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Latitudinal variation in the reproductive biology of the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea)

Abstract Population structure and reproductive ecology of the burrowing ghost shrimp *Callianassa filholi* Milne-Edwards, 1878 were studied in populations along a latitudinal gradient throughout New Zealand during the breeding season. Size-frequency distributions revealed unimodal populations, with predominantly sexually mature shrimp. All populations showed an unbiased sex-ratio, and there appeared to be no significant difference in size (carapace length, CL) between sexes. At the same time, CL and size at maturity differed significantly between populations; however, a general increase in sizes from north to south was not consistent throughout the latitudinal range studied. The timing of the breeding cycle differed significantly between populations, and breeding started earlier in southern populations. Number of embryos (fecundity) increased linearly with female CL at each location, but rates differed significantly between populations. Embryo size was not related to number of embryos, and the former increased significantly with latitude. With the exception of embryo size, observed differences in body size/size at maturity and reproductive timing between *C. filholi* populations are thought to be determined by food availability rather than temperature. Thus, further study is suggested on these aspects of thalassinid reproductive biology.

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Introduction

Thalassinidean shrimps occupy burrows of varying complexity and design in intertidal and subtidal soft-sediment environments (Nash et al. 1984; Griffis and Suchanek 1991). Their sediment turnover activities, associated with burrow construction/maintenance and feeding, have been shown to impact the structural and geotechnical properties of the substratum (Tudhope and Scoffin 1984), and, consequently, on important ecosystem functions such as nutrient exchange (Koike and Mukai 1983) and benthic community-structure (e.g. Bird 1982; Posey 1986). Despite their ecological importance, relatively little is known about the population and, especially, the reproductive biology of thalassinid species (Tamaki et al. 1996; Thessalou-Legaki and Kiortsis 1997). This deficiency is emphasised by the lack of information on environmental adaptations of shrimp populations. Environmental conditions, i.e. temperature, have been demonstrated to impact intertidal decapod populations (Jones and Simons 1983), so it can be expected that thalassinideans would show similar adaptations in relation to their environment. Thus, the present study aimed at investigating intraspecific differences in population structure and reproductive biology of a relatively understudied thalassinid shrimp. *Callianassa filholi* Milne-Edwards, 1878 is endemic to New Zealand, and has been recorded throughout the country from Stewart Island (47°S) in the south (Milne-Edwards 1878) to the Bay of Islands (35°S) in the North Island (Auckland Institute and Museum). Populations occur in sandy sediment, in predominantly intertidal and shallow subtidal habitats, although the species has also been found at sites 60 m deep (National Institute for Water and Atmospheric Research, Wellington, New Zealand). Previous studies of *C. filholi* have focused on the biology of two populations in the South Island, in which breeding occurred from midwinter to summer (Devine 1966; Berkenbusch and Rowden 1998). In order to compare reproductive characteristics between *C. fiholi*

populations, the samples collected covered the previously established main reproductive period.

Materials and methods

Samples

Six *Callianassa filholi* Milne Edwards, 1878 populations were sampled throughout New Zealand, from 37°01′S to 46°26′S (Fig. 1). Whilst representing similar habitats (e.g. sandy tidal flats, between 1 to 2.8 m above low water) and providing easy access for collection, intertidal sites were selected to account for the species' latitudinal range. Populations were simultaneously (± 1 d) sampled on three occasions, at the beginning and end of spring and the middle of summer (September November 1997 and January 1998). During each collection, 30 burrows (identified by sediment-expulsion mounds on the surface) were haphazardly selected, and inhabiting shrimp were captured with a yabby pump (Manning 1975). Despite the potential bias, i.e. for the collection of small individuals, this method was deemed adequate for an effective collection of the target adult shrimp. Collected specimens were anaesthetised (7.5% magnesium chloride in freshwater) for 5 h prior to fixation in 10% formalin/seawater.

In the laboratory, shrimp were counted, sexed and measured; morphological measurements (to the nearest 0.1 mm using a stereomicroscope with a measuring eye-piece) included carapace length (CL; from the tip of the rostrum to the posterior margin of the carapace), and maximum primary chela prodopus width. Shrimp of unidentified sex (0 to 1.6% of the total sample at each location) were omitted from the analysis. Females with embryos were recorded, and embryos were classified by visual assessment into three developmental stages, modified after stages identified by Boolootian et al. (1959): I, round shape, un-eyed (Stages 1 to 4); II, oval shape, eye-pigment visible (Stages 5 to 8); III, oval shape, eye-pigment and distinct tails visible (Stages 8 to 9). After removal from female pleopods, embryos were counted and a subsample ($n = 50$) was measured (minimum and maximum diameter to the nearest 50 μm). Because of potential loss of embryos during incubation, only Stage I embryos were included in fecundity estimates and subsequent analysis.
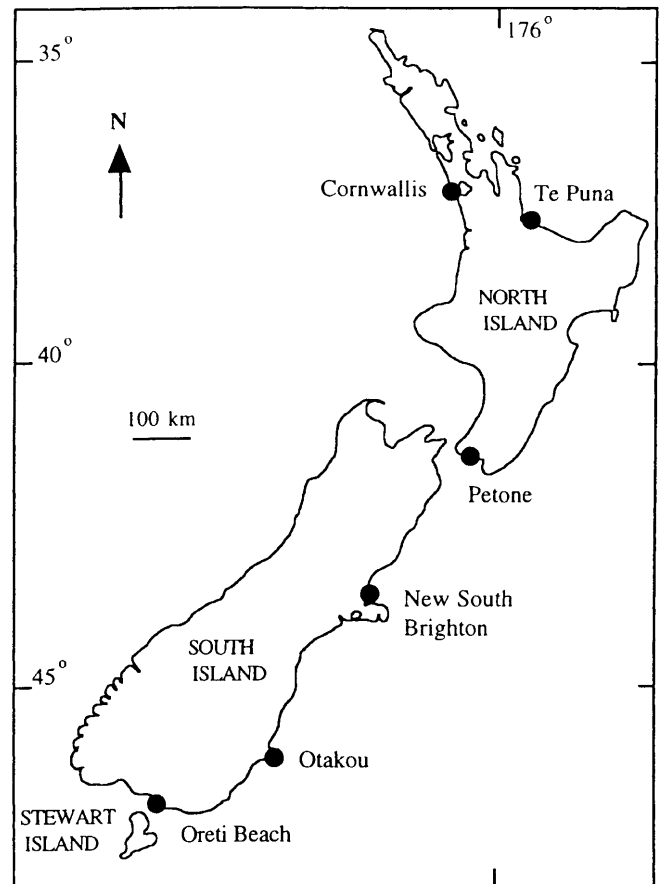
Data analysis

For each population, shrimp were classed following convention into 1 mm size-classes. Size at maturity was ascertained by analysing allometric growth of the primary chela in relation to CL, using REGRANS (Pezzuto 1993) for males, and CL of the smallest female in berry within each population for females. General linear models were applied to assess size differences between locations; the relationship between size and latitude, between size (CL) of ovigerous females and number of embryos (Stage I) were determined by least-squares linear regressions. Fecundity between populations was compared using ANCOVA.


Fig. 1 Sampling sites for *Callianassa filholi* populations (●) in New Zealand

Results

Each *Callianassa filholi* population exhibited an unbiased sex-ratio (Table 1) and, with the exception of the Petone population, a similar size-frequency distribution and unimodal population structure (Fig. 2). Modal size ranged from 5 mm (Te Puna) to 10 mm CL (Petone and Oreti Beach), with a modal class of 8 mm CL in three of the populations (Cornwallis, New South Brighton, Otakou). Post-larval/small juvenile and very large adult shrimp appeared to be scarce within population samples, however, very large adults constituted a second cohort

Table 1 *Callianassa filholi*. Sample size, mean ($\pm$ SE) carapace length (*CL*), size at maturity, and sex-ratio of populations at each site (*M* males; *F* females)

Site	Sample size (M/F)	Mean CL (mm) $\pm$ SE		Size (CL mm) at maturity		Sex-ratio (M:F)	χ^{2*}
		M	F	M	F		
Cornwallis	49/70	7.3 $\pm$ 0.5	7.9 $\pm$ 0.2	8.7	5.6	0.71	0.068
Te Puna	36/28	6.3 $\pm$ 0.3	5.6 $\pm$ 0.3	6.7	4.8	1.29	0.317
Petone	40/50	11.0 $\pm$ 0.7	11.5 $\pm$ 0.6	11.5	7.5	0.78	0.249
New South Brighton	102/102	8.7 $\pm$ 0.2	8.5 $\pm$ 0.2	8.2	7	1.01	0.944
Otakou	61/63	7.5 $\pm$ 0.5	7.6 $\pm$ 0.4	8.0	6.5	0.98	0.857
Oreti Beach	123/130	9.3 $\pm$ 0.4	9.2 $\pm$ 0.3	10.0	6.8	0.95	0.707

* all $P > 0.05$

Fig. 2 *Callianassa filholi.* Size-frequency distributions of populations at each location for all sampling occasions (*filled bars* males; *open bars* females; *values in parentheses* sample sizes)

Carapace length (mm)
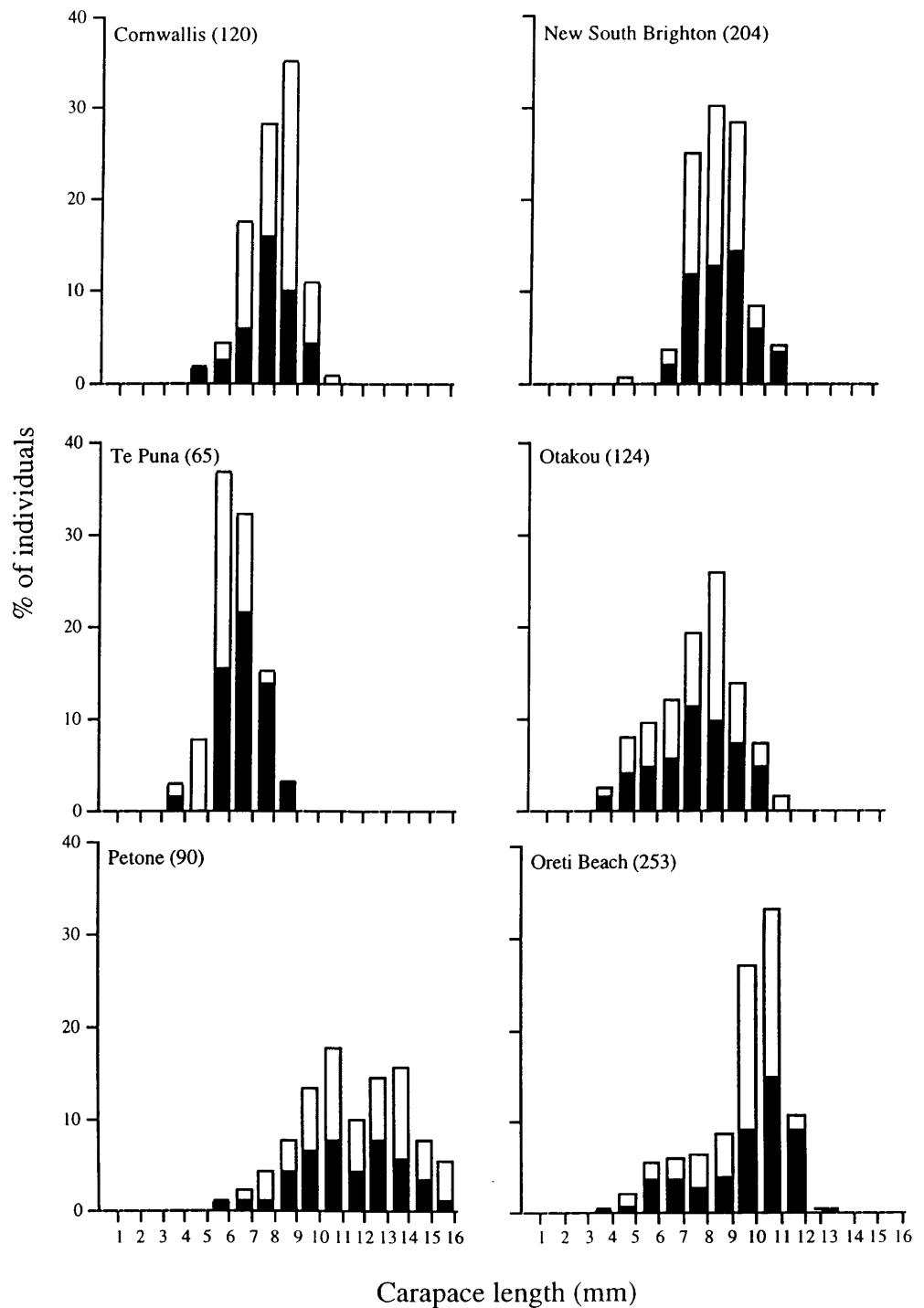
(mode 13 mm CL) at Petone which resulted in a bimodal population structure.

Within each population, male and female *Callianassa filholi* were present in the majority of size classes and there was no statistical difference in CL between sexes (two-way ANOVA, $n = 854$, $F = 0.0016$, $P > 0.05$). However, there was a significant difference in CL between populations ($F = 113.21$, $P \leq 0.0001$), with shrimp size at Petone greatly exceeding that of males and females from any other site. Size at maturity displayed a similar pattern: both sexes reached maturity at smaller sizes at Cornwallis and Te Puna than shrimp in southern populations, whilst shrimp at Petone attained sexual maturity at the largest size of any population (Table 1). Despite an apparent trend of decreasing size with decreasing latitude, neither mean CL nor size at maturity appeared to be significantly related to latitude (Table 2).

The timing of the reproductive cycle varied between populations, with distinct differences between the most southern and northern populations (Fig. 3). In the

Table 2 *Callianassa filholi.* Regression analysis for size parameters and latitude between populations ($n = 6$)

Parameter	r^2	F	P
Mean CL			
Both sexes	0.138	0.638	0.469
Size at maturity			
Males	0.455	3.34	0.1417
Females	0.840	0.365	0.5783

North, at Cornwallis, the proportion of ovigerous females increased from moderately high levels during spring to a peak in midsummer, when > 50% of ovigerous females still carried Stage I embryos. In contrast, southern populations appeared to breed earlier: at Oreti Beach most reproductive females were in berry at the beginning of spring, but the proportion dramatically declined in midsummer. At Petone, the proportion of ovigerous females remained at the same level (~60%), and ovigerous females carrying Stage II and III embryos were present throughout spring and summer.
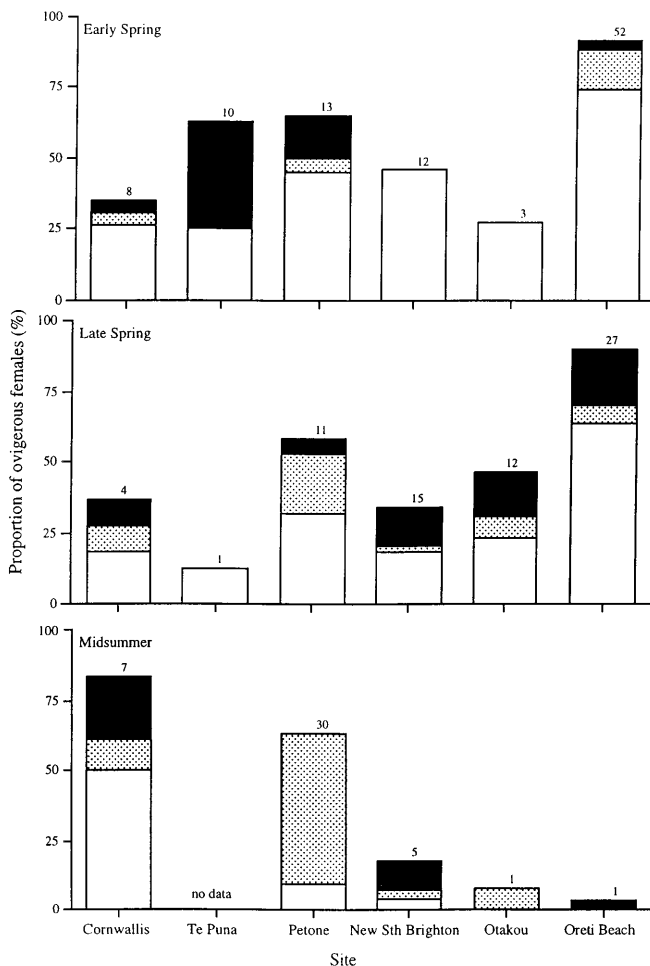

Fig. 3 *Callianassa filholi.* Proportion of reproductive females in berry and proportion of Stage I to III embryos in each population on each sampling occasion (*Numbers on bars* numbers of ovigerous females; *open bars* Stage I; *stippled bars* Stage II; *filled bars* Stage III)

There was a significant relationship between CL of ovigerous females and number of embryos (Stage I) in the populations at four of the locations. Because of small sample sizes ($n < 10$), no regressions were attempted for Te Puna and Otakou, although the limited data appear to suggest a similar trend (Fig. 4). Number of embryos (fecundity) increased linearly with female size, but varied amongst ovigerous females within populations. The relationship between female size and fecundity differed significantly between populations (ANCOVA; $n = 102$, slopes: $F = 4.6681$, $P < 0.01$; intercepts: $F = 10.728$, $P \leq 0.0001$), i.e. fecundity was significantly higher at Petone than New South Brighton, where fecundity was at the lowest level (Table 3). Embryo size (Stage I) did not appear to be significantly related to embryo number (all $P > 0.05$), but size (diameter) did show a significant increase with latitude ($n = 6$, $F = 10.8$, $P < 0.05$), ranging from 464 µm at Cornwallis to 684 µm at Oreti Beach (Fig. 5).

Discussion

All *Callianassa filholi* populations exhibited an unbiased sex-ratio throughout spring and summer. A previous study of *C. filholi* at Otakou found the population to be female-dominated over a 16 mo period; however, during part of this time the sex-ratio was unbiased amongst adult shrimp (Berkenbusch and Rowden 1998). Sex-ratio in thalassinidean shrimp has been reported to vary between species, size classes and seasons, often with females prevailing over males amongst adult shrimp (e.g. Tunberg 1986; Vaugelas et al. 1986; Tamaki et al. 1997). Although this general trend of female-biased sex-ratio has been linked to the loss of males from fighting, migration or predation (Felder and Lovett 1989; Dumbauld et al. 1996), it remains unproven what determines sex-ratio in thalassinid populations (Dworschak 1998).

The population structure at each site revealed that populations consisted mainly of adult *Callianassa filholi*, with few juveniles present during spring and summer. This agrees with previous findings for *C. filholi* populations, in which sexually mature adults were present throughout the year while the presence of postlarval/small juvenile shrimp varied with season (Devine 1966; Berkenbusch and Rowden 1998). Whilst it is possible that sampling by yabby pump introduces a bias (Rowden and Jones 1994), the agreement with earlier studies confirms that scarcity of small juveniles is a seasonal occurrence. Thus, the data implies that recruitment in all populations occurred after mid-summer. The bimodal population structure at Petone resulted from the presence of large adults, indicating a possible lifespan of 3 to 4 yr for *C. filholi*. This lifespan estimate is consistent with Devine's (1966) suggestion for the New South Brighton population, but slightly longer than the estimate of 2 to 3 yr for the population at Otakou (Berkenbusch and Rowden 1998).
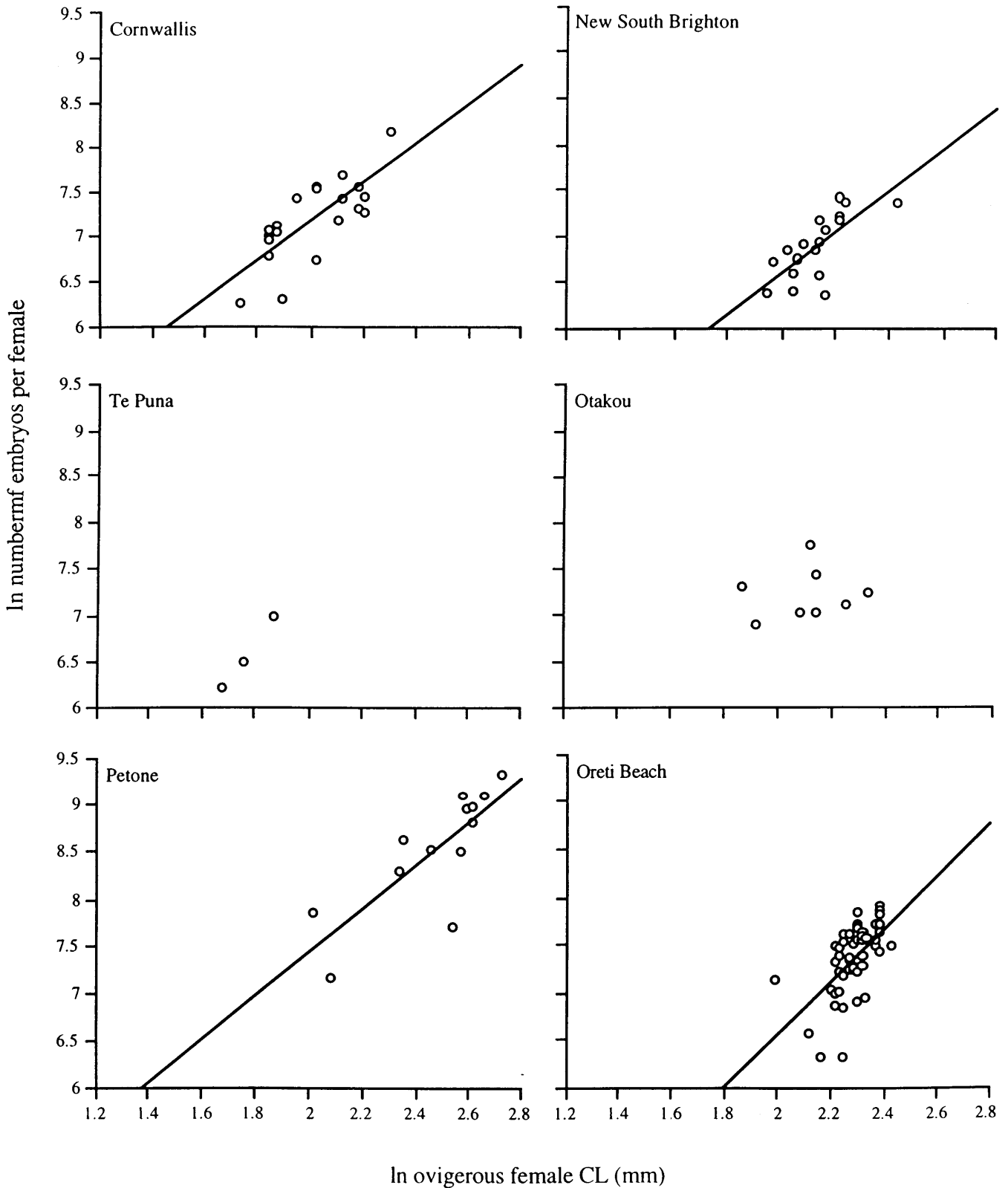
Fig. 4 *Callianassa filholi*. Relationship between number of embryos and carapace length (*CL*) of ovigerous females in each population on each sampling occasion plotted on natural logarithmic scale (see Table 3 for regression equations)

Comparison of sizes between populations, revealed significant differences in modal size, mean CL, and size at maturity for male and female *Callianassa filholi*. Differences in size between *C. filholi* populations were not significantly related to latitude. In particular, sizes in

Table 3 *Callianassa filholi*. Number of embryos per female and regression equations for each population determining relationship between size (carapace length, *CL*) of female and number of embryos (*EN*) (*Dashes* no regressions attempted)

| Location	No. embryos/female	Regression equation	r^2	F	P	(n)
Cornwallis	520/267	lnEN = 2.822 + 2.179 lnCL	0.573	24	0.0001	(20)
Te Puna	498/1081	–	–			(3)
Petone	1303/11296	lnEN = 2.834 + 2.309 lnCL	0.639	19.5	0.001	(13)
New South Brighton	575/1672	lnEN = 2.147 + 2.228 lnCL	0.526	17.8	0.0007	(18)
Otakou	992/2348	–	–			(8)
Oreti Beach	558/2710	lnEN = 1.088 + 2.739 lnCL	0.343	25.6	≤0.0001	(51)

the Petone population exceeded sizes in other populations, including those further south. This finding is surprising given the well-documented link between increasing latitude (and associated decreasing temperature) and corresponding increasing body size/size at maturity in marine fauna (Kinne 1970; Levinton and Monahan 1983). In New Zealand, where seawater temperature decreases along a latitudinal gradient (Heath 1985), a previous study of another intertidal decapod, the mud crab *Helice crassa*, found that size parameters of ovigerous females corresponded significantly to latitude (Jones and Simons 1983). It is evident that observed differences in size between *C. filholi* populations cannot be solely explained by increasing latitude/decreasing temperature, and that other factors need be considered when attempting to account for the noted differences. Variation in size between populations of the thalassinid shrimp *Upogebia africana* within an estuary have been significantly related to distance from the estuary mouth (Hanekom and Erasmus 1988). These authors attributed the decrease in shrimp size with increasing distance from the estuary mouth to a corresponding decrease in food and oxygen input during flood tides. Similarly, Dumbauld et al. (1996) suspected food supply to be a controlling factor for growth of the thalassinids *Neotrypaea californiensis* and *Upogebia pugettensis* inhabiting a North American tidal flat. For deposit-feeding callianassids, food supply is intrinsically linked to the organic content of the substratum, and anecdotal evidence suggested that *C. subterranea* from an organically enriched site exhibited larger sizes than shrimp from a site with considerably lower organic content (see Rowden and Jones 1995). Whilst low organic content in near surface sediments has been reported for Cornwallis (within Manukau Harbour, 0.03 to 0.52%: Thrush et al. 1991), New South Brighton (<1%: Devine 1966), and Otakou (0.7 to 1.7%: Berkenbusch unpublished data) 5 to 10 fold higher values were noted at Petone (5.6%: Goff et al. 1998). No data are available for Te Puna nor Oreti Beach, but organic content is generally very low on sandy beaches (Steele 1976; McLachlan 1983).

This suggests that food availability at Petone could play a more important role in determining size in *Callianassa filholi* populations than temperature. Similar observations for a filter-feeding decapod, the porcellanid crab *Petrolisthes elongatus*, support this suggestion, as ovigerous females exhibited larger sizes at this particular location than at sites either north or south (see Jones 1977). This indicates that, for deposit-feeding callianassids, the relative importance of temperature is dependent on environmental conditions at the site, and may be exceeded by food availability in determining body size of populations.

Differences in the timing of the reproductive season between *Callianassa filholi* populations were reflected in a comparatively late breeding season at the northern site compared to populations further south. The reproductive cycle at Cornwallis, the most northern site, is compatible with those of other thalassinid species which breed from spring to summer/autumn (Witbaard and Duineveld 1989; Felder and Griffis 1994). Conversely, populations further south started breeding early, and previous studies of *C. filholi* identified the start of the reproductive season to be mid-winter (Devine 1966; Berkenbusch and Rowden 1998). Differences in the timing of the reproductive cycle between locations within estuaries have also been observed in *Neotrypaea californiensis* and *Upogebia pugettensis* (Bird 1982; Dumbauld et al. 1996), with populations closer to the estuary mouth extruding eggs earlier than those within the estuary. Thus, it appears that initiation and length of the breeding season in thalassinids is not necessarily determined by a relative increase in temperature, as is general believed to be the case for marine invertebrates (Kinne 1970; Hill 1977), but may also be linked to food availability (Chao et al. 1995).

Within each *Callianassa filholi* population studied, fecundity increased with ovigerous female size; a similar relationship has been reported for other temperate
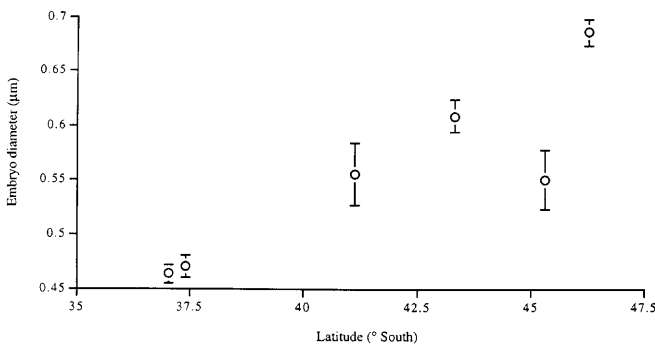
Fig. 5 *Callianassa filholi*. Embryo (Stage I) diameter as a function of latitude for each population on all sampling occasions (*vertical bars* = 2 SE)

species (Hill 1977; Hanekom and Erasmus 1988; Dumbauld et al. 1996; Thessalou-Legaki and Kiortsis 1997). Whilst fecundity estimates from New South Brighton in the present study are consistent with findings of 600 to 1500 embryos/female by Devine (1966) at the same site, the great variation between fecundity estimates found in the present study highlights the importance of environmental factors in controlling fecundity of thalassinids. A comparison of *Upogebia pusilla* populations found great variability in number of embryos between females from different locations and over time (Dworschak 1988). A factor which is likely to affect fecundity, i.e. the number of embryos per brood, is the number of broods per female per season (Hill 1977). It has been postulated for a number of thalassinid species that females produce several broods per season (Hailstone and Stephenson 1961; Rowden and Jones 1994; Tamaki et al. 1996). On the other hand, no evidence for multiple breeding has been found for *Neotrypaea californiensis*, *Upogebia pugettensis* and *Sergio mirim* (Dumbauld et al. 1996; Pezzuto 1998). Whilst there was no unequivocal evidence to indicate more than one brood per season for female *C. filholi* at Otakou (Berkenbusch and Rowden 1998), Devine (1966) noted a multiple breeding season for the population at New South Brighton. The data from the present study does not resolve this discrepancy, and it remains unclear if female *C. filholi* carry consecutive broods and what might determine the number of broods per season in thalassinid shrimps.

The observed increase in embryo size with increasing latitude for *Callianassa filholi* populations could be related to temperature determining incubation time and embryonic development. *C. filholi* have been found to brood for 5 to 6 wk at New South Brighton (Devine 1966), and it is likely that incubation time would decrease as temperature increases (Wear 1974), with a concomitant decrease in the size of embryos (Efford 1969). Thus, latitudinal differences in embryo size between *C. filholi* populations may be explained by protracted embryonic development at the lower temperatures experienced as latitude increases, and consequently account for the lack of a significant relationship between number and size of embryos.

The present study indicates that intraspecific differences in the reproductive biology of *Callianassa filholi*, i.e. mean size at maturity and fecundity, are not necessarily imposed by temperature, but may be explained by food availability. At the same time, increasing embryo size does appear to correspond to increasing latitude, indicating that incubation time increases as temperature decreases.

Whilst six populations, covering the latitudinal/temperature range of *Callianassa filholi* were studied in the present investigation, caution is necessary in inferring too widely from such observations. Further research into the reproductive biology of *C. filholi* and other thalassinid shrimp is required in order to (1) investigate the precise role of food in determining size at maturity and number of broods per season, and (2) the role of temperature in controlling embryo size and subsequent larval development.

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