

Population biology of the ghost shrimps, *Trypaea australiensis* and *Biffarius arenosus* (Decapoda: Thalassinidea), in Western Port, Victoria.

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Abstract

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This study compared the population biology of two co-existing species of ghost shrimps, *Trypaea australiensis* Dana 1952 and *Biffarius arenosus* (Poore 1975), over a two year period at Warneet and Crib Point in Western Port, Victoria, south-eastern Australia. Overall, the sex ratio in populations of *T. australiensis* varied considerably (male and female biases were found at different times) whereas the sex ratio of *B. arenosus* was generally 1:1 or female biased. A male biased sex ratio was found in the juvenile size class of populations of *T. australiensis* (both years) and *B. arenosus* (one year only). Both species reproduced in spring and summer in Western Port and juveniles appeared to recruit into the populations all year round. The embryo and clutch size of *T. australiensis* females was significantly larger than *B. arenosus*, and a significant relationship between female body size and clutch size (but not embryo size) was found for both species. Comparisons between this and other population studies of *T. australiensis* and *B. arenosus* were made to highlight any latitudinal variation in the reproduction and breeding biology of these species along the eastern coast of Australia.

Keywords

Thalassinidea; ghost shrimp; Western Port; population biology; benthic invertebrates

Introduction

Thalassinidean ghost shrimps are considered key fauna in benthic habitats. There is significant interest in their influence on community composition of benthic environments (Branch and Pringle, 1987; Posey et al., 1991; Dittman, 1996; Berkenbusch et al., 2000) and their key role in changing sediment conditions (Abu-Hilal et al., 1988; de Vaugelas and Buscail, 1990; Forster and Graf, 1992; Bird et al., 2000; Katrak and Bird, 2003). Thalassinidean ghost shrimps have been identified as ecosystem engineers (Berkenbusch and Rowden, 2003) because bioturbation and bioirrigation of the sediment significantly alters its physical and chemical structure (Webb and Eyre, 2004; Grigg et al., 2007). Due to their important role in “engineering” the surrounding environment, thalassinidean ghost shrimps have been suggested as possible indicators of community composition and sediment properties (Posey, 1986; Nicholls, 2002). It is therefore important to fully understand their population biology, including the stability of populations, fecundity, sex ratios and reproductive periods.

The ghost shrimps, *Trypaea australiensis* and *Biffarius arenosus*, are distributed widely along the south and east coasts of Australia where they dominate benthic, soft-sediment marine habitats (Poore and Griffin, 1979). The population biology of *Trypaea australiensis* has been well studied in both northern and southern regions (Hailstone and Stephenson, 1961; Coleman, 1981; Kenway, 1981; McPhee and Skilleter,

2002a; Rotherham and West, 2007; Rotherham and West, 2009). In contrast, little is known about the population biology of *Biffarius arenosus*, with just one study carried out in the 1970s in Western Port, Victoria (see Coleman, 1981).

A comparison of studies of *T. australiensis* in north and south-eastern Australia provide evidence that biological measures such as fecundity and the timing of reproduction can vary for different populations of the same species of thalassinidean (Hailstone and Stephenson, 1961; Coleman, 1981; Kenway, 1981; McPhee and Skilleter, 2002a). Differences in the biology of spatially separated populations of invertebrate species have been reported for other species of thalassinidean. A study of *Callinassa filholi* found differences in the time and length of the reproduction period, the size of individuals at maturity and the rates of fecundity between populations from northern and southern New Zealand (Berkenbusch and Rowden, 2000). The primary cause of the variation was thought to be food availability at the different sites. In contrast, a number of studies (e.g. Kubo et al. (2006)) attributed latitudinal differences in thalassinidean embryo size amongst individuals of the same species to variations in water temperature. Differences in the size of individuals of *Upogebia africana* were related to variation in food availability and salinity of the water column (Hanekom and Erasmus, 1988). Given that the population biology of any given marine species can vary over space and time it is essential to understand the local population biology of species of ecological significance, such as ghost shrimps.

This study aims to describe the population biology of *T. australiensis* and *B. arenosus* in Western Port, Victoria and to compare the findings with previous studies. A particular focus is the population biology of *Biffarius arenosus* as very few studies have investigated the biology of this species. The population biology of *T. australiensis* is described here to compare with the other detailed studies from around Australia, particularly the recent work by Rotherham and West (2009). The opportunity to compare the biology of *T. australiensis* and *B. arenosus* of present day populations in Western Port, with the study by Coleman (1981) conducted 30 years ago provides the means to critically assess whether the population structure is consistent over time. Understanding the stability and variability in the population biology of these species in time and space is essential in order to consider ghost shrimps as key species or indicators of ecological condition in benthic habitats.

Methods

Sampling procedure

Individuals of the ghost shrimps *Trypaea australiensis* and *Biffarius arenosus* were collected from Warneet and Crib Point (38°13' S, 145°18' E), in Western Port, Victoria, Australia

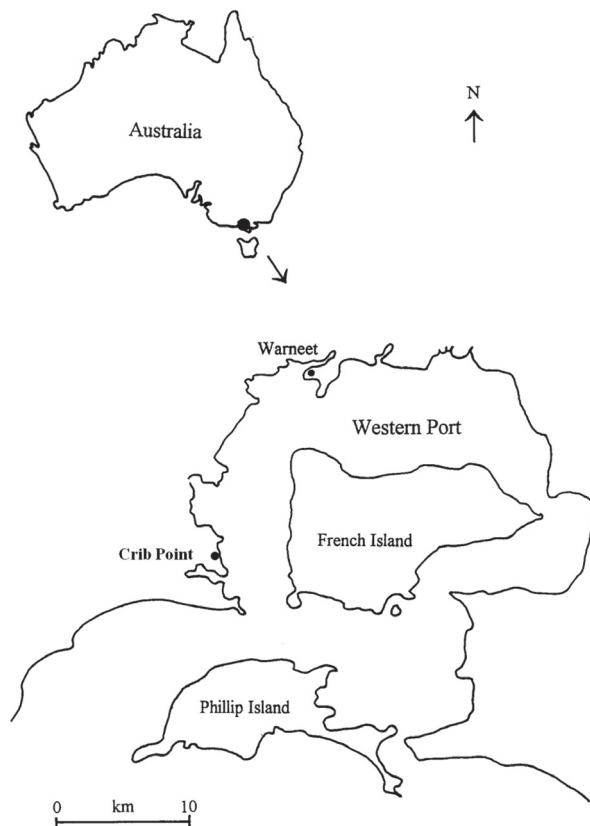


Figure 1. Map of Australia showing the study sites located in Western Port: Warneet and Crib Point.

(fig. 1). Individuals measured and examined for this population biology study were collected as part of a larger study, so methods of collection varied between years.

From April 2004 to March 2005, 6 large cores (25 cm diameter, 40 cm depth) were collected randomly along the mudflat between the high tide mark and the low tide mark at Warneet, once a month. Sediment within the cores was removed using a hand held suction pump, or bait pump. Sediment was directly pumped into a 1mm mesh sieve. All of the ghost shrimp individuals were collected from this sieve using forceps and placed in 70% ethanol for storage and analysis. From March 2006 to March 2007, ten medium cores (15 cm diameter, 40 cm depth) were collected from Warneet monthly. In April 2006 and then from October 2006 to April 2007 ten medium cores (15 cm diameter, 40 cm depth) were also collected each month from Crib Point, Western Port. Each core was removed intact and sediment from the cores was sieved through a 1 mm mesh sieve. All ghost shrimps were removed using forceps and stored in 70% ethanol for analysis. Frequent and intensive bait pumping for ghost shrimp was observed at Warneet during the 2006 sampling period so additional sampling was conducted at Crib Point to ensure individuals of all size classes, including large ovigerous females, were represented. Collection of ghost shrimps for bait can target larger individuals in a population (McPhee and Skilleter, 2002b), and therefore, the reduced period of sampling (seven months) was chosen to target individuals during the breeding season.

The variation in size of the cores used for collection in 2004/05 and 2006/07 may have impacted the number and size of individuals collected and therefore data from each year was analysed separately and general comparisons across years were made. Rotherham and West (2003) found that there was no significant difference in the catches of *Trypaea australiensis* or the precision of catches using two different sized cores (0.04 and 0.07 m²), so it is presumed that comparisons in the current study across years will give a true representation of populations patterns despite the differences in core size used.

In the laboratory, all individuals collected in all samples were measured for carapace length (CL) and the sex was recorded. The sex was determined by the presence (female) or absence (male) of the 2nd pair of pleopods. The number of ovigerous females was recorded along with the development (eyed or uneyed) of the embryos. Carapace length was measured to 0.01 mm using a digital pair of callipers under a dissecting microscope, from the tip of the rostrum to the mid-dorsal posterior edge of the carapace.

Ovigerous females of *B. arenosus* and *T. australiensis* were selected with stage 1 embryos only (as described by Rodrigues (1976) (cited in Kubo et al. 2006)). Stage 1 embryos are tightly packed and round with a uniformly distributed yolk and no eye spots. Clutch size (CS, number of embryos per female) was quantified for each female by removing all embryos from the first and second pairs of pleopods under a dissecting microscope (magnification X 40). The shortest and longest diameters of the first 20 embryos from each female were measured under a compound microscope with a calibrated ocular micrometer (magnification X 40 or X 100). The formula

for an ellipsoid was used to calculate the volume of each embryo: Embryo volume $\text{mm}^3 = \pi LS^2/6$ (where L and S are the longest and shortest diameter respectively, measured to the nearest 0.01 mm). Mean embryo volume was calculated for each female. For comparison with data presented in Rotherham and West (2009), mean embryo diameter was calculated from all maximum and minimum embryo diameters measured for all individuals within a species.

Statistical analysis

Size frequency histograms and plots of the proportion of ovigerous females were created in Microsoft Excel 2007. Chi squared analyses were done using SPSS version 13.0 to statistically test if the sex ratio differed significantly from 1:1 for *T. australiensis* and *B. arenosus* overall for 2004–2005 and 2006–2007 and seasonally within these years. Sex ratio was compared at Warneet and Crib Point separately and for juveniles and adults separately.

Size cohorts were identified for *T. australiensis* and *B. arenosus* each month (or sampling period) using Bhattacharya's (1967) graphical method of fitting normal (Gaussian) components to length-frequency histograms with the modal progression analysis routine in the computer program FISAT II (FAO-ICLARM, 2005). Visually estimated cohort means (as obtained with Bhattacharya's method in FISAT II) were then refined using the NORMSEP optimisation procedure in FISAT II. No progression of the cohort means was observed for data collected for either *T. australiensis* or *B. arenosus* each month indicating that individuals collected each month were not from the same cohort. Consequently, no further analysis of growth from length-frequency data was conducted. Instead, the cohort means calculated for each month were represented with an arrow on the length-frequency histograms for each species and each year.

The clutch size and mean embryo volumes of ovigerous females were compared between species using t-tests in SPSS version 15.0. Data for these parameters were normally distributed (Shapiro-Wilks test, $p > 0.05$) but tests for equality of variance (Levene's test) showed variances were not equal ($p < 0.05$). Despite variance not being equal, t-tests were still used but the significance level was reduced to $p < 0.001$ to reduced the chance of a type I error occurring. The relationships between embryo volume, clutch size and carapace length (as CL^3) were explored for both species using a Pearson's product-moment correlation. The significant relationship between clutch size to carapace length (as CL^3) was then analysed using linear regression. The line of best fit for each significant linear relationship was plotted.

Results

Population structure of *Trypaea australiensis*

In 2004–2005, a total of 712 *Trypaea australiensis* were collected across the 12 months. Of these, 600 specimens could be sexed. There were 347 males and 253 females resulting in an overall sex ratio of 1.4:1 (males: females) which was significantly different from 1:1 ($\chi^2 = 14.727$, $\text{df} = 1$, $p < 0.001$). When considering juveniles and adults separately the overall sex ratio

was 4.8:1 (males: females) for juveniles ($\chi^2 = 88.862$, $\text{df} = 1$, $p < 0.001$) and for 0.69:1 (males: females) for adults ($\chi^2 = 11.174$, $\text{df} = 1$, $p = 0.001$) both significantly different from 1:1. Seasonally, there were generally two cohorts of *T. australiensis*, one with a mean carapace length between 3–5 mm and the other cohort at mean carapace length between 7–10 mm (fig. 2, see arrows). The smaller cohort (presumably juvenile *T. australiensis*) can be detected using Bhattacharya's method in all months except April, June, August, September and January 2004–2005. However, juveniles also seem to be present (though not normally distributed) in April, July, August and September. This suggests recruitment into the population throughout the year. From April to September 2004 there was a significant sex bias towards males (13.7:1, 16:0, 15.5:1, 3.9:1, 3.5:1, 4:0 respectively) in juvenile ($\text{CL} < 5$ mm) *T. australiensis* ($\chi^2 = 32.818$, 16.00, 25.485, 11.765, 5.556, 11.560, $p < 0.05$ respectively) but not adult *T. australiensis* until August where the sex bias was towards females 0.4:1 ($\chi^2 = 6.429$, $\text{df} = 1$, $p = 0.011$). In September 2004, only four juveniles were collected and these were all males, however there was a significant sex biased towards females in adults 0.2:1 (males: females) ($\chi^2 = 11.560$, $\text{df} = 1$, $p = 0.001$). From October 2004 to March 2005 the sex ratio did not differ significantly from 1:1, although juveniles in March 2005 did show a sex ratio significantly different from 1:1 with a bias towards males (7.5:1, $\chi^2 = 9.941$, $\text{df} = 1$, $p = 0.002$). In 2006–2007, a total of 381 *T. australiensis* were collected across ten months at Warneet. Of these 212 were males and 169 were females resulting in a male sex bias of 1.3:1 which was significantly different from 1:1 ($\chi^2 = 5.765$, $\text{df} = 1$, $p = 0.016$). When considering juveniles and adults separately out of 90 juveniles collected there was no significant difference in the sex ratio from 1:1 ($p = 0.206$) however, there was a significant sex bias towards males (1.3:1) for the 291 adults ($\chi^2 = 4.167$, $\text{df} = 1$, $p = 0.041$). Seasonally throughout 2006–2007 at Warneet, the sex ratio for *T. australiensis* seemed to vary as in 2004–2005, however when tested with a chi-square test there was no significant deviation in the sex ratio from 1:1 in any month for adults or juveniles ($p > 0.05$) except in September 2006 when adult males outnumbered adult females 4.3:1 ($\chi^2 = 6.250$, $\text{df} = 1$, $p = 0.012$). In 2006–2007 at Warneet, the two distinct cohorts seen in 2004–2005 were again apparent in all months except December 2006 however a bimodal size distribution was not as clear (see arrows on fig. 3). In August 2006, there were three cohorts identified with the third cohort of mean carapace length 9–10 mm. Higher numbers of juveniles ($\text{CL} < 5$ mm) were seen in May 2006 and February 2007 although the juveniles or smallest cohort (CL 3–4 mm) were present in May, July, August, September and February (fig. 3) indicating some recruitment throughout the entire sampling period. At Crib Point in 2006–2007, a total of 386 *T. australiensis* were collected across seven months. Of these shrimps 225 were males and 161 were females resulting in a sex ratio of 1.4:1 (males: females) which was significantly different from 1:1 ($\chi^2 = 10.611$, $\text{df} = 1$, $p = 0.001$). For juveniles and adults separately at Crib Point, there was no significant difference in the sex ratio of adults from 1:1 ($p > 0.05$) but there was a significant difference in the sex ratio of juveniles from 1:1. For juvenile *T. australiensis* at Crib Point, the sex ratio was significantly male biased (1.8:1, $\chi^2 = 11.267$, df

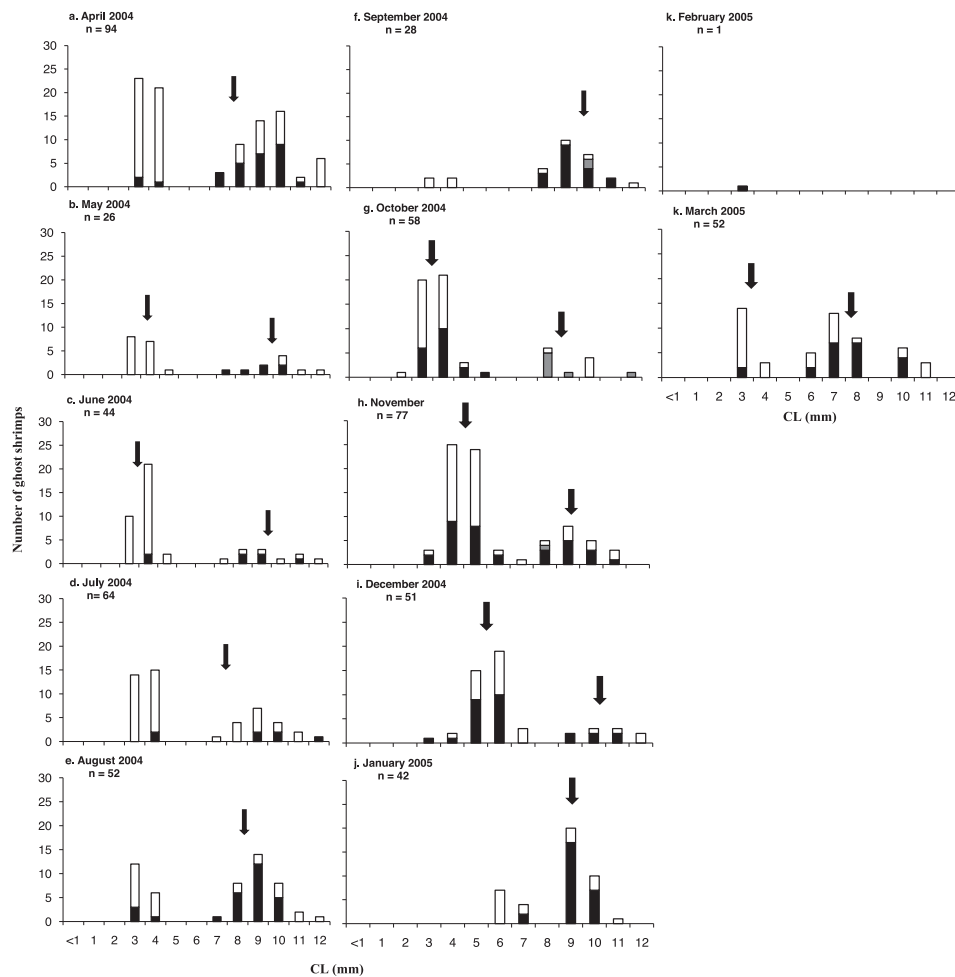


Figure 2. Carapace length (CL) size frequency distributions for *Trypaea australiensis* collected at Warneet, Western Port in 2004-2005. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows show mean CL length of the cohorts identified using FISAT II

= 1, $p = 0.001$). When each sampling occasion was considered separately, it was found that the sex ratio did not differ from 1:1 ($p > 0.05$) for any sampling occasion except for juveniles in April 2006. In April 2006 at Crib Point, the juvenile sex ratio was significantly male biased (4.8:1, 15.114, $df = 1$, $p < 0.001$). At Crib Point there was generally only one cohort of individuals identified through graphical methods, except in February and April 2007 where there were two cohorts identified with mean carapace lengths of 4-5 and 7-8 mm (fig. 4). Although generally only one cohort was identified graphically at Crib Point, there were small individuals (< 5 mm CL) present in all months.

Overall the sex ratio for *T. australiensis* populations at Warneet in 2004-2005 and at Crib Point in 2006-2007 was the same (1.4 males: 1 female). The overall sex ratio at Warneet 2006-2007 was also very similar (1.3 males: 1 female) indicating some consistencies in these populations across years and sites.

Reproduction of *Trypaea australiensis*

In 2004-2005, a low proportion of ovigerous females (10 out of 248 females) were collected. These ovigerous females were found in September, October and November 2004 (fig. 5a). During this period, ovigerous females had uneyed (early development) and eyed (late development) embryos.

In 2006-2007, a total of 19 ovigerous females out of 169 females were collected at Warneet. These ovigerous females were found in a similar period to 2004-2005, which was September, November and December 2006, although there was a higher proportion of ovigerous females found in November and December 2006 than in November and December 2004 (fig. 5c). The ovigerous females in September carried early stage developed embryos with no eyes while the later ovigerous females collected in November and December had late stage developed embryos with clear eyes. At Crib

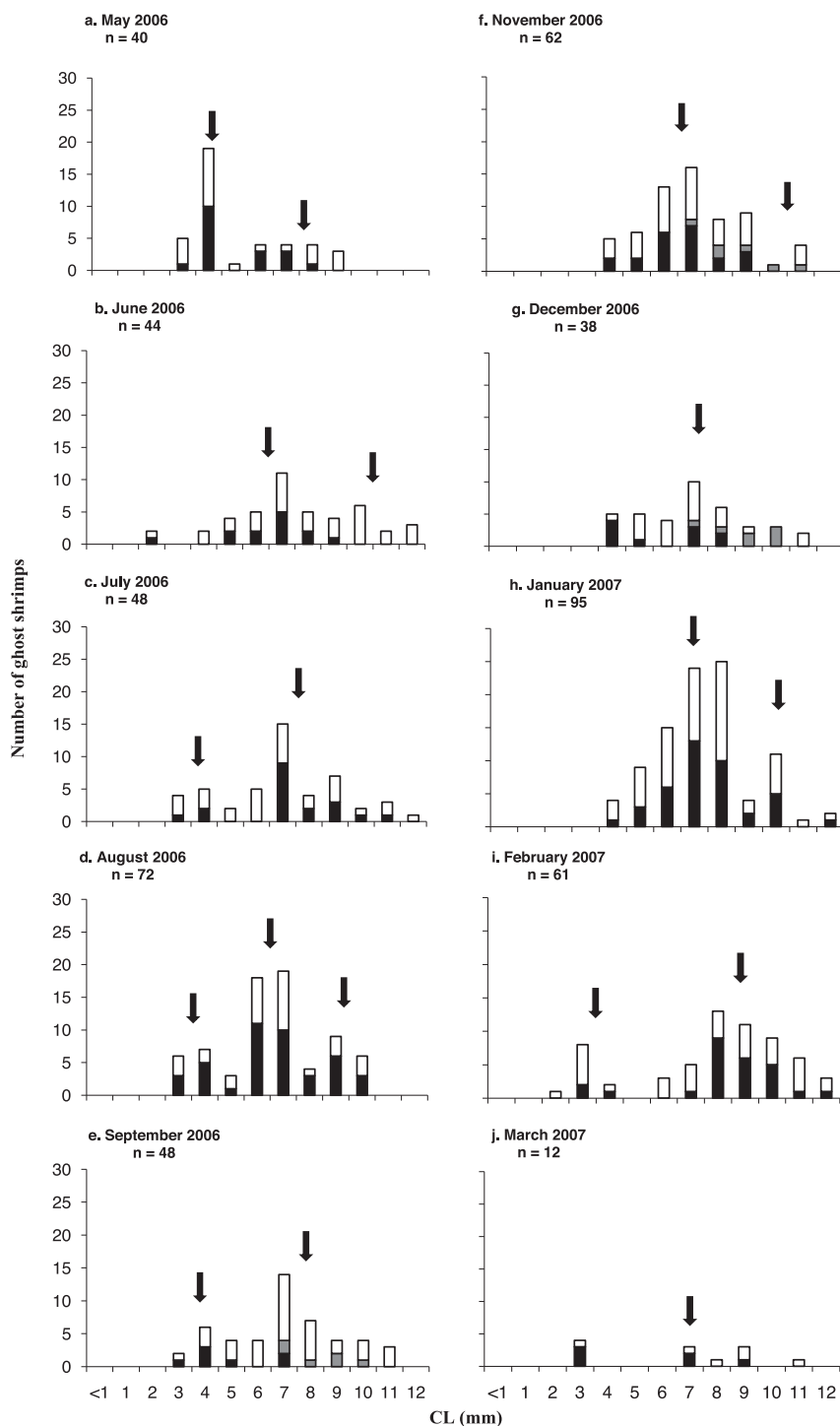


Figure 3. Carapace length (CL) size frequency distributions for *Trypaea australiensis* collected at Warneet, Western Port in 2006-2007. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows show the mean CL length of cohorts identified using FISAT II.

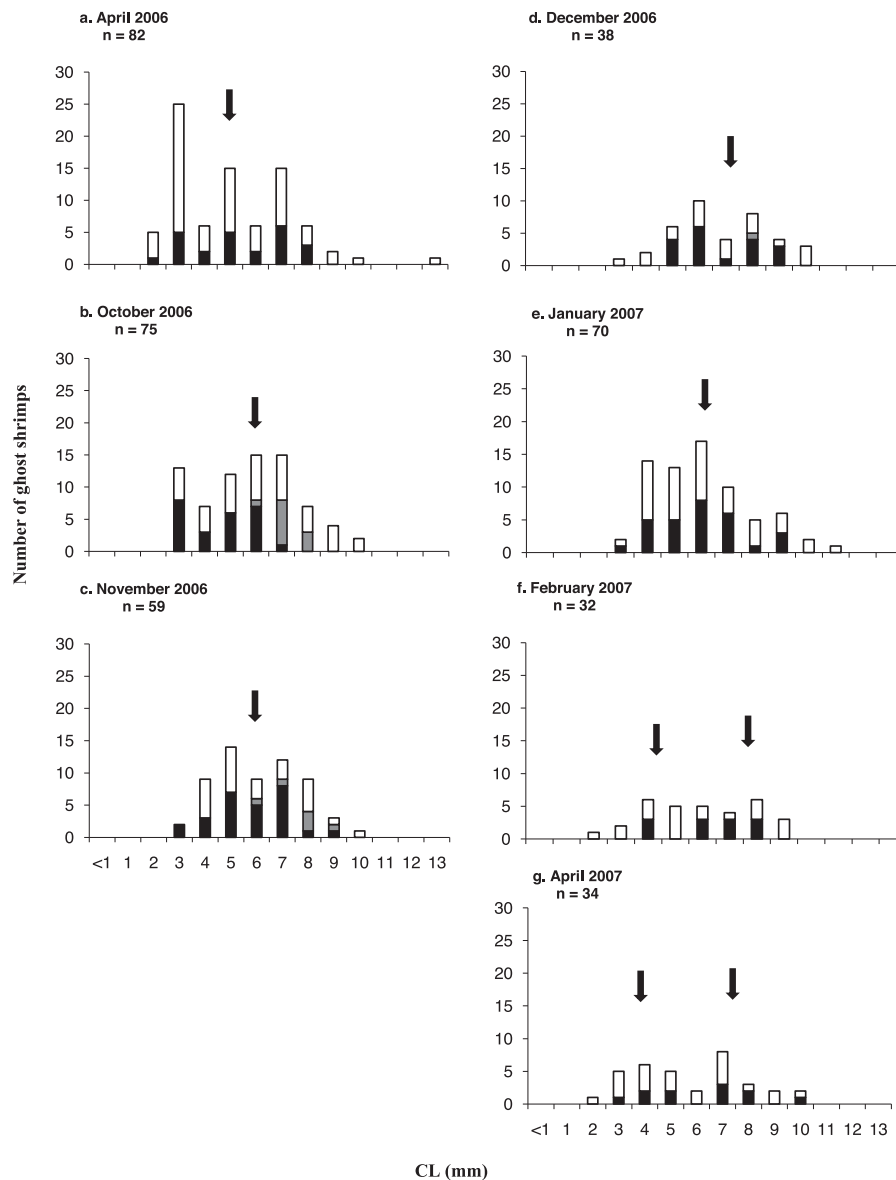


Figure 4. Carapace length (CL) size frequency distributions for *Trypaea australiensis* collected at Crib Point, Western Port in 2006-2007. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows show mean CL of the cohorts using FISAT II.

Point, a total of 18 ovigerous females out of 161 females were collected. These ovigerous females were found in October, November and December 2006 again the same period as at Warneet in 2004-2005 and 2006-2007 (fig. 5e).

Population structure of *Biffarius arenosus*

In 2004-2005 a total of 436 *Biffarius arenosus* individuals were collected across 12 months. Of these 368 specimens could be sexed. There were 185 males and 183 females resulting in a sex ratio of 1:1 (males: females). When considering

juveniles (CL < 3mm) and adults separately it was found that there was a sex ratio of 2.3:1 (males: females) for juveniles which is significantly different from 1:1 ($\chi^2 = 8.643$, df = 1, $p = 0.003$). There was no significant difference in sex ratio from 1:1 in adult *B. arenosus* individuals. Seasonally in 2004-2005, the sex ratio rarely deviated from 1:1 (males: females). There was a significant male sex bias in juveniles in March 2004 (6:0, $\chi^2 = 6$, df = 1, $p = 0.014$) however this is most likely due to very few juveniles being collected. In January 2005, there was a significant female sex bias in adult *B. arenosus* (8:0, χ^2

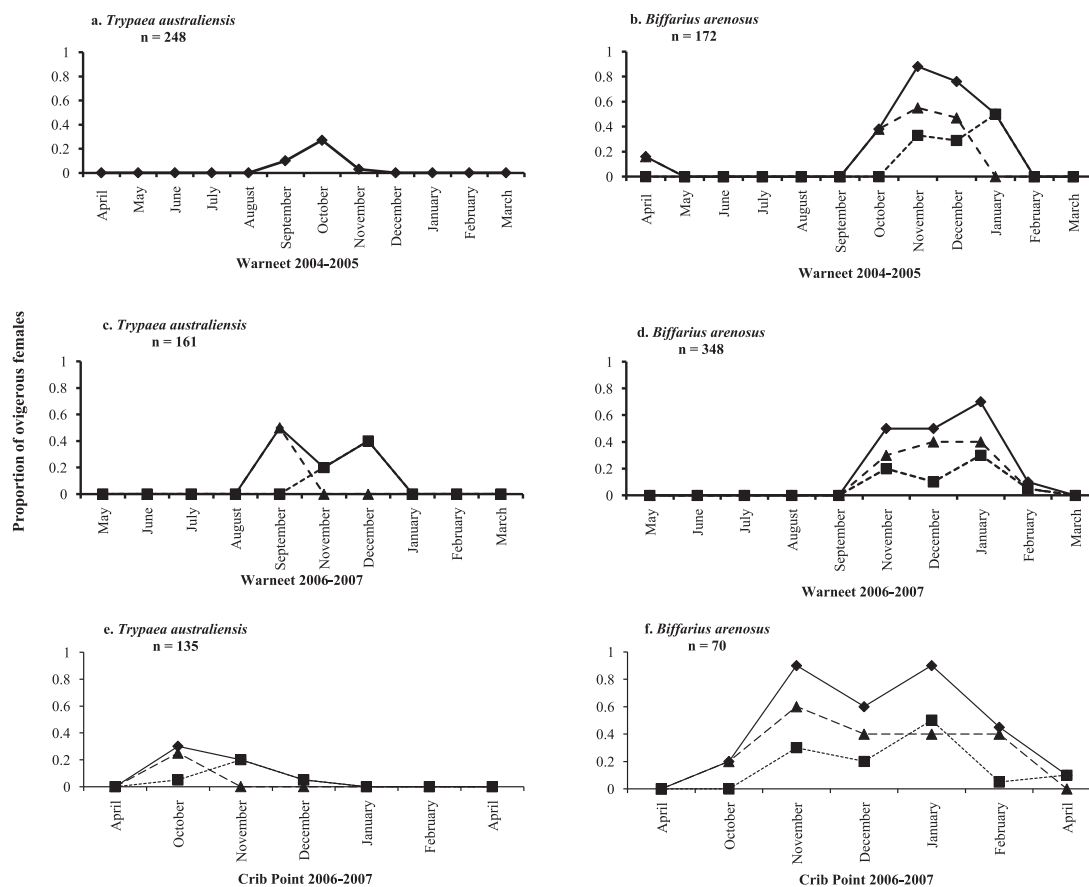


Figure 5. Proportion of ovigerous females for April 2004 to March 2005 (a. *Trypaea australiensis*, b. *Biffarius arenosus*) and March 2006 to May 2007 (c. *T. australiensis*, d. *B. arenosus*) at Warneet, Western Port. Proportion of ovigerous females for April 2006, October 2006 - February 2007 and April 2007 (e. *T. australiensis*, f. *B. arenosus*) at Crib Point, Western Port. Solid line is total proportions of ovigerous females, triangles with dashed line is proportion of ovigerous females with uneyed embryos and squares with dashed line is proportion of ovigerous females with eyed embryos.

= 8, df = 1, $p = 0.005$), however as with the juveniles in March, the sex ratio is most likely due to only eight individuals being collected. Throughout the 12 month period there only seemed to be one cohort of individuals (CL 4-5mm, fig. 6). Juveniles (CL < 3mm) were present in all months indicating recruitment into the population throughout the sampling period (fig. 6).

In 2006-2007 a total of 631 *B. arenosus* individuals were collected at Warneet of which 283 were males and 348 were females. This was a sex bias towards females (0.8:1 males: females) which was significantly different from 1:1 ($\chi^2 = 6.696$, df = 1, $p = 0.010$). Overall of the 239 juveniles there was a sex ratio of 1.1:1 (males: females) which was not significantly different from 1:1 ($p > 0.05$) and of the 388 adults there was a sex ratio of 0.7:1 (males: females) which was significantly different from 1:1 ($\chi^2 = 12.629$, df = 1, $p < 0.001$). Seasonally at Warneet there was a significant sex bias towards males for juvenile *B. arenosus* in January 2007 (5:1, $\chi^2 = 5.333$, df = 1, $p = 0.021$) and a significant bias in the sex ratio towards females for adults in January 2007 (0.5:1, $\chi^2 = 5.000$, df = 1, $p = 0.025$) and in February 2007 (0.5:1, $\chi^2 = 5.453$, df = 1, $p = 0.020$). There were no other

sampling times at Warneet in which the sex ratio was significantly different from 1:1. As in 2004-2005, there appears to be only one cohort of individuals of *B. arenosus* throughout the sampling period in 2006-2007 at Warneet (CL 4-5 mm, fig. 7 see arrows) with juveniles (CL < 3 mm) present at all sampling periods.

At Crib Point in 2006-2007, a total of 140 *B. arenosus* individuals were collected across seven months. Of these 138 specimens could be sexed. There were 57 males and 81 were females resulting in a female biased sex ratio of 0.7:1 (males: females) which was significantly different from 1:1 ($\chi^2 = 4.174$, df = 1, $p = 0.041$). For juveniles and adults separately at Crib Point, there was no significant difference in the sex ratio of juveniles from 1:1 ($p > 0.05$) but there was a significant difference in the sex ratio of adults from 1:1 resulting in a female bias (0.56:1, $\chi^2 = 9.308$, df = 1, $p = 0.002$). When each sampling occasion was considered separately at Crib Point, it was found that the sex ratio did not differ from 1:1 ($p > 0.05$) for any sampling occasion. When comparing the size frequency histograms for *B. arenosus* at Crib Point it can be seen that there was only one cohort of individuals present each month (CL 4-5

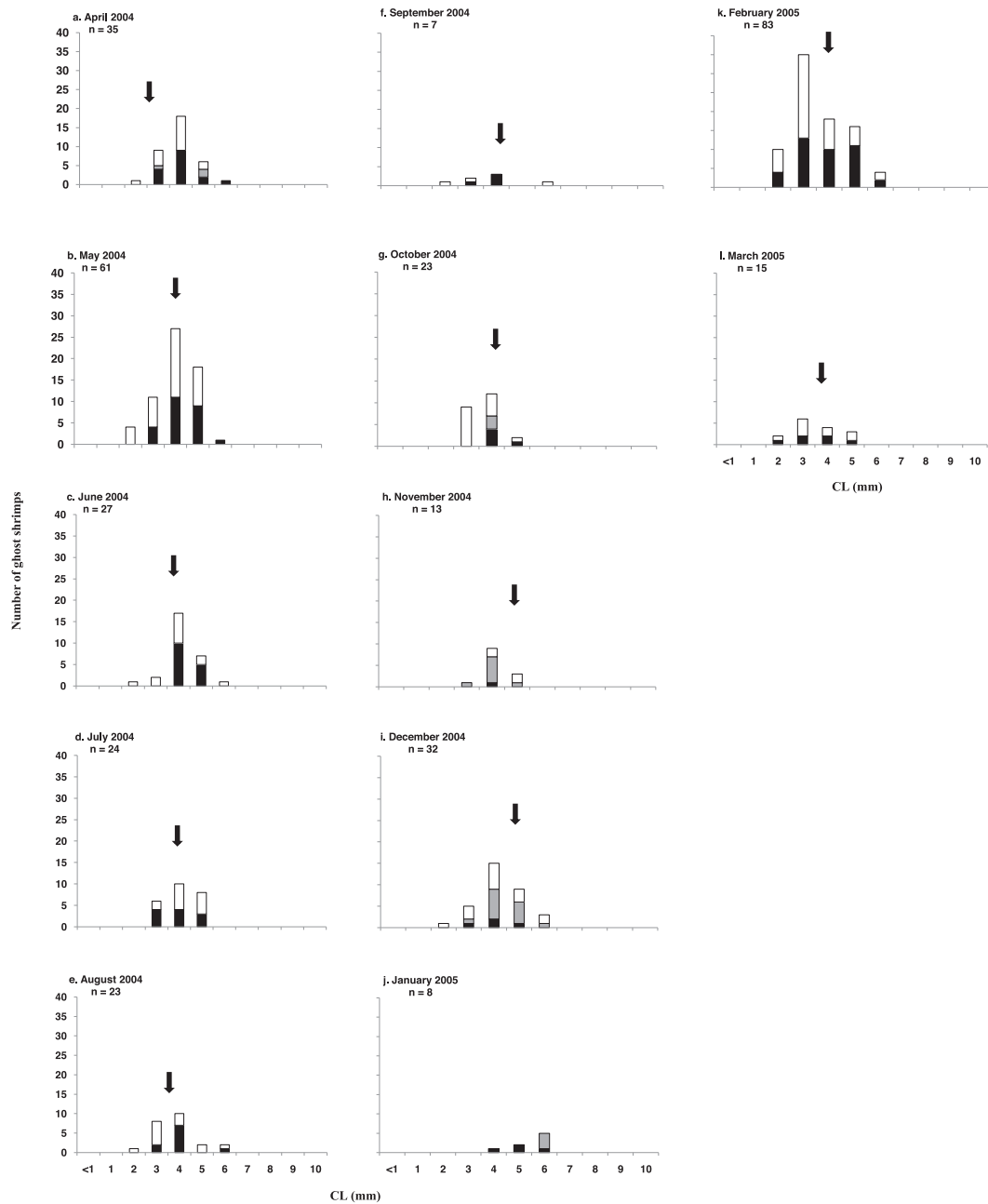


Figure 6. Carapace length (CL) size frequency distributions for *Biffarius arenosus* collected at Warneet, Western Port in 2004-2005. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows show mean CL of cohorts as calculated in FISAT II.

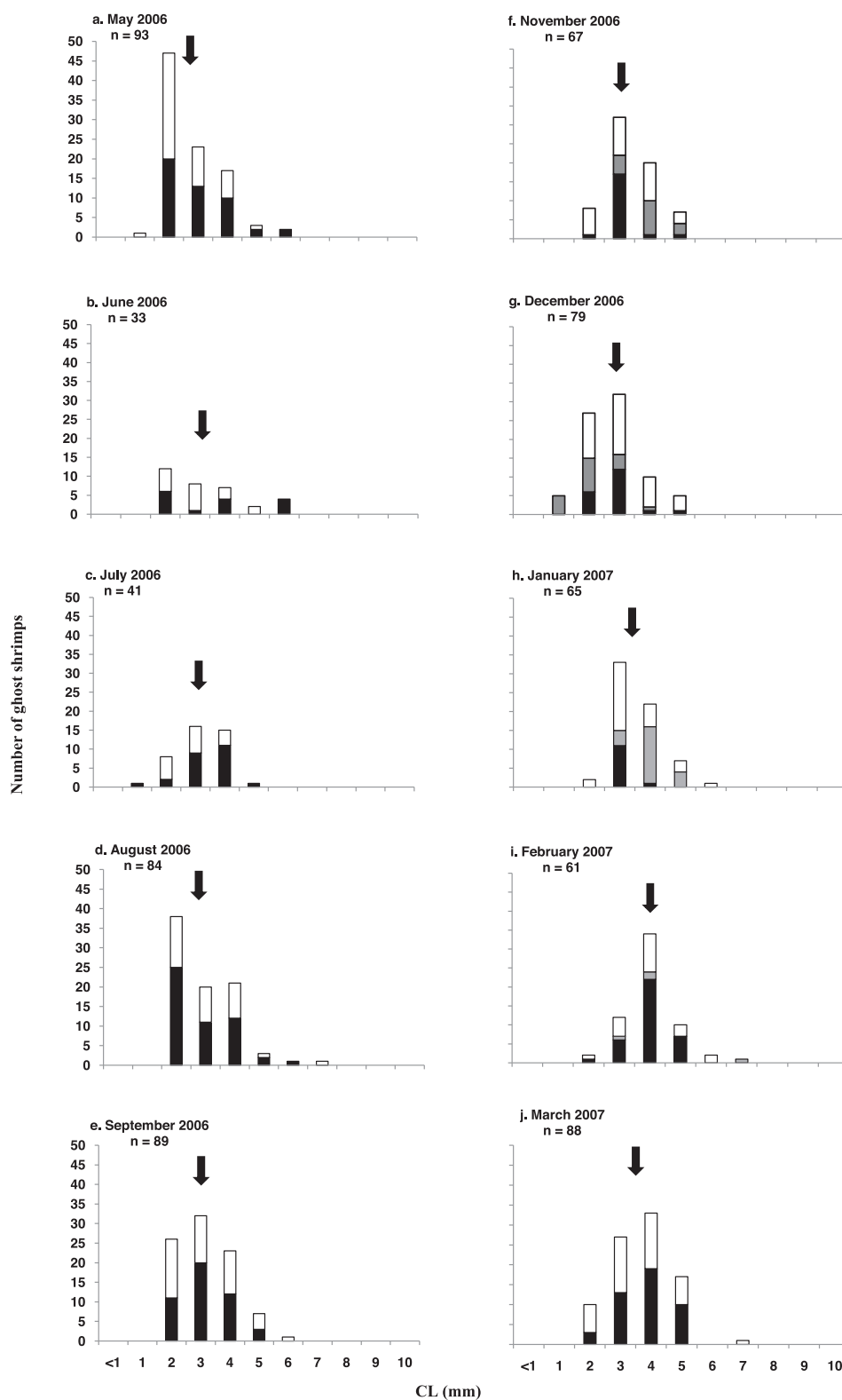


Figure 7. Carapace length (CL) size frequency distributions for *Biffarius arenosus* collected at Warneet, Western Port in 2006-2007. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows indicate mean CL of cohorts calculated in FISAT II.

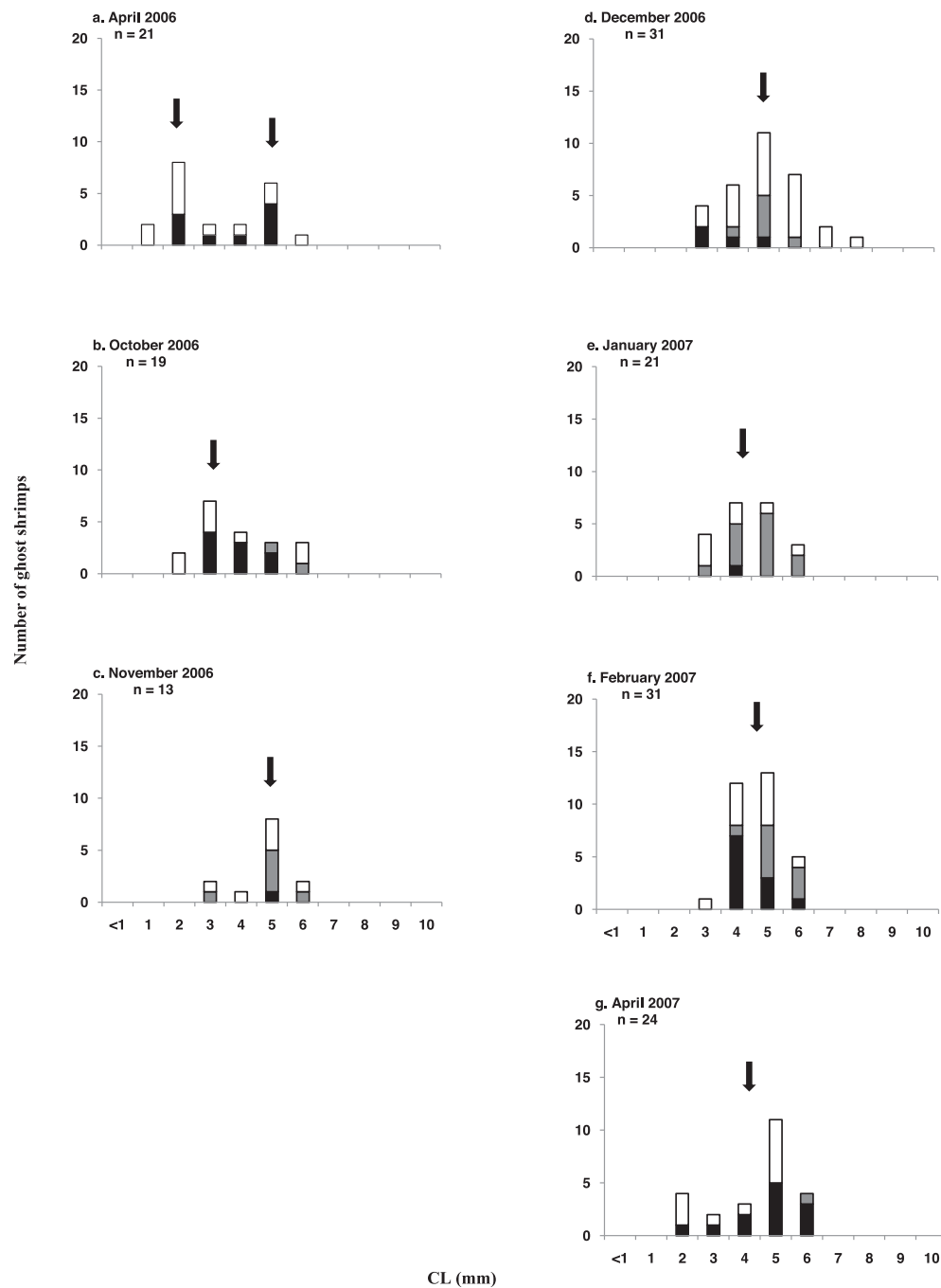


Figure 8. Carapace length (CL) size frequency distributions for *Biffarius arenosus* collected at Crib Point, Western Port in 2006-2007. Non-ovigerous females are shown by black bars, ovigerous females by grey bars and males by open bars (n = number of shrimp collected). Individuals are grouped into size classes by rounding to the closest mm from two decimal places. Arrows show mean CL for cohorts as calculated in FISAT II.

mm, fig. 8, see arrows) except in April 2007 where there were two cohorts identified at mean carapace length 2-3mm and 5-6mm. This second cohort may represent a higher number of juveniles entering these populations in this month. The other months are consistent with data from Warneet, indicating a similar size structure in the populations from both sites.

Overall in 2004-2005 and 2006-2007 at Warneet, there was little change in the sex ratio of *B. arenosus* both overall and throughout time (1:1, 0.8:1 and 0.7:1 respectively). There was also only one cohort of individuals throughout the sampling periods and juveniles were present in most samples.

Reproduction of *Biffarius arenosus*

In 2004-2005 a total of 31 ovigerous females out of 172 females were collected. The reproductive period, as represented by the presence of ovigerous females, occurred with a small peak in April 2004 and then from September 2004 to February 2005 (fig. 5b). There was a clear succession in the presence of ovigerous females with early stage developed (eyed) embryos and ovigerous females with late stage developed (uneyed) embryos. Eyed embryos were present on ovigerous females from September to January with a peak in November while uneyed embryos were present on females from October to February with a peak in February (fig. 5b).

In 2006-2007 at Warneet a total of 63 ovigerous females out of 348 females were collected. The reproductive period occurred from September 2006 to March 2007 (fig. 5d). This is the same pattern as occurred in 2004-2005 however the reproductive period was slightly longer with ovigerous females present in January and February in 2007. The succession in the

stage of embryo development seen in 2004-2005 was not as apparent in 2006-2007 with uneyed embryos present on females from November to March and eyed embryos present also from November to March (fig. 5d). At Crib Point there were 24 ovigerous females out of a total of 81 females collected in 2006-2007 and the period of ovigerous females was generally consistent with 2004-2005 and 2006-2007 at Warneet. Ovigerous females were found at Crib Point from October 2006 to February 2007 and again in April 2007 (fig. 5f).

Embryo and clutch size

Embryo size (expressed as volume, mm^3) for *T. australiensis* (mean \pm SD = $0.33 \pm 0.05 \text{ mm}^3$, $n = 380$) was significantly larger than for *B. arenosus* ($0.10 \pm 0.02 \text{ mm}^3$, $n = 400$) (t-test; $t = 19.1$, $n = 37$, $p < 0.001$). The relationships between embryo volume (mm^3) and female body size (as carapace length, mm) for both *B. arenosus* and *T. australiensis* are shown in fig. 9. The correlations between embryo volume and total length ($r = 0.249$ for *B. arenosus* and $r = -0.047$ for *T. australiensis*) were not significant ($p > 0.05$).

The mean clutch size for *T. australiensis* (313 ± 226) was significantly larger than for *B. arenosus* (96 ± 54) (t-test; $t = 4.7$, $df = 37$, $p < 0.001$). A significant relationship between clutch size and female body size (as carapace length, mm) was detected for both *B. arenosus* (ANOVA; $F = 20.62$, $df = 18$, $p < 0.001$, $r^2 = 0.51$) and *T. australiensis* (ANOVA; $F = 53.09$, $df = 17$, $p < 0.001$, $r^2 = 0.74$) (fig. 10). The linear regression equations for *B. arenosus* ($y = 1.38x - 22.03$) and *T. australiensis* ($y = 0.82x - 241.66$) describe the relationship between clutch size and female body size for each species.

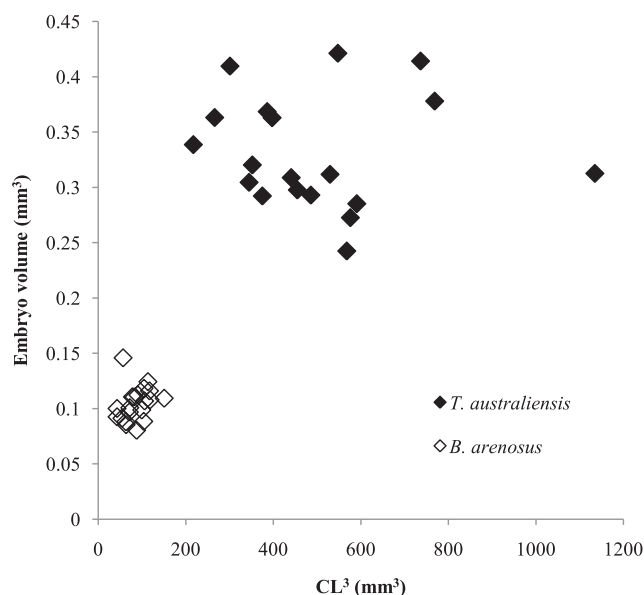


Figure 9. Relationships between embryo volume (mm^3) and body size ($\text{CL}^3 = \text{carapace length}^3$) for females of *Trypaea australiensis* and *Biffarius arenosus*. Embryos were from females collected from March 2006 to May 2007 at Warneet and Crib Point, Western Port.

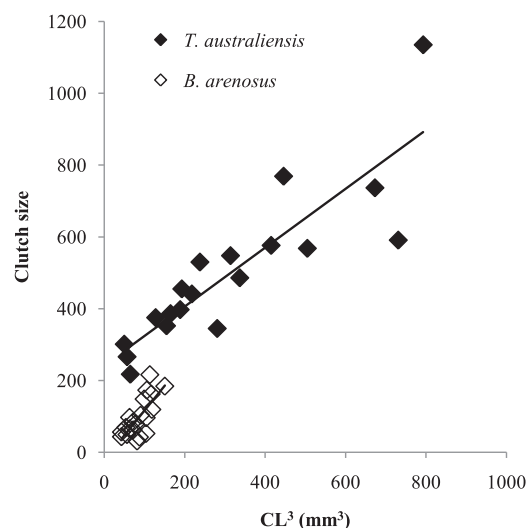


Figure 10. Linear regression of clutch size (number of embryos per female) and body size ($\text{CL}^3 = \text{carapace length}^3$) for females of *Trypaea australiensis* and *Biffarius arenosus*. Females were from March 2006 to May 2007 sampling at Warneet and Crib Point, Western Port.

Table 1. Comparison of the size of the smallest male and female, the largest male and female, the smallest ovigerous female, the mean embryo size (uneyed) (diameter and volume), the clutch size range, the reproductive period (by presence of ovigerous females), season at time of reproduction (main reproductive season) and the presence of juveniles for *Trypaea australiensis* collected in a number of studies throughout Australia. All size measurements are for carapace length (CL) in mm.

Locality	Western Port, Victoria	Western Port, Victoria	Moreton Bay, Queensland	Western Port, Victoria	Cleveland Bay, North Queensland	Moreton Bay, Queensland	Port Hacking, New South Wales	Shoalhaven River, New South Wales	Moruya River, New South Wales
Smallest male collected (CL mm)	2-3	2-3	3-5	2-3	3 - 6*	-	2	2	2
Smallest female collected (CL mm)	3-4	2-3	3-5	3-4	4 - 6*	-	3	3	3
Largest male collected (CL mm)	12	12	16	14-15	15*	-	14	15	11
Largest female collected (CL mm)	12	12	15	11-12	16*	-	12	13	10
Smallest ovigerous female collected (CL mm)	8	7	8	5-6	5*	3	7	6	5
Embryo volume (mm³)	-	0.19-0.63	-	-	-	-	-	-	-
Embryo diameter (mm)	-	0.70-1.16	-	-	-	-	-	-	-
Mean embryo diameter (mm)	-	0.87	-	-	-	-	0.61	0.67	0.61
Clutch size (range)	-	50-793	-	-	92-2236	-	723-3259	663-4738	636-1363
Reproductive period	Aug-Dec	Aug-Jan	Mar-Nov - with peaks in April and Sept	Aug - Jan - with a major peak in September	May - Oct - with major peaks in May and Aug	Oct, Mar, July, Aug, Dec and Feb	Jan-Oct - with a major peak in Feb-Mar	Jan-Aug - with a major peak in Feb-Mar	Jan-May - with a major peak in Jan-Feb
Main reproductive season	Spring	Spring	Autumn	Spring	Autumn/Winter	All seasons	Summer/Autumn	Summer/Autumn	Summer
Presence of juveniles	All months except Jan	All months	Spring	All months except Mar, Apr and July	-	All seasons	Spring and Summer	Spring and Summer	Spring and Summer
Reference	Current study 2004 -2005	Current study 2006 -2007	Hailstone and Stephson 1961	Coleman 1981	Kenway 1981	McPhee and Skilleter 2002a	Rotherham and West 2007, 2009	Rotherham and West 2007, 2009	Rotherham and West 2007, 2009

* CL calculated using the linear equations described in Hailstone & Stephenson (1961): Male CL = 0.242 TL - 1.686; Female CL = 0.19 TL + 0.410.

Table 2. Comparison of the size of the smallest male and female, the largest male and female, the smallest ovigerous female, the mean embryo size (uneyed) (diameter and volume), the clutch size range, the reproductive period (by presence of ovigerous females), season at time of reproduction (main reproductive season) and the presence of juveniles for *Biffarius arenosus* collected in a number of studies throughout Australia. All size measurements are for carapace length (CL) in mm.

Locality	Western Port, Victoria	Western Port, Victoria	Western Port, Victoria
Smallest male collected (CL mm)	2-3	1-2	1-2
Smallest female collected (CL mm)	2-3	2-3	2-3
Largest male collected (CL mm)	6	8	8-9
Largest female collected (CL mm)	6	6	7-8
Smallest ovigerous female collected (CL mm)	3-4	3-4	4-5
Embryo volume (mm ³)	-	0.06-0.22	-
Embryo diameter (mm)	-	0.48-0.77	-
Mean embryo diameter (mm)	-	0.55	-
Clutch size (range)	-	31-216	-
Reproductive period	Sept - Feb	Sept - Feb, Mar - May	Aug - Nov, Nov - Mar
Main reproductive season	Spring	Spring/ Summer	Spring/ Summer
Presence of juveniles	Apr-June, Aug - Sept, Dec, Feb - Mar	All months	Mar- June, Sept - Oct
Reference	Current study 2004-2005	Current study 2006-2007	Coleman 1981

Discussion

There were general consistencies in the population structure and reproductive periods for *Trypaea australiensis* and *Biffarius arenosus* compared with previous studies. In particular, the current study showed very similar results to the study by Coleman (1981) from Western Port with the only main difference being slightly smaller *T. australiensis* males collected in the current study (Table 1). Similar sized individuals and the same reproductive period was found for *B. arenosus*. However, smaller ovigerous females of *B. arenosus* were found in the current study compared with Coleman (1981, Table 2). Hence, the smallest size limit of juveniles of *B. arenosus* can be revised to a carapace length of < 3 mm rather than a carapace length of < 4 mm as suggested by Coleman (1981).

Further differences in the biology of *T. australiensis* exist between the southern and northern Australian populations (see Table 1). In Moreton Bay, Queensland, the smallest male *T. australiensis* were 1–2 mm larger than the smallest male found in Western Port (Hailstone and Stephenson, 1961 compared to the current study). Also the largest male and female *T. australiensis* individuals were approximately 4 mm larger than the largest males and females found in the current study (Hailstone and Stephenson, 1961). In Cleveland Bay, North Queensland the smallest and largest males and females

collected were also larger (approximately 4 mm) than those found in Western Port in the current study (Kenway, 1981). Size differences in ovigerous females of *T. australiensis* are also apparent with the smallest ovigerous females found in Moreton Bay (Hailstone and Stephenson, 1961) being larger (8 mm CL) than the ovigerous females found in Western Port (5-6 mm CL, Coleman 1981). In contrast, males and females collected from populations in south-eastern New South Wales were similar in size to those found in Western Port (Rotherham and West, 2009).

Latitudinal or site differences in sizes of individuals of the same species have been found for a number of different organisms throughout Australia. For example the carapace width of western rock lobster (*Panulirus cygnus*) females that carry two broods of embryos, has been found to decline progressively with decreasing latitudes (de Lestang and Melville-Smith, 2006), the size of individuals and growth rate of near-shore tropical squids *Loliolus noctiluca* was found to decrease from northern Queensland to southern New South Wales (Jackson and Moltschaniwskyj, 2001) and the mangroves *Avicenna marina*, are found to be up to 15 metres taller in northern areas of Australia than in Western Port, Victoria (Edgar, 2001). Reasons for the differences in sizes of individuals between latitudes include increases in growth rate due to warmer temperatures (Lonsdale and Levinton, 1985), latitudinal changes in food availability (Dumbald et al., 1996)

and limiting environmental properties such as temperature or salinity (Hanekom and Erasmus, 1988). For thalassinidean shrimps, Berkenbusch and Rowden (2000) found differences in the size of latitudinally different populations of the species *Callianassa filholi*. They found that there was no consistent trend in size differences from north to south with the mid-latitude populations growing to larger sizes than the other populations studied and it was suggested that food availability may have been the determining factor in the geographical differences in size of this species.

The size of the smallest ovigerous female did not vary substantially between northern and southern populations of *T. australiensis* (ranged from 5 - 8 mm, Table 1) however, the ovigerous females collected by McPhee and Skilleter (2002a) in Moreton Bay were much smaller (3 mm CL) than any reported elsewhere (Hailstone and Stephenson, 1961; Coleman, 1981; Kenway, 1981; Rotherham and West, 2009). Rotherham and West (2009) suggested that the small *T. australiensis* females reported in McPhee and Skilleter (2002a) were probably misidentified *B. arenosus*.

Another major difference between northern and southern Australian studies of *T. australiensis* occurs in the timing of the reproductive period (as shown by the presence of ovigerous females). In Moreton Bay and Cleveland Bay (Hailstone and Stephenson, 1961; Kenway, 1981; McPhee and Skilleter, 2002a), some of the reproductive period was in spring and summer but there was also a main peak in autumn and winter. In south-eastern New South Wales, reproductive period also peaked in summer with ovigerous females still present in the population in early Autumn (Rotherham and West, 2009). In contrast, the reproductive period in Western Port was restricted to spring and summer (Coleman, 1981, the current study 2004-2005 and 2006-2007). Hailstone and Stephenson (1961) found that greater than 90 percent of females were ovigerous in the main reproductive period (April) in Moreton Bay, which is similar to the proportions found by Coleman (1981) in Western Port, and Rotherham and West (2009) in south-eastern New South Wales. However, McPhee and Skilleter (2002a) found only 5.1% of females to be ovigerous, which is similar to the current study where 4% and 14% of *T. australiensis* females were found to be ovigerous in 2004-2005 and 2006-2007 respectively. This is an interesting finding as the most recent studies found less ovigerous females than studies conducted over 20 years earlier, perhaps a reflection of the large increase in collection of these species for bait in these areas during this period (McPhee and Skilleter, 2002b; Contessa and Bird, 2004). It has been suggested that large individuals are collected for bait in preference to smaller individuals (McPhee and Skilleter, 2002b) and this would include removing sexually mature or ovigerous females from the populations. Future studies may consider comparing the number of ovigerous females to see if this trend continues in areas of heavy bait collection.

More variability in the population structure of *T. australiensis* and *B. arenosus* was seen in the sex ratio of males to females. A variable sex ratio was found for *T. australiensis* while the sex ratio of *B. arenosus* was generally 1:1 or female biased. The sex ratio for *T. australiensis* was

significantly female biased in August and September 2004-2005 and then significantly male biased in June and September 2006 and February and April 2007. Variability in sex ratio from male to female bias was also seen at Crib Point for *T. australiensis*. The sex ratio for *B. arenosus* was much less variable than for *T. australiensis* in the current study. Rarely, the ratio varied from 1:1 in 2004-2005 at Warneet and 2006-2007 at Crib Point. In 2006-2007 at Warneet there was a significant sex bias towards females. In the study by Coleman (1981), sex ratios were not statistically described but size frequency histograms for males and females of *T. australiensis* and *B. arenosus* seem to show an even number of males and females. This was variable in some months, consistent with the current findings.

For many species of thalassinidean shrimps (including previous findings of *T. australiensis*) a sex ratio of 1:1 [*Nihonotrypaea harmandi* (as *Callianassa japonica*); Tamaki et al., 1997, *Callianassa filholi*; Berkenbusch and Rowden, 1998] or a sex ratio biased towards females has been found (*T. australiensis*; Hailstone and Stephenson, 1961, *T. australiensis*; Kenway, 1981, *Lepidophthalmus* (as *Callianassa*) *louisianensis*; Felder and Lovett, 1989, *Callichirus major*; Botter-Carvalho et al., 2007; *T. australiensis*; Rotherham and West, 2009). There are a few exceptions where a male biased sex ratio occurs such as the study by Kevrekidis et al. (1997) that found *Upogebia pusilla*, to have a predominantly male sex bias in the Evros Delta, Aegean Sea. Rowden and Jones (1994) also found a male biased sex ratio for *Callianassa subterranea* in the North Sea. Although there are suggestions for sex bias in the literature, such as the loss of males through fighting, migration or predation (Felder and Lovett 1989; Dumbauld et al. 1996) or bias due to sampling gear efficiency (Rowden and Jones, 1994), it really is unclear how or why sex ratio bias occurs (Dworschak, 1998).

Interestingly in this study, there was a male biased sex ratio in the smaller individuals or juveniles (*T. australiensis* CL < 5 mm and *B. arenosus* CL < 3 mm) in 2004/ 2005 for *T. australiensis* and *B. arenosus* and in 2006/ 2007 at Crib Point for *T. australiensis* only. Rotherham and West (2009) also found a male biased sex ratio in the small size classes (< 6 mm CL) of populations of *T. australiensis* in south-eastern New South Wales. Other studies have reported a consistent male sex bias in smaller individuals of ghost shrimps even when there is a female sex bias in adults. For example, in Piedade Beach, north eastern Brazil, the sex ratio of *Callichirus major* was male biased in smaller individuals under 7 mm carapace length (Botter-Carvalho et al., 2007). Botter-Carvalho et al., (2007) suggested that although it is uncertain why a male biased sex ratio occurs in smaller individuals there may be some sampling bias imposed by using a bait pump to collect shrimps. Bait pumping has been suggested to selectively favour the collection of females as they occupy higher positions in the burrow more frequently (Rowden and Jones, 1994). Males are also faster and more vigorous in escaping the sampling technique of bait pumping (Botter-Carvalho et al., 2007). In the current study a male biased sex ratio in juveniles was found at Warneet for both *B. arenosus* and *T. australiensis* in 2004-2005 and not 2006-2007 at Warneet. This supports

the idea that bait pumping may preferentially collect females in the larger sizes as individuals collected in 2004–2005 were collected using a bait pump and in 2006–2007 they were removed through hand excavation of cores. Therefore, it is unclear if there are any ecological explanations of the variable sex ratio found in this study or if it is simply a product of the sampling efficiency.

In both 2004–2005 and 2006–2007, the population of *T. australiensis* comprised of two cohorts of individuals. This supports Hailstone and Stephenson's (1961) suggestion that this species lives for two years. There was however, no progression of these cohorts through time, again similar to findings of Hailstone and Stephenson (1961) and Coleman (1981) who suggested that a lack of progression in the mean size of cohort modes can imply a negligible growth rate or balanced recruitment and loss in the population. Individuals move into the population through larval recruitment (Dakin and Colefax, 1940; Hailstone and Stephenson, 1961) but it has also been suggested that individuals of *T. australiensis* could move between areas by burrowing or crawling on the surface of the substratum (Hailstone and Stephenson, 1961; Coleman, 1981) resulting in a highly dynamic population structure for this species.

For *B. arenosus*, generally only one cohort of individuals was seen each month in both 2004–2005 and 2006–2007. As with *T. australiensis* there was no progression of the mean carapace length of the cohorts of *B. arenosus* over time, prohibiting any estimation of growth. Coleman (1981) found similar results for *B. arenosus* in Western Port in 1981. No progression in the mean carapace lengths through time may suggest that as with *T. australiensis* the population is highly dynamic with constant recruitment and/or migration into the population. Alternatively, with only one cohort present each month this species may only live for one year. No data is available on the development of *B. arenosus*, either larval stages or growth parameters therefore further study is needed so that inferences can be made about the age and life cycle of this species.

The fecundity of each species was shown through measurements of clutch and embryo size. The clutch size was positively correlated with the size of females for both species, which is consistent with many other studies of thalassinidean shrimps (e.g. Dworschak, 1988; Berkenbusch and Rowden, 2000; Kubo et al., 2006; Rotherham and West, 2009). *Trypaea australiensis* had significantly larger embryos and a significantly larger clutch size than *B. arenosus*, a result which is not surprising since *T. australiensis* females are much larger than *B. arenosus* females.

Rotherham and West (2009) found that *T. australiensis* had on average smaller embryos in the Moruya River, New South Wales than the mean embryo sizes found in the current study for *T. australiensis* in Western Port. This pattern of smaller embryo size occurring at higher latitudes (New South Wales compared with Victoria) is consistent with Berkenbusch and Rowden (2000) who found that the embryo size of *Callianassa filholi* increased significantly with higher latitudes. The sites sampled by Berkenbusch and Rowden (2000) that showed differences in embryo sizes were separated

by greater than 5° in latitude which is similar to the degree of separation between the sites sampled by Rotherham and West (2009) and the sites sampled in the current study. Kubo et al. (2006) also found a latitudinal gradient in the size of ghost shrimps (*Nihonotrypaea japonica* and *N. harmandi*) embryos, again with the smaller embryos at higher latitude. Berkenbusch and Rowden (2000) summarised literature that showed that food availability may be a driving factor of latitudinal differences in embryo size. In contrast, Kubo et al. (2006) attributed latitudinal differences in embryo size to differences in temperature. For example, the higher the latitude the cooler the water and therefore the larger the embryo size [as seen for *N. japonica* (cooler waters) and *N. harmandi* (warmer waters)] (Kubo et al., 2006). Further evidence for temperature being the primary factor is shown by Kubo et al. (2006) for *N. japonica* in Ariake Sound, where embryos produced in winter to spring were larger than embryos produced in summer. In Australia, it is unknown whether it is temperature, food availability or some other factor that leads to a latitudinal difference in the embryo size of *T. australiensis* however as Rotherham and West (2009) describe, there is a known temperature gradient from north (lower latitudes) to south (higher latitudes) along the east coast of Australia suggesting that temperature may be the primary factor for latitudinal differences in Australia.

The clutch size of *T. australiensis* was also reported by Rotherham and West (2009). The range of clutch sizes for *T. australiensis* in the current study is at the lower end of this range found in Rotherham and West (2009). This may be due to a 'trade-off' in the need for *T. australiensis* to produce larger embryos in cooler waters in Victoria and therefore less embryos and a smaller clutch size. This was suggested as a possible reproductive trait of *N. japonica* by Kubo et al. (2006) where the embryos produced in winter were larger and the clutch size was reduced due to the need to produce embryos with higher nutrients to withstand 'nutritional stress' brought about by winter conditions (Paschke et al., 2004).

Kubo et al. (2006) compared the population biology, particularly fecundity, of many thalassinidean shrimp species from around the world. From these comparisons it was shown that shrimps with similar embryo and clutch sizes had very similar life history traits. For example, *Nihonotrypaea harmandi* and *N. petalura* have similar embryo volumes to *Callianassa filholi*, *C. subterranean* and *Neotrypaea californiensis* all of which have four or five zoeal stages and relatively long planktonic periods (>15 days). Seven other species in this comparison (*Callichirus* (as *Callianassa*) *kraussi*, *Neocallichirus* (as *Callianassa*) *kewalramanii*, *Callichirus major*, *Lepidophthalmus louisianensis*, *L. sinuensis*, *Pestarella tyrrhena*, and *Sergio mirim*) had larger embryos and had only two to three planktotrophic/lecithotrophic zoeal stages with shorter planktonic periods (<14 days). This comparative information is useful in predicting the type of life history pattern that a particular species might have. There have been a number of studies on the life history of *Trypaea australiensis* that show the number of zoeal stages and planktonic period for this species. However for *Biffarius arenosus*, there is very little information. The mean embryo

volume of *Biffarius arenosus* found in the current study falls into the group of species reported by Kubo et al. (2006) that have smaller embryos ($<0.180\text{ mm}^3$) and therefore it is predicted that *B. arenosus* would have around 4-5 zoeal stages and a relatively longer planktonic period. The embryos of *Trypaea australiensis* fall into the group of species reported by Kubo et al. (2006) that have larger embryos (embryo volume $>0.180\text{ mm}^3$) and this suggests that the life cycle of *T. australiensis* would have two to three zoeal stages. Unfortunately, these predictions need to be taken with some caution as previous studies of the life history of *T. australiensis* have showed that *T. australiensis* has six larval planktonic stages with a relatively long period of larval development (up to 6 weeks) (Dakin and Colefax, 1940; Hailstone and Stephenson, 1961), a result which is not consistent with the evidence presented by Kubo et al. (2006). Therefore, although this summary by Kubo et al. (2006) is useful in making some predictions about the life history of these species (particularly *B. arenosus*) further laboratory studies are required to definitively observe the life cycle of these species.

Conclusions

This study has provided information about the population structure of *T. australiensis* and *B. arenosus* that confirms previous findings about these species in Western Port (Coleman, 1981), but shows some key differences between Western Port populations and northern and eastern Australian populations (Hailstone and Stephenson, 1961; Kenway, 1981; McPhee and Skilleter, 2002a; Rotherdam and West, 2007; Rotherham and West, 2009). It also provides new information on the fecundity of both species, in particular *B. arenosus*. The main differences between findings from this study and others occurred in the time of breeding seasons and small variations in the timing of recruitment of juveniles into the populations. There was also significant evidence that there are latitudinal differences in the size of individuals and the fecundity of *T. australiensis* along the east coast of Australia. These findings are consistent with other latitudinal studies of ghost shrimp biology around the world (e.g. Berkenbusch and Rowden, 2000; Kubo et al., 2006) and suggest that further environmental data should be collected alongside population data so that factors contributing to these latitudinal differences can be determined. Furthermore, given that there are some differences in the population dynamics of the same species of ghost shrimps at different latitudes, any studies investigating ghost shrimps for use as indicators of benthic habitats need to take into account local differences in population biology.

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