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POPULATION DYNAMICS OF THE BURROWING GHOST SHRIMP *CALLIANASSA FILHOLI* ON AN INTERTIDAL SANDFLAT IN NEW ZEALAND

(DECAPODA: THALASSINIDEA)

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ABSTRACT

Population samples of the burrowing ghost shrimp *Callianassa filholi* Milne-Edwards, 1878 were taken on an intertidal sandflat in Otago Harbour, south-eastern New Zealand, monthly over a period of 16 months. The spatial population distribution appeared to be contagious in autumn and early winter, and random from mid-winter to summer. The population density did not show any significant difference over the sampling period, with a mean density of 16 individuals m^{-2}. Overall the sex ratio was significantly biased towards females (mean male:female ratio = 1:1.5). Visual inspection of size frequencies indicated the presence of a bimodal population. Large animals (7-14 mm carapace length [CL]) were present throughout the year and no significant difference in CL was observed between sexes. Post-larval shrimp ($CL \leq 3$ mm) were present in spring and summer, which together with developing juveniles constituted a second group of smaller animals (< 7 mm CL). Regression analysis of allometric growth showed the size of maturation to be 8 mm CL for females and 9 mm CL for males. Only females of $CL \geq 8$ mm carried eggs and these ovigerous females were present from mid-winter to mid-summer, with all reproductive females bearing eggs in November (spring). Data obtained suggest that the *Callianassa filholi* population is stable, with low mortality and recruitment rates and that individuals have a lifespan of 2-3 years.

INTRODUCTION

Thalassinid shrimps have attracted growing attention with respect to their bioturbatory role in various processes that occur in soft-sediment environments. Their bioturbation activities have been demonstrated to have a profound impact on the geotechnical (Tudhope & Scoffin 1983; Vaugelas 1985; Colin et al. 1986), chemical (Koike & Mukai 1983; Powilleit & Graf 1996) and biological (Branch & Pringle 1987; Tamaki 1988) characteristics of the habitat. As a consequence callianassids, in particular, are often considered as a central component of benthic communities (Suchanek 1983; Alongi 1986; Tamaki 1988). Despite this recognition, there are still relatively few detailed studies concerning callianassid population biology (Hailstone & Stephenson 1961; Devine 1966; Forbes 1977; Bird 1982; Tamaki & Ingole 1993; Rowden & Jones 1994). The paucity of information is probably due to the shrimps' cryptic lifestyle which makes field observations and sampling of shrimp populations difficult. As a consequence, knowledge on the population biology of callianassids is limited and often biased. This is particularly so for *Callianassa filholi*, the burrowing ghost shrimp endemic to New Zealand. *Callianassa filholi* has been reported from locations throughout New Zealand, ranging from intertidal sandflats (Devine 1966; Morton & Miller 1968; Gillespie & Asher 1995) to subtidal habitats with depths of 63 m (NIWA). Despite an ealier study (Devine 1966), little detail is known about the biology and ecology of *Callianassa filholi*. In order to address this shortfall a comprehensive study is currently examining intertidally occurring populations of *Callianassa filholi*. The present paper reports on aspects of the species' population biology.

It should be noted that the systematic status of *Callianassa filholi* is currently under review. In all likelihood it will be assigned to a different genus in the future (R.B. Manning pers. comm.).

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MATERIALS AND METHODS

Field collection. The present study was carried out at Otakou, an intertidal sandflat in Otago Harbour, southeastern New Zealand (Fig. 1). The study site encompassed 0.25 km^2, consisting of well sorted sand, with a tidal range of 1.4 to 2.2 m (Fussell 1979). The *Callianassa filholi* population was sampled, monthly from June 1995 to September 1996, by taking 6 to 9 random cores (0.25m^2 surface area to a depth of 50 cm). [The number of cores taken on each occasion was dependent on logistical constraints. Core depth was chosen to exceed the maximum burrow depth (40 cm) determined by resin casting, unpublished data]. The contents of each core were sieved on 1 mm mesh and the retained material sorted for ghost shrimp, both by eye (larger individuals) and stereomicroscope (smaller individuals). Shrimp were anaesthetised (7.5% magnesium chloride in freshwater) for 5 h prior to fixation in 10 % formalin/seawater.

Laboratory analysis. Collected *Callianassa filholi* were identified using a diagnostic key (Chilton 1907) counted and visually checked for parasitism. Morphological measurements were made to the nearest 0.1 mm using a stereomicroscope with a measuring eye-piece. Measurements included carapace length (CL; tip of the rostrum to the posterior margin of the carapace), and maximum primary chela propodus width (ChW). In addition, the position of the enlarged

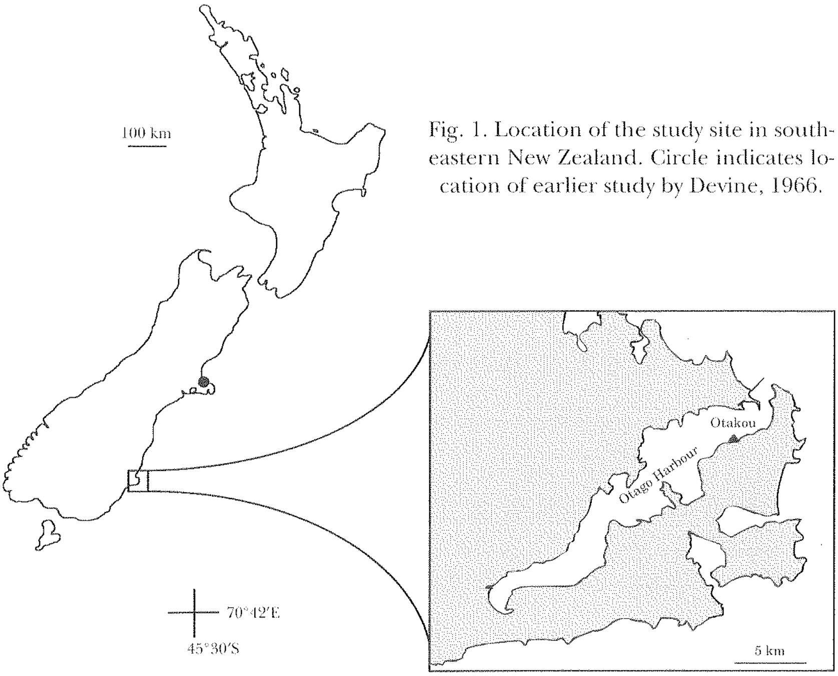

Fig. 1. Location of the study site in south-eastern New Zealand. Circle indicates location of earlier study by Devine, 1966.

primary chela was recorded. Sex was determined for individuals larger than 3 mm CL by presence (females, biramous) and absence (males) of anterior pleopods. Shrimp were classed following convention into 1 mm size category intervals. Shrimp smaller than 3 mm CL were classed as post-larval (pl). The proportion of reproductive females in berry was recorded for each sampling occasion.

Data analysis. The spatial distribution of the shrimp population was examined by calculation of a variance:mean ratio Index of Dispersion (Elliot 1977). Allometric growth of the primary chela in relation to CL was analysed to ascertain size at maturation, using REGRANS (Pezzuto 1993). In comparison, repetitive standard least square regression and subsequent assessment of the total residual sum of squares were applied. Size at maturation was then defined by the value with lowest combined sum of the squared residuals (SSR) for the regressions. Type of relative growth was determined from the allometric coefficients calculated from subsequent log-transformation of the subdivided data (see Lovett & Felder 1989). Individuals with a damaged carapace, damaged or missing chelae were precluded from the sample measured.

RESULTS

Population distribution and density. The population distribution of *Callianassa filholi* at Otakou showed temporal variation (Table 1). At the beginning of the

Table 1: Summary of population details of *Callianassa fiholi* at Otakou between June 1995 and September 1996.

Month	Number of $0.25 m^2$ cores	Total number of shrimp	Mean density (individuals/m^2)	Index of Dispersion ($I = \delta^2/mean$)	χ^2 ($I[n-l]$)	P	Sex ratio (Male/Female)	P	Primary chela ratio (left/right)
June	8	34	17	1.19	8.35	n.s.	0.5	n.s.	0.92
July	9	27	12	1.58	12.67	n.s.	0.6	n.s.	0.83
August	8	12	6	2.29	16.00	<0.05	0.6	n.s.	3.00
September	6	33	22	1.44	7.18	n.s.	0.5	<0.05	1.18
October	8	25	12	1.59	11.14	n.s.	0.8	n.s.	1.38
November	8	30	15	1.81	12.67	n.s.	0.9	n.s.	1.11
December	8	26	13	0.86	6.00	n.s.	0.6	<0.05	2.20
January	6	35	23	1.19	5.97	n.s.	1.1	n.s.	0.87
February	9	34	15	1.31	10.47	n.s.	0.4	<0.01	1.67
March	8	23	11	2.23	15.61	<0.05	1.1	n.s.	0.78
April	9	36	16	2.56	20.50	<0.01	0.4	<0.05	1.29
May	7	44	25	2.53	15.17	<0.025	0.4	<0.005	0.72
June	8	37	18	3.39	23.74	<0.005	0.7	n.s.	1.36
July	7	38	21	1.77	10.63	n.s.	0.8	n.s.	1.73
August	9	30	13	2.40	19.22	<0.025	1.0	=1.00	1.10
September	9	33	15	2.93	23.43	<0.005	0.5	n.s.	1 .00

Table 2. Distribution of sex ratio amongst different size classes of *Callianassa filholi* at Otakou (combined data, all months).

Size class (mm CL)	M/F-Ratio	χ^2	P
≥3	2.67	2.3	0.13
≥4	2.00	1.3	0.25
≥5	1.40	0.3	0.56
≥6	0.93	0.0	0.85
≥7	0.39	8.7	0.00
≥8	0.30	17.9	0.00
≥9	0.43	17.6	0.00
≥10	0.63	5.6	0.02
≥11	1.10	0.1	0.76
≥12	1.13	0.1	0.81
≥13	2.00	0.3	0.56

sampling period in 1995, the population distribution did not appear to be significantly different from random, in winter (June, July, except for August), spring (September, October, November) and summer (December, January and February 1996). However, in 1996 the population was contagiously distributed in autumn and winter (March, April, May, June, August, except for July) and at the beginning of spring (September). The monthly mean density was not significantly different (ANOVA, $P>0.10$) and the mean population density across all months was found to be 16 individuals m^{-2} (Table 1).

Sex ratio. The sex ratio varied with season and size class, being almost equal or equal in November, January, March, July and August 1996 and biased towards females in all of the other months. This bias was significant in some months (September and December 1995, February, April and May 1996). Overall, the prevalence of females was statistically significant (χ^2 =25.8; $P<0.001$, n= 477) with a mean male:female-ratio of 1:1.5, ie. 62% females (Table 1). When distinguishing between size classes (total for all months), females were significantly more abundant than males in the middle range of size classes (≥ 7, 8, 9, 10 mm CL), males were more abundant (though not significantly so) amongst smaller size classes (≥ 3, 4, 5 mm CL) and the two largest size classes (≥ 13mm and 14 mm CL – the latter class containing only a single male), whilst the sex ratio was almost equal when considering shrimp of ≥ 6, 11 and 12mm CL (Table 2).

Handedness. No clear pattern for the occurrence of handedness by individuals was apparent. When individuals from both sexes over the entire sampling period were combined, the ratio of handedness within the population appeared to be almost equal (L/R=1.16) (Table 1); there was no statistically significant variation of right- or left-handedness exhibited by shrimp across all months (χ^2 =2; $P>0.1$, n =369). For some months there was a higher proportion of left-handedness (e.g. August 1995: 75%) or right-handedness (e.g. May 1996: 58%), whilst at other times the ratio of left- to right-handedness was almost equal or equal (November 1995, August and September 1996). There was no

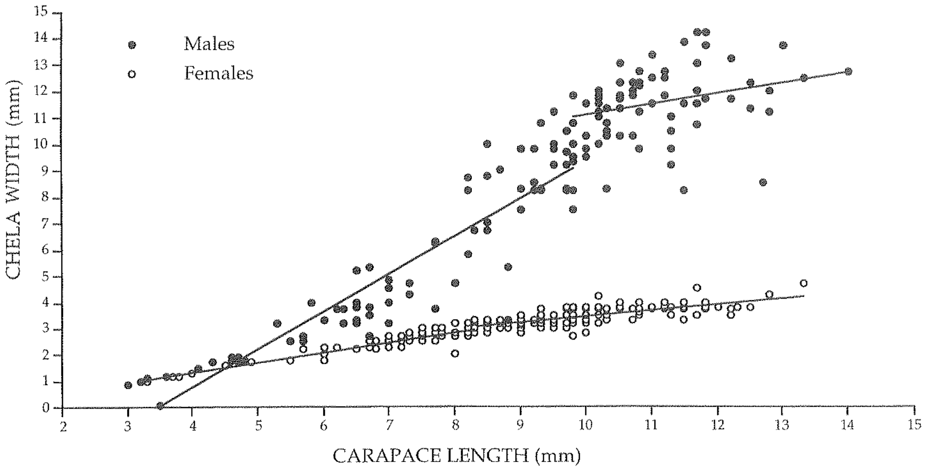

Fig. 2. Primary chela width (mm) in relation to carapace length (mm) of male and female *Callianassa filholi*. Transition points were determined at 9.8 mm CL for males (ChW=1.437xCL-4.989, n=82, r=0.918, $P<0.001$ and ChW=0.406xCL+7.032, n=68, r=0.292, $P<0.05$) and 8.3 mm CL for females (ChW=0.381xCL-0.196, n=63, r=0.926, $P<0.001$ and ChW=0.225xCL+1.216, n=173, r=0.734, $P<0.001$).

significant preference for left- or right-handedness within sexes, although it was observed that males were more often left-handed (total L/R=1.24, $\chi^2=2$; $P>0.1$, $n = 166$) and females more often right-handed (total L/R=0.70, $\chi^2=0.4$; $P>0.5$, $n = 203$).

Relative growth and sexual maturity. Allometric growth of the primary chela in relation to carapace length was used to determine size at maturation. Results of the data analysis by REGRANS suggested male shrimp reach sexual maturity at 9.8 mm CL whilst females become mature at 8.3 mm CL (Fig. 2). Iterative subsetting data analysis determined size at maturity to be 10 mm CL for males, and

Table 3. Sum of the squared residuals (SSR) values from iterative subset data of hypothesized maturation lengths after linear regressions of carapace length and primary chela width of *Callianassa filholi*.

	CL	SSR	CL	SSR	Combined SSR
Males	<10.5	156.76	≥10.5	82.46	239.22
	<10.0	130.18	≥10.0	103.07	233.25
	<9.5	98.52	≥9.5	149.37	247.89
	<9.0	86.61	≥9.0	159.21	245.82
	<8.5	34.89	≥8.5	219.03	253.92
Females	<9.5	3.81	≥9.5	6.44	10.25
	<9.0	2.79	≥9.0	7.39	10.18
	<8.5	2.33	≥8.5	7.85	10.18
	<8.0	1.04	≥8.0	9.34	10.38
	<7.5	0.67	≥7.5	9.83	10.5

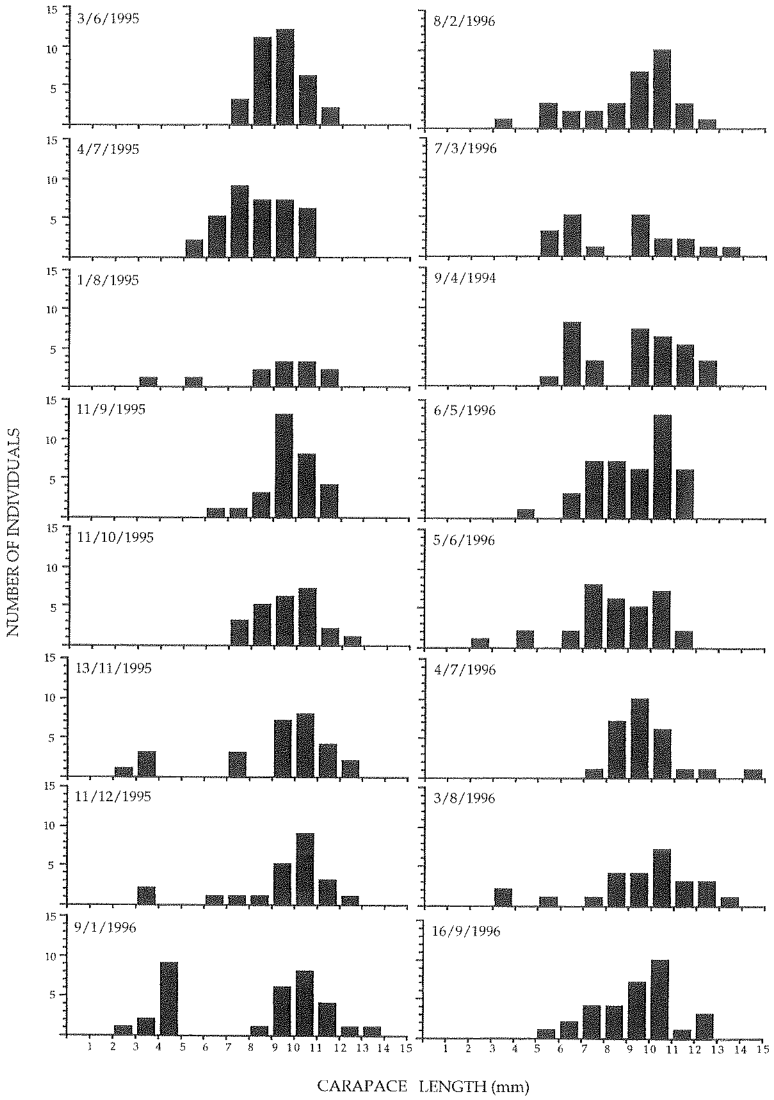

Fig. 3. Size (carapace length) frequency distributions of *Callianassa filholi* at Otakou between June 1995 and September 1996.

8.5-9.0 mm CL for females (Table 3). Before reaching maturity, primary chela size increased isometrically in females and allometrically (positive) in males. Beyond the size at maturation, major chela growth became negatively allometric for both sexes. The difference in chela growth before and after maturation was significant for both, males and females (ANCOVA, both $P < 0.0001$), so that transition points could be accepted. The slow isometric growth of primary che-

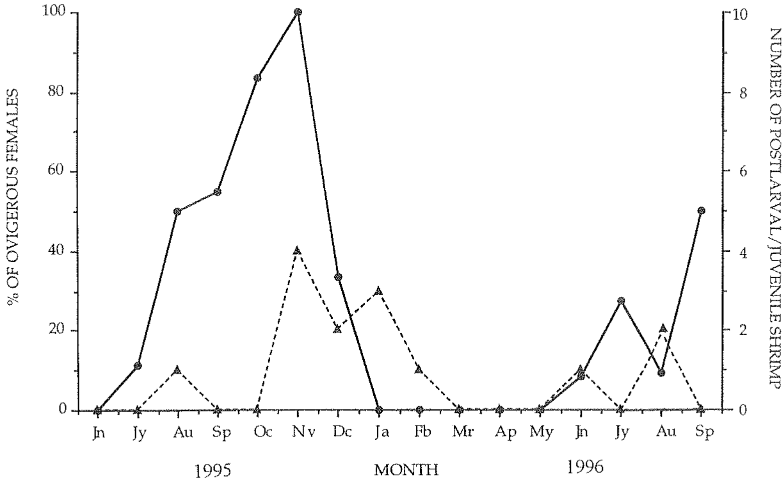

Fig. 4. Proportion of reproductive females (CL ≥ 8 mm) in berry (solid line) and presence of post-larval and small juvenile (CL ≤ 4 mm)(dashed line) *Callianassa filholi* between June 1995 and September 1996.

lae in females before maturation results in considerably smaller sized chelae than for males. Taking into account the transition points indicated by both relative growth analysis techniques, it is considered that the size of maturation can be accepted to be ≥ 9 mm CL for males, and ≥ 8 mm CL for females (all but one of the ovigerous females collected [n=58] was found to be smaller than this suggested maturation length).

Population size structure. Size-frequency distributions show a bimodal population structure, representing sexually mature adults and post-larvae/juveniles (Fig. 3). Sexually mature shrimp were present throughout the entire year, constituting one cohort (modes 9/10 mm CL). Post-larval/juvenile shrimp clearly began recruiting to the population at the end of spring (November). During the course of the summer these developing juveniles comprised a second cohort (mode 4 mm CL). In autumn, juveniles grew towards sexual maturity (mode 6 mm CL) and recruited to the adult population from late autumn (May) onwards (modes 7 and 8 mm CL). By winter (July), the population returned to a situation dominated by mature adults, with the occurrence of small numbers of juveniles in the population during June, 1996 and August, 1995/6. There was no statistically significant difference in carapace length between sexes (Two-way ANOVA, n = 451, P>0.05), nor between sexes over time (P>0.25). Mean carapace length (both sexes) over time showed significant variation between some months (P<0.01) but did not display any apparent trend, nor seasonal variation.

Reproduction and post-larval settlement. Ovigerous females began appearing in the population during July, 1995 and their presence increased to a maximum in

November, when all reproductive females (≥ 8 mm CL) carried eggs. Numbers declined in December and no berried females were found in January, 1996. In June, 1996, ovigerous females started appearing in the population again, exhibiting an apparent increase with one sharp decline in August. Post-larval shrimp and juveniles ≤ 4 mm were present in November 1995 through to February 1996, and discretely in June 1996 and August 1995/96 (Fig. 4).

Parasitism. No infestation by obvious parasites was observed in *Callianassa filholi.*

DISCUSSION

The temporal variation apparent in the spatial distribution of the *Callianassa filholi* population at Otakou differs from the observations of Devine (1966), who recorded *Callianassa filholi* burrows at South Brighton to be contagiously distributed throughout the period of study. However, his results were based on counts of burrow openings at the surface rather than direct counts of individuals from core samples. Devine (1966) did note that the number of burrow openings does not necessarily represent the number of individuals present, as burrows may be occupied by one male together with two or more females. It has been documented for thalassinids that the relationship between burrow openings and shrimp present is indeed very variable (Dumbauld et al. 1996). In particular, population estimates based on burrow openings are likely to be distorted when shrimps are known to share burrows (eg. *Callichirus armatus,* Vaugelas et al. 1986). Burrow sharing and interconnection of burrows has also been suggested for *Neotrypaea affinis* (MacGinitie & MacGinitie 1968), *Trypaea australiensis* (Hailstone & Stephenson 1961) and *Neotrypaea californiensis* (MacGinitie 1934). In addition, it has been postulated that mating occurs in interconnected burrows (e.g. Felder & Lovett 1989) and that young postlarval shrimp can initially excavate their own burrows in the wall of a parent burrow (e.g. *Callianassa kraussi,* Forbes 1973). Such adult-adult and adult-juvenile burrow relationships are likely to affect the spatial population distribution observed (Tuck et al. 1994). Observations on the spatial distribution pattern of thalassinids are scarce, however, temporal variation in spatial distribution has been noted previously (e.g. *Callianassa subterranea,* Rowden & Jones 1994). At Otakou, it appears that varying proportions of the population share burrows, with variations apparent in the number and gender combinations observed per burrow (unpublished data). It is possible that burrow sharing occurs part of the time and is related to distinct periods in the shrimp's lifecycle, such as mating and juvenile recruitment.

No significant variations in population density of *Callianassa filholi* were found at the study site, which exhibited a relatively low mean population density (16 m^{-2}). Callianassids demonstrate a wide range of population densities, sometimes in excess of 400 individuals m^{-2} (e.g. *Callianassa bouvieri,* Dworschak & Pervesler 1988; *Neotrypaea californiensis,* Dumbauld et al. 1996). The findings of the present study are consistent with the low population densities recorded for thalassinid species from similar intertidal habitats (e.g. 20 m^{-2}, *Callianassa japonica*, Koike & Mukai 1983; 10 – 40 m^{-2}, *Callichirus islagrande*, Felder & Griffis 1994). The *Callianassa filholi* population did not show any drastic changes in spatial density, as has been observed for other intertidal occurring species, where margins of dense shrimp beds may be marked by a dramatic decline in shrimp numbers (e.g. *Neotrypaea californiensis*, 100 individuals m^{-2} to 2-3 individuals m^{-2} over a horizontal distance of 2 m, Posey 1986). Aggressive behaviour by confronting individuals has been suggested to serve as a density controlling factor, and has been recorded numerously for other species (MacGinitie 1934; Buchanan 1963; Berrill 1975; Griffis & Chavez 1988; Felder & Lovett 1989; Rowden & Jones 1994). However, no aggressive interactions were noted in *Callianassa filholi* (pers. obs.).

The female biased sex ratio in the *Callianassa filholi* population at Otakou is consistent with the findings of the earlier study of the same species by Devine (1966), and those of other callianassids, e.g. *Trypaea australiensis* (Hailstone & Stephenson 1961), *Lepidophthalmus louisianensis* (Felder & Lovett 1989) and *Callianassa subterranea* (Witbaard & Duineveld 1989). Whilst the sex ratio varied among juvenile size classes, females became significantly more abundant, relative to males, with the increasing maturity of the individuals. This facet of the population structure has also been observed for *Neotrypaea californiensis*, and it has been suggested that this bias might be attributed to the loss of large males from the population due to fighting or predation (Dumbauld et al. 1996). *Callianassa filholi* has been found to constitute an important prey species for the swimming crab *Ovalipes catharus* in localised areas (Wear & Haddon 1987) and its occurrence has also been noted occasionally in the stomach contents of bentho-pelagic fish (e.g. *Auchenoceros punctatus*, R. Ardern pers. comm.).

The relationship between primary chela allometry and sexual maturity has been used in several studies to determine size at maturation for callianassids (e.g. Tucker 1930; Rodrigues 1985; Dworschak in press). Primary chela growth in both sexes has been found to have similar rates before reaching maturity, after which primary chela growth becomes positively allometric for males and almost isometric or negatively allometric for females (e.g. *Lepidophthalmus louisianensis*, Felder & Lovett 1989; *Callianassa subterranea*, Rowden & Jones 1994). Growth of primary chelae for *Callianassa filholi* is isometric for females and positively allometric for males, before reaching sexual maturity, so that growth rates differ between sexes. After reaching sexual maturity, both sexes display negative allometry in primary chelae growth, which is unusual for males.

The observed growth rates and sizes for primary chelae of male and female *Callianassa filholi* are consistent with the findings of Devine (1966), who applied linear regressions to the total data for each sex. Differences in primary chela growth between sexes result in one significantly enlarged chela in males opposed to almost similar sized and much smaller chelae in females. Such differentiation in chelae size between sexes is consistent with observations of other callianassids (e.g. Hailstone & Stephenson 1961; Felder & Griffis 1994). The lack of any pattern of left- or right-handedness apparent for *Callianassa filholi* has also been documented for *Callianassa bouvieri* (Dworschak & Pervesler 1988), *Lepidophthalmus louisianensis* (Felder & Lovett 1989), *Callianassa subterranea* (Rowden & Jones 1994), *Neotrypaea californiensis* (Labadie & Palmer 1996), *Callianassa candida*, and *Callianassa tyrrhena* (Dworschak, in press). It has not been established categorically what purpose the enlarged primary chela serve, but Labadie & Palmer (1996) inferred from chela morphometry that it is used in fighting and mating, a view that conforms to suggestions made in earlier studies (Buchanan 1963; Felder & Lovett 1989; Tunberg 1986). Although *Callianassa filholi* were never observed displaying aggressive behaviour, it is likely that the difference in chela morphology between males and females reflect distinct behavioural traits (Felder & Lovett 1989).

The bimodal population found at the present site supports the results of Devine (1966) who also found a bimodal population at South Brighton consisting of mature adults and juveniles. He similarly found mature adults throughout all seasons, with the presence of juveniles varying throughout the year. The population appears to exhibit low mortality and recruitment rates, with size-frequency distributions comparable to those of other thalassinids, in which the population is dominated by mature individuals with very few small juveniles being present (e.g. *Upogebia deltaura*, Tunberg 1986). Tunberg (1986) explained the observed size-frequency pattern by suggesting that there was a depth-age zonation, i.e. juveniles were found in shallower water than adults. A similar size-frequency pattern has been found for *Callianassa japonica*, where adult shrimp appear to positively affect larval settlement and subsequent recruitment success (Tamaki & Ingole 1993). Due to limited monthly data, no cohort progression rates could be calculated. However, a visual assessment of growth in mean carapace length for both cohorts over the sampling period were estimated for *Callianassa filholi* (see Felder & Griffis 1994). According to Tamaki et al. (1996) female *Callianassa japonica* become mature in approximately the first year after recruiting to the benthic population, and a similar observation has been made for *Callianassa subterranea* (Rowden & Jones 1994). In the period before *Callianassa filholi* juveniles reach sexual maturity, the mean carapace length was found to increase by 6 to 7 mm. This growth rate is similar to previous estimates of first year growth for callianassids, which include 9.5 mm for *Trypaea australiensis* (Hailstone & Stephenson 1961), 6 mm for *Callianassa kraussi* (Forbes 1977), 6 to 7 mm for *Callichirus islagrande* and 3 to 9 mm for *Lepidophthalmus louisianensis* (Felder & Griffis 1994). Mature *Callianassa filholi* adults grow at a slightly slower rate, with mean carapace length increasing by a further 4 to 5 mm. Large animals are present in the population, but not in high enough numbers to suggest a third year class as Devine (1966) postulated for the South Brighton population. If cohort modes represent year classes, the lifespan of *Cal-*

lianassa filholi, derived from data in the present study, is 2, possibly 3 years. This estimate is slightly more conservative than the 3 to 4 year lifespan suggested by Devine (1966), who also inferred that *Callianassa filholi* grow slower in the first year than in the second. Although data from the present study does not support this interpretation, the mean growth rate is compatible with the one suggested by Devine (1966). A lifespan of 2 to 3 years appears to be consistent with findings for other callianassids e.g. *Trypaea australiensis* (2 years, Hailstone & Stephenson 1961), *Lepidophthalmus louisianensis* (2-2.5 years, Felder & Lovett 1989), *Callianassa kraussi* (3 years, Forbes, 1977) and *Callianassa subterranea* (2-3 years, Rowden & Jones 1994). The breeding season, from early/mid-winter through to mid-summer, indicated by the proportion of ovigerous females, agrees with the extent of the breeding season observed in the previous study of *Callianassa filholi* (Devine 1966). The breeding season seems unusual when compared to other callianassids, for which breeding occurs from spring to summer/autumn (Felder & Griffis 1994; Forbes 1977; Tamaki et al. 1996; Thessalou-Legaki & Kiortsis 1997; Witbaard & Duineveld 1989). Devine (1966) believed that the extensive breeding season of *Callianassa filholi* incorporated a second egg laying period for larger females. So-called "double" breeding seasons have been noted and postulated for other species (e.g. *Trypaea australiensis,* Hailstone & Stephenson 1961; *Callianassa subterranea,* Rowden & Jones 1994). However, the results of the present study of *Callianassa filholi,* indicate only a single maximum of egg bearing females in the early summer. Though arguably, the occurrence of small numbers of post-larval/juvenile shrimp in June 1996 and August 1995/96 might be considered as circumstantial evidence for a second egg laying period, the existence of a double breeding season for *Callianassa filholi* at the study site remains unproven. The appearance of the main cohort of post-larval and small juvenile shrimp corresponds to the indentified breeding season, initially with a delay of 8 weeks after the first presence of ovigerous females. Taking into account a brooding period of 5.5 weeks (Devine 1966), data indirectly suggests that larval *Callianassa filholi* spend about 3 weeks in the plankton prior to settling and recruiting to the benthic population. Devine (1966) postulated the larval life to last up to 5 months, but strangely he did not account for the continuous hatching and recruitment of the larvae to the plankton during the breeding season. The planktonic life suggested by the present study is compatible to the planktonic life estimated for other callianassid species by the same method (10 weeks, Johnson & Gonor 1982, 4 weeks, Rowden & Jones 1994; 3.5 weeks, Tamaki et al. 1996).

Obvious parasites such as bopyrids and rhizocephalans have been noted in numerous thalassinid species from different locations e.g. *Callianassa tyrrhena* (Dworschak, in press), *Callianassa subterranea* (Rowden & Jones 1994), *Calocarides coronatus* (Høeg & Lützen 1985), *Upogebia pusilla* (Dworschak 1987), *Upogebia deltaura,* and *Upogebia stellata* (Astall et al. 1996). *Callianassa filholi* appears to be free of obvious parasites, which is consistent with the findings of Devine

(1966). A complete lack of parasitism of callianassid populations is generally less frequently noted (e.g. *Callianassa candida,* Dworschak in press), and the reason(s) for this situation remain unknown.

Despite the many interesting aspects of the life of *Callianassa filholi* which have been confirmed or revealed by the present study, it is apparent that further work is required to provide a more comprehensive picture of the population biology of this, and other, callianassid shrimps. The authors suggest that the following themes warrant further investigation:

1. The circumstances and nature of mating behaviour.
2. The factors which influence the temporal occurrence and duration of the breeding season(s).
3. The relationship between larval recruitment to the plankton and subsequent benthic settlement.
4. The relationship between spatial population distribution and distinct life-cycle periods.
5. The factors which influence the promotion of a low and stable population density.

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