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Population Structure and Life History Characteristics of *Euastacus bispinosus* and *Cherax destructor* (Parastacidae) in the Grampians National Park, Australia

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Abstract.— Despite being the most widely distributed and cultured freshwater crayfish species in Australia, relatively little is known about the ecology of *Cherax destructor* outside of captivity. Similarly, few ecological studies have been conducted on the large and threatened stream dwelling Australian freshwater crayfish *Euastacus bispinosus*. A series of seasonal sampling surveys over two years investigated the population structure, life history and reproductive timing of *C. destructor* in fire dam habitats, and of *E. bispinosus* in channel (stream) habitats, in the Grampians National Park in south-west Victoria, Australia. *Cherax destructor* individuals in the largest size class (50 – 59.95 mm OCL) were not abundant during the study, while those belonging to the 0 – 9.95 mm OCL size class were more frequent in summer than at other times of year, suggesting synchronous recruitment in fire dam habitats. Individuals in the reproductively active mid-size classes were also frequent in summer. For *E. bispinosus*, sex ratios in spring always favoured females, although there were no clear trends for other times of year. Gravid *E. bispinosus* females were found in winter and spring throughout the study, and were sexually mature at a smaller size than has previously been reported. [*Keywords*.— *Cherax destructor*; *Euastacus bispinosus*; life history; population structure; reproductive timing; sex ratios].

INTRODUCTION

Crayfish populations are known to comprise a large proportion of the biomass in many freshwater ecosystems (Hogger 1988). However, despite this knowledge, relatively few comprehensive studies have been conducted on the population structure or life histories of crayfish populations in their natural habitat. In Australia, most studies have focused on species of recreational and commercial importance, and many have been conducted from an aquacultural perspective.

Euastacus bispinosus

Euastacus bispinosus (Clark) is a large stream dwelling freshwater crayfish endemic to southwestern Victoria, and is classified as a threatened species by the Victorian State Government. Few ecological studies have been conducted on this species, however two studies have focused on population characteristics of wild populations. The first was a preliminary survey of three *Euastacus* species conducted by Barker (1992), and the second was a more detailed study of *E. bispinosus* reproduction by Honan and Mitchell (1995a). Honan and Mitchell (1995a) found that in the lower Glenelg River catchment, *E. bispinosus* spawn in late summer-autumn, brood over winter and release juveniles in spring and summer. However, as with many species of *Euastacus,* the ecology of this species remains poorly understood.

Cherax destructor

Cherax destructor (Clark), although not endemic to the Grampians region, is the most widely distributed, heavily cultured, and perhaps the most extensively studied species of freshwater crayfish in Australia. Despite this, relatively few studies have examined the ecology of this species in habitats largely undisturbed by human activities.

Previous studies on *C. destructor* have focused on aquacultural potential (Frost 1974), taxonomy and distribution (Lawrence et al. 2000a), habitat variation (Lawrence et al. 2000b), sex ratios obtained from intra- and inter-subspecific crosses within and between *C. destructor destructor* and *C. destructor albidus* (Clark) sourced from wild populations and commercial suppliers (Austin and Meewan 1999). *Cherax destructor* reproduction, development and breeding were studied by Johnson (1979), other studies have examined aspects of the species biology in farm dams in far-western New South Wales (Reynolds 1980), and the ecological role of *C. destructor* within billabongs (waterholes formed by cut-off bends in a river) of the Ovens River floodplain in north-eastern Victoria (Brooks 1997). Beatty et al. (2005a) studied the threat posed by the introduced *C. destructor* to the endemic crayfish fauna in the Hutt River region of Western Australia. Lake and Sokol (1986a) investigated the habitat, factors influencing catchability, population structure, density and standing crop, sex ratios, breeding, growth and moulting, length-weight relationships, and diet of *C. destructor* in two dams in Victoria. The breeding period of *C. destructor* has been reported to extend from spring to early autumn (Lake and Sokol 1986b; Morrissy and Cassells 1992; Beatty et al. 2005b).

Life History Strategies

Life history strategies of freshwater crayfish are often classified as either summer or winter brooders. According to Honan and Mitchell (1995a) summer brooders generally have an

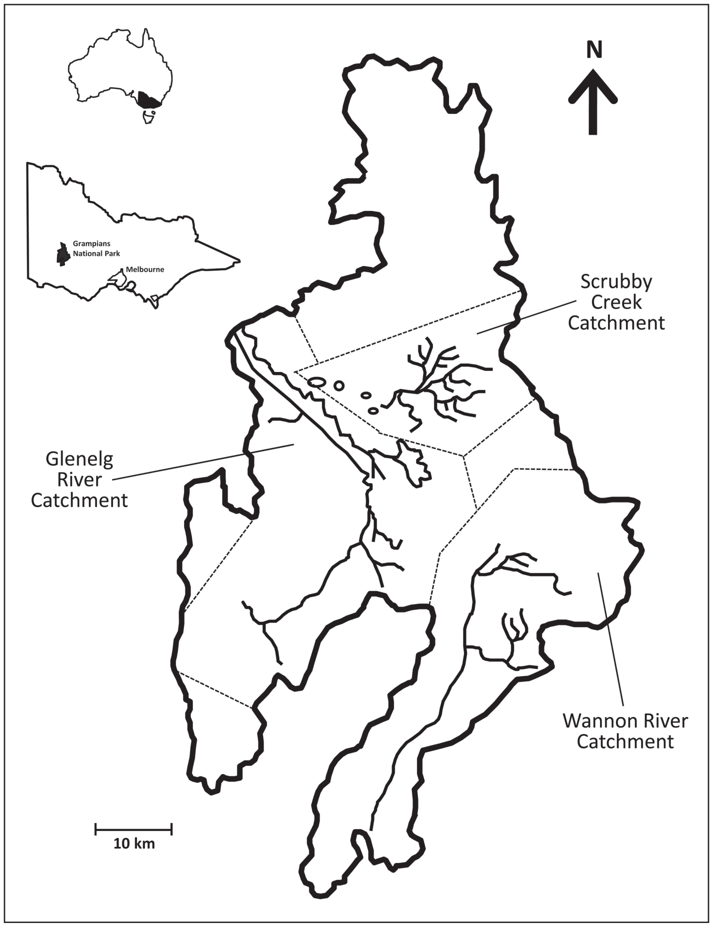

Figure 1. Location of the Grampians National Park in Victoria and the locations of the Wannon River, Glenelg River, and Scrubby Creek Catchments within the Grampians National Park.

asynchronous spawning regime during the short summer breeding period that may include multiple spawning events, have short life spans, exhibit rapid growth, and have relatively high fecundities with small eggs. These species are often able to colonise habitats modified and disturbed by humans, with their high fecundities and rapid growth rates enabling populations to increase rapidly in size, traits typical of generalist species. *Cherax destructor* has previously been classified as a generalist, inhabiting a range of habitats including desert mound springs, alpine streams, subtropical creeks, rivers, billabongs, water holes, ephemeral lakes, and swamps (Beatty et al. 2005a).

In contrast, Honan and Mitchell (1995a) describe the life history strategy of a winter brooder as including a long life span, slow growth, relatively large size at sexual maturity, low fecundity, and large egg size: traits characteristic of a specialist species. *Euastacus bispinosus* can be classified as a specialist crayfish species, typically occurring only in stream habitats with good water quality.

This paper investigates and contrasts the population structure, life history and reproductive timing of the generalist species *C. destructor* in fire dam habitats, and the specialist species *E. bispinosus* in channel (stream) habitats, in the Grampians National Park in south-west Victoria, Australia.

These habitats are quite distinct from those of previous studies on these species, as they are located within National Park boundaries, and therefore not subject to the usual anthropogenic disturbances associated with private properties, in particular agricultural activities.

MATERIALS AND METHODS

This study was part of a larger project investigating the ecology and biology of the unique and diverse freshwater crayfish fauna of the Grampians National Park. As part of the larger study, the study area was partitioned into three catchments; the Wannon River Catchment, the Scrubby Creek Catchment, and the Glenelg River Catchment (Figure 1). Within these catchments, two replicate sites of each of the habitat types (channels and fire dams) were selected for seasonal surveys.

The fire dams in the study area were created as water reseviors for fighting bushfires, are discrete constructed units within a watershed, and have their own small catchment areas. Fire dams are therefore different to the other common habitat types found in the study area which are typically connected by a floodplain for some of the year. It is possible that several of the fire dams in the Grampians National Park were artificially stocked with *C. destructor* at some point, however sufficient time has passed, and the *C. destructor* fire dam populations resemble typical populations found in more natural ponds or lakes.

Eight seasonal surveys were conducted over 24 months from spring 2003 to winter 2005. All sites, in all catchments, were sampled in each season of both years: spring (September – November), summer (December – February), autumn (March – April, and winter (June – August). The seasonal sampling surveys employed both day and night sampling, so as to include diurnal variations in activity, and different sampling techniques were used for day and night sampling. Day sampling involved a series of random 30-second dip-net (250 µm mesh) sweeps of a 25 m^2 area in lentic habitats (or the littoral zone of fire dams) or a 50 m length of channel habitats for one hour. Crayfish were marked with nail varnish so that any individuals recaptured in night sampling could be identified. Night sampling involved the use of three box bait traps (baited with beef liver) which were placed randomly

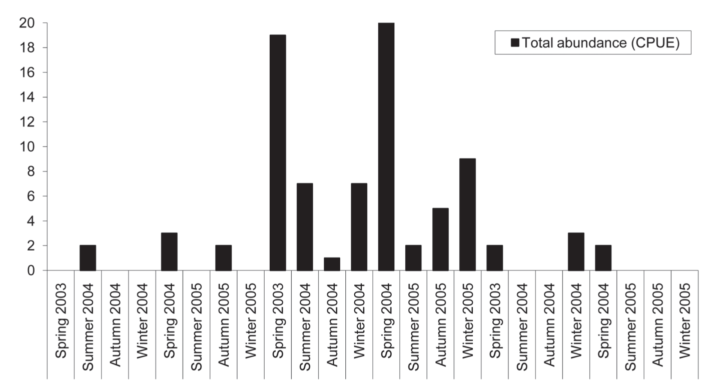

Figure 2. Total abundance of *E. bispinosus* in the Wannon River, Scrubby Creek, and Glenelg River catchments in the Grampians National Park, for each year and season.

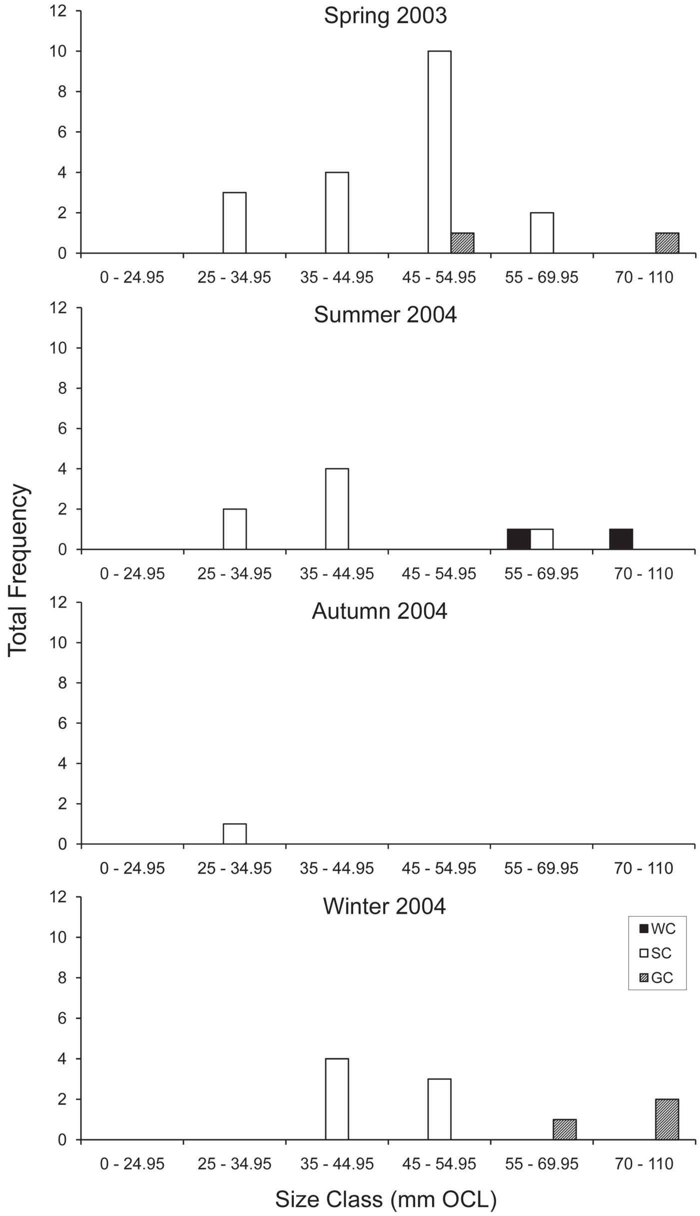

Figure 3. Total frequencies of *E. bispinosus* in each size class in the Wannon River catchment (WC), Glenelg River catchment (GC), and Scrubby catchment (SC), in spring 2003, summer, autumn, and winter 2004.

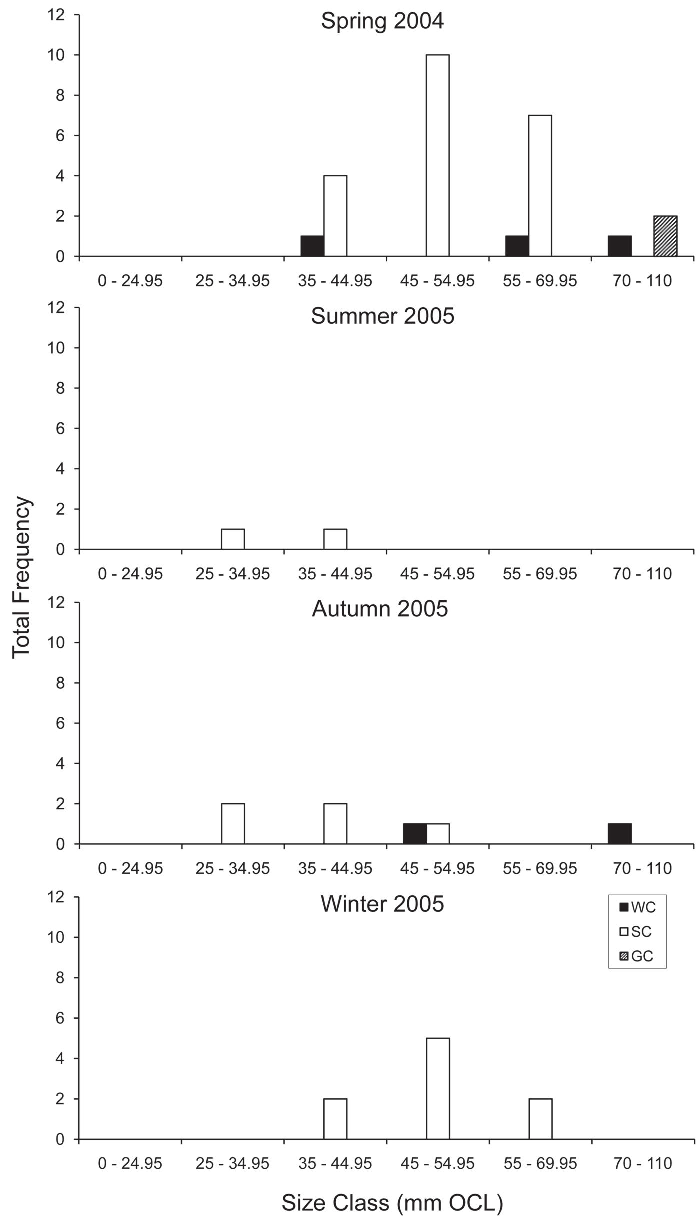

Figure 4. Total frequencies of *E. bispinosus* in each size class in the Wannon River catchment (WC), Glenelg River catchment (GC), and Scrubby catchment (SC), in spring 2004, summer, autumn, and winter 2005.

at each site sampled that day. Traps were left in place overnight and collected the next morning. Captured crayfish were sorted on trays, and specimens placed in holding containers until sampling at a particular site was completed. Each crayfish was identified to species, OCL was measured to the nearest 0.05 mm, sex was determined, details of gravid females were recorded, any evidence of moulting was noted (i.e., soft shells), and all specimens were released unharmed. Seasonal data for each species from all sites within a given catchment were pooled, and data was plotted using bar charts.

RESULTS

Over the course of this study a total of 85 *E. bispinosus* and 1093 *C. destructor* were captured. Data for one site in the Glenelg River catchment were predominantly derived from night sampling (using traps), as on most sampling occasions this site was deemed unsafe to sample with a dip net because it had very steep, slippery clay banks.

Euastacus bispinosus

In total, 48 female and 37 male *E. bispinosus* were captured during this study. *Euastacus bispinosus* occurred exclusively in channel habitat, and was found in all three catchments and at four sites. *Euastacus bispinosus* was more abundant in the Scrubby Creek catchment than in the Wannon River or Glenelg River catchments (Figure 2).

The highest abundances of *E. bispinosus* were recorded in the Scrubby Creek catchment in spring in both years, while abundances were also high in winter in both years, and summer 2004. During the periods of peak abundance sex ratios favoured

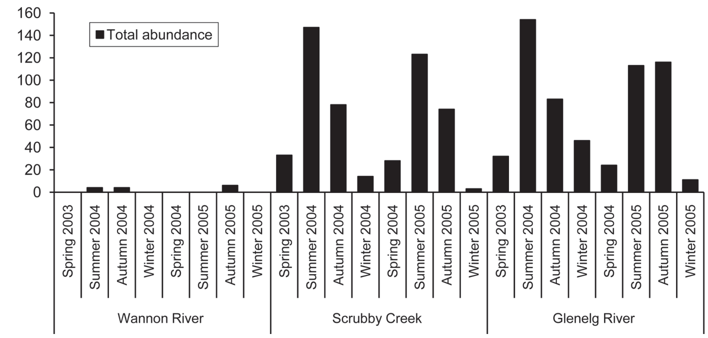

Figure 5. Total abundance of *C. destructor* in fire dams in the Wannon River, Scrubby Creek, and Glenelg River catchments in the Grampians National Park, for each year and season.

females (male:female ratio spring 2003, 6:13; spring 2004, 3:4). Several individuals were also captured in spring in the other two catchments (Figure 2) but the abundances were much lower and gave little indication of the sex ratios.

Size distributions of *E. bispinosus* differed between seasons and years in the Scrubby Creek catchment (Figures 3 and 4), and the size of *E. bispinosus* was more normally distributed than in the other catchments, probably due to the larger sample size obtained there. Larger *E. bispinosus* (45.00 – 110.00 mm OCL) were caught during spring and winter in both years than during summer and autumn, when catches were generally comprised of smaller individuals (25.00 – 44.95 mm OCL). Individuals captured in the Glenelg River and Wannon River catchments only occurred in the three largest size classes, with the exception of one individual found in the 35.00 – 44.95 mm OCL size class in the Wannon River catchment in spring 2004.

Gravid females were captured during winter and spring throughout the study period, but only in the Scrubby Creek catchment; and only seven individuals were captured. Two of the gravid females were captured in spring 2003, one in winter 2004, two in spring 2004, and two in winter 2005, respectively. Gravid *E. bispinosus* females ranged in size from 48.40 mm OCL to 62.90 mm OCL, therefore, for the purposes of this study females 48.40 mm OCL or larger were considered as sexually mature. No gravid females were found in the Wannon River or Glenelg River catchments throughout the study, although some were certainly large enough to be considered sexually mature. Three additional gravid females were captured in the Scrubby Creek catchment during the course of a separate and unrelated study in winter 2004. The season when they were captured, and their size at sexual maturity (OCL 56.40 mm, 57.50 mm, and 63.40 mm), were in accord with the results of this present study. It was not possible to determine the size at sexual maturity of males.

No abnormalities in reproductive structures (i.e., aberrant gonopores) were noted in any of the *E. bispinosus* captured in this study.

Cherax destructor

Cherax destructor were more abundant in fire dams in the Scrubby Creek and Glenelg River catchments than in the Wannon River catchment (Figure 5). In all three catchments *C. destructor* was more abundant in summer and autumn of both years, with the lowest abundances generally recorded in winter.

While numbers captured in the Wannon River catchment were low, where females were captured, they were always more frequent than males (Table 1). Overall, in the Scrubby Creek catchment, a clear pattern of sex ratios changing with season was evident (although this pattern was only detected in one of the two sites studied). Females were less frequently captured than males during the spring of both years, summer 2004, and winter 2005, while in autumn of both years and winter 2004 sex ratios switched to favour females, and in summer 2005 sex ratios were equal (Table 1). No other consistent patterns in sex ratios were detected for this species at the other site in the Scrubby Creek catchment, or in the Glenelg River Catchment, although females were generally more abundant than males.

In all catchments, and throughout the study the frequency of individuals in the largest size class (50 – 59.95 mm) was very low, and no *C. destructor* in this size class were found in autumn or winter in either year (Figures 6 and 7). In contrast, individuals belonging to the four smallest size classes (0 – 9.95 mm through 30 – 39.95 mm) were more frequent in summer and autumn of both years, and somewhat less frequently captured in spring and winter.

Gravid *C. destructor* were only recorded in summer, where three females were found carrying eggs and two females carrying juveniles. These crayfish measured 21.70 mm, 28.00 mm, 23.60 mm, 38.30 mm, and 22.00 mm OCL, respectively. Therefore, for the purposes of this study, females 21.70 mm OCL or larger were considered as sexually mature. It was not possible to determine the size at sexual maturity of males.

Soft-shelled female *C. destructor* were most abundant in spring and summer 2004 (Figure 8). In this study 392 soft-shelled females and 30 soft-shelled males were captured. No evidence of moulting was detected in winter.

Table 1. *Cherax destructor* sex ratios by catchment and year (nd. denotes no data).

Catchment	M:F Ratio By Year and Season							
	Spring 2003	Summer 2004	Autumn 2004	Winter 2004	Spring 2005	Summer 2005	Autumn 2005	Winter 2005
Wannon River	nd.	0:4	0:4	nd.	nd.	nd	1:2	nd
Scrubby Creek	4:3	16:13	1:4	0:2	19:9	1:1	2:3	2:1
Glenelg River	17:15	66:77	37:46	25:21	11:13	55:57	47:69	5:6

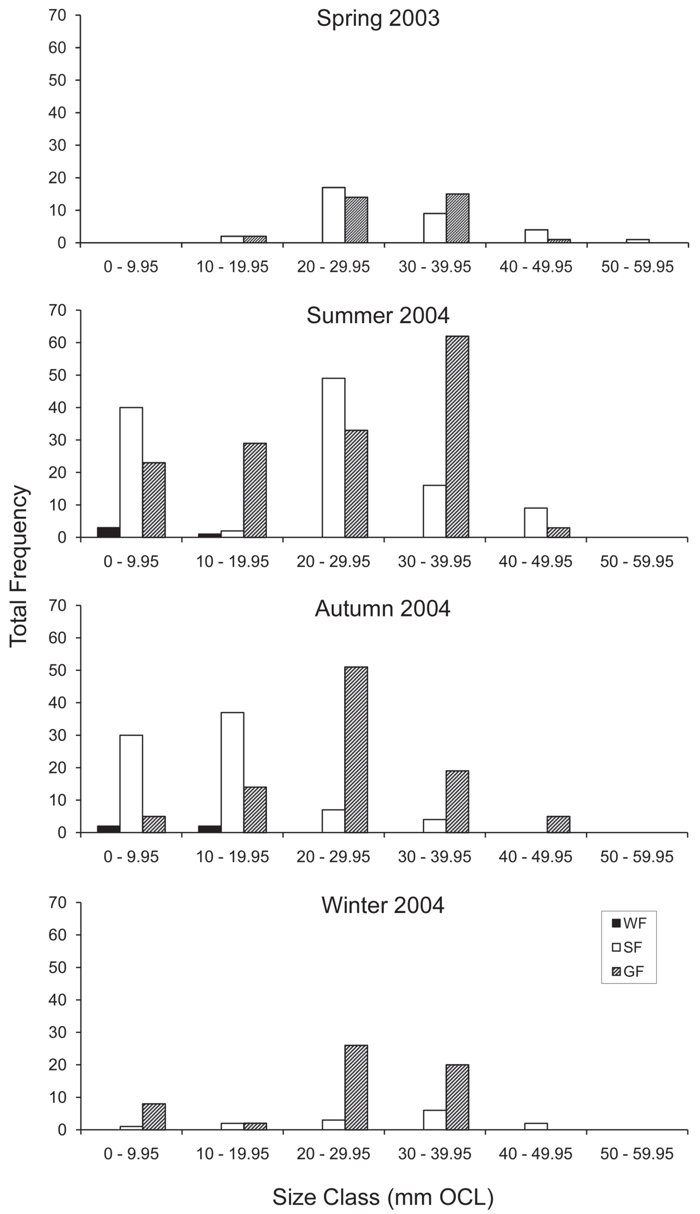

Figure 6. Total frequencies of *C. destructor* in fire dams in each size class in the Wannon River catchment (WF), Glenelg River catchment (GF), and Scrubby catchment (SF), in spring 2003, summer, autumn, and winter 2004.

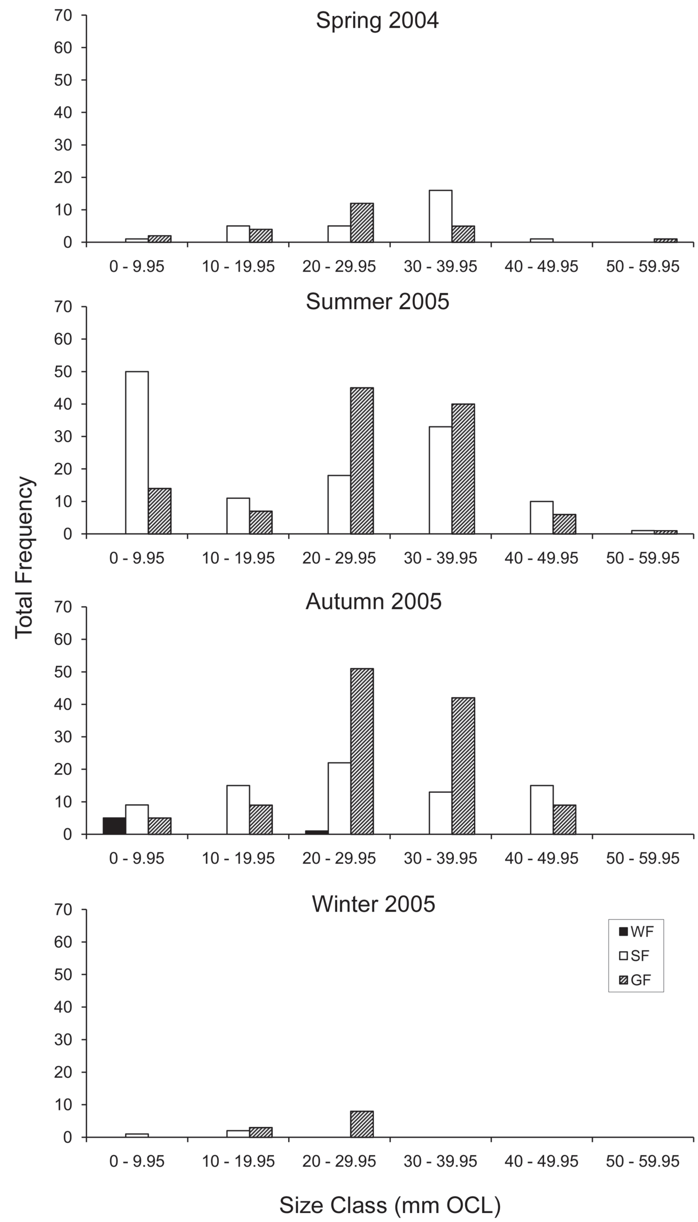

Figure 7. Total frequencies of *C. destructor* in fire dams in each size class in the Wannon River catchment (WF), Glenelg River catchment (GF), and Scrubby Creek catchment (SF), in spring 2004, summer, autumn, and winter 2005.

DISCUSSION

Euastacus bispinosus

Abundance and sex ratios

The number of *E. bispinosus* captured over the course of this study is comparable to other field ecology studies previously conducted on *Euastacus* species (Lintermans and Rutzou 1991; Barker 1992; Honan and Mitchell 1995a; Turvey and Merrick 1997). Despite this, it is difficult to draw any definite conclusions about the annual patterns displayed in sex ratios and population structure of this species in the Grampians National Park.

Reported sex ratios for most captured freshwater crayfish species change during the year (including for *Euastacus spinifer* (Heller) from New South Wales; Turvey and Merrick 1997). Generally there is a trend that adult males dominate catches during the breeding period since gravid females are trap-shy but at other times of year the sex ratio is 1:1 (Abrahamsson 1971; Lake and Sokol 1986a). Breeding season is the period of time from the first spawning event to the release of the last clutch of juveniles, whereas brooding season refers to the period when females are berried and subsequently carrying young under their abdomens. We found a similar result for *E. bispinosus* in the Scrubby Creek catchment when sex ratios favoured males during the breeding period, autumn and winter 2005. However, this pattern did not hold for other seasons during the study, with females dominating catches in spring 2003, winter and spring 2004 and summer 2005, coinciding with the timing of brooding of this species. Similarly, a study of *E. bispinosus* in the lower Glenelg River catchment (Honan and Mitchell 1995c) reported higher catches of females

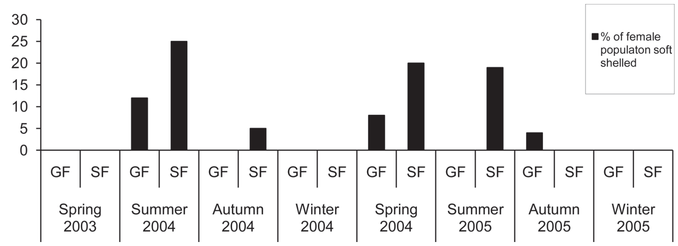

Figure 8. Percentage of the *C. destructor* female population in fire dams in the Glenelg River (GF) and Scrubby Creek catchments (SF), that were soft-shelled in each year and season.

than males during brooding season, but a 1:1 sex ratio at other times of year. Catches of *E. bispinosus* (Barker 1992) in May and June 1990 in the lower Glenelg River catchment showed similar results with sex ratios favouring females (although the sample sizes were small). Turvey and Merrick (1997) found deviations from the 1:1 male to female ratio among small *E. spinifer*, and reported a general scarcity of large males. This was attributed to the respective presence and absence of precocious (small but sexually mature) males.

Very small *E. bispinosus* were rarely captured in the current study, which concurs with the findings of Turvey and Merrick's (1997) study of *E. spinifer* where few juvenile individuals were captured despite a much larger sample size. In addition, at one of their study sites, juveniles were most abundant during the period spring to mid-autumn which concurs with the findings of this study. Turvey and Merrick (1997) also found only small numbers of large crayfish.

Unlike populations studied in the lower Glenelg River catchment (Honan and Mitchell 1995a) where 17% of crayfish captured at one study site had aberrant gonopores, the current study found no crayfish with aberrations. Whatever the cause of aberrations elsewhere is, it has apparently not affected the upstream populations in the Grampians National Park.

Population structure

In the current study the majority of *E. bispinosus* were between 35.00 and 69.95 mm OCL, while the majority of *E. bispinosus* captured by Honan and Mitchell (1995b) were between 35 and 110 mm OCL. Their study was conducted in two lowland tributaries of the Glenelg River, downstream of the Grampians National Park, where water temperatures are higher. Warmer temperatures and associated lowland river conditions may explain the larger size, and different population structure of *E. bispinosus* found in the lower Glenelg River compared with the headwaters. Alternatively, the differences between the lowland and upland populations may be the result of genetic isolation.

Euastacus bispinosus has previously (prior to 2006) been the target of recreational fishing (both inside and outside of National Parks); with the minimum legal capture size in the Glenelg River system being 100 mm carapace length and the bag/possession limit being one male only (taking of females prohibited), with no closed season on males. However, since February 2006, this fishery has been closed as a result of declines in population sizes due to drought and bushfire (Stevens 2006, personal communication). Only two of the 37 male *E. bispinosus* captured in this study were minimum legal size, and most of the larger crayfish caught were female, so it is possible that previous recreational fishing has played a role structuring the size distributions and sex ratios in the Grampians National Park.

Over-fishing has been suggested as a strong determinant of crayfish abundance in the past for other large and recreationally important crayfish species (Lintermans and Rutzou 1991). While the previous recreational fishing laws may have assisted in preserving the relative population abundance of *E. bispinosus* they may also have had an unforeseen effect on the current sex ratios, population structure, and possibly the size of sexual maturity of this species. Male *E. bispinosus* in the lower Glenelg river have been reported to often dominate the largest size classes (Honan and Mitchell 1995c). It has been suggested that mature male crayfish may regulate the growth and mortality rates of other individuals in a population, thus restricting the recruitment of juveniles (Momot 1993). If this is true of *E. bispinosus* populations, the removal of larger males from a population may have further consequences in the Glenelg River catchment.

Reproduction and life history

Compared to the Scrubby Creek catchment, the absence of gravid females, individuals in the smaller size classes, and higher abundances in the larger size classes in the other two catchments, might be the indirect result of illegal fishing pressure on larger reproductively active individuals, or that females were not reproducing in those areas. It is also possible that the sampling protocols (i.e., frequency of sampling, or sampling equipment) were not suitable for capturing the gravid females, or smaller individuals.

The size at sexual maturity determined in this current study for female *E. bispinosus* (48.40 mm OCL) is considerably smaller than that reported previously (58 mm OCL) by Honan and Mitchell (1995b) in the lower Glenelg River. This difference could possibly be due to the higher altitude and associated lower water temperatures, and/or the smaller dimensions of stream channels in the upper reaches of the Glenelg River. Water temperature has been suggested as the most important factor affecting growth rates, and cooler temperatures are known to reduce growth rates of freshwater crayfish (Mason 1978; Lowery 1988; Hamr and Richardson 1994). Slow growth rates and other life history characteristics have been linked to higher altitude (Hamr and Richardson 1994), genetic factors (Wenner et al. 1985), and Morgan (1986) reported that female *Euastacus armatus* (von Martens) from small streams matured at much smaller sizes than those in large watercourses. Growth and size at sexual maturity could also be influenced by other physicochemical water parameters, in particular calcium availability.

Cherax destructor

Abundance and sex ratios

In all three catchments *C. destructor* was most abundant in summer and autumn of both years. These peak abundances corresponded with the driest time of year (least rainfall) in the

Grampians National Park, but may also be attributed to the fact that *C. destructor* most commonly inhabits fire dam habitats, which unlike other habitat types in the region, are relatively unaffected by the seasonal wetting-drying cycle. Lake and Sokol (1986a) also found *C. destructor* to be most abundant during the period January to early March.

In certain circumstances in the study area, it appears that the general activities and timing of reproduction in this species need not be strictly dictated by seasonal rainfall events.

Cherax destructor abundances appeared lower in winter throughout the study and a common trend of sex ratios favouring males in winter was observed. Other studies have reported various sex ratios for *Cherax* species, including males more common than females in mid-late autumn (Beatty et al. 2005b), through 1:1 (Lake and Sokol 1986a), to favouring females (Woodland 1967). Deviations from a 1:1 sex ratio in wild populations may result from a number of factors including method of capture and catchability, growth rate and or mortality, internal parasites and/or symbionts (Austin and Meewan 1999). In the current study, females brooding eggs in winter may have remained in burrows or behaved in a cryptic manner, which could explain the lower abundances observed during this period.

Population structure

During summer 2005 in the Scrubby Creek catchment the 0 – 9.95 mm size class exhibited the highest frequency suggesting that many juvenile *C. destructor* had been recruited into the population after being released from their mother's pleopods. Populations in this and in the Glenelg River catchment exhibited a similar pattern of higher frequencies of the smallest size class and moderate frequencies of the mid size classes in both summers (compared to other times of year).

Release of brooded juveniles in the Scrubby Creek catchment may have occurred slightly later in the year than the Glenelg River catchment, as in both years the frequency of individuals in the 0 – 9.95 mm size class remained high in autumn, while the Glenelg River catchment displayed reduced frequencies in autumn compared to summer. High abundances of juveniles during autumn have been reported elsewhere in Victoria (Lake and Sokol 1986b).

We observed fewer *C. destructor* belonging to the smallest size class, and an increase in the 20 – 29.95 mm size class in autumn each year in the Glenelg River catchment, probably due to the growth of the previously observed abundant juveniles. Juvenile *C. destructor* do moult frequently and thus grow throughout the year (bar winter) (Reynolds 1980). In the Glenelg River catchment, *C. destructor* frequently occurred in the size classes 20 – 29.95 mm and 30 – 39.95 mm throughout this study, which is similar to the findings of Brooks (1997). However, in summer 2004 and winter 2005 in the Glenelg River catchment, some individuals in the 10 – 10.95 mm size class were present, suggesting either an aging population which reproduces infrequently (i.e., not at any particular time of year) is present, or that only a very small number of individuals are reproducing (perhaps in early summer), and that the sampling protocols in this study did not detect it. Perhaps those small *C. destructor* occurring in both winters were the result of late hatching and subsequent slow growth, or some small portion of the young-of-year class grew very slowly. It is also possible the low numbers of smaller crayfish, and increased frequency of larger crayfish, were attributable to cannibalism of the juveniles by the larger adult crayfish.

Although different size-frequency patterns were shown throughout both years, high frequencies of *C. destructor* in the smallest size class (0 – 9.95 mm) in summer and autumn were generally apparent. This general pattern varied in magnitude from year to year and from catchment to catchment and probably results from the exact timing of juvenile recruitment into the populations studied. These data suggest that synchronous reproduction occurs in *C. destructor* populations in fire dams in the Grampians National Park.

Reproduction and life history

The minimum size at sexual maturity (as determined by gravid females), of 21.70 mm OCL in this study, is comparable to the findings of Beatty et al. (2005a) from Western Australia, who found female *C. destructor* sexually mature at 17 mm OCL. The range 17 mm – 21.70 mm OCL is somewhat smaller than female size at sexual maturity previously reported: 31.58 mm OCL (Lake and Sokol 1986b), through to 38.8 mm OCL (Reynolds 1980).

The small number of gravid females captured restricted our ability to thoroughly examine the life history of this species in the populations studied. However, the available data suggest that preparatory moulting, spawning and the brooding of eggs and juveniles, occur sometime during the period of late spring to early autumn. This seasonal timing, and multiple spawning events within this period, have been previously reported for this species in a number of other studies (Clark 1936; Frost 1974; Beatty et al. 2005a, 2005b). Therefore, it is likely that *C. destructor* inhabiting fire dams in the Grampians National Park also underwent several spawning events during the protracted breeding period reported, as juveniles were found in the populations throughout the study.

The absence of soft-shelled females in winter of either year, and the majority of soft shelled females being captured in spring and summer, is in accord with reports that mature female *C. destructor* moult mainly in spring and summer (Reynolds 1980).

CONCLUSIONS

Both *E. bispinosus* and *C. destructor* in the Grampians National Park were found to exhibit the same general life history characteristics as those reported in previous studies elsewhere, with the exceptions that *E. bispinosus* were generally smaller in size compared to its downstream counterparts and had a smaller size at sexual maturity. *Cherax destructor* in fire dams were also found to have a reduced size, and reduced size at sexual maturity compared to populations elsewhere, which could be due to high density of crayfish, and limited food availability in fire dams. It is also possible that some of the differences found in the Grampians populations of *E. bispinosus* and *C. destructor*, might be attributable to the higher altitude, and cooler water temperatures in the study area.

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