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LATITUDINAL VARIATION IN REPRODUCTIVE CHARACTERISTICS OF A MUD CRAB, *HELICE CRASSA* (GRAPSIDAE)

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ABSTRACT

The population structure and reproductive biology of the burrowing mud crab *Helice crassa* Dana, 1851 were studied in relation to latitude. Populations from 11 sites in New Zealand between latitudes of 35° South (lowest) and 46°27′ South (highest) were sampled during November and December 1980. Crab densities (crabs$\cdot$m^{-2}) were correlated significantly with latitude and were higher at low than high latitudes. In general, population size structures were similar, and each population had few large individuals (carapace width > 14.0 mm), an unbiased sex ratio and a size-frequency distribution skewed in favor of juvenile and small crabs (carapace width ≤ 6.0 mm). However, maximum crab size, size of maturity of females, and numbers of eggs carried per female increased significantly with increased latitude. Volumes and dry weights of eggs differed significantly between populations, but independently of latitude. Nevertheless, percentage swelling of eggs during embryonic development did increase significantly from low to high latitudes. The data are discussed in relation to general trends and hypotheses proposed currently for latitudinal effects on marine invertebrate populations.

Variations in the reproductive ecology of a single species from different areas of its geographical range have been examined for few marine invertebrates, yet such studies are an important prerequisite for understanding the reproductive adaptations to environment (Sastry, 1970). General trends of reproductive response with change in latitude, however, have been proposed and discussed previously (Giese, 1959; Vernberg, 1962), and these form the background to the present work. The endemic mud crab *Helice crassa* Dana, 1851 (Grapsidae) was chosen for the study as it has an extensive geographical distribution in New Zealand, extending from the tip of the North Island to a southern limit in Stewart Island (Dell, 1968). In addition, the ecological requirements of this species are relatively well studied and long-term descriptions of its population structure are available for two South Island locations (Nye, 1977; Jones, 1980). Crabs construct burrows in well-drained, compacted sediments above mid-tide level, and have behavioral, structural, and physiological adaptations to semi-terrestrial conditions (Hawkins and Jones, 1982; Hawkins et al., 1982; Jones, 1977a; 1981; Jones and Simons, 1982; Shumway and Jones, 1981). *H. crassa* is active on the surface during low tide and feeds mainly on organic matter extracted from surface mud (Fielder and Jones, 1979).

The objectives of this study were to examine the variability in population structure and reproductive biology of *Helice crassa* from sites along its geographical range, and to correlate these with latitude and habitat.

MATERIALS AND METHODS

Eleven populations of *Helice crassa*, encompassing almost its entire geographical range, were sampled during November and December 1980 (Fig. 1, Table 1). This period was chosen because numbers of ovigerous females for studied populations of *H. crassa* peaked at this time in different geographical locations (Wear, 1970; Nye, 1977; Jones, 1980), allowing them to be collected in relatively high numbers. In addition, a restricted collection period reduced to a minimum any likely temporal changes in population structure and reproduction (Diaz, 1980; Jones, 1980). The substratum at each location

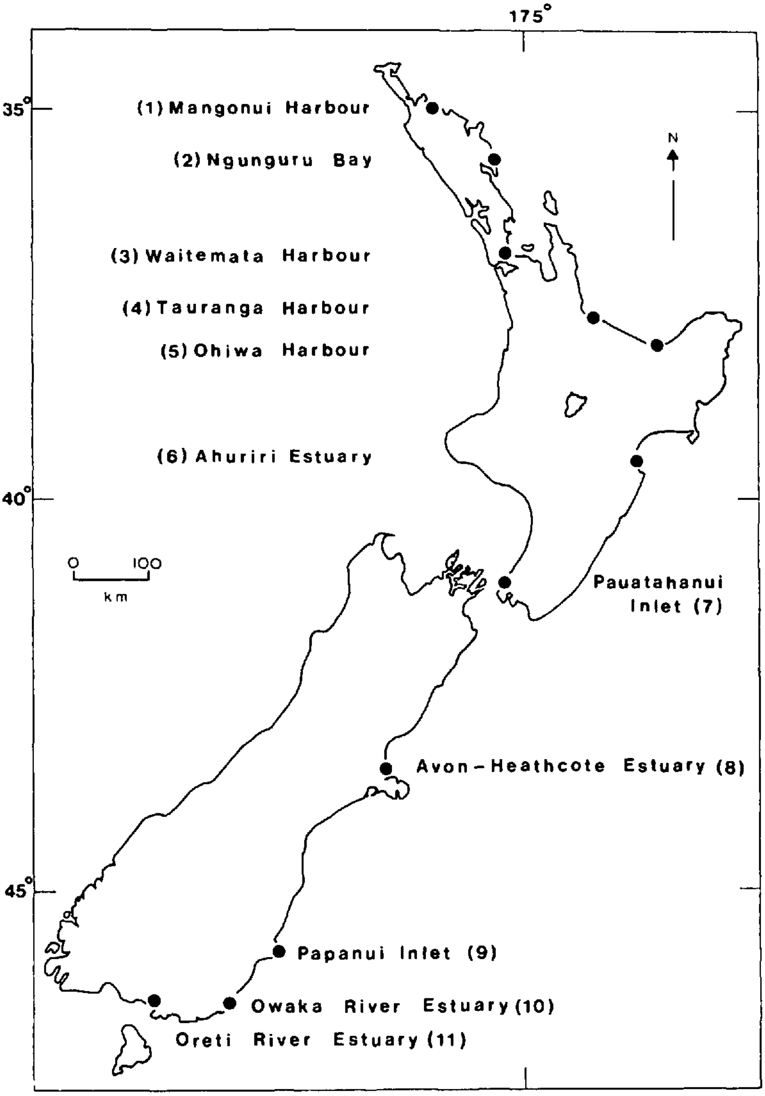

Figure 1. Locations of crab sampling sites in the North Island (Sites 1–7) and South Island (Sites 8–11) of New Zealand.

was ranked following a subjective scale used previously by Boyden and Little (1973), viz., sand (large particles), sandy mud (mixture of large and fine particles), mud (fine particles), and fluid mud (thixotropic).

Field Measurements

Collection methods were identical and two types of crab samples were taken at each site. Firstly, the population structure was investigated using quadrats (0.25 m^2) which were thrown randomly within the zone of occurrence of *Helice crassa* (Jones and Simons, 1982). The area within the quadrat was excavated, the spoil searched and all crabs preserved in 10% sea water formalin. The number of quadrats taken and the excavation depth were determined by crab density and maximum burrow penetration respectively (Table 1). Secondly, collections of ovigerous females only were made by

Table 1. Density of *Helice crassa* calculated from 0.25 m² quadrats

Site	Latitude (°S)	Location	Sampling Date (1980)	Habitat	Substratum	No. Quadrats	Depth Quadrat (cm)	No. Crabs	Density (Crabs m^{-2})
1	35°	Mangonui Harbour	10 Dec.	Mangrove	Fluid mud	4	16	462	462
2	35°40′	Ngunguru Bay	9 Dec.	Mangrove	Sandy mud	8	16	340	170
3	36°50′	Waitemata Harbour	6 Dec.	Mangrove	Fluid mud	2	16	186	372
4	37°41′	Tauranga Harbour	4 Dec.	Mangrove	Fluid mud	4	14	352	352
5	38°	Ohiwa Harbour	3 Dec.	Marine inlet	Sand	12	15	117	39
6	39°30′	Ahuriri Estuary	30 Nov.	Estuary	Sandy mud	8	10	551	275.5
7	41°05′	Pauatahanui Inlet	15 Dec.	Marine inlet	Sandy mud	12	16	446	148.7
8	43°33′	Avon-Heathcote Estuary	26 Nov.	Estuary	Mud	4	10	251	251
9	45°50′	Papanui Inlet	18 Nov.	Marine inlet	Sand	8	12	176	88
10	46°27′	Owaka River Estuary	20 Nov.	Estuary	Sandy mud	8	15	297	148.5
11	46°22′	Oreti River Estuary	23 Nov.	Estuary	Sand	16	15	244	61

checking undisturbed burrows. These were stored separately in 10% sea water formalin, and were not included in the descriptions of population structure, but used in the investigation of reproductive biology.

Laboratory Measurements

Each crab collected by the quadrat method was measured (maximum carapace width [cw]) to the nearest 0.1 mm with hand-held vernier calipers (cw > 6.0 mm) or a micrometer scale in a stereoscopic microscope (cw ≤ 6.0 mm), and assigned to one of the following classes: (1) juvenile, (2) male, (3) non-ovigerous female and (4) ovigerous female. Individuals of cw ≤4.0 mm were difficult to sex and were grouped arbitrarily as juveniles (Jones, 1980). Ovigerous females were then used to supplement the other collections of this crab class for each site and were examined as described below.

After measuring the maximum cw of each ovigerous female as described previously, all eggs were removed from the pleopods and their stage of development categorized using the following morphological features: Stage 1—recently oviposited, full of yolk and lacking cleavage; Stage 2—cleavage but no eye pigment; and Stage 3—embryos with eyes (Jones, 1980; Simons and Jones, 1981). Five eggs from each brood were selected at random and their longest and shortest diameters measured to the nearest 0.01 mm with a micrometer eyepiece in a stereoscopic microscope. Eggs were almost spherical and mean egg volume was calculated from the formula $\frac{1}{6}\pi \ell^3$ (where ℓ is the mean of the two diameters). These measurements were taken within 6 weeks of collection and storage in 10% sea water formalin during this period had no measurable influence on egg volume. Numbers of eggs carried per female were estimated using a dry weight technique. Eggs were washed in distilled water, a subsample of 500 was counted as a reference, and both the reference and the rest of the brood were dried to constant weight. Egg numbers were calculated from the total dry weight using the weight of the reference sample.

All measured data were tested for association with latitude using the Spearman Rank Correlation Coefficient (r_s) (Siegel, 1956). As substratum and density may influence life history traits (Mooij-Vogelaar et al., 1973; Simons and Jones, 1981), measurements were tested also for association with these variables. Substratum was not correlated significantly with latitude ($r_s = 0.58$, $n = 11$, $P > 0.05$), allowing the influence of these variables to be examined independently.

RESULTS

Crab Density

Densities were correlated significantly with latitude ($r_s = 0.68$, $n = 11$, $P < 0.05$) and substratum ($r_s = 0.93$, $n = 11$, $P < 0.01$), and decreased with increases in both latitude and sediment particle size (Table 1).

Population Structure

The size groupings used in the frequency histograms were selected arbitrarily as a convenient method for data presentation (Fig. 2). In general, the shape of the size-frequency distributions was similar, and each population had few large individuals (cw > 14.0 mm), a frequency distribution skewed in favor of juveniles and small crabs (cw ≤ 6.0 mm), and an unbiased sex ratio (Table 2). The population at the Oreti River Estuary (Site 11), however, had few small crabs, and was biased in favor of large individuals and females (Fig. 2). In addition, whereas the proportion of females carrying eggs (expressed as a percentage of all females collected) varied between 9 and 35% for populations at Sites 1–10, 50% of the females were ovigerous at the Oreti River Estuary (Fig. 2, Table 2). Previously, Nye (1977) reported an equal sex ratio for *Helice crassa* at Papanui Inlet (Site 9). Similarly, Jones (1980) showed an unbiased sex ratio for this species in November and December in the Avon-Heathcote Estuary (Site 8), although the overall sex ratio for 21 months of sampling at the latter site was biased towards males.

The proportion of small crabs (cw ≤ 6.0 mm) and of ovigerous females in each population was not correlated with latitude, substratum or crab density ($P > 0.05$). The cw of the largest male ($r_s = 0.67$, $n = 11$, $P < 0.05$) and largest female crab ($r_s = 0.77$, $n = 11$, $P < 0.05$), however, was associated significantly with

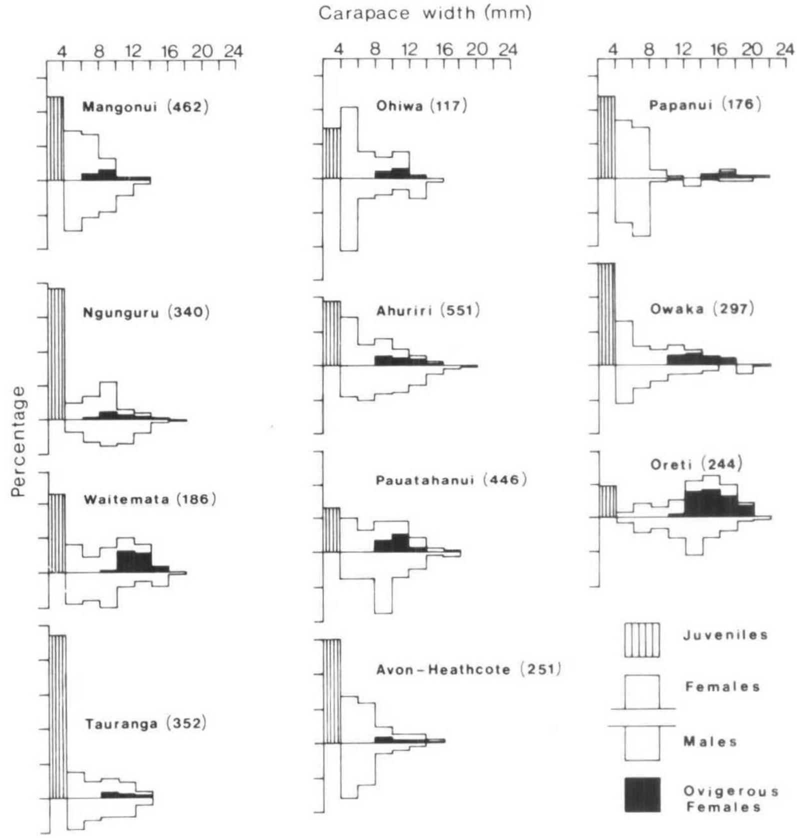

Figure 2. Frequency histograms of carapace width for *Helice crassa* populations based solely on crabs collected by the quadrat method. Sample numbers are given in parentheses, and the ordinate is marked in units of ten. Further details are given in Table 2.

latitude, such that maximum cw increased from low to high latitudes. Crab size was not associated with population density or substratum ($P > 0.05$).

Size-Frequency of Ovigerous Females

Details of the numbers and frequency distributions of ovigerous females are shown in Figure 3. Insufficient numbers of ovigerous females precluded examination of the reproductive biology of *Helice crassa* at Ohiwa Harbour (Site 5).

Most frequency distributions were unimodal and the size of the modal class increased significantly with increase in latitude ($r_s = 0.72$, $n = 10$, $P < 0.05$). The same trend was found for the mean cw of ovigerous females ($r_s = 0.73$, $n = 10$, $P < 0.05$), and for the cw of the smallest ($r_s = 0.78$, $n = 10$, $P < 0.01$) and largest ovigerous female ($r_s = 0.88$, $n = 10$, $P < 0.01$). These size measurements generally were not correlated with substratum or population density ($P > 0.05$), except that the cw of the largest ovigerous female in each population increased with decrease in crab density ($r_s = 0.68$, $n = 10$, $P < 0.05$). Taking the cw of the smallest ovigerous female as an approximation of sexual maturity for females in each population (Giese, 1959; Jones, 1980; Simons and Jones, 1981), indicated that size at puberty increased from low to high latitudes.

Table 2. Details of the *Helice crassa* populations based on the 0.25 m^2 quadrats (sex ratios tested by χ^2)

	Carapace Width (mm)												Sex Ratio	
	Males				Females				Ovigerous Females					
Site	n	$\bar{x}$	SD	Largest	n	$\bar{x}$	SD	Largest	n	$\bar{x}$	SD	Range	(♀♀:1♂)	Significance Level Different from 1:1
1	184	7.3	2.3	13.8	143	6.6	1.8	13.5	22	8.9	1.2	7.6–13.3	0.90	n.s.
2	112	9.4	2.7	16.7	78	7.9	2.2	14.1	19	9.8	1.5	7.4–12.4	0.87	n.s.
3	53	8.9	3.2	17.3	47	8.1	2.7	13.0	25	12.1	1.5	9.7–15.2	1.36	n.s.
4	99	7.9	2.6	13.6	73	7.5	2.6	14.0	15	10.6	1.6	8.0–12.6	0.89	n.s.
5	50	7.8	2.1	12.9	45	6.7	2.4	13.2	5	10.2	1.1	8.9–11.7	1.0	n.s.
6	189	9.2	3.1	18.6	159	7.0	2.5	15.2	42	11.3	1.8	8.7–15.9	1.06	n.s.
7	211	9.1	2.9	17.6	133	8.1	2.9	14.6	45	10.8	1.6	8.1–16.4	0.84	n.s.
8	86	6.6	1.9	13.6	80	6.9	2.4	16.0	9	11.1	2.0	8.5–14.1	1.03	n.s.
9	65	7.7	3.5	19.6	63	6.6	2.6	20.9	6	16.9	1.2	15.1–18.5	1.06	n.s.
10	92	8.9	4.4	20.8	84	7.2	2.6	14.7	30	13.5	1.9	10.1–17.0	1.24	n.s.
11	94	12.4	3.6	21.7	63	12.0	3.7	19.5	63	15.4	2.0	11.8–19.6	1.34	0.05

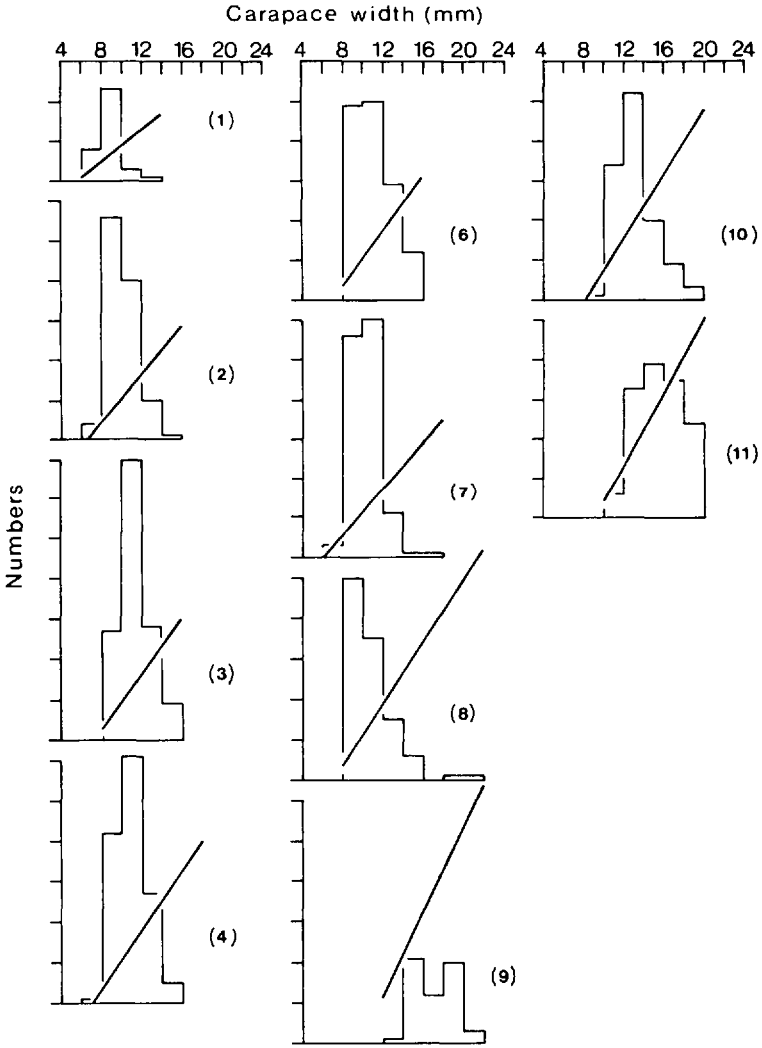

Figure 3. Frequency histograms of carapace width (ordinate in units of ten) and regression lines relating egg numbers with carapace width (ordinate in units of five thousand) of ovigerous female *Helice crassa* (combined data from quadrats and additional collections; sites numbered as in Fig. 1; r values for fitted regression lines ranged from 0.83–0.92).

Egg Numbers

For each population, there was no difference between stage of egg development and number of eggs carried per female, therefore all egg stages were combined. These data indicated that no mortality occurred during embryonic development for each population and supported the same conclusion reached earlier for this species at the Avon-Heathcote Estuary (Site 8) (Jones, 1980). Regression lines were fitted by least squares to data relating egg numbers with cw of ovigerous females and differences between lines were tested by analysis of covariance (Snedecor and Cochran, 1968) (Table 3). Results show that numbers of eggs increased linearly with increase in female cw (Fig. 3), although there were significant inter-populational differences (Table 3). For example, ovigerous females of all sizes at

Table 3. Comparison of regression lines given in Figure 3 by analysis of covariance. Sites are numbered as in Table 1 and levels of significance are indicated as: ns = not significant, * = 5%, ** = 1%, *** = 0.1%

Slope values

Sites	1	2	3	4	6	7	8	9	10	11
1										
2	**									
3	***	ns								
4	**	ns	ns							
6	**	ns	ns	ns						
7	**	ns	**	***	*					
8	**	ns	ns	ns	ns	**				
9	**	***	***	***	***	***	***			
10	**	**	*	ns	**	***	ns	*		
11	***	***	***	**	***	***	**	ns	ns	

Intercept values

Sites	1	2	3	4	6	7	8	9	10	11
1										
2	ns									
3	ns	***								
4	ns	ns	***							
6	ns	ns	**	*						
7	ns	ns	***	ns	*					
8	ns	*	***	ns	***	ns				
9	*	*	ns	*	ns	ns	*			
10	**	***	*	***	***	***	***	ns		
11	***	***	*	***	**	***	***	ns	ns	

Mangonui Harbour (Site 1) carried significantly fewer eggs than females at the southernmost locations sampled (Sites 9–11). Large females at Mangonui Harbour carried significantly fewer eggs than similarly-sized females at any other site. Numbers of eggs carried by females at Sites 9–11 were not significantly different; however, egg numbers at these high latitude sites were significantly greater than those from other locations.

Intercept and slope values for the regression lines were correlated significantly with latitude ($r_s = 0.81$, $n = 10$, $P < 0.01$) and density ($r_s = 0.66$, $n = 10$, $P < 0.05$), but not with substratum ($P > 0.05$). The major trend was an increase in egg numbers with increased latitude for crabs of similar sizes, and a secondary trend of a decrease in egg numbers with increased density.

Egg Volume

Egg volume measurements and interpopulational differences are shown in Tables 4 and 5 respectively. The data compare well with egg volumes published previously for *Helice crassa* (Wear, 1970; Jones, 1980).

Volumes of Stage 1 eggs differed significantly between some populations (Table 5). The smallest eggs were found at the Avon-Heathcote Estuary (Site 8) and the largest at the Oreti River Estuary (Site 11). Differences in Stage 1 egg volumes were independent of latitude, substratum, crab density, and female carapace width ($P > 0.05$).

Eggs from each site increased in volume during embryonic development (Jones, 1980), but there were differences in the proportion of swelling between populations (Table 4). In general, eggs from South Island locations showed greater increase in

Table 4. Variation in mean egg volumes of *Helice crassa* (based on mean volume of 5 eggs for each n value)

	Egg Volume (nℓ)						
	Stage 1			Stage 3			
Site	n	$\bar{x}$	S	n	$\bar{x}$	S	% Volume Increase
1	5	12.65	1.41	5	15.50	1.68	22.5
2	22	12.27	1.85	37	15.18	1.17	23.7
3	91	12.77	2.22	10	14.14	1.15	10.7
4	58	12.65	2.40	44	15.49	1.92	22.5
6	53	10.94	1.96	30	13.87	3.45	26.8
7	57	12.97	2.21	17	16.27	2.17	25.4
8	71	7.26	0.77	12	10.50	1.44	44.6
9	7	13.37	2.23	48	23.14	3.21	73.1
10	9	11.11	1.40	62	20.85	2.82	87.7
11	41	14.20	2.03	69	19.36	3.02	36.3

volume than those from the North Island. Percentage increases were correlated significantly with latitude ($r_s = 0.89$, $n = 10$, $P < 0.01$) and substratum ($r_s = 0.71$, $n = 10$, $P < 0.05$). These differences in volume changes resulted in the pattern of comparison for Stage 3 eggs shown in Table 5. Volumes of late stage eggs at the Avon-Heathcote Estuary (Site 8) were significantly smaller than at other sites, and those at Sites 9–11 were significantly greater than at other sites. Volumes of Stage 3 eggs were not associated significantly with latitude, substratum or population density ($P > 0.05$).

Table 5. Comparison of egg volume data from Table 4 using the Student's *t*-test carried out at 5% level of significance. Sites are numbered as in Table 1 (ns = not significant, * = 5%)

Stage 1 eggs

Sites											
1											
2	ns										
3	ns	ns									
4	ns	ns	ns								
6	*	*	*	*							
7	ns	ns	ns	ns	*						
8	*	*	*	*	*	*					
9	ns	ns	ns	ns	*	ns	*				
10	ns	ns	*	*	ns	*	*	*			
11	*	*	*	*	*	*	*	ns	*		
	1	2	3	4	6	7	8	9	10	11	Sites

Stage 3 eggs

Sites											
1											
2	ns										
3	ns	*									
4	ns	ns	*								
6	ns	ns	ns	*							
7	ns	ns	*	ns	*						
8	*	*	*	*	*	*					
9	*	*	*	*	*	*	*				
10	*	*	*	*	*	*	*	*			
11	*	*	*	*	*	*	*	*	*		
	1	2	3	4	6	7	8	9	10	11	Sites

Table 6. Variation in egg dry weight of *Helice crassa* (based on dry weight of 500 eggs for each n value)

Sites	Egg Dry Weight (mg)						% Change in Dry Weight
	Stage 1			Stage 3			
	n	$\bar{x}$	S	n	$\bar{x}$	S	
1	5	1.98	0.19	5	1.42	0.16	−28.2
2	20	2.10	0.27	38	1.89	0.29	−10.0
3	91	1.94	0.34	10	1.79	0.26	−7.7
4	57	1.93	0.29	44	1.77	0.28	−8.3
6	63	1.97	0.27	29	1.88	0.28	−4.6
7	54	1.87	0.23	17	1.89	0.23	+1.1
8	71	1.86	0.32	11	1.69	0.29	−9.1
9	7	2.53	0.35	47	2.49	0.29	−1.6
10	8	2.39	0.57	61	2.34	0.42	−2.1
11	40	2.59	0.41	69	2.20	0.28	−15.1

Egg Dry Weight

The dry weight of Stage 1 eggs differed significantly between some sites (Table 7). These differences were not related to differences in egg volume or latitude ($P > 0.05$), but were associated with substratum ($r_s = 0.65$, $n = 10$, $P < 0.05$). Dry weight of eggs increased with increase in sediment particle size.

At each site except Pauatahanui Inlet (Site 7), eggs lost weight during embryonic development (Table 6). Percentage weight decreases were not correlated with latitude, substratum or crab density ($P > 0.05$). The dry weight of Stage 3 eggs

Table 7. Comparison of egg dry weights from Table 6 using the Student's *t*-test carried out at 5% level of significance. Sites are numbered as in Table 1 (ns = not significant, * = 5%)

Stage 1 eggs

Sites	1	2	3	4	6	7	8	9	10	11
1										
2	ns									
3	ns	*								
4	ns	*	ns							
6	ns	ns	ns	ns						
7	ns	*	ns	ns	*					
8	ns	*	ns	ns	*	ns				
9	*	*	*	*	*	*	*			
10	ns	ns	*	*	*	*	*	ns		
11	*	*	*	*	*	*	*	ns	ns	

Stage 3 eggs

Sites	1	2	3	4	6	7	8	9	10	11
1										
2	*									
3	*	ns								
4	*	ns	ns							
6	*	ns	ns	ns						
7	*	ns	ns	ns	ns					
8	ns	ns	ns	ns	ns	ns				
9	*	*	*	*	*	*	*			
10	*	*	*	*	*	*	*	*		
11	*	*	*	*	*	*	*	*	*	

was associated significantly with latitude ($r_s = 0.67$, $n = 10$, $P < 0.05$) and substratum ($r_s = 0.86$, $n = 10$, $P < 0.01$) and increased with increase in both latitude and sediment particle size.

DISCUSSION

Latitude per se can have no effect on the biology of organisms. Environmental factors which vary with latitude such as temperature and photoperiod, however, do directly influence life history characteristics of marine crustaceans. Most studies implicate temperature as the major factor affecting growth and reproductive output (Giese, 1959; Vernberg, 1962; Sastry, 1966; Kinne, 1970), although temperature–photoperiod interactions may also be significant (Armitage and Landau, 1982). Long-term temperature measurements were not available for all collection sites used in this study; however, published data for New Zealand show clearly that sea water temperatures decrease as latitude increases (Garner, 1969; Jones, 1977b; 1980). The significant correlations with latitude found here for *Helice crassa* are assumed to reflect this inverse relationship with temperature although confirmation awaits laboratory investigation (Ernest and Blake, 1981).

Population Density

Densities of *Helice crassa* were inversely correlated with latitude and substratum (subjective particle size), the latter having the more significant level of association. Substratum type is known to influence densities of burrowing invertebrate fauna of particulate shores (Little and Boyden, 1976; Van Dolah, 1978). The effect of substratum was particularly evident at Ngunguru Bay (Site 2) and Ohiwa Harbour (Site 5) which, in spite of being at relatively low latitudes, had population densities much lower than sites from higher latitudes. Observations from previous work (Jones and Simons, 1982) and during this study show that *H. crassa* burrows into compacted substrata, and habitat selection is the result of territorial and feeding behavior (Jones and Simons, 1982) and respiratory adaptations (Hawkins and Jones, 1982; Hawkins et al., 1982). As highest crab densities were measured in muddy sediments, especially mangrove swamps, and as *H. crassa* is a detrital feeder (Fielder and Jones, 1979), we suggest that availability and quality of food has an important influence on population density. Sediment organic content is positively related to the amount of mud present (Newell, 1979).

Population Structure

Population size-structures were generally biased towards small individuals, suggesting that samples were taken during a period of recent recruitment. A similar size-frequency pattern for the November–December period at Site 8 was reported previously by Jones (1980). These findings indicate that population characteristics and recruitment periodicity of *Helice crassa* are similar along its geographical range for the same time of year and also between years at the same locality. The same conclusions were made for the mole crab *Emerita talpoida* (Diaz, 1980). The population of *H. crassa* at the Oreti River Estuary (Site 11) was quite different from the general pattern and the reasons for this exception are unknown.

Crab Size

Size data for *Helice crassa* support the well-documented observation that final body size and size of maturity of marine animals increase with increasing latitude (Vernberg, 1962; Kinne, 1970; Annala et al., 1980; Hastings, 1981). These trends are often related to temperature and metabolic differences along a latitudinal range. Low temperature slows growth rates and leads to delayed attainment of sexual maturity, whereas higher temperatures are thought to stimulate growth and initiate early ovarian development (Kinne, 1970; Annala et al., 1980; Armitage and Landau, 1982). Explanations other than temperature include influences of density and predation. Chittleborough (1976) suggested that high crayfish densities retard growth by increasing intraspecific encounters and reducing food intake per individual, resulting in smaller size at first breeding. As there was no significant correlation between population density and size of maturity for *H. crassa,* this hypothesis does not appear valid for our data. Recently, Wallerstein and Brusca (1982) proposed that size-selective fish predation influenced idoteid isopod body size. The authors argue cogently that higher predation pressure from a more diverse fish community at low latitudes has resulted in selection for smaller size of maturity and reduced maximum body size compared with higher latitudes. Consideration of this hypothesis in relation to our findings, however, requires an assessment of the importance of *H. crassa* to the diets of fish feeding in the littoral zone. Preliminary data indicate that this mud crab species is utilized more by fish in northern compared with southern New Zealand (Webb, 1973; Kilner and Akroyd, 1978).

Egg Numbers

In general, individuals of similar size are said to produce more eggs per brood at high compared with low latitudes (Vernberg, 1962). For marine crustaceans, however, egg numbers carried per female may also be independent of latitude (Efford, 1969) or higher at low compared with high latitudes (Reaka, 1979). Egg numbers for *Helice crassa* increased significantly from low to high latitudes, and this trend is consistent with the finding that egg numbers are related inversely with temperature (Woodward and White, 1981). Of the various hypotheses advanced to explain this relationship the following are pertinent. At high temperatures, rapid growth and high metabolism result in less energy going into egg production than at lower temperatures (Diaz, 1980). Furthermore, reduction in energy for egg production may result from the inability of females to mobilize sufficient food reserves to keep pace with the increased number of broods produced sequentially under high compared with lower temperatures (Wear, 1974). Two strategies to reduce egg production energy costs have been proposed: a decrease in egg numbers and a reduction in the energetic contribution to each egg (Price, 1974). Both strategies appear to have been adopted by *H. crassa* at lower latitudes. Alternatively, at low temperatures, females with slower growth and reduced metabolism may channel more energy into producing more eggs, each with high nutritional reserves (Woodward and White, 1981). This hypothesis offers an explanation of how a decrease in potential fecundity caused by reduced breeding periods at high compared with low latitudes (Giese, 1959; Jones, 1977b) may be negated.

Rather than egg numbers per female as an indication of reproductive productivity, some estimation of fecundity (total numbers of eggs produced per population per year) would be more valuable. For example, Fusaro (1980) has indicated that although egg numbers for the sand crab *Emerita analoga* do not change with latitude, the proportion of egg-carrying females and the duration of egg development does, for they are related directly with temperature; at high temperatures more broods are produced and more females become ovigerous within a reproductive season than at colder temperatures. Until more demographic information becomes available for *Helice crassa,* the suggestion that increased egg production at high latitudes may compensate for reduction in other aspects of reproductive response at different latitudes remains unresolved.

Egg Volume

Marine invertebrate eggs of the same stage of development often show a trend of increasing volume with increasing latitude (Vernberg, 1962; Barnes and Barnes, 1965; Efford, 1969; Van Dolah and Bird, 1980). Data for some crustaceans, however, indicate that egg volume is independent of latitude (Diaz, 1980; Woodward and White, 1981). The volume of Stage 1 eggs of *Helice crassa* were not associated with latitude, and the adaptive significance, if any, of the interpopulation differences reported here for Stage 1 egg volumes remains unanswered.

Percentage volume increases during development measured here were less than that reported previously for *Helice crassa* (Wear, 1970) and for decapods generally (Wear, 1974); however, Jones (1980) recorded no significant increase in volume for this mud crab species at the Avon-Heathcote Estuary.

Egg Dry Weight

Egg volume and egg dry weight were not correlated, suggesting that egg volume does not necessarily indicate the amount of material an egg can contain (Hermans, 1979). Significant differences in egg dry weight, which may reflect important differences in organic composition (Turner and Lawrence, 1979), were apparent between populations of *Helice crassa.* Heaviest eggs occurred at the three most southern sites, and it is possible that more yolk is deposited in these eggs to nourish the developing embryo over the protracted incubation period likely at colder temperatures (Wear, 1974). Late stage eggs at these high latitude sites also had a greater volume than those from lower latitudes and this size difference may be an adaptation for enhanced survival for the planktonic larvae at colder temperatures (Thorson, 1950; Efford, 1969).

In conclusion, several reproductive attributes have been shown to vary significantly between populations of *Helice crassa* from different parts of its geographical range. Some responses were correlated significantly with latitude and implicate temperature and its relationships with metabolic adaptation, whereas others were associated with population density and substratum. Clearly, such variations must be taken into account in descriptions and discussions of life history patterns and strategies (Hicks, 1979; Turner and Lawrence, 1979).

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