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Observations on Shell Form and its Ecological Significance in Thaisid Gastropods of the Genus *Lepsiella* in New Zealand

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Abstract

This paper is concerned with the ecological significance of variation in shell form within the thaisid gastropod genus *Lepsiella* in New Zealand. Shell form has been investigated by measurement of shell height and breadth, aperture length and width, the diameters of consecutive whorls, apical angle, shell weight, and shell capacity, although in many cases shell height and shell breadth could not be measured because of erosion. *L.albomarginata* has been studied intensively at 4 stations in the South Island, and *L. scobina* less intensively at 6 stations in the North and South Islands. Comparisons of pairs of characters between stations have been tested by regression analysis and analysis of covariance where appropriate. Shells of *L. albomarginata* are relatively taller and narrower, and have a thicker wall, at a very sheltered station (Hakahaka Bay) than at more wave-exposed stations. *L. scobina (sensu stricto)*, characterised by the presence of spiral ribs on the shell, exhibits less striking but comparable differences in shell shape. In laboratory tests in a tidal tank the thicker-shelled *L. albomarginata* from a sheltered station (Hakahaka Bay in Port Underwood) was much better able to resist attack by the shore crab *Hemigrapsus edwardsi* than was *L. albomarginata* from a nearby wave-exposed station (Whites Bay, near Cape Campbell, South Island). *L. scobina* from both stations was resistant to attack. *H. edwardsi* abounds at sheltered stations, but is missing from wave-exposed rock reefs such as those at Whites Bay, so that the ability to survive encounters with shore crabs is ecologically important to *L. albomarginata* inhabiting sheltered stations. *L. scobina* occupies a lower zone on the shore, where it is probably liable to encounter other more powerful predators. Its spiral ribs probably strengthen the shell. We do not know to what extent differences in shell form and thickness depend on environmental factors, and to what extent they originate genetically. Thin shells are associated with an abundance of mussels *(Mytilus edulis* ssp. *aoteanus* or *Modiolus neozelanicus)*. There is an interesting possibility that a scarcity of mussels or other food caused by superior non-specific predators might result in the production of better-protected *Lepsiella*.

Introduction

The thaisid gastropod *Lepsiella scobina* (Quoy and Gaimard) and the subspecies (or closely related independent species?) *L. scobina* ssp. *albomarginata* (Deshayes) (Suter, 1913; see Powell, 1962, for nomenclature) occupy in New Zealand niches corresponding closely to that filled by *Nucella lapillus* (L.) on North Atlantic shores. They feed mainly on barnacles and mussels of several species, but are also capable of eating various other common shore animals (see Luckens, 1966). Photographs of a range of *Lepsiella* shells are shown in Fig. 1. *L. scobina (sensu stricto)* is provided with spiral ribs (3 on the body whorl), whereas these are missing from *L. albomarginata* (Suter, 1913). The spiral ribs of *L. scobina* end at the outer lip, and are conspicuous in profile (Fig. 1d-g). As the shell grows the advancing outer lip overlaps the middle and lower spiral ribs of the preceding whorl, so that only the upper rib remains visible.

Places mentioned in this paper are shown in the map of New Zealand in Fig. 2. Fearon (1962; summarised by Knox, 1963) has shown that *Lepsiella scobina* is mainly a northern form, extending southwards as far as the north shore of the South Island, whereas *L. albomarginata* occurs all around the South Island and in some parts of the North Island as well. *L. scobina* also occurs in Lyttleton Harbour, which is outside its geographically continuous range. In some areas where both forms occur together there are intermediate forms also, with only 1 or 2 spiral ribs.

We are concerned in this paper with the occurrence and ecological significance of differences in shell form. Subjectively, the shells of *Lepsiella albomarginata* and *L. scobina* from very sheltered localities appear taller and narrower than those from the open coast. Unfortunately, nearly all the shells of *L. albomarginata* from wave-exposed localities in New Zealand are so badly eroded at the spire that accurate measurements cannot be made of shell height. However, a limited number of perfect and practically perfect shells were found at Taylor's Mistake, an open bay with intertidal reefs near Christchurch, well-known from the survey by Knox (1953). Therefore we first report on a detailed study of these shells and of shells from Hakahaka Bay, a very sheltered

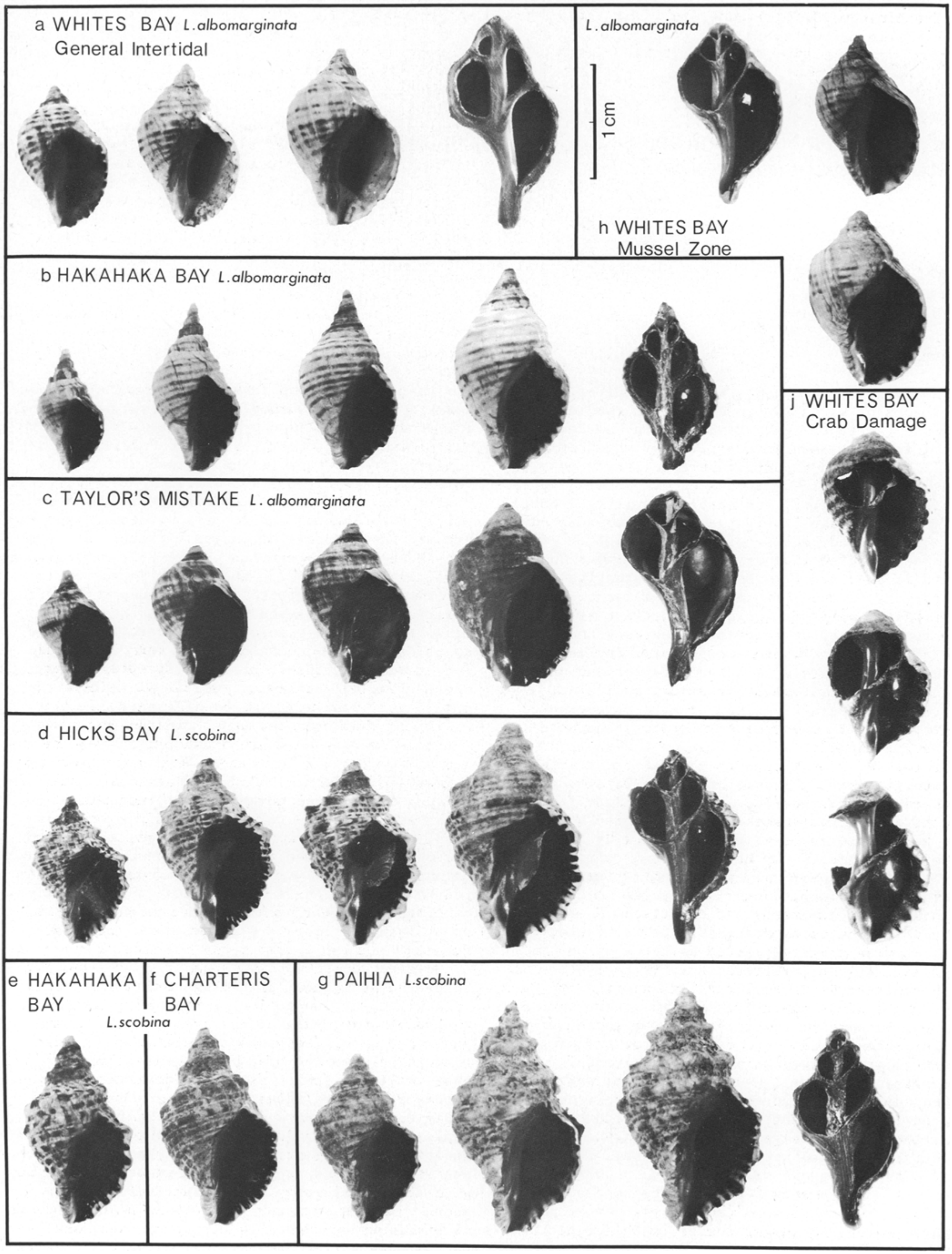

Fig. 1. *Lepsiella albomarginata* and *L. scobina* from various stations. In shells shown in vertical section, the plane of the cut is at right angles to the aperture. In (j), damage by crabs was incurred in an experiment involving *Hemigrapsus edwardsi*

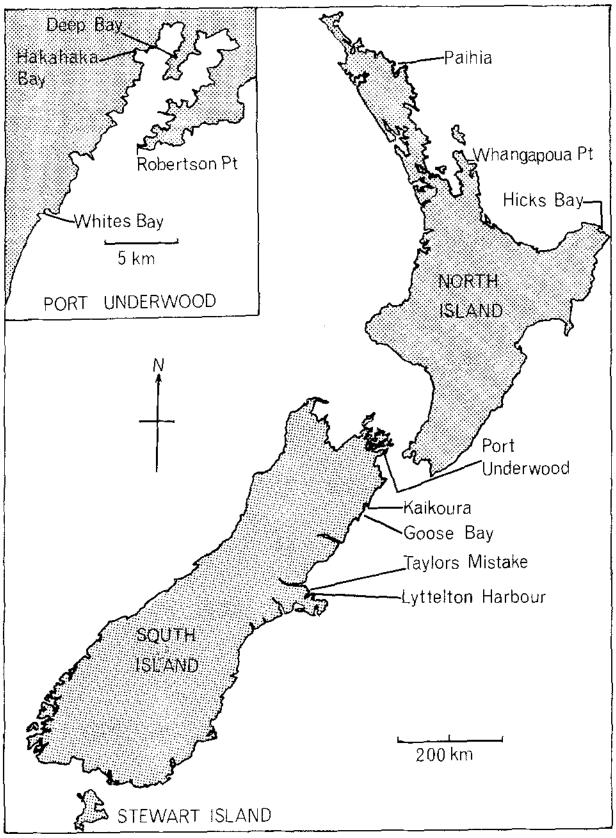

Fig. 2. Map of New Zealand. Inset: Port Underwood

bay within the much larger bay known as Port Underwood (Fig. 2).

The results from these two contrasting stations are supported by a further comparison of slightly less perfect shells of *Lepsiella albomarginata* by means of measurements not seriously impaired by minor damage to the apex: shell capacity, shell weight, diameters of the body whorl and preceding whorl, and apical angle, all as defined later. The results of this comparison are examined in the light of D'Arcy Thompson's (1917) theoretical treatment of the perfect logarithmically spiral shell, towards which gastropod shells approximate. The relevant characteristics for a "turbinate" shell, of essentially conical proportions, are the apical angle (2θ), the spiral angle (α), and the ratio of the breadth of consecutive whorls (R). The "spiral angle" is the angle between a radius intersecting the outer surface and a tangent to the surface at that point of intersection. Diagrams illustrating these characteristics are given by Moore (1936), who has discussed their application to *Nucella lapillus*. For a turbinate shell the relation is:

$$\mathrm{Tan}\,\alpha = \frac{2.72 \sin \theta}{\mathrm{Log}\ R} .$$

Our data permit the calculation of α from apical angle and whorl ratio.

Extensive studies were also carried out on *Lepsiella albomarginata* from two other stations (Whites Bay, exposed to north and east, and Kaikoura, exposed to north), except that shells from these places were too eroded for measurement of apical angle. Additional samples of *L. albomarginata* and *L. scobina* were collected from various stations in the North and South Islands and were used for the measurement of successive whorl diameters. These stations include two extremely sheltered harbours or estuaries (Charteris Bay in Lyttleton Harbour and Paihia in the Bay of Islands) where *L. scobina* is noticeably taller and narrower than on the open coast.

Finally, we describe differences in the resistance of *Lepsiella albomarginata* from different localities to attack by the shore crab *Hemigrapsus edwardsi*. Here also we found a parallel with *Nucella lapillus* (see Kitching *et al.*, 1966). It was in fact the discovery of the differences in resistance to crabs which led us to examine the differences in shell form.

Variation in Shell Form

Methods

Collections of *Lepsiella* spp. were made from each locality by picking up all living specimens seen until a sufficient number, normally 40 to 100 shells, had been collected. Usually at least two collections were made in each locality, and some localities were visited several times. Some care was taken to include both small and large specimens (if available), but no other selection was made. In general, laborious programmes of measurement were carried out on one complete collection from each locality, whereas a second or larger collection was used for more limited programmes. Damaged shells which would lead to faulty results were discarded.

The various linear shell measurements are shown in Fig. 3a, b. "Outside" Vernier steel callipers were used, and all measurements, including aperture length and width, were made from outside. The margin of the aperture at the columella was taken as the outer border of the glossy lining of the aperture. The diameter of the body whorl (D_0) was measured from the upper margin of the aperture around the body whorl along one of the shell striae to the opposite side: this is the line along which the upper lip would advance, forming a suture, if further growth of the shell were to occur. For comparison we measured the whorl diameter (D_{-1}) along the suture exactly one gyre of the spiral above this. These measurements of whorl diameter are illustrated in Fig. 3b. The apical angle was measured between straight lines tangential to the body whorl and preceding whorl; arrows at the points of contact are shown in Fig. 3c.

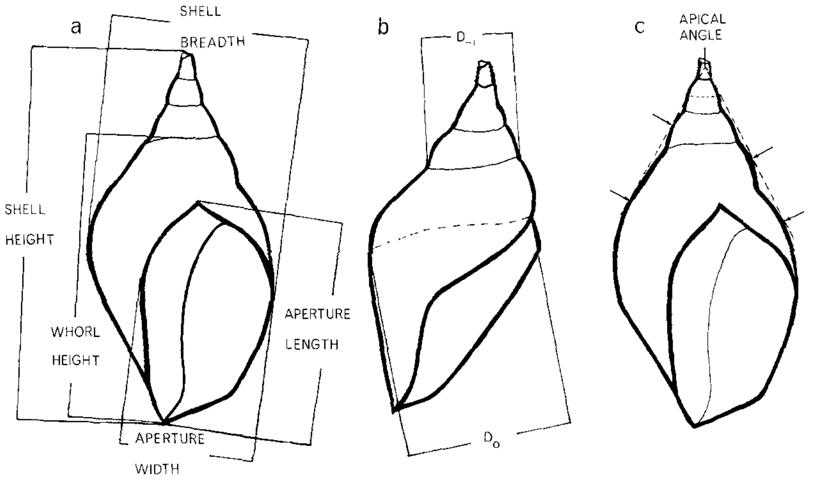

Fig. 3. Linear and angular measurements used for comparing shells. In (c), arrows indicate the points of contact of the two lines subtending the apical angle

For measurement of shell weight, the specimens (already stored for 1 month or more without preservative) were twice boiled for 1 h in 10% KOH to remove any remains of the body of the animal. The shells were then washed, reboiled in distilled water, and dried in a warm dry room. The dry shells were weighed and immersed in water in a flask, which was then evacuated to remove air locks and fill the spire of the shells with water. Finally, the shells were lifted in turn from the water, allowed to dry on the outside, and re-weighed full of water. The difference between dry and full weights is a measure of the shell capacity.

All these measurements were analysed by linear regression, quadratic regression where appropriate, and by analysis of covariance, by means of computer programs prepared for us by Dr. D. Aikman. These programs derive the appropriate regressions and provide the evidence required to test first the significance of linear regression slopes and then whether a significant reduction in the residual variance is obtained by the use of a quadratic relationship. They provide for comparisons by t or F tests of the results of treating two collections as part of a single population with a combined regression or as two separate populations each with its own regression. They also provide estimates of the mean value and standard error of one variable for stated values of the other, so that comparisons may readily be made between members of a series of stations in respect of a standard size of shell. All these values are appropriate for the interpretation of relationships as found within the size range of shells actually available and collected, and they provide a means of studying changes with size and so, by implication, with age. Clearly, however, the relation between any pairs of measured characteristics must in fact originate at the origin, and the occurrence of a significant intercept in our regressions implies that there has been a change in slope during an early growth period inadequately represented in our collections.

Results

The linear measurements illustrated in Fig. 3a were made on 31 perfect *Lepsiella albomarginata* shells from Hakahaka Bay and on 14 perfect shells from Taylor's Mistake. In comparisons between these two groups of shells, very significant differences were found between each pair of measured characteristics, as judged from rectilinear regressions (taken either way). Either the slopes differ, or if not the analysis of covariance shows a significant difference between the populations. A few of these comparisons are summarised in Table 1, and aperture measurements in relation to shell height are plotted in Fig. 4. As illustrated in Fig. 1b, c, the shells from Hakahaka Bay are taller and narrower and have narrower apertures than those from Taylor's Mistake. The body whorl and the aperture also occupy a smaller proportion of the shell height in the Hakahaka Bay shells.

All the shells of *Lepsiella albomarginata* from Hakahaka Bay conform to the characteristic "Hakahaka Bay" type, as do all in a collection made from Deep Bay - another sheltered bay in Port Underwood. All those from Taylor's Mistake conform to the "Taylor's Mistake" type. The linear measurements were carried out only on the rather small number of unworn Taylor's Mistake shells in order to obtain reliable values.

Measurements carried out on large samples showed no significant difference in the spiral angle (α), calculated separately for each shell, between Hakahaka Bay and Taylor's Mistake. The apical angle and whorl ratio were both very significantly smaller for Hakahaka Bay than for Taylor's Mistake, and these two differences balance out in the calculation of spiral angle. Apical angle decreased significantly at both stations with increase of shell capacity (as a measure of shell size), and there is a corresponding decrease in whorl ratio at Hakahaka Bay; however, whorl ratio varied too much at Taylor's Mistake to reveal any significant trend. Table 2 summarises the data on which these conclusions are based. If spiral angle can be regarded as constant for the species, then local differences in shell proportions can be described adequately in terms either of apical angle or of whorl ratio.

Table 1. *Lepsiella albomarginata*. Comparisons of pairs of measurements (mm) of shells of specimens from Hakahaka Bay (collected 8 January and 27 February, 1971) and Taylor's Mistake (collected 17 March, 1971)

Ordinate	Abscissa	Hakahaka Bay (n = 31)		Taylor's Mistake (n = 14)		Comparison of slopes (t)	Analysis of covariance (t)
		Slope	Intercept	Slope	Intercept		
Shell breadth	Shell height	0.77	0.19	0.90	−0.09	1.92	3.92
Whorl height	Shell height	0.49	0.70	0.64	−0.09	2.83	6.99
Aperture length	Shell height	0.55	1.0	0.75	−0.03	4.39	9.39
Aperture width	Shell height	0.35	−0.25	0.45	0.01	2.13	12.06
Aperture width	Aperture length	0.59	−0.47	0.60	0.04	0.17	5.27
Aperture width	Shell breadth	0.42	0.01	0.50	0.34	1.53	9.76

The relationship of the diameter of the main body whorl (D_0) to that of the preceding whorl (D_{-1}) for *Lepsiella albomarginata* at Hakahaka Bay, Whites Bay, Kaikoura, and Taylor's Mistake is illustrated in Fig. 5. Statistical information is given in Table 3, which includes the regression constants and standard errors for a quadratic fit where this gives a significant improvement. Although all these collections of *L. albomarginata* differ very significantly from each other, the distributions for the Whites Bay (general intertidal) and Kaikoura shells overlap substantially and are intermediate between the other two. The Hakahaka Bay and Taylor's Mistake collections represent extreme opposites, with no overlap except for very small shells. Estimates of D_0 for stated

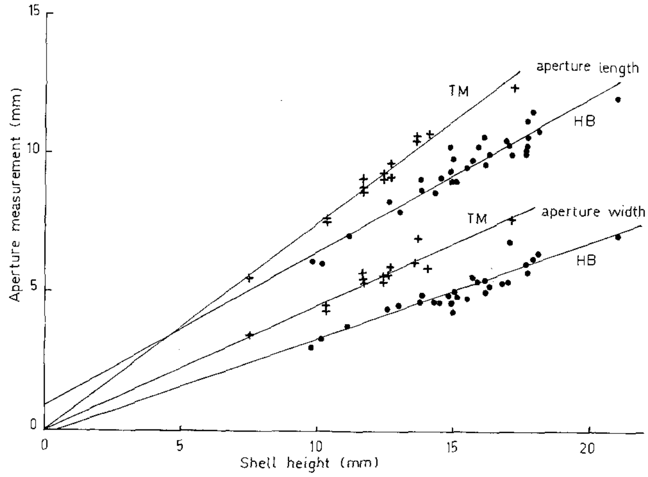

Fig. 4. *Lepsiella albomarginata*. Aperture measurements in relation to shell height for shells from Taylor's Mistake (TM) and Hakahaka Bay (HB)

Table 2. *Lepsiella albomarginata*. Statistical variables for shell shape of specimens from Hakahaka Bay (collected 8 January 1971) and from Taylor's Mistake (collected 12 March, 1971); means ± standard error. Shell capacity (v) is used as a measure of shell size. NS: Not significant

Station	No. of shells	Regression for whorl ratio ($R = D_0/D_{-1}$) where $R = a + bv$		Whorl ratio for v = 0.25 ml	Regression for apical angle (2θ) where $2\theta = a + bv$		Apical angle vor v = 0.25 ml	Spiral angle (α)
		a	b		a	b		
Hakahaka Bay	42	1.81±0.03	−0.966±0.113	1.60±0.01	68±2	−63±6.7	52±0.8	80.35±0.17
Taylor's Mistake	46	R=2.01±0.03	NS	2.01±0.03	88±1.6	−24±5.8	82±0.8	80.43±0.19

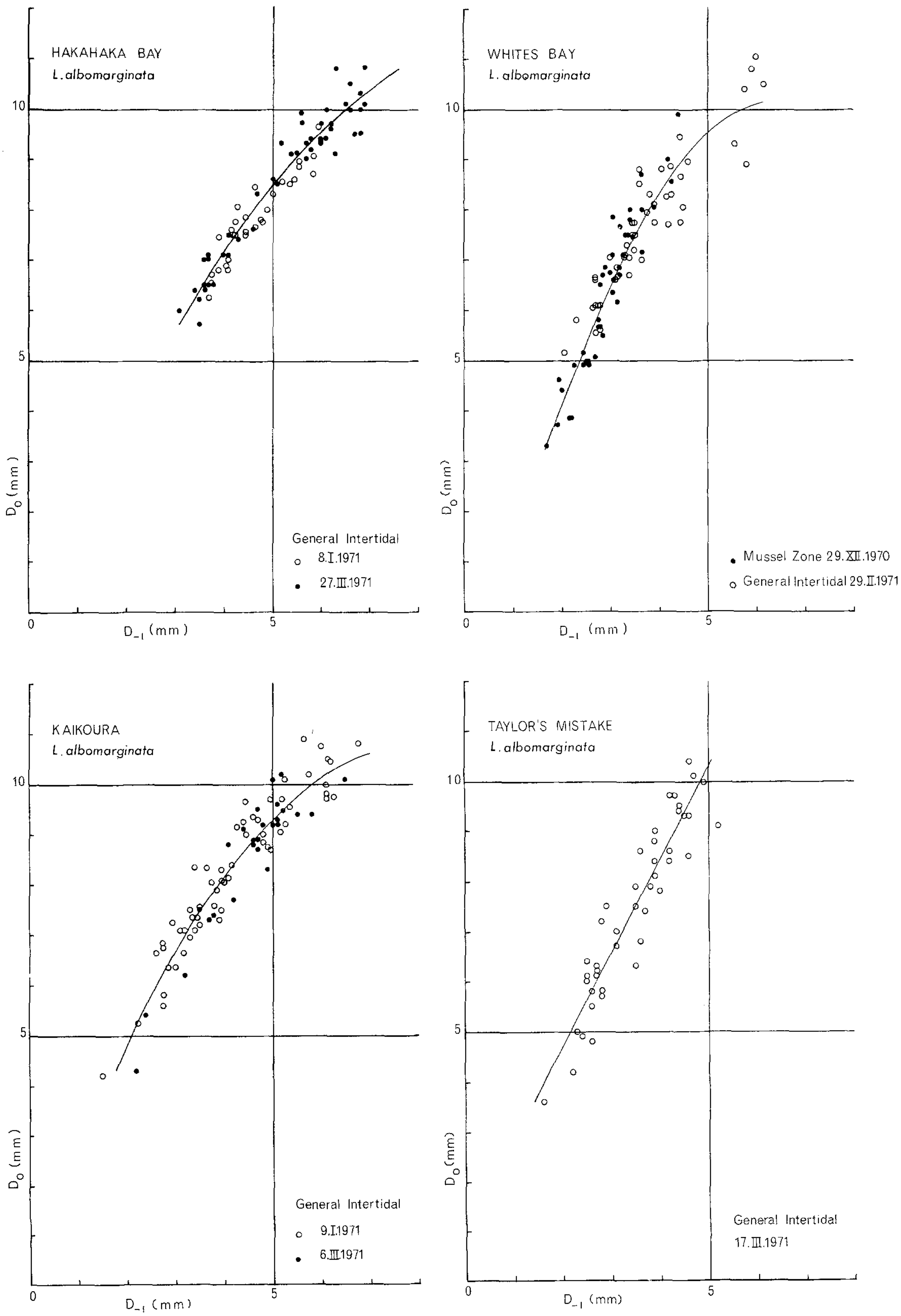

Fig. 5. *Lepsiella albomarginata*. Relation of D_0 (diameter of body whorl) to D_{-1} (diameter of preceding whorl), measured as shown in Fig. 3b, for 4 stations

Table 3. *Lepsiella* spp. Regressions describing relation of diameter of body whorl (D_o) to diameter of preceding whorl (D_{-1}) (in mm) according to rectilinear equation ($D_o = a + b D_{-1}$), or quadratic equation ($D_o = a + b D_{-1} + c D_{-1}^2$) if improvement is significant; each estimate ± standard error

Species	Collection area	Date of collection	No. of shells	a	b	c	Estimate of D_o where D_{-1} = 2.5 mm	5.0 mm
L. albomarginata	Hakahaka Bay	8 Jan., 1971; 27 Feb., 1971	77	−0.59 ± 1.04	2.41 ± 0.42	−0.12 ± 0.041	4.67 ± 0.25	8.42 ± 0.06
	Whites Bay (general shore)	29 Feb., 1971	47	2.86 ± 0.30	1.28 ± 0.76	-	6.07 ± 0.12	9.27 ± 0.12
	Whites Bay (mussel zone)	29 Dec., 1970	44	0.69 ± 0.37	2.38 ± 0.12	-	5.26 ± 0.09	11.22 ± 0.26
	Whites Bay (combined)		91	−2.26 ± 0.66	3.80 ± 0.35	−0.29 ± 0.045	5.44 ± 0.09	9.56 ± 0.11
	Kaikoura	9 Jan. & 6 March, 1971	89	−0.06 ± 0.59	2.79 ± 0.28	−0.18 ± 0.032	5.78 ± 0.11	9.34 ± 0.06
	Taylor's Mistake	17 March, 1971	45	0.98 ± 0.39	1.86 ± 0.11	-	5.62 ± 0.14	10.26 ± 0.19
	Charteris Bay	14 March, 1971	53	3.49 ± 0.32	0.96 ± 0.07	-	5.88 ± 0.15	8.28 ± 0.05
Intermediate	Charteris Bay	14 March, 1971	11	3.67 ± 1.00	1.00 ± 0.18	-	6.19 ± 0.55	8.70 ± 0.14
L. scobina	Charteris Bay	14 March, 1971	33	−4.24 ± 2.72	4.20 ± 1.07	−0.315 ± 0.104	4.29 ± 0.72	8.88 ± 0.06
	Hakahaka Bay	8 Jan., 1971	50	1.75 ± 0.38	1.45 ± 0.08	-	5.36 ± 0.18	8.98 ± 0.07
	Whites Bay	8 Jan., 1971	32	−3.28 ± 2.13	3.68 ± 0.81	−0.21 ± 0.076	4.64 ± 0.61	9.99 ± 0.14
	Paihia	12 April, 1971	149	1.64 ± 0.23	1.38 ± 0.04	-	4.75 ± 0.24	8.55 ± 0.04
	Hicks Bay	5 April, 1971	27	2.40 ± 0.62	1.54 ± 0.14	-	6.23 ± 0.29	10.07 ± 0.13
	Whangapoua Point (Typical)	2 April, 1971	45	2.55 ± 0.72	1.50 ± 0.17	-	6.29 ± 0.32	10.03 ± 0.16
	(2 major ribs)	2 April, 1971	55	−5.03 ± 2.15	5.06 ± 0.94	−0.41 ± 0.101	5.08 ± 0.45	10.13 ± 0.11
	(combined)	2 April, 1971	100	−1.47 ± 1.72	3.48 ± 0.78	−0.235 ± 0.087	5.75 ± 0.34	10.03 ± 0.10

values of D_{-1} (2.5 and 5.0 mm) are also given in Table 3, and provide a useful basis for comparison, the standard deviations of these estimates being calculated from the variances and covariances of the parameters of the appropriate regressions. These estimates reflect the general differences in shell proportions, and are less liable than some other measurements to distortion through erosion.

Measurements of shell weight and capacity were made on *Lepsiella albomarginata* from the same 4 stations. Shells from Taylor's Mistake are lighter, in relation to shell capacity, than those from Hakahaka Bay, Whites Bay (general shore collection), or Kaikoura (Fig. 6). Statistically there are significant differences between all pairs of stations except Hakahaka Bay and Kaikoura, which give the highest estimates of shell weight for stated values of shell capacity (Table 4). Whites Bay shells are intermediate, and shells from Taylor's Mistake and from the mussel zone at Whites Bay (exposed only at low water) are the lightest. Taylor's Mistake shells and those from the mussel zone at Whites Bay do not differ significantly. They are also much thinner than those from Hakahaka Bay, as is obvious from inspection of shells cut vertically into halves (Fig. 1). It is evident that differences in shell thickness are the main cause of differences in shell weight for a given shell capacity, although the Taylor's Mistake shells are also a slightly more economical shape.

Measurements of whorl diameters were also made on *Lepsiella scobina* from Hakahaka Bay (sheltered), Whites Bay (exposed), Charteris Bay (sheltered, in Lyttleton Harbour), and in the North Island from Paihia (very sheltered, in Bay of Islands), and Whangapoua Point and Hicks Bay (both fully exposed to north-east) (Fig. 7; Table 3). Although the differences are less striking than for *L. albomarginata*, *L. scobina* shells from sheltered stations have a lower estimated value of D_0 for $D_{-1} = 5.0$ mm (Table 3). Some specimens from Charteris Bay appear to be intermediate between *L. scobina* and *L. albomarginata*, having less than 3 spiral ribs. Many specimens from Whangapoua Point have the upper and middle spiral ribs well developed, and two or three poorly developed lower ribs. They do not differ convincingly in whorl ratio from typical *L. scobina* from that station.

Predation Tests

Material and Methods

Preliminary tests were carried out with submerged cages in Hakahaka Bay to see if crabs of various species could break open various species of thaisid gastropods. Work was then transferred to the Edward Percival Marine Station, Kaikoura. Experiments were carried out here in a tidal tank on batches of *Lepsiella albomarginata* and *L. scobina* placed together with the shore crab *Hemigrapsus edwardsi*, which is found on many sheltered beaches under boulders.

Slabs of rock within the zone of *Lepsiella albomarginata* were removed from the reefs near Seal Point, Kaikoura, to the tidal tank. These slabs were covered with the barnacle *Chamaesipho columna*, which is the normal food of *L. albomarginata* at Kaikoura. The tops of the rocks were exposed to air during simulated low tide and covered with water during high tide. Crevices between the rocks provided hiding places which the *Hemigrapsus edwardsi* occupied by day: at night the crabs emerged to forage. The tidal controls were set to give 6 h of low water and 6 h of high water per cycle. During high water the volume of water was

Table 4. *Lepsiella albomarginata*. Regressions describing relation of shell weight (w) (in g) to shell capacity (v) (in ml) according to linear equation ($w = a + bv$), or quadratic ($w = a + bv + cv^2$) if improvement is significant; each estimate ± standard error

Station	Date of collection	No. of shells	a	b	c	Estimates of w where v = 0.25 ml	0.5 ml
Hakahaka Bay	27 Feb., 1971	45	-0.04 ± 0.030	2.01 ± 0.101	-	0.46 ± 0.012	0.96±0.026
Whites Bay (general shore)	27 Feb., 1971	71	-0.06 ± 0.015	1.78 ± 0.07	-	0.38 ± 0.007	0.83±0.020
Whites Bay (mussel zone)	29 Dec., 1970	38	0.013 ± 0.007	1.13 ± 0.036	-	0.29 ± 0.004	0.58±0.012
Whites Bay (combined)	-	109	0.0035 ± 0.023	1.17 ± 0.19	0.85 ± 0.35	0.35 ± 0.008	0.80±0.023
Kaikoura	6 & 16 March, 1971	56	-0.09 ± 0.026	2.15 ± 0.075	-	0.45 ± 0.011	0.99±0.016
Taylor's Mistake	17 March, 1971	74	-0.002 ± 0.010	1.10 ± 0.032	-	0.27 ± 0.048	0.55±0.008

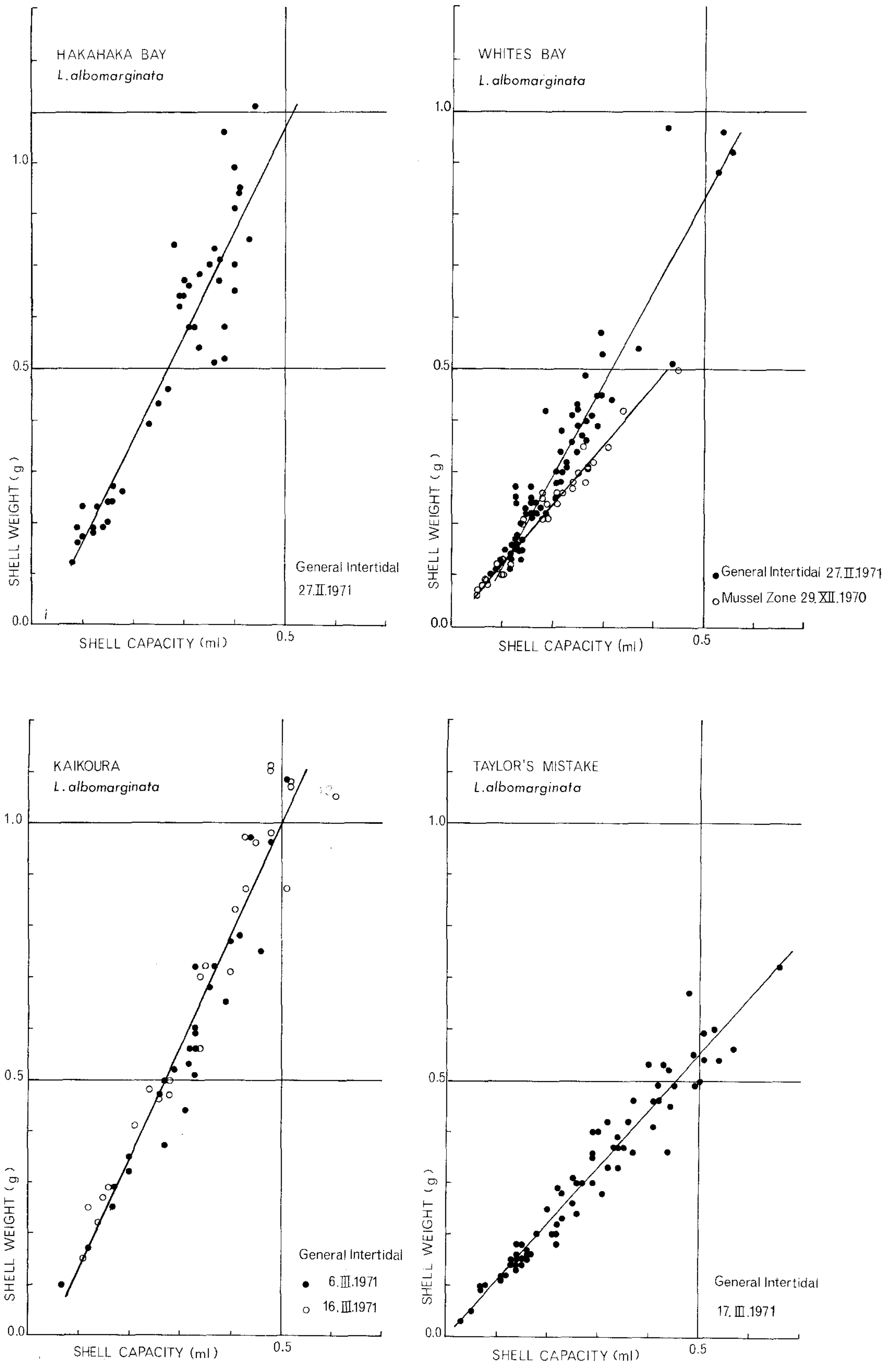

Fig. 6. *Lepsiella albomarginata*. Relation of shell weight to shell capacity for 4 stations

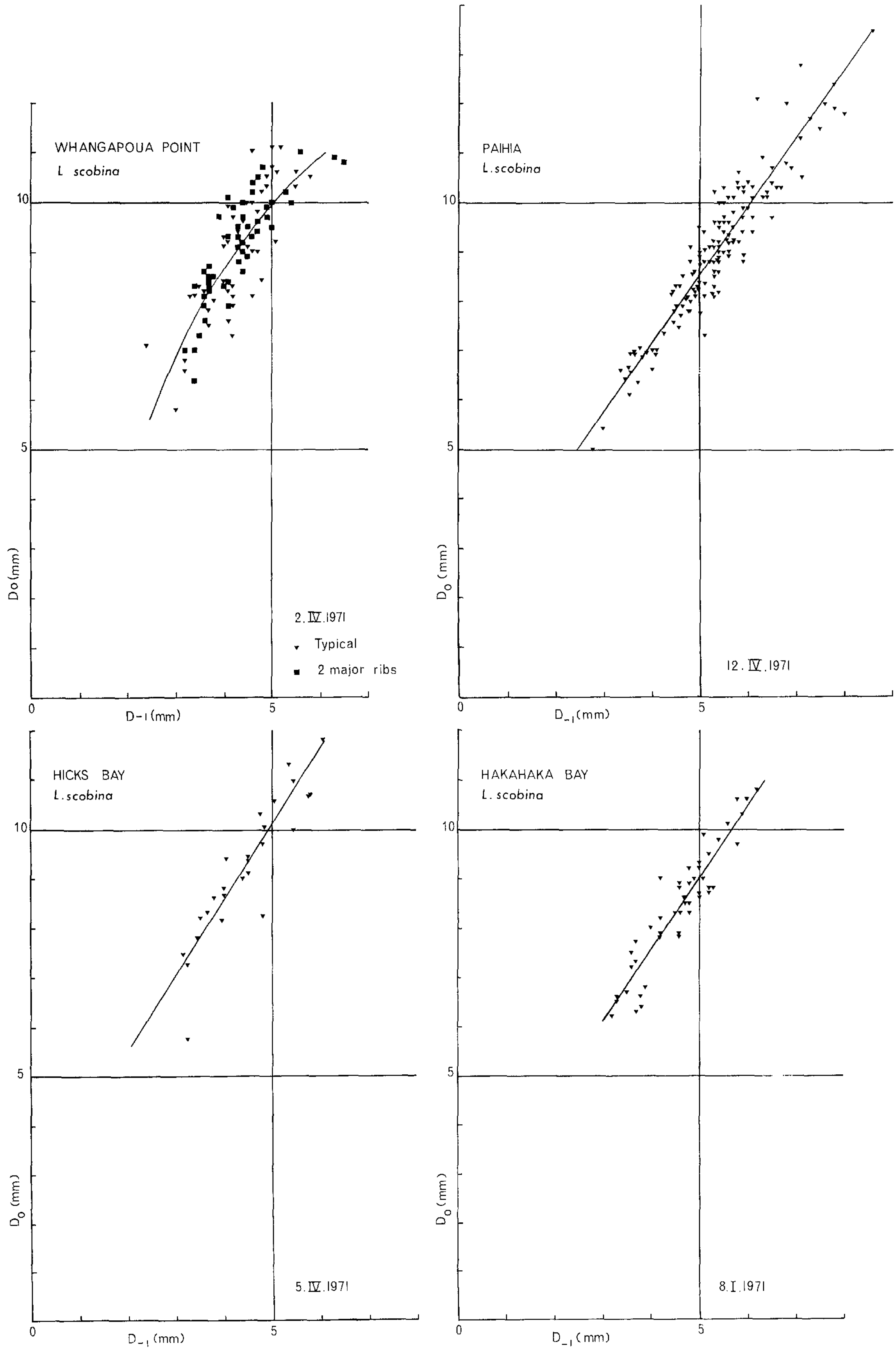

Fig. 7. *Lepsiella scobina*. Relation of D_0 to D_{-1} for 4 stations

64 l, the depth was 16 cm and the rocks were fully covered. At the change from high to low water the circulation was cut off and the water in the tank siphoned off to leave a depth of 3 cm. The top of the tank was covered with mesh polythene to prevent escape.

Results

The results of these experiments are shown in Tables 5-8. In the first experiment 12 *Hemigrapsus edwardsi* destroyed about half the 100 *Lepsiella albomarginata* (collected at Kaikoura) within a period of 5 days (Table 5). This implied a much greater susceptibility than had been found in preliminary experiments carried out with submerged cages at Hakahaka Bay.

Accordingly, in the next two experiments with the tidal tank, the resistance of *Lepsiella* spp. from two different habitats was compared. *L. scobina* was found to be very resistant to attack by *Hemigrapsus edwardsi* (Table 6). *L. albomarginata* from Hakahaka Bay was resistant but from Whites Bay was susceptible (Tables 6 and 7). The combined losses of *L. albomarginata* from Whites Bay amounted to 65 out of 150, and only 6 out of 150 for specimens from Hakahaka Bay. Although the susceptible size classes, as judged by height, were not equally distributed, the results leave no doubt about the preferential destruction of Whites Bay specimens. In fact shell capacity (representing bulk of body) would probably be a more fitting basis for comparison, and if compared in this way the vulnerability of shells from Whites Bay would appear even more striking. The cube root of shell capacity is a linear function of shell height, in accordance with the regressions summarised in Table 9. Shells from Whites Bay are equivalent in capacity to Hakahaka Bay shells larger by 2 to 3 of the size classes used in Tables 6 and 7.

Finally, the tidal tank was subdivided by a partition allowing the passage of water but not *Lepsiella*. Six large male *Hemigrapsus edwardsi* and 50 *L. albomarginata* were placed on the left side,

Table 5. *Lepsiella albomarginata*. Survival of specimens from Kaikoura in tidal tank in presence of *Hemigrapsus adwardsi*; 6 male crabs, carapace width 29, 31, 33, 35, 37, 37 mm; 6 females, 27, 30, 31, 31, 31, 33 mm. Experiment started 3rd and finished 8th January, 1971

Height (mm)	No. present at start	No. present after 5 days	Losses
16 - 18	8	8	0
10 - 15	82	37	45
7 - 9	10	2	8

Table 6. *Lepsiella albomarginata* and *L. scobina*. Survival of specimens from Hakahaka Bay and from Whites Bay in tidal tank in presence of *Hemigrapsus edwardsi*. Experiment started 8th and finished 13th January, 1971. The same crabs were used as in Table 5

Species and station		Height (mm) 10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
L. albomarginata Whites Bay	No.at start	0	0	6	6	7	8	9	2	2	1	1	1	2	2	2	1	50
	No.after 5 days	0	0	0	4	1	7	5	2	2	1	1	1	2	0	2	1	29
	Losses	0	0	6	2	6	1	4	0	0	0	0	0	0	2	0	0	21
Hakahaka Bay	No.at start	1	0	0	2	3	6	9	9	5	10	3	1	1	0	0	0	50
	No.after 5 days	0	0	0	2	3	6	9	8	5	10	2	1	1	0	0	0	47
	Losses	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	3
L. scobina Whites Bay	No.at start	0	0	0	2	2	2	1	9	3	8	9	9	1	3	0	1	50
	No.after 5 days	0	0	0	2	2	2	1	9	3	8	9	9	1	3	0	1	50
	Losses	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hakahaka Bay	No.at start	0	0	0	0	4	5	17	9	9	4	1	1	0	0	0	0	50
	No.after 5 days	0	0	0	0	4[a]	5	16[b]	9	7	3	1	1	0	0	0	0	46
	Losses	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	4

[a] 1 specimen with body whorl and siphon badly damaged.

[b] 2 specimens with body whorl badly damaged.

Table 7. *Lepsiella albomarginata*. Survival of specimens from Hakahaka Bay and from Whites Bay in tidal tank in presence of *Hemigrapsus edwardsi*; 6 male crabs, carapace width 26, 29, 31, 31, 32, 33 mm; 6 female crabs, carapace width 24, 24, 26, 26, 27 mm. Experiment started 28 February and finished 6 March, 1971

Station		Height (mm)														Total
		10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Hakahaka Bay	No. at start	0	0	2	3	12	9	8	9	13	15	19	5	2	3	100
	No. after 7 days	0	0	2	3	12	9	8	8	13	15	18	5	1	3	97
	Losses	0	0	0	0	0	0	0	1	0	0	1	0	1	0	3
Whites Bay	No. at start	1	3	18	24	12	18	5	7	4	2	4	1	1	0	100
	No. after 7 days	0	1	5	9	7	12	3	7	4	2	4	1	1	0	56
	Losses	1	2	13	15	5	6	2	0	0	0	0	0	0	0	44

Table 8. *Lepsiella albomarginata*. Survival of specimens from Goose Bay, on the open east coast near Kaikoura, in tidal tank in presence of male or female *Hemigrapsus edwardsi*. Experiment started 13th and finished 20th March, 1971

Experimental animals	Position in tank Left side			Right side		
H. edwardsi						
No. and sex	6 males			6 females		
Carapace widths (mm)	34, 35, 36, 37, 37, 37			31, 31, 32, 33, 35, 38		
L. albomarginata[a]						
Height (mm)	15	13	9-11	15	13	9-11
No. at start	8	22	20 (50)	8	22	20 (50)
After 7 days	2	1	0 (3)	8	22	20[b] (50)
Losses	6	21	20 (47)	0	0	0 (0)

[a]Total numbers are given in parentheses.

[b]1 specimen had outer lip chipped.

and 6 large female *H. edwardsi*, of about the same size range as the males, together with 50 *L. albomarginata* on the right side. The *L. albomarginata* were in 3 size ranges, distributed equally to both sides. The *H. edwardsi* were from Kaikoura and the *L. albomarginata* from nearby Goose Bay. After 7 days only 3 *L. albomarginata* survived in the presence of the male crabs, but all those with the female crabs survived (Table 8). Male *H. edwardsi* have much larger chelae. *L. albomarginata* from Goose Bay somewhat resemble in appearance the thin-shelled specimens found at Taylor's Mistake, and from the experiment they appear to have been more vulnerable than those from Whites Bay.

Taylor's Mistake is a very popular site for the collection of marine biological material. For this reason, in the interests of conservation, *Lepsiella* was not collected here for the predation experiments. However, in view of the fact that their shells are thin, we believe that (if tested) *L. albomarginata* from Taylor's Mistake would have been found to be very vulnerable to *Hemigrapsus edwardsi*.

The shells broken by crabs in these experiments were all of medium size or rather small. Many were broken into small pieces, but those shells which were not completely broken up had the body whorl and the whorl above it broken open, with little or no damage to the outer lip (Fig. 1j). They had clearly been crushed.

Discussion

Variation within the *Lepsiella* group in New Zealand involves the presence or absence of the 3 knobbly spiral ribs, the overall shape of the shell - tall and narrow or short and broad - and the thickness of the shell. Although sculptural features often show very great variation within a single species of thaisid (e.g. Clench, 1947; Kincaid, 1957), it is generally and no doubt correctly considered that such features are determined genetically and that they may be used - with discretion - for the separation of species. It seems likely that *L. scobina* and *L. albomarginata* are genetically distinct, even though intermediate forms occur in some places.

The situation is much less clear in respect of overall shell shape and shell thickness. Field data are difficult to interpret, and the question will probably only be settled by means of experiments. Tall narrow shells of *Lepsiella albomarginata* and *L. scobina* clearly tend to be associated

Table 9. *Lepsiella albomarginata*. Regressions of relation of cube root of shell capacity ($\sqrt[3]{v}$) (in ml) to shell height (h) (in mm) according to linear equation ($\sqrt[3]{v} = a + bh$). A quadratic fit gave no significant improvement. Each estimate ± standard error

Station	Date of collection (1971)	No. of shells	a	b	Estimate of $\sqrt[3]{v}$ for h = 15 mm
Hakahaka Bay	27 Feb.	44	-0.049 ± 0.034	0.041 ± 0.002	0.57 ± 0.006
Whites Bay	27 Feb.	68	0.091 ± 0.019	0.039 ± 0.0015	0.68 ± 0.005
Kaikoura	6 and 16 March	55	0.110 ± 0.021	0.036 ± 0.001	0.64 ± 0.004
Taylor's Mistake	17 March	72	0.026 ± 0.018	0.049 ± 0.001	0.72 ± 0.004

with sheltered conditions, and short broad shells with exposure to waves, as in the case of *Nucella lapillus*. Exposure to waves is often associated with differences in the nature and quantity of available food. Moore (1936) attributed differences in the shell form of *N. lapillus* to diet (mussels or barnacles), but Staiger (1954, 1957) has described differences in the chromosomes of this species associated with habitat, and he attributed to these the differences in shell form. Using a related species, *Thais lamellosa*, on San Juan Island (Washington State, USA) Spight (1973) found that the shell was relatively shorter and broader at certain more wave-exposed stations where barnacle populations are dense. In experimental tanks in the laboratory, however, the offspring of broad or narrow specimens all developed as the narrow form, even though growth was rapid. He therefore attributed the differences in shape found in the "field" to some other unknown environmental factor. There is evidence that in limpets the shape may be influenced by the posture associated with holding on (Moore, 1934). For *Patella aspera*, very depressed shells are found in very sheltered conditions permitting prolonged relaxation (Ebling *et al.*, 1962). So far as *Lapsiella* is concerned, the supply of food, the direct influence of water movement, and other unknown environmental variables all deserve consideration.

In Hakahaka Bay the chief foods available to *Lepsiella* are the barnacles *Elminius modestus* (under boulders) and *Chamaesipho columna* (on outcrops of solid rock). The mussel *Mytilus edulis* ssp. *aoteanus* forms a zone low in the intertidal region on solid rock or occasionally on very large boulders, but such places are limited in extent. In Whites Bay *Lepsiella* was obtained from a promontory of solid rock, ending in an arch. Here *C. columna* extends over much of the intertidal region, but gives way to *M. edulis* ssp. *aoteanus* and the green mussel *Perna canaliculata* lower down. *M. edulis* ssp. *aoteanus* forms a dense and extensive zone just above the level of low water of spring tides. At Kaikoura *C. columna* was found on certain reefs only, and only these were inhabited by *L. albomarginata*; there were no mussels near them. At Taylor's Mistake intertidal crevices were filled with the small mussel *Modiolus neozelanicus*, on which *L. albomarginata* was clustered, and there were many *C. columna* on the open surface of the rock. The shells of all *L. albomarginata* from Taylor's Mistake and of the rather small specimens taken in the sample from the mussel zone on the Whites Bay promontory (Fig. 1c, h) were very thin. It is quite possible that abundant food, easily obtained, promoted a rapid growth in the body without a corresponding increase in rate of shell secretion. Larger shells at Whites Bay tended to be thicker as well as higher up on the shore, but we do not know whether there is an upward migration of *L. albomarginata* from the mussel zone to the *C. columna* zone above. The differences in shell shape between stations might equally plausibly be attributed to environmental or to genetic influences, but we suspect that the latter play some part.

Have the differences in shell shape and thickness any ecological significance? The sheltered-water form of *Nucella lapillus* was found to be much more resistant to attack by crabs (Kitching *et al.*, 1966), and even so crabs destroy a significant proportion of the population (Feare, 1970). The shore crab *Hemigrapsus edwardsi*, used in our tests, is abundant on sheltered boulder-strewn shores in the South Island of New Zealand, but is missing from rock-reefs on the open coast where shelter is lacking. It is therefore fitting that *Lepsiella* living in sheltered habitats should be sufficiently protected to enable most individuals to survive chance encounters with these abundant predators, while those living on wave-exposed shores may be less well protected, at least when young. The struggle for existence is keen, and the cost of extra shell weight must be weighed against the advantage gained. Over-protection would probably entail unacceptable disadvantages, and it seems that *L. albomarginata* is finely adjusted to the risks of its habitat. We do not know to what extent shell shape, as such, affects the ability of *Lepsiella* to resist crushing by crabs; it is clear, however, that shell thickness is important, and also that ribs (where present) are likely to confer additional protection.

Where both *L. albomarginata* and *L. scobina* occur together, the latter, with its ribs and knobs, usually occurs in a lower (but often overlapping) zone, where it is likely to meet more powerful predators. Other New Zealand thaisids which are ribbed - *Lepsithais lacunosus* (Bruguière) of southerly distribution and *Neothais scalaris* (Menke) of northerly distribution - also occupy the lower shore, and no doubt face the same or greater risks. We have not investigated the ecological significance of the wider shell aperture of specimens from wave-exposed coasts, but we suspect that, as in the case of *Nucella lapillus*, this is associated with a large foot and thus with a better grip, as originally suggested by Colton (1922) and demonstrated by Kitching *et al.* (1966). It seems likely that both environmental and genetic influences determine shell form, in a manner shaped by natural selection to provide the best ecological advantage, and it is possible that some degree of individual plasticity is advantageous. For instance, scarcity of food caused by the presence of superior general predators might result in slower growth and in the development of thicker shells. It is known that progressive starvation can lead to thickening at the growing edge of the shell of *N. lapillus* (Bryan, 1969). On the other hand, genetic variation, acting within the limitations imposed by overall environmental conditions such as sea and air temperature (e.g. Largen, 1967), might also provide a local variation of phenotype appropriate to local conditions. In either case it seems that these differences are ecologically important.

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Literature Cited

Bryan, G.W.: The effects of oil-spill removers ('detergents') on the gastropod *Nucella lapillus* on a rocky shore and in the laboratory. J. mar. biol. Ass. U.K. *49*, 1067-1092 (1969)

Clench, W.J.: The genus *Purpura* and *Thais* in the Western Atlantic. Johnsonia *2*, 61-92 (1947)

Colton, H.S.: Variation in the dog whelk, *Thais (Purpura* auct.*) lapillus*. Ecology *3*, 146-157 (1922)

Ebling, F.J., J.F. Sloane, J.A. Kitching and H.M. Davies: The ecology of Lough Ine. XII the distribution and characteristics of *Patella* species. J. Anim. Ecol. *31*, 457-470 (1962)

Feare, C.J.: Aspects of the ecology of an exposed shore population of dog-whelks *Nucella lapillus* (L.). Oecologia (Berl.) *5*, 1-18 (1970)

Fearon, C.E.: Studies in the biology and taxonomy of the thaisid gastropod *Lepsiella* Iredale. Thesis for the degree of Master of Science with Honours, University of Canterbury 1962

Kincaid, T.: Local races and clines in the marine gastropod *Thais lamellosa* Gmelim: a population study, 75 pp. Seattle: Calliostoma Co. 1957

Kitching, J.A., L. Muntz and F.J. Ebling: The ecology of Lough Ine XV. The ecological significance of shell and body form in *Nucella*. J. Anim. Ecol. *35*, 113-126 (1966)

Knox, G.A.: The intertidal ecology of Taylor's Mistake, Banks Peninsula. Trans. R. Soc. N.Z. *81*, 189-220 (1953)

- Problems of speciation in intertidal organisms with special reference to New Zealand shores. Publs Syst. Ass. *5*, 1-199 (1963)

Largen, M.J.: The influence of water temperature upon the life of the dog-whelk *Thais lapillus* (Gastropoda, Prosobranchia). J. Anim. Ecol. *36*, 207-214 (1967)

Luckens, P.A.: Competition and predation in shore zonation at Leigh. Ph.D. Thesis, Auckland University 1966

Moore, H.B.: The relation of shell growth to environment in *Patella vulgata*. Proc. malac. Soc. Lond. *21*, 217-222 (1934)

- The biology of *Purpura lapillus* L. Shell variation in relation to environment. J. mar. biol. Ass. U.K. *21*, 61-89 (1936)

Powell, A.W.B.: Shells of New Zealand, 203 pp. Christchurch. N.Z.: Whitcombe and Tombs Ltd. 1962

Spight, T.M.: Ontogeny, environment, and shape of a marine snail *Thais lamellosa* Gmelin. J. exp. mar. Biol. Ecol. *13*, 215-228 (1973)

Staiger, H.: Der Chromosomendimorphismus beim Prosobranchier *Purpura lapillus* in Beziehung zur Ökologie der Art. Chromosoma *6*, 419-478 (1954)

- Genetical and morphological variation in *Purpura lapillus* with respect to local and regional differentiation of population groups. Année biol. *33*, 251-258 (1957)

Suter, H.: Manual of the New Zealand Mollusca, 1120 pp. Wellington, N.Z.: Government Printer 1913

Thompson, D'Arcy, W.: On growth and form, 793 pp. Cambridge: University Press 1971

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