, December 1st was assigned as the hatching date; allowing for embryo development. The relationship of the OCL range of a cohort, within each monthly length–frequency distribution, to the previous and subsequent months was used to assign that cohort as either 0+ or 1+.

A modified version of the von Bertalanffy growth curve of Hanumara & Hoenig (1987) was fitted to the mean OCL distributions of either the one (0+) or two (0+ and 1+) age cohorts of *C. destructor* present in each month in the Hutt River. As growth is most rapid in the first few months of life in freshwater crayfish due to greater moult frequency (Reynolds, 2002), the modification of the equation was undertaken so that it was assumed that the maximum growth rate occurred in young *C. destructor*, i.e., less than approximately 5 months (de Lestang et al., 2003):

$$\mathrm{OCL}_t = \begin{cases} OCL_\infty\left\{1-\exp\left[-\left\{\frac{K(t-t'_0)}{12}+\frac{CK}{2\pi}\sin 2\pi\frac{(3)}{12}\right\}\right]\right\} \\ \text{if } t < t_s+3 \\ OCL_\infty\left\{1-\exp\left[-\left\{\frac{K(t-t'_0)}{12}+\frac{CK}{2\pi}\sin 2\pi\frac{(t-t_s)}{12}\right\}\right]\right\} \\ \text{if } t \geq t_s+3 \end{cases} \quad (4)$$

where OCL_t is the orbital carapace length estimate at age t months, 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 ($t_0 = t'_0 - (6C/\pi)\sin(0.5\pi)$), C determines the relative amplitude of the seasonal oscillation (where $0 \leq C \leq 1$) and t_s determines the phase of seasonal oscillation relative to t_0.

The instantaneous total mortality rate (Z, 1 year^{-1}) of *C. destructor* in the Hutt River was determined by employing a catch curve that plotted the natural logarithms of numbers surviving over age (Beverton & Holt, 1957; Ricker, 1975). An age-frequency distribution was generated via the creation of a length-converted catch curve (Pauly, 1983; King, 1995):

$$\ln\left[\frac{N_i}{\Delta t}\right] = \alpha - Zt_i \quad (5)$$

where N_i is the number of individuals in size class i, Δt the time taken to grow through the size class i, t_i is the relative age of the size class i, t_i is a constant and Z is the instantaneous total mortality rate (1 year^{-1}). The relative ages were determined using the inverse of the modified seasonal von Bertalanffy growth equation with $t_0 = 0$ as only relative ages were required (King, 1995).

The empirical equation of Pauly (1980) was used to estimate the instantaneous natural mortality rate (M, 1 year^{-1}).

$$\ln(M) = -0.0152 - 0.279\ln(L_\infty) + 0.6543\ln(K) + 0.463\ln(T) \quad (6)$$

where $L_\infty(\mathrm{OCL}_\infty)$ and K are the growth parameters of the modified seasonal von Bertalanffy growth equation and T is the average mean annual water temperature in the Hutt River. The instantaneous rate of fishing mortality (F, 1 year^{-1}) was determined using the equation (King, 1995):

$$F = Z - M \quad (7)$$

The exploitation rate (E) was then determined using the equation of Quinn & Deriso (1999):

$$E = \frac{F}{Z} \quad (8)$$

Results

Present distribution of Cherax destructor *in Western Australia*

Cherax destructor was recorded at 15 sites in the main channel and/or tributaries of the following major rivers of the Pilbara Drainage Division: Hutt, Bowes, Chapman, Greenough and Irwin rivers (Fig. 1). In the Southwest Coast Drainage Division, it was captured at 26 sites in the main channel, tributaries and/or water-supply dams constructed on the tributaries of the: Arrowsmith, Hill, Avon, Canning, Murray, Harvey, Vasse, Gunyulgup, Blackwood, Warren, Kalgan,

Gairdner, Fitzgerald and Phillips rivers (Fig. 1). *Cherax destructor* was also captured in Canegrass Swamp, a natural water body, and the Malcolm, Niagra and Bromus public water-supply reservoirs; located on natural watercourses in the Zone of Uncoordinated Drainage (see Fig. 1).

Environmental variables

The mean water temperatures for the Hutt River were reflective of the Mediterranean climate of the region; ranging from a minimum of 16.3 °C in August to a maximum of 27.7 °C in February. Day-lengths for nearby Geraldton increased from a minimum of 618 min in mid-winter to a maximum of 840 min in mid-summer.

Reproductive biology

The smallest mature female and male *C. destructor* captured during the spawning period measured 17 and 20 mm OCL, respectively (Fig. 2). The logistic regression analysis yielded an OCL_{50} of 21.6 mm OCL (95% confidence limits = 20.7, 22.4 mm OCL) and 26.5 mm OCL (95% confidence limits = 25.8, 27.1 mm OCL) for female and male *C. destructor*, respectively (Fig. 2). The OCL_{95} of female and male *C. destructor* was 28.0 mm OCL (95% confidence limits = 26.6, 29.6 mm OCL) and 31.2 mm OCL (95% confidence limits = 29.7, 32.8 mm OCL), respectively (Fig. 2).

Immature ovaries (stages I and II) were dominated by oogonia and chromatin nucleolar oocytes (stage I), with stage II ovaries also containing perinucleolar oocytes that had a size range of 100–600 μm with a modal ovarian diameter of 100–200 μm (Table 1 and Fig. 3). Perinucleolar oocytes continued to be present in stages III, IV, V, VI and VII ovaries with a bimodal distribution of mean oocyte diameters developing from stage IV. There was only one ovigerous female (stage VII) captured and it contained all developmental stages of oocytes (Fig. 3), including an apparent resorbing un-released yolk granule oocyte (mean diameter 1180 μm) (Table 1).

Virgin (immature, stage I) testes were very small, with a clear testicular mass and a thin, clear thread-like vas deferens that did not contain spermatophores. Maturing virgin (stage II) testes were semi-opaque and slightly thickened with discernable spermatocyte bundles, the vas deferens was thin and clear, and lacked spermatophores. Mature stages (III–VI) contained bundles of spermatozoa within spermatophores in the vas deferens, with stages V and VI also displaying clear distal regions of the vas deferens that lacked spermatophores (Table 2).

The temporal pattern in the mean oocyte diameter frequency distribution of *C. destructor* in the Hutt River was indicative of a protracted spawning period from July to January. Oocytes that had undergone primary vitellogenesis (100–600 μm) were found in all months of the year, whereas oocytes greater than 1000 μm (late yolk vesicle and yolk granule, Table 1) were found in females in all months aside from February and March. The onset of spawning occurred in July with the maximum oocyte size of *C. destructor* being 900, 1200, 1400, 1800 and 1650 μm in March, April, May, June and July, respectively.

The temporal trend in ovarian maturation also suggested a prolonged spawning period occurred (Fig. 4). Females with stage III gonads, which had completed primary vitellogenesis and contained late perinucleolar oocytes, were present in all months (Fig. 4). The percentage of stage VI (ripe) ovaries increased from 8.3% in May to 13.1 and 28.6% in June and July, respectively (Fig. 4). The single ovigerous individual (stage VII) was captured in August (Fig. 4). Stage VI ovaries continued to be recorded until December and were found in 4.6% of females (Fig. 4).

The temporal pattern in the developmental stages of the testes of male *C. destructor* in the Hutt River also suggested that an extended spawning period had occurred (Fig. 4). Between July and August, the percentage of male *C. destructor* with stages V increased from 0 to 3.7%, and those with stage VI rose from 0 to 18.5% (Fig. 4). The percentage of spawning (stage VI) testes then declined progressively to be present in 2.2% of male *C. destructor* in December (Fig. 4).

The trend in the mean GSI of mature *C. destructor* also supports the spawning period elucidated by the analysis of the temporal patterns in oocyte development and gonad stage development (Fig. 5). The mean GSI of mature female *C. destructor* increased from a minimum of 0.65 ($\pm$0.18 S.E.) in February to a maximum of 2.69

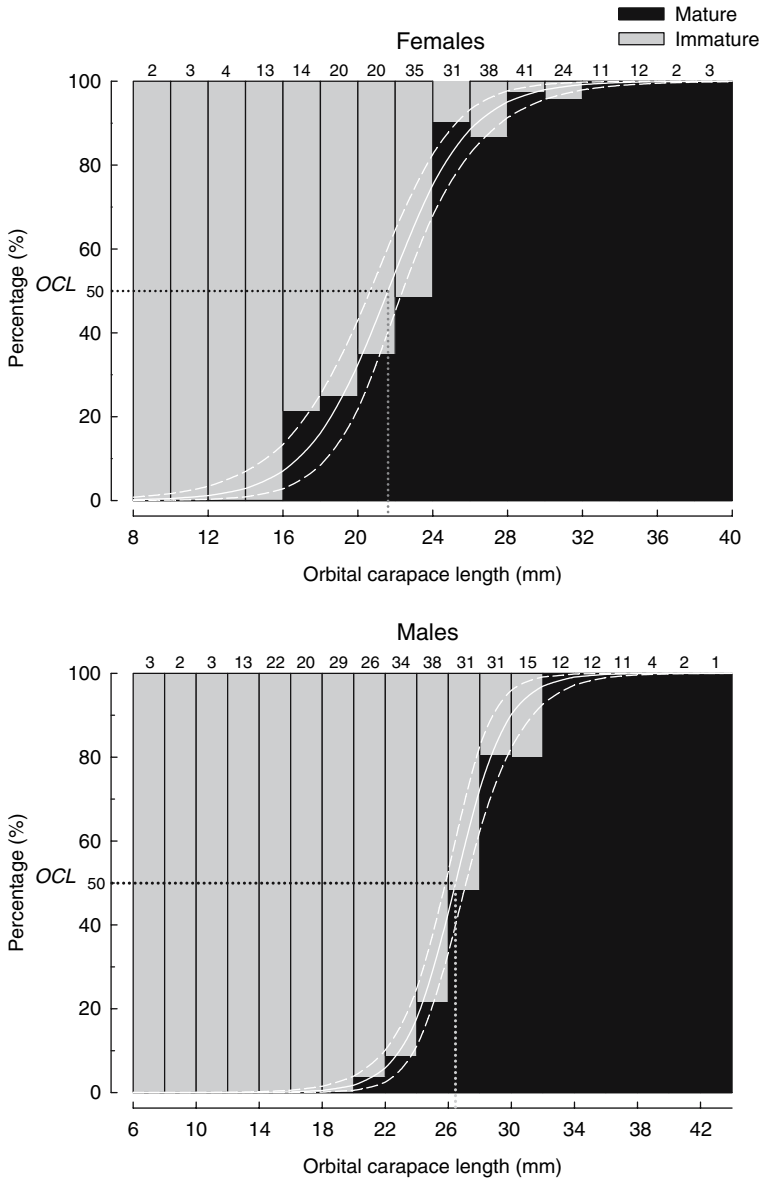

Figure 2. Percentage contributions of immature (i.e., stages I/II) and maturing/mature (i.e., stages III–VII and III–VI for females and males, respectively) gonadal development stages in sequential 2 mm OCL intervals of female and male *Cherax destructor* during the breeding season in the Hutt River, i.e., May to January. N.B.: The logistic curves (including 95% confidence limits) were fitted to the percentage contributions of *C. destructor* with maturing/mature gonads. The number of *C. destructor* in each length interval is given at the top of each column.

($\pm$1.15 S.E.) in July. The GSI then gradually declined to 1.27 ($\pm$0.25 S.E.) in December (Fig. 5).

A similar temporal trend was found in the mean GSI of mature males during the spawning period (Fig. 5). The major rise in the mean GSI of mature males occurred simultaneously with the rise in female GSI from May to July (Fig. 5) before gradually declining to 0.34 ($\pm$0.04).

The gradual decline in mature GSIs between July and December combined with the occurrence of stage VI gonads and also those stages that were

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

Ovarian stage	Mean GSI (±1 S.E.)	Macroscopic description	Maximum oocyte diameter (μm)	Histological description
I/II. Virgin/maturing virgin	0.35 ± 0.06	Thin strand like (stage I) or slightly thickened creamy yellow (stage II) ovaries.	600	Ovarian matrix dominated by oogonia, chromatin nucleolar and perinucleolar oocytes. Post-ovulatory follicles also present in recently spent ovaries.
III. Developing	0.70 ± 0.04	Thickened and bright orange oocytes visible in the ovarian matrix.	800	Perinucleolar oocytes that have increased in size reflecting primary vitellogenesis having occurred present. Ovarian epithelium that consists of flattened follicle cells is visible surrounding developing oocytes. Oogonia also present.
IV. Developed	1.43 ± 0.08	Thick with light-green oocytes dominating ovarian matrix and occasional orange oocytes also visible.	1100	Perinucleolar oocytes and oogonia continue to be present, however, ovarian matrix dominated by oocytes undergoing secondary vitellogenesis with yolk globules clearly visible in the cytoplasm.
V. Mature	2.65 ± 0.13	Swollen and large dark-green oocytes clearly dominate matrix.	1600	Larger oocytes with yolk granules and vesicles dominating the ovarian matrix surrounded by ovarian epithelium. Perinucleolar oocytes continue to be present.
VI. Ripe	3.71 ± 0.22	Very swollen with very large, dark grey-green oocytes dominating the ovarian matrix.	1900	Oocytes continue to increase in size with cytoplasm completely consisting of yolk vesicle and large yolk granules. Perinucleolar oocytes continue to be present.
VII. Spent	0.96	Predominantly creamy-yellow matrix with orange and green oocytes present throughout.	1200	Perinucleolar oocytes continue to be present along with post-ovulatory follicles and large, apparently unspent ova.

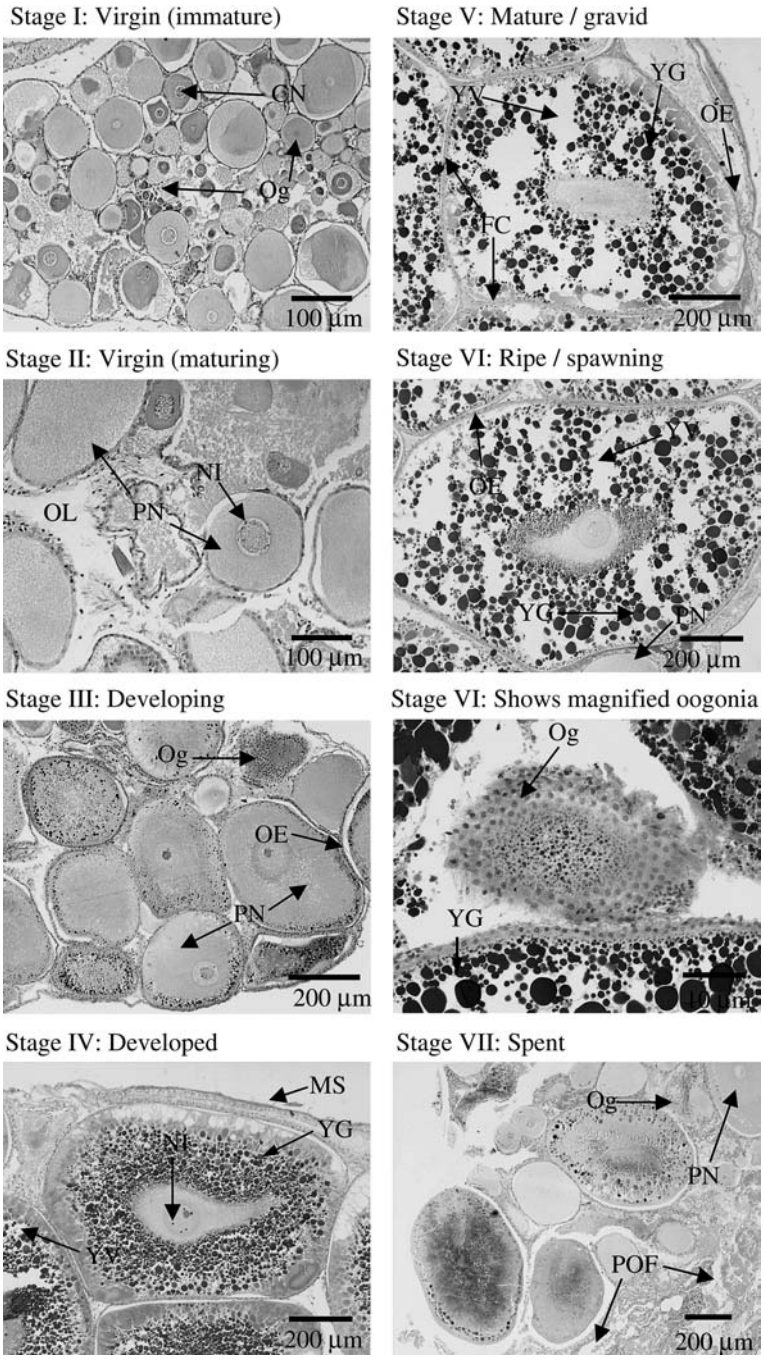

Figure 3. Microscopic appearance of the different ovarian developmental stage of *Cherax destructor* from the Hutt River, Western Australia. CN = Chromatin nucleolar; NI = nucleoli; YG = yolk granule; YV = yolk vesicle; POF = post-ovulatory follicle; FC = Follicle cell; OE = Ovarian epithelium; OL = Ovarian lumen; Og = Oogonia; PN = perinucleolar oocyte.

re-maturing suggest strongly that *C. destructor* in the Hutt River had an extended breeding season in which it could spawn more than once.

The one ovigerous *C. destructor* captured during the study in the Hutt River, which was recorded in August, had an OCL of 37 mm and a

Table 2. Macroscopic descriptions of the different stages of testicular development for male *Cherax destructor* (adapted from Beatty et al., 2003)

Testicular stage	Mean GSI (±1 S.E.)	Macroscopic description
I. Virgin	0.17 ± 0.01	Very thin testes, strand-like transparent vas deferens
II. Maturing virgin	0.27 ± 0.02	Slightly thickened testes and vas deferens
III. Mature	0.35 ± 0.02	Thickened testes, opaque vas deferens
IV. Gravid	0.41 ± 0.03	Swollen testes, milky opaque vas deferens
V. Spawning	0.44 ± 0.03	Swollen, milky vas deferens with distal region being less opaque than proximal and mid regions
VI. Spent	0.53 ± 0.03	Well developed testes and relatively flattened, clear distal region of the vas deferens

pleopodal fecundity of 263. The ovarian fecundity of 21 female *C. destructor* (size range of between 32 and 39 mm OCL) ranged from 149 to 295 with a mean of 210.2 (±9.24 S.E.). The relationship between the F_o and OCL of 21 *C. destructor* was best described by the quadratic equation: $F_o = 0.698\text{OCL}^2 - 36.751\text{OCL} + 671.056$, $R = 0.627$.

Growth and mortality

The sex ratio of *C. destructor* in the Hutt River was 1 female: 1.066 males. The length–frequency distributions of *C. destructor* largely supported the spawning periods ascertained by the above analysis of the temporal trends in gonadal and oocyte development with newly released individuals first captured in November (size range of between 6 and 14 mm OCL and a mode of 10.6 mm OCL) estimated to be 2-month-old allowing for a relatively short, 1 month, incubation period prior to hatching, i.e., based on birth (hatching) in September (Figs. 6 and 7). The estimation of the incubation period is based on the study of Mitchell & Collins (1989), who found a short brooding period (i.e., egg and hatchling attachment) of 60 days between previous mating and re-spawning for *C. albidus* (now synonymised with *C. destructor sensu* Austin et al., 2003) and also that of (Rouse & Yeh, 1995) who found a 1-month incubation period.

The growth curve was fitted to the subsequent modes of the monthly normal distributions of OCL cohorts from ages 1 (January) to 12 (December) months (Figs. 6 and 7). The mode of the normal distribution of this subsequent 0+ cohort increased progressively to 13.9, 25.2 and 29.7 mm OCL in March, September and December at ages 3, 9 and 12 months, respectively (Fig. 6).

The modified seasonal von-Bertalanffy growth equation displayed a good fit to the modes of the monthly normal distributions of OCL cohorts (coefficient of determination 0.9989) (Table 3 and Fig. 7). The equation yielded values for K, OCL_∞ and t_0 of 51.25 mm, 0.78 and −1.54 (Table 3). Using the growth equation, the predicted OCLs of *C. destructor* at ages 6 and 12 months were 18.5 and 29.0 mm OCL, respectively (Table 3 and Fig. 7).

The length-converted catch curve revealed a total instantaneous mortality rate for *C. destructor* in the Hutt River of 2.91 year^{-1} (Table 3 and Fig. 8). From the empirical formula of Pauly (1980), the instantaneous natural mortality was 1.09 year^{-1} and therefore fishing mortality and exploitation rates were 0.62 and 1.82 year^{-1}, respectively (Table 3).

Discussion

Distribution of Cherax destructor *in Western Australia*

The current study confirmed the presence of *C. destructor* in natural water bodies of the Pilbara Drainage Division as previously recorded by Morrissy & Cassells (1992) and Jasinska et al. (1993). In contrast to these studies, and that of Austin (1985) who collected *C. destructor* from wild systems outside of the 'yabbie exclusion zone' in the Southwest Coast Drainage Division of Western Australia, this study also documents the

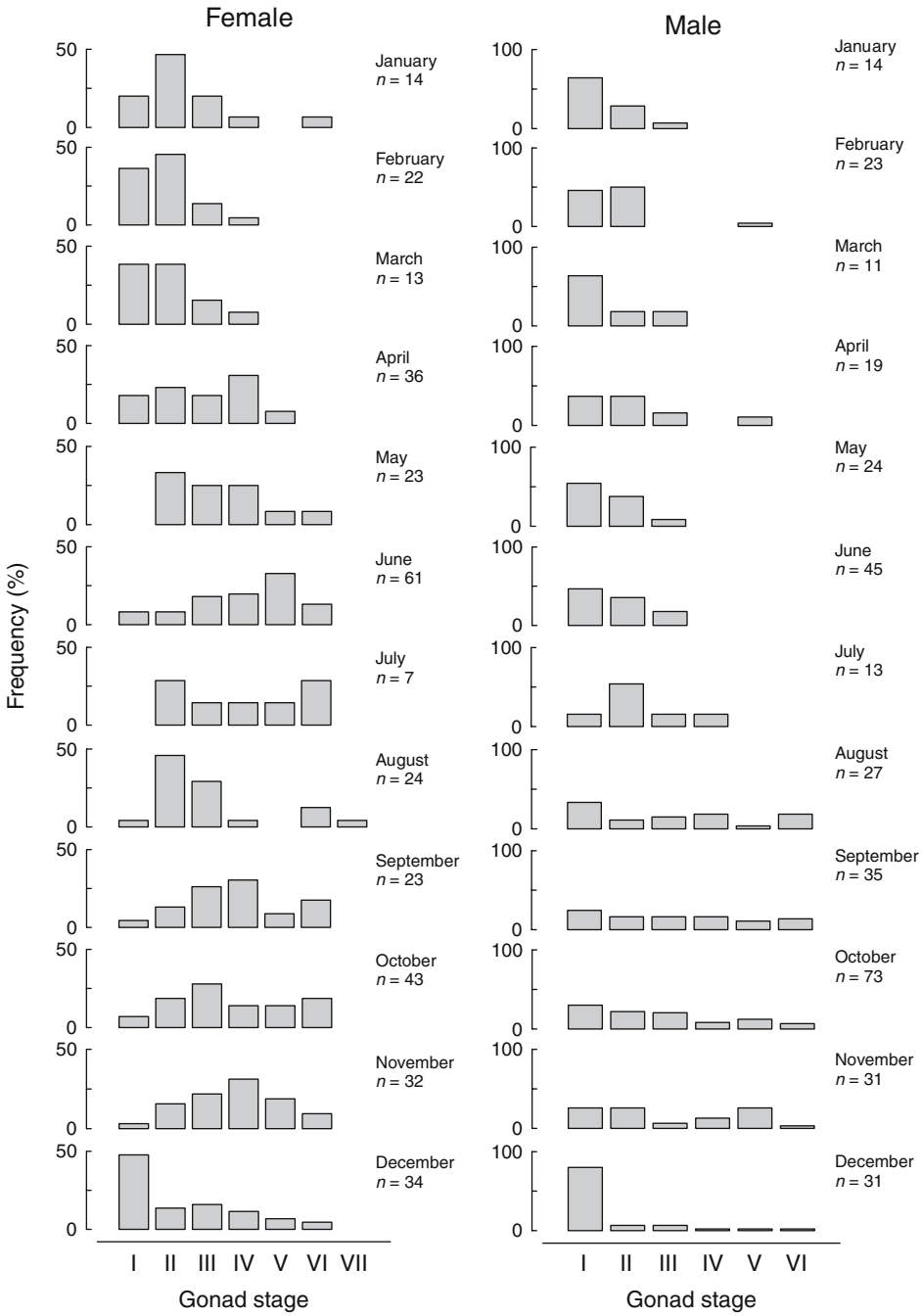

Figure 4. Monthly frequencies of different gonad developmental stages of female and male *Cherax destructor* in the Hutt River.

presence of this species in wild systems in the Zone of Uncoordinated Drainage and within the 'yabbie exclusion zone' (Fig. 1).

Many of the aquatic systems in the Southwest Coast Drainage Division have become salinised, which has resulted in a reduction in the inland ranges of native fish and crayfish species (Morrissy, 1978; Morgan et al., 2003). The ability of *C. destructor* to tolerate relatively high salinities (~12 ppt in Mills & Geddes, 1980), coupled with

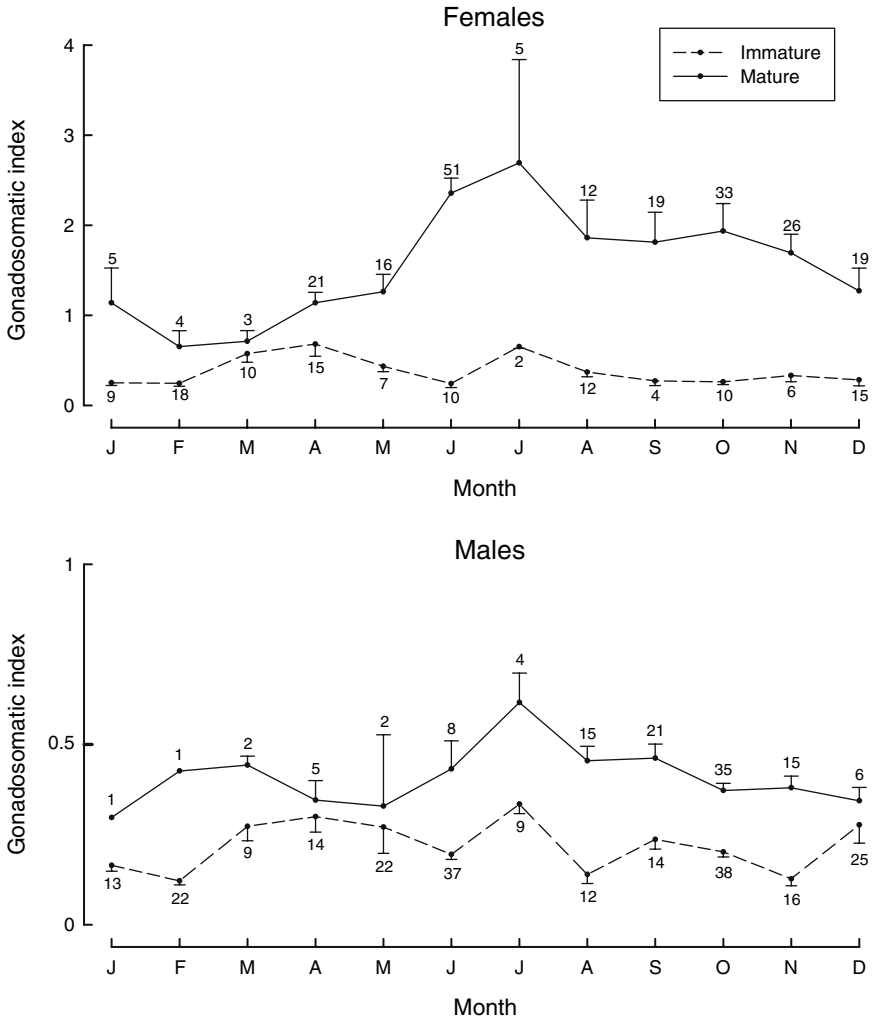

Figure 5. Mean gonadosomatic indices (±1 S.E.) for female and male *Cherax destructor* in the Hutt River with gonad stages I/II (i.e., immature) and gonad stages III–VII and III–VI (i.e., mature/maturing) for females and males, respectively.

its tolerance of hypoxic conditions (Morris & Callaghan, 1998), would be conducive to it further expanding its range in southwestern Australia. The potential impact on the structure and function of aquatic ecosystems in southwestern Australia, and particularly those occupied by endemic freshwater crayfishes, is of major concern given the life history parameters exhibited by *C. destructor* in the Hutt River (see below).

Reproductive biology

Abdu et al. (2000) and Beatty et al. (2003, 2005) clearly demonstrated that histological examination provides a very precise description of ovarian development in freshwater crayfishes. Furthermore, Beatty et al. (2005) showed that patterns in the frequencies of female gonadal development stages (based on histological examination) provided an accurate description of their reproductive biology. Thus, although only one ovigerous female was captured in the current study, presumably as a result of the burrowing behaviour of ovigerous females (e.g., Beatty et al., 2005), the use of the above techniques is likely to provide the most accurate description of the reproductive biology of *C. destructor*. The capture of juveniles in every month further supports the descriptions of the

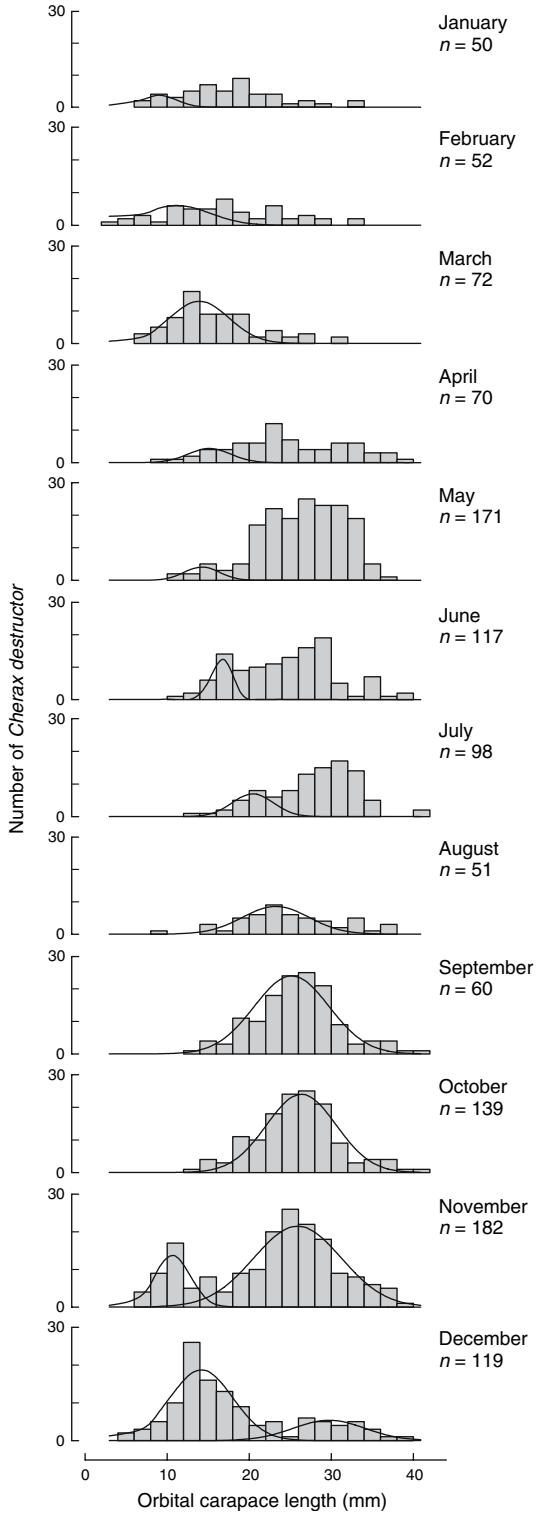

Figure 6. Orbital carapace length–frequency histograms in each month for *Cherax destructor* in the Hutt River. Normal distributions have been fitted to the one or two size cohorts present in each month used to fit the von Bertalanffy growth curve. N.B.: n = sample size.

reproductive biology of this species provided below.

The spawning period of *C. destructor* in the Hutt River occurred between July and January (Figs. 4 and 5) and was similar to that recorded in farm dams in southwestern Western Australia, where newly released juveniles were found throughout the period between October and February (Morrissy & Cassells, 1992). Given the prolonged spawning period, it is likely that *C. destructor* underwent multiple spawning events as evidenced by GSIs and length–frequency distributions with newly released juveniles being captured in November and again in January (Fig. 6).

The initiation of secondary vitellogenesis in the current study occurred from stage III as revealed by the presence of early yolk vesicles (Table 1). Of particular note was the presence of this stage in all months, this is in contrast to their absence in *C. cainii* in all months from June to November, inclusive (Beatty et al., 2003). Based on specimens of *C. albidus* (*C. destructor sensu* Austin et al., 2003) held in aquaria McRae & Mitchell (1995) proposed that, following spawning, ovaries were held in a constant state of readiness, with oocytes present at the end of primary vitellogenesis able to undergo secondary vitellogenesis (increase in mean size from 400 to 2000 μm) rapidly. In a later study, McRae & Mitchell (1997) noted that, provided the female *C. destructor* was not ovigerous and had sufficient nutritional reserves, the presence of males was a cue for rematuration. Thus, the demonstrated ability of *C. destructor* to undergo rapid ovarian rematuration and the fact that males were always present, further supports our argument that this species underwent multiple spawning in the Hutt River, and is likely to be able to spawn multiple times in other southwestern Australian systems given such favourable conditions.

Multiple spawning has previously been documented in the invasive freshwater crayfish, *Procambarus clarkii* (Girard, 1852) (Gutiérrez-

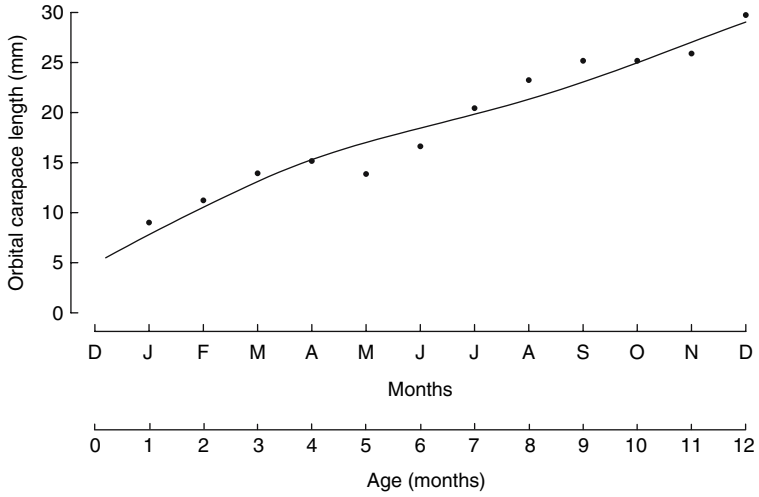

Figure 7. Modified seasonal von Bertalanffy growth curves of *Cherax destructor* in the Hutt River. Curves are fitted to the monthly mean orbital carapace lengths at age of the 0+ and 1+ cohorts.

Yurrita & Montes, 1999). Those authors considered that such a reproductive strategy allowed it to become established in new and varied environments. At high densities *P. clarkii* was found to have the ability to alter the structure and function of ecosystems, becoming an ecosystem engineer (keystone) species (Gutiérrez-Yurrita & Montes, 1999 and references therein). Given the previously mentioned wide range of impacts that introduced species of freshwater crayfish may have, the establishment of *C. destructor* in the Hutt River would have likely resulted in it altering the structure and function of this ecosystem and others in which it has become established (Fig. 1).

Life-history strategies of freshwater crayfishes have previously been placed into two categories; winter and summer brooders. Many crayfishes that are considered invasive species (e.g., *P. clarkii*, Gutiérrez-Yurrita & Montes, 1999) are summer brooders. Summer brooders generally have strategies that include: short brooding periods in summer; an a-synchronous spawning regime within the breeding period (that may include multiple spawning events); the ability to exist in a wide range of permanent and temporary aquatic systems; relatively high fecundities with small eggs; rapid growth rates and a short life span (Honan & Mitchell, 1995). Many of these traits are typical of those generally associated with *r*-selected life-histories. *Cherax destructor* in the Hutt River therefore displayed life-history traits consistent with a summer-brooding, *r*-selected species (Table 3).

The ability to undergo multiple spawning, when conditions are suitable undoubtedly aids in the ability of *C. destructor* to occupy temporary habitats and rapidly colonise a range of new aquatic environments. This strategy is also exhibited by the endemic congener *C. quinquecarinatus*, which also occupies a wide variety of temporary and permanent habitats in this region (Table 3, Beatty et al., 2005). By contrast, the large sympatric endemic *C. cainii* only spawns once during its breeding period, occupying permanent aquatic systems (Table 3, Beatty et al., 2003, 2004). The reproductive strategy exhibited by *C. destructor* would have enabled it to rapidly proliferate in the Hutt River; attaining a similar density to that of *C. cainii* (Beatty et al., 2004) that was translocated into this system prior to the introduction of *C. destructor* (Morrissy & Cassells, 1992). Similarly, its establishment in other aquatic systems in Western Australia would be aided by its reproductive strategy; potentially enabling it to become the most abundant crayfish species in many of those systems.

Growth

The length–frequency distribution of *C. destructor* in the Hutt River revealed the main recruit-

Table 3. Comparison of life-history parameters for: *Cherax destructor* in the Hutt River, *Cherax cainii* in Lake Navarino (Beatty et al., 2003) and the Hutt River (Beatty et al., 2004), and *Cherax quinquecarinatus* in Bull Creek (Beatty et al., 2005)

Parameter	*Cherax destructor*	*Cherax cainii*	*Cherax quinquecarinatus*
Habitat range	Perennial/ephemeral	Perennial	Perennial/ephemeral
Habitat of population studied	Perennial river	Perennial river + reservoir	Perennial stream
Breeding period	July–January	July–December	August–February
Potential for multiple spawning?	Yes	No	Yes
Spawning rate of mature females (%)	29	10–96	43
Ovarian fecundity	210	443	82
Length at first maturity (OCL_{50}, mm OCL)	Females = 21.6; Males = 26.5	Females = 32.1–70.4; Males = 28.6–39.6	Females = 18.8; Males = 24.5
OCL_∞ (mm)	51.25	101.9	Females = 59.6; Males = 73.8
K	0.78	0.42	Females = 0.29; Males = 0.25
t_0 (month)	−1.54	1.54	Females = 0.18; Males = 0.44
C	0.36	0.37	Females = 1.00; Males = 0.71
t_s	0	3.85	Females = 8.64; Males = 5.83
Age at OCL_{50} (months)	Females = 9; Males = 11	Females = 36; Males = 16	Females = 19; Males = 19
Size at age 12 months (mm OCL)	29.0	27.9	Females = 14.7; Males = 14.1
Z (1 year^{-1})	2.91	1.79	Females = 2.34; Males = 1.95
M (1 year^{-1})	1.09	0.60	Females = 0.55; Males = 0.48
F (1 year^{-1})	1.82	1.19	Females = 1.78; Males = 1.47
E	0.62	0.66	Females = 0.76; Males = 0.75

N.B.: Breeding period refers the period from initial spawning through the release of juveniles from pleopods of females. Spawning rate of mature females is based on the maximum percentage of mature females that possessed stage VII (i.e., ovigerous), stage V (mature) or VI (gravid) ovaries in any month during the breeding period. 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 of the growth curve, Z is the instantaneous rate of total mortality determined by a length converted catch curve, M is the instantaneous rate of natural mortality, F is the instantaneous rate of fishing mortality and E is the exploitation rate.

ment period (juvenile release) was spring/early summer as supported by initial capture of 0+ individuals in November. However, the protracted spawning period of *C. destructor* in the Hutt River resulted in another recruitment event occurring in January, which subsequently became the most easily discerned cohort thereafter until the following December, at 12 months of age. The cause of the apparent higher survivorship of the progeny of the second spawning event in November than the initial, more major event that occurred in August is unknown but a period of high juvenile mortality appears to have occurred in early summer.

Extended hatching periods and highly variable individual growth rates, resulting in a considerable

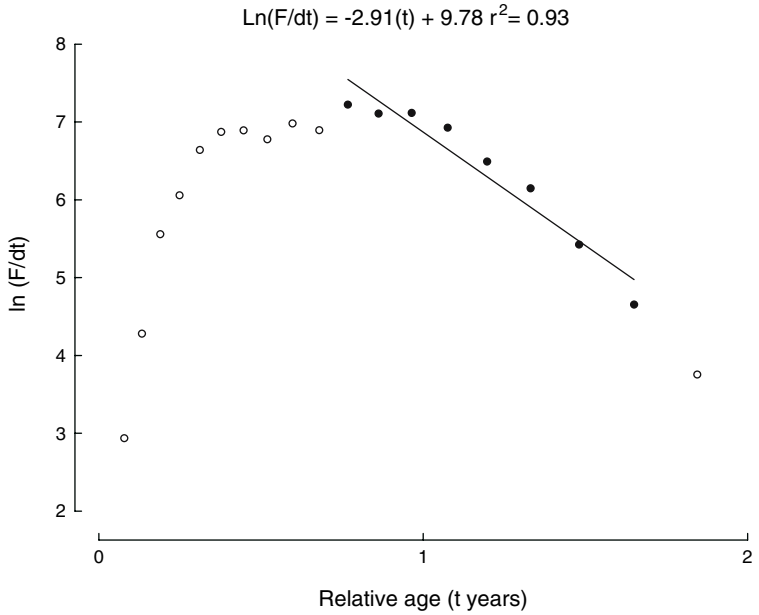

Figure 8. Length-converted catch curve of *Cherax destructor* in the Hutt River. N.B.: Slope of the regression line represents the instantaneous mortality rate (Z) and data points with open circles were excluded as they represent mean ages that were not fully recruited (ascending data points) or those with small sample sizes (less than 10 individuals).

overlap of successive age groups, complicate size-frequency analyses in freshwater crayfishes (e.g., Morrissy, 1975; Jones, 1981; Gutiérrez-Yurrita & Latournerié-Cervera, 1999). Whilst there was a high degree of overlap in cohorts in the Hutt River population of *C. destructor*, the extremely high coefficient of determination estimated for the modified seasonal von Bertalanffy growth curve suggest a good description of growth for the first 12 months (Fig. 6).

Although the growth rate of *C. destructor* in the Hutt River was comparable to that recorded for *C. cainii* in that system (Beatty et al., 2004), the OCL_{∞} was less, i.e., ca. 51 mm OCL for *C. destructor* cf. ca. 102 mm OCL for *C. cainii* (Table 3). However, as the K was greater for *C. destructor* (0.78 cf. 0.42 for *C. cainii*), its length at 12 months of age (29 mm OCL) was as great as that of *C. cainii* in the Hutt River (ca. 28 mm OCL, Table 3, Beatty et al., 2004). Furthermore, based on the lengths at first maturity estimated in this study, the majority of the population of *C. destructor* will have reproduced by this time, whereas female *C. cainii* matured much later and at a much larger size (i.e., OCL_{50} for female *C. cainii* in this system was ca. 70 mm OCL equating to an age of ca. 36 months (Table 3, Beatty et al., 2004). *Cherax destructor* in the Hutt River also had a much greater growth rate compared with that recorded for the endemic *C. quinquecarinatus* in a permanent stream in southwestern Western Australia (K for *C. destructor* and *C. quinquecarinatus* were 0.78 and 0.25–0.29, respectively) and attained a far larger size after 1 year (29 and ca. 14 mm OCL for *C. destructor* and *C. quinquecarinatus*, respectively) (Table 3).

Size is a major factor determining the outcome of competitive interactions between individual freshwater crayfish (e.g., Momot & Leering, 1986; Pavey & Fielder, 1996). Chelae size is also important in determining the outcome of agonistic encounters (Gherardi et al., 1999). As *C. destructor* is adapted to burrowing in temporary environments, it possesses chelae of considerable size (see also Austin & Knott, 1996), and, based on size attained in its first year, it would be capable of competing with *C. cainii* and out-competing the relatively small *C. quinquecarinatus* for resources (Table 3).

Mortality

The estimate of total mortality of *C. destructor* in the Hutt River was 2.91 year^{-1}, relatively high compared to that for *C. cainii* in the Hutt River (1.79 year^{-1}) (Table 3, Beatty et al., 2004). *Cherax quinquecarinatus* was also found to have a relatively high total mortality rate in a permanent Western Australian stream (2.34 and 1.95 year^{-1} for females and males, respectively (Table 3, Beatty et al., 2005)). The exploitation rate recorded here (0.62) suggests that most of the total instantaneous mortality of *C. destructor* in the Hutt River was due to fishing mortality. The main sampling site had very easy public access relative to the remainder of the Hutt River, which largely passes through privately owned land. Therefore, a relatively high level of fishing pressure may be expected at this site, particularly in light of the good palatability of this species and the fact that its capture in Western Australia is not restricted by fishery regulations (cf. the 3 weeks allowed for the recreational capture of the highly sought after *C. cainii*).

Conclusions

Cherax destructor has become established in many wild aquatic systems in Western Australia in the past decade. The ability of *C. destructor* to withstand relatively extreme physicochemical conditions would help to facilitate this establishment. Life history traits described for *C. destructor* in the Hutt River are typical of an invasive, *r*-strategist crayfish species, i.e., an extended breeding period with multiple spawning events, a high spawning frequency, a rapid growth rate and the attainment of maturity at the end of its first year of life (Table 3). These traits are likely to have facilitated the proliferation of this species in the Hutt River and also aided its establishment in other Western Australian systems. Furthermore, the comparison of life-history traits of *C. destructor* determined in the present study with those recently described for the endemic congeners *C. cainii* and *C. quinquecarinatus*, suggests that it has the potential to become the most abundant species of crayfish once established in an aquatic system that houses these endemics. Given the uniqueness of the freshwater crayfish fauna of the Southwest Coast Drainage Division of Western Australia, the recent spread of *C. destructor* into wild aquatic systems in the region is of serious concern.

Acknowledgements

Many thanks to M. Allen, M. Maddern and M. Johnson for help with sampling. We would like to express much gratitude to S. de Lestang, A. Hesp and N. Hall for advice regarding the sections on growth and maturity. The provision of additional distributional data by Dr Brett Molony and C. Astbury, Department of Fisheries Government of Western Australia is appreciated. Funding was provided by Murdoch University, the Department of Fisheries Government of Western Australia and the National Heritage Trust.

References

Abdu, U., G. Yeheskel & A. Sagi, 2000. Oocyte development and polypeptide dynamics during ovarian maturation in the red-claw crayfish *Cherax quadricarinatus*. Invertebrate Reproduction and Development 37: 75–83.

Austin, C. M., 1985. Introduction of the yabbie, *Cherax destructor* (Decapoda: Parastacidae) into southwestern Australia. Western Australian Naturalist 16: 78–82.

Austin, C. M. & B. Knott, 1996. Systematics of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in south-western Australia: electrophoretic, morphological and habitat variation. Australian Journal of Zoology 44: 223–258.

Austin, C. M., T. T. T. Nguyen, M. M. Meewan & D. R. Jerry, 2003. The taxonomy and phylogeny of the '*Cherax destructor*' complex (Decapoda:Parastacidae) examined using mitochondrial 16S sequences. Australian Journal of Zoology 51: 99–110.

Beatty, S. J., D. L. Morgan & H. S. Gill, 2003. The reproductive biology of the large freshwater crayfish *Cherax cainii* in south-western Australia. Marine and Freshwater Research 54: 597–608.

Beatty, S. J., D. L. Morgan & H. S. Gill, 2004. Biology of a translocated population of the large freshwater crayfish, *Cherax cainii* Austin and Ryan, 2002 in a Western Australian river. Crustaceana 77: 1329–1351.

Beatty, S. J., D. L. Morgan & H. S. Gill, 2005. Life history and reproductive biology of the gilgie *Cherax quinquecarinatus*, a freshwater crayfish endemic to south-western Australia. Journal of Crustacean Biology 25: 251–262.

Beverton, R. J. H. & S. J. Holt, 1957. On the dynamics of exploited fish populations. United Kingdom Ministry of

Agriculture, Fisheries and Food, Fisheries Investigations, Series 2 (19), 533pp.
Butler, IV M. J. & R. A. Stein, 1985. An analysis of the mechanisms governing species replacements in crayfish. Oecologia 66: 168–177.
de Lestang, S., N. Hall & I. C. Potter, 2003. 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. Journal of Crustacean Biology 23: 908–919.
Gherardi, F., S. Barbaresi & A. Raddi, 1999. The agonistic behaviour in the red swamp crayfish, *Procambarus clarkii*: functions of the chelae. Freshwater Crayfish 12: 233–243.
Gutiérrez-Yurrita, P. J. & J. R. Latournerié-Cervera, 1999. Ecological features of *Procambarus digueti* and *Procambarus bouvieri* (Cambaridae), two endemic crayfish species of Mexico. Freshwater Crayfish 12: 605–619.
Gutiérrez-Yurrita, P. J. & C. Montes, 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Doñana National Park, Spain, and implications for species management. Freshwater Biology 42: 561–574.
Hanson, J. M., P. A. Chambers & E. E. Prepas, 1990. Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. Freshwater Biology 2: 69–80.
Hanumara, R. C. & N. A. Hoenig, 1987. An empirical comparison of a fit of linear and non-linear models for seasonal growth in fish. Fisheries Research 5: 351–381.
Hill, A. M., D. M. Sinars & D. M. Lodge, 1993. Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. Oecologia 94: 303–306.
Holdich, D. M., 1988. The dangers of introducing alien animals with particular reference to crayfish. Freshwater Crayfish 7: 15–30.
Honan, J. A. & B. D. Mitchell, 1995. Reproduction of *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and trends in the reproductive characteristics of freshwater crayfish. Australian Journal of Marine and Freshwater Research 46: 485–499.
Horwitz, P., 1990. The translocation of freshwater crayfish in Australia: potential impact, the need for control and global relevance. Biological Conservation 54: 291–305.
Horwitz, P. & M. Adams, 2000. The systematics, biogeography and conservation status of species in the freshwater crayfish genus *Engaewa* Riek (Decapoda: Parastacidae) from south-western Australia. Invertebrate Taxonomy 14: 655–680.
Horwitz, P. & B. Knott, 1995. The distribution and spread of the yabbie *Cherax destructor* complex in Australia: speculations, hypotheses and the need for research. Freshwater Crayfish 10: 81–91.
Jasinska, E. J., B. Knott & N. Poulter, 1993. Spread of the introduced yabbie, *Cherax* sp. (Crustacea: Decapoda: Parastacidae), beyond the natural range of freshwater crayfishes in Western Australia. Journal of the Royal Society of Western Australia 76: 67–69.
Johnson, H. T., 1979. Reproduction, development and breeding activity in the freshwater crayfish *Cherax destructor* (Clark), M. Sc. Dissertation. University of Sydney, New South Wales, Australia.
Jones, J. B., 1981. Growth of two species of freshwater crayfish (*Paranephrops* spp.) in New Zealand. New Zealand Journal of Marine and Freshwater Research 15: 15–20.
King, M., 1995. Fisheries Biology, Assessment and Management. Fishing News Books. Oxford, England.
Lodge, D. M., M. W. Kershner, J. E. Aloi & A. P. Covich, 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75: 1265–1281.
Lodge, D., R. A. Stein, K. M. Brown, A. P. Covich, C. Broenmark, J. E. Garvey & S. P. Klosiewski, 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology 23: 53–67.
McRae, T. G. & B. D. Mitchell, 1995. Studies on ovarian development in the yabbie, *Cherax albidus*. Freshwater Crayfish 10: 521–531.
McRae, T. G. & B. D. Mitchell, 1997. Control of ovarian rematuration in the yabbie, *Cherax destructor* (Clark). Freshwater Crayfish 11: 299–310.
Mills, B. J. & M. C. Geddes, 1980. Salinity tolerance and osmoregulation of the Australian freshwater crayfish *Cherax destructor* Clark (Decapoda: Parastacidae). Australian Journal of Marine and Freshwater Research 31: 667–676.
Mitchell, B. D. & R. O. Collins, 1989. Development of field-scale intensive culture techniques for the commercial production of the yabbie (*Cherax destructor/albidus*). Centre for Aquatic Science Report 89 (1). Warnambool Institute of Advanced Education, Warnambool, Victoria, Australia.
Momot, W. T., 1995. Redefining the role of freshwater crayfish in aquatic ecosystems. Reviews in Fisheries Science 3: 33–63.
Momot, W. T. & G. M. Leering, 1986. Aggressive interaction between *Pacifastacus lenuisculus* and *Orconectes virilis* under laboratory conditions. Freshwater Crayfish 6: 87–93.
Morgan, D. L., D. C. Thorburn & H. S. Gill, 2003. Salinization of southwestern Western Australian rivers and the implications for the inland fish fauna – the Blackwood River, a case study. Pacific Conservation Biology 9: 161–171.
Morris, S. & J. Callaghan, 1998. The emersion response of the Australian yabbie *Cherax destructor* to environmental hypoxia and the respiratory and metabolic responses to consequent air-breathing. Journal of Comparative Physiology B 168: 389–398.
Morrissy, N. M., 1975. Spawning variation and its relationship to growth rate and density in the marron, *Cherax tenuimanus* (Smith). Fisheries Research Bulletin of Western Australia 16: 1–32.
Morrissy, N. M., 1978. The past and present distribution of marron, *Cherax tenuimanus*, in Western Australia. Fisheries Research Bulletin of Western Australia 22: 1–38.
Morrissy, N. M. & G. Cassells, 1992. Spread of the introduced yabbie *Cherax albidus* Clark 1936 in Western Australia. Fisheries Research Bulletin of Western Australia 92: 1–27.
Nyström, P. B., W. Bronmark & C. Graneli, 1996. Patterns in benthic food webs: a role for omnivorous crayfish?. Freshwater Biology 36: 631–646.
Nyström, P., C. Bronmark & W. Graneli, 1999. Influence of an exotic and a native crayfish species on a littoral benthic community. Oikos 85: 545–553.

Nyström, P. B. & J. A. Strand, 1996. Grazing by a native and an exotic crayfish on aquatic macrophytes. Freshwater Biology 36: 673–682.

Olsen, T. L., D. M. Lodge, G. M. Capelli & R. J. Houlihan, 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 48: 1853–1861.

Pauly, D., 1980. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer. 39: 175–192.

Pauly, D., 1983. Length-converted catch curves: a powerful tool for fisheries research in the tropics (part 1). Fishbyte 1: 9–13.

Pavey, C. R. & D. R. Fielder, 1996. The influence of size differential on agonistic behaviour in the freshwater crayfish, *Cherax cuspidatus* (Decapoda, Parastacidae). Journal of Zoology 238: 445–447.

Quinn, T. J. II. & R. B. Deriso, 1999. Quantitative Fish Dynamics. Blackwell Science, Oxford, United Kingdom.

Reynolds, J. D., 2002. Growth and reproduction. In Holdich, D. M. (ed.), The Biology of Freshwater Crayfish. Blackwell Science, Oxford, United Kingdom, 152–191.

Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin, 191.

Rouse, D. B. & H. S. Yeh, 1995. Factors influencing spawning of *Cherax quadricarinatus* in indoor hatcheries. Freshwater Crayfish 10: 605–610.

Schnute, J. & D. A. Fournier, 1980. A new approach to length–frequency analysis: growth structure. Canadian Journal of Fisheries and Aquatic Science 37: 1337–1351.

Stenroth, P. & P. Nyström, 2003. Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. Freshwater Biology 48: 466–475.