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Morphometric variation in *Haliotis iris* (Mollusca:Gastropoda): analysis of 61 populations

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Abstract Relationships of shell height, shell width, shell weight, foot weight, dry foot weight, and total weight were examined with shell length for *Haliotis iris* from different localities. Mean length varied among 61 localities explaining more than 70% of the variation in the other parameters which covaried with length. Significant sources of variation in mean length included latitude (sea surface temperature) and relative exposure. Variation in all morphometric parameters occurred among localities but such variation, although significant, was generally not large (< 10 % of mean values). Although the spatial scales examined included 100s of km, the largest morphometric variation shown was between neighboring localities (200 m apart). This and the high residual variation in any morphometric parameter for *H. iris* from any location indicated that morphometric variation occurred over small spatial scales. The suggestion that some localities of *H. iris* were "stunted" with small average lengths and had individuals with relatively peaked shells and greater weights compared with those from other localities, was not supported by our results.

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INTRODUCTION

The New Zealand fishery for abalone (*Haliotis iris*) is managed over large coastal areas each of which supports many discrete populations of *H. iris* (Schiel 1992; McShane et al. 1994). However, the demography and morphometrics of *H. iris* can vary over much smaller areas than those which are used to manage the fishery (McShane et al. 1994). The disaggregate structure of abalone stocks (Sluczanowski 1984, 1986) means that generalizations about population parameters such as growth, recruitment and survival can be imprecise or misleading because of spatial variation (McShane 1995). Growth of abalone can vary considerably among populations (Shepherd & Hearn 1983; McShane et al. 1988; Sloan & Breen 1988; Day & Fleming 1992) as can recruitment (McShane & Smith 1991) and morphometrics (McShane et al. 1988; Sloan & Breen 1988). Moreover, size limits may give varying protection to different breeding stocks because of different growth rates (McShane 1992).

The *H. iris* fishery is managed on a basis of regulating the size of animals captured (shell length) and the total weight of animals caught in each management area (annual catch quota; Schiel 1992; McShane et al. 1994). Commercial fishers of this species have suggested that some populations have relatively few individuals that grow above the legal minimum size of 125 mm shell length, and suggest that these "stunted" populations were comprised of individuals with deeper shells and heavier weight than "normal" populations. If these suggestions were true, as we seek to test here by considering variation in morphometrics among *H. iris* from different localities, then exploitation strategies based on limits on shell length may be inappropriate.

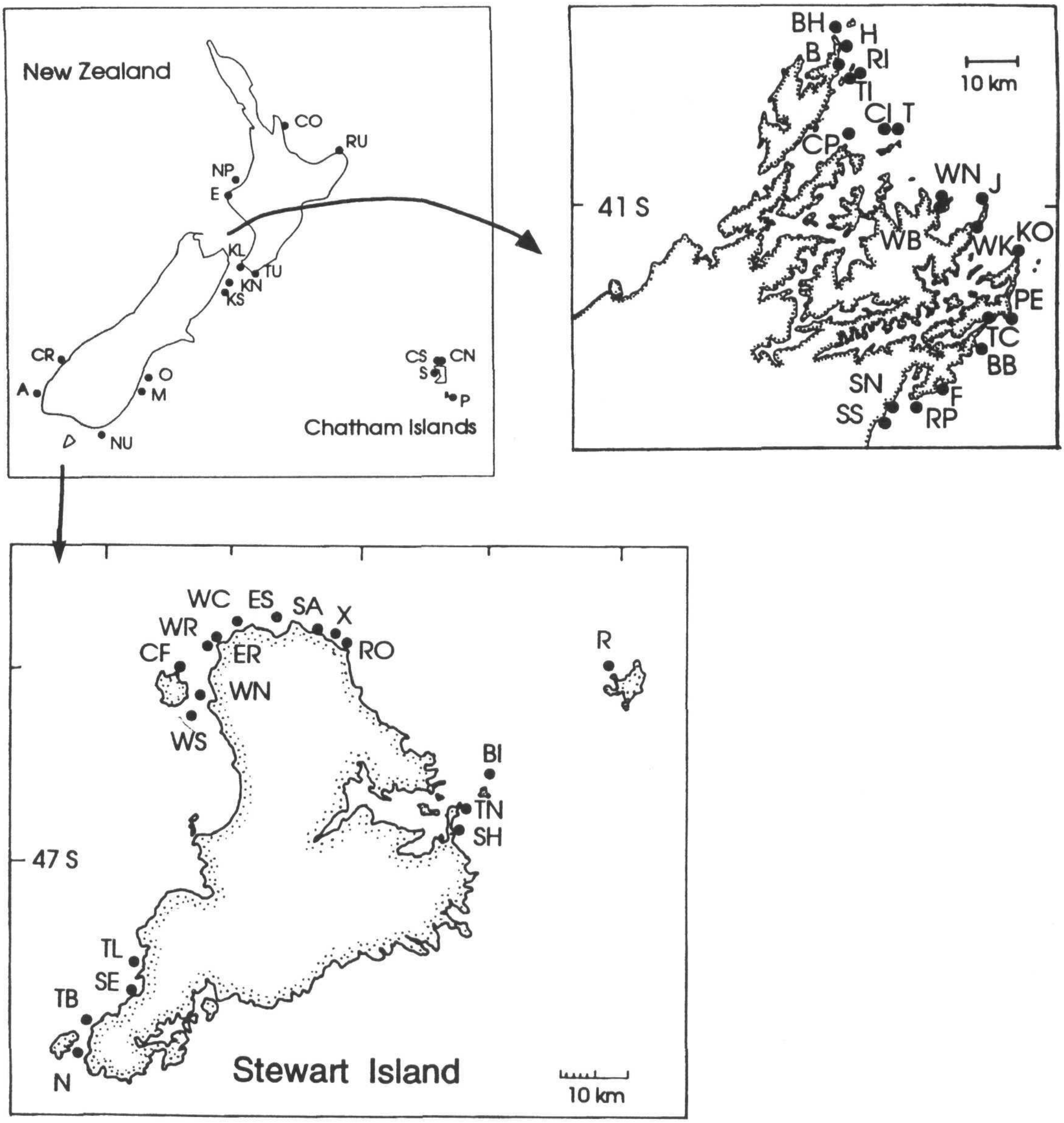

Fig. 1 Locality map for morphometric studies of *Haliotis iris*.

MATERIALS AND METHODS

Haliotis iris from 61 localities around New Zealand were sampled (Fig. 1). The localities were selected on the basis of their commercial importance (McShane et al. 1994) and because of putative differences in growth rates (Schiel & Breen 1991). The localities chosen had a variety of different habitats and levels of wave exposure, and ranged over 10 degrees of latitude (Table 1). Morphometric variation was therefore considered over a range of spatial scales (from 200 m to 1000 km, Fig. 1). In general, *H. iris* from any locality were sampled only once (during 1980–1983 or 1989, Table 1). However, at Karori Light, *H. iris* were sampled during 1982 and 1989 (Table 1).

Table 1 Summary data for *Haliotis iris* sampled from different localities included in morphometric studies. Data are shown for mean shell length (SL) and sample size (N). Relative wave exposure is indicated as exposed (E), moderate (M) or sheltered (S). Analyses for covariates with shell length are recovery (foot weight as a percent of total weight, R), shell weight (SW) or dry foot weight (DW). Shell width and shell height were measured at all locatities.

Code	Locality	Date	N	SL (s.e.)	Exposure	Analyses
A	Anchor Island	7/82	57	140.8(1.1)	M	DW
BI	Bench Island	9/89	48	125.9(1.9)	M	R,SW
BH	Billhook Bay	10/89	62	109.6(2.2)	E	R,SW
B	Black Beach	10/89	50	123.6(1.9)	S	R,SW
BB	Bushby Bay	11/82	54	117.8(1.8)	M	DW
CN	Cape Young (Nth)	3/82	52	116.1(1.7)	E	DW
CS	Cape Young (Sth)	3/82	52	112.0(1.7)	E	DW
C	Chalky Inlet	7/82	57	141.8(1.2)	E	DW
CI	Chetwode Island	10/89	53	118.8(1.8)	E	R,SW
CP	Clay Point	10/89	51	113.2(1.8)	E	R,SW
CR	Coal River	7/82	60	126.3(1.2)	E	DW
CF	Codfish Island	7/82	60	139.6(1.3)	M	DW
CO	Coromandel	11/82	59	97.2(0.6)	M	DW
ER	East Ruggedy	9/89	73	132.6(1.3)	E	R,SW
ES	Smoky Cape (east)	9/89	96	124.0(1.2)	M	R,SW
E	Cape Egmont	4/82	56	80.3(0.9)	E	DW
F	Fighting Bay	11/82	55	135.2(1.3)	M	DW
G	Gisborne	7/81	56	100.0(1.0)	M	
H	Hapuku Rocks	10/89	58	119.6(1.7)	E	R,SW
J	Cape Jackson	12/81	49	127.9(1.9)	E	
KN	Kaikoura (Nth)	1/83	53	127.5(1.7)	E	DW
KS	Kaikoura (Sth)	1/83	57	108.3(1.7)	E	DW
K	Kakanui Point	8/82	54	120.4(2.4)	E	DW
KL	Karori Light	7/82,10/89	286	126.3(0.9)	M	R,SW,DW
KO	Cape Koamaru	12/81	60	120.7(1.2)	E	DW
L	Laura's Leg	9/89	69	110.8(2.3)	S	R,SW
M	Moeraki	5/82	56	110.3(0.9)	E	DW
N	Nicholson Bay	9/89	98	138.7(1.7)	S	R,SW
NP	New Plymouth	4/82	57	70.3(0.9)	S	DW
NU	The Nuggets	5/82	52	112.0(1.6)	E	DW
O	Oamaru	8/82	38	126.9(1.4)	M	
PH	Palmer Head	3/83	56	120.3(1.3)	E	DW
PE	Perano Head	10/89	57	109.4(1.8)	E	
RI	Rangitoto Is.	3/83	56	116.7(1.7)	M	DW
RP	Robertson Point	10/89	53	109.4(1.9)	E	R,SW
R	Ruapuke Is.	7/82	39	143.9(1.4)	E	DW
RU	Cape Runaway	12/80	63	116.0(1.0)	E	DW
RO	Rollers Beach	9/89	95	122.7(1.2)	M	R,SW
SA	Saddle Point (Nth)	9/89	90	111.0(1.4)	M	R,SW
P	Sandy Point	3/82	49	139.8(2.0)	E	DW
SE	South Easy Harbour	9/89	93	143.7(1.3)	M	R,SW
SN	Staircase (Nth)	10/89	63	120.5(3.0)	E	R,SW
SS	Staircase (Sth)	10/89	65	124.0(1.8)	E	R,SW
SH	Steep Head	9/89	78	114.6(2.2)	M	R,SW
S	Stony Creek	3/82	55	112.9(1.5)	M	DW
T	Te Kakako Is	10/89	50	119.4(1.8)	M	R,SW
TN	The Neck	9/89	60	122.8(1.8)	S	R,SW,DW
TL	Three leg woodhen	9/89	100	136.4(1.4)	S	R,SW
TI	Tinui Island	10/89	64	109.1(1.9)	M	R,SW
TP	Tongue Pt.	11/82	60	115.4(2.3)	E	DW
TC	Tory Channel	11/82	59	110.2(1.9)	M	DW
TB	Tupari Bay	9/89	66	138.9(1.0)	M	R,SW
TU	Cape Turikirae	2/82	58	142.9(1.4)	E	DW
WK	Waikawa	12/81	50	114.1(1.5)	S	
W	Waituna (Nth)	9/89	91	133.1(1.8)	E	R,SW
WS	Waituna (Sth)	9/89	132	145.4(1.3)	E	R,SW
WN	Waitui Bay (Nth)	9/89	54	125.9(1.5)	M	R,SW
WB	Waitui Bay (Sth)	10/89	46	126.0(1.1)	M	R,SW
WC	West of Cave Point	10/89	84	125.4(1.1)	M	R,SW
WR	Ruggedy (West)	9/89	91	124.3(1.6)	E	R,SW
X	Christmas Village	1/83	100	118.9(1.5)	M	R,SW,DW

For comparison among localities, exposure was subjectively assessed according to a three point scale: exposed i.e. localities are exposed to frequent heavy seas; moderate, i.e. localities are exposed to occasional heavy seas; and sheltered, i.e. localities are rarely exposed to heavy seas (Table 1).

At each locality, research divers collected all *H. iris* seen until a sample of at least 40 individuals was taken. Only emergent, probably mature, individuals were collected, as immature *H. iris* are generally cryptic (McShane 1995). Total weight, shell weight, foot weight (pedal sole minus viscera), shell length, shell width and shell height were examined, but at some localities, not all of these parameters were measured (Table 1).

The length and width of each shell was measured to the nearest millimetre with vernier calipers. Shell height was measured with an apparatus which measured the the distance between the ventral plane of the shell and the highest part of the shell (Newman 1968; McShane et al. 1988). Shell length, width and height are referred to here as length, width and height, respectively. Total weight was recorded to the nearest gram after removal of epizoic matter, and the foot was weighed after dissection from the shell and viscera. The dry weights of the foot and shell were measured to the nearest 0.1 gram after drying to constant weight at 100°C. The sex of each animal was recorded whenever possible.

For comparison of morphometric parameters of *H. iris* between localities where more than 40 specimens were collected (Table 1), a random subsample of 40 was used to conform to a balanced analysis of variance (ANOVA). Regression analyses with length as the independent variable were done. The relationship between weight (W) and length (L) was assumed to be:

$$W = aL^b$$

Weight and length were therefore converted to natural logarithms so that regression analysis could be used to estimate the constants *a* and *b*.

For comparison of morphometric relationships between localities, parameters covarying with length were tested for homogeneity of slopes. Pairwise comparisons of slopes after ANOVA were done using the minimum significant difference (at $P = 0.05$) established by the Tukey-Kramer method (Sokal & Rohlf 1981, p508). Populations of similar mean length were also compared directly with analyses of variance (ANOVA) after homogeneity of variances was tested with Cochran's test. If necessary, data were transformed (ln x+1). Pairwise comparisons of means were done after ANOVA with SNK tests (Underwood 1981).

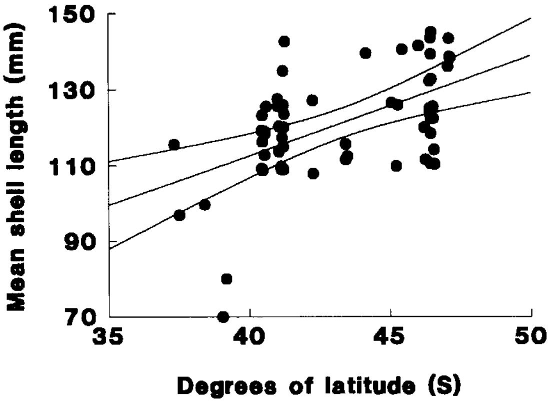

Fig. 2 Variation in mean shell length of *Haliotis iris* with latitude. Standard errors for mean values are within the widths of the symbol. 95% confidence intervals are shown about the regression line.

RESULTS

There were significant differences in mean length among localities ($F_{60,2379} = 61.8$, $P < 0.001$, Table 1). Even neighboring localities differed in mean length (Waituna Nth < Waituna Sth and Ruggedy west < Ruggedy east, by SNK tests $P < 0.05$) but other neighboring localities had similar mean lengths (e.g., Staircase Nth = Staircase Sth, Waitui Bay Nth = Waitui Bay Sth). There was no significant difference in the mean length of *H. iris* sampled from Karori Light between sampling periods (1982 vs 1989; $F_{1,285} = 5.1$, $P < 0.001$).

About 28% of the variation in mean length of *H. iris* between localities could be explained by latitude (Fig. 2) but the relative exposure was also a significant source of variation in mean length ($F_{2,4015} = 4.0$, $P < 0.05$, Fig. 3). All parameters that covaried with length (width, height, and weight) showed similar differences among localities.

The relationships of width and height with length differed among localities (least squares slopes compared: localities × width, $F_{30,2244} = 5.9$, $P < 0.001$; locality × height, $F_{30,2289} = 5.5$, $P < 0.001$). Although statistically significant, the differences between localities for width covarying with length were not large relative to differences in the relationship of height with length (Mean-Square

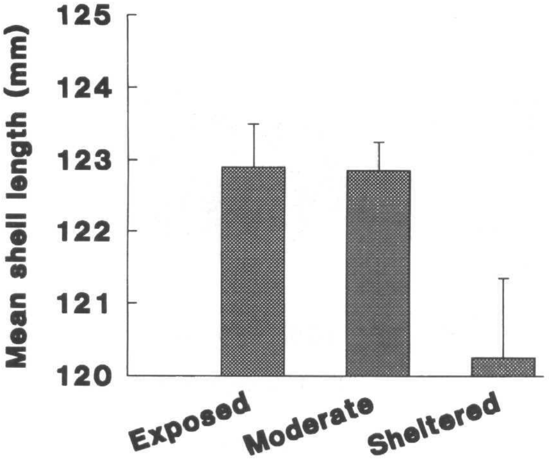

Fig. 3 Variation in the shell length of *Haliotis iris* with relative exposure (see text for details). Data are means with s.e.

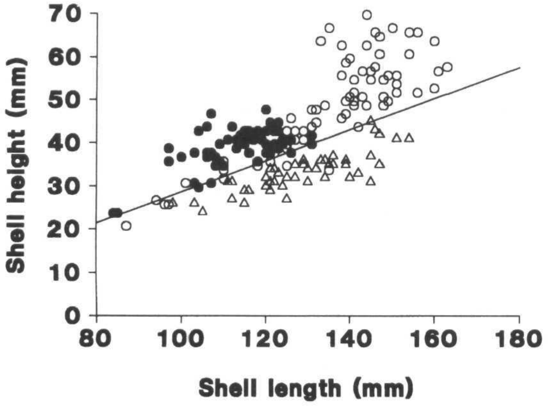

Fig. 4 Relationship of shell height with shell length of *H. iris*. Least squares regression is shown for pooled data from all localities. Localities with uneven distribution of residuals about the regression are shown: Stony Creek ((●), Sandy Point (o) and Cape Jackson ((△). Skewed residual variation also occurred for Waituna (Nth), Billhook Bay and Bushby Bay but, for clarity, these localities are not shown.

(popn) = 512.3 (height vs length); 102.0 (width vs length). These differences in the morphometric relationships for *H. iris* from different localities were evident from the residual variation of mean width or height vs mean length for individual localities (Figs. 4, 5). Localities with highly skewed

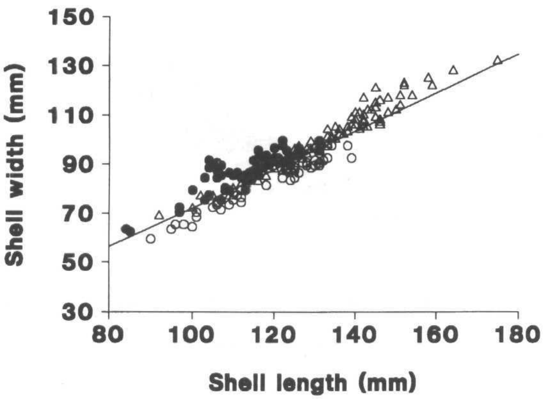

Fig. 5 Relationship of shell width with shell length of *H. iris*. Least squares regression is shown for pooled data from all localities. Localities with uneven distribution of residuals about the regression are shown: Stony Creek ((●),Waituna (Nth) ((△), and Te Kakako (o). Skewed residual variation also occurred for Oamaru, Saddle Point (Nth), Billhook Bay and Bushby Bay but, for clarity, these localities are not shown.

residual variation from the mean height/length relationship included Billhook Bay, Stony Creek, Sandy Point, Cape Jackson, Waituna Nth and Bushby Bay (Fig. 4). Localities with high residual variation from the mean width/length relationship included Te Kakako Island, Waituna Nth, Saddle Point (Nth), Stony Creek and Oamaru (Fig. 5). The other localities examined had an even distribution of residuals for the regression of height or width versus length.

Comparison of mean heights for localities with similar mean lengths (about 110 mm) revealed that *H. iris* from Billhook Bay had significantly smaller heights than the other localities (Tinui Island, Robertson Point, Laura's Leg, Saddle Point (Nth), Clay Point and Steep Head) (by ANOVA and SNK test, $F_{6,\,343} = 2.66$, $P < 0.05$). All other localities with similar mean lengths had similar mean heights (by ANOVA, $P > 0.05$) except for those of about 135 mm mean length. ANOVA and SNK tests revealed that *H. iris* from Waituna (Nth) had greater mean height than Three Leg Woodhen ($F_{4,245} = 7.82$, $P < 0.001$); SNK tests revealed that the other localities, East Ruggedy, Nicholson Bay and Tupari Bay had similar but intermediate mean heights.

On a local scale, *Haliotis iris* from Waituna (Nth) were significantly higher and wider than those individuals of similar length from a

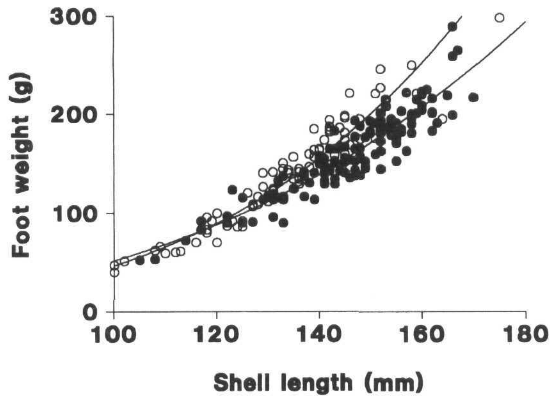

Fig. 6 Relationship of foot weight (FW) to shell length (L) for neighboring localities at Waituna. Data are shown for Waituna (Nth) (o) and Waituna (Sth) ((●). Regressions of $FW = aL^b$ are shown in each case.

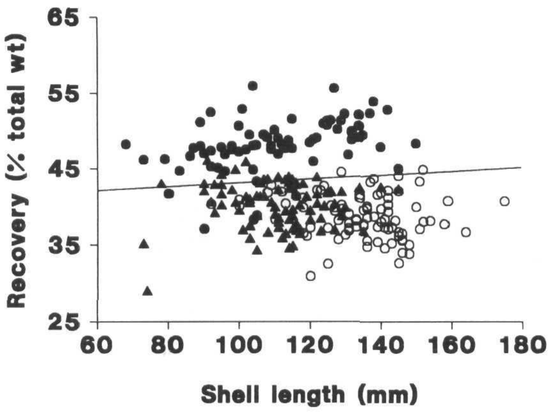

Fig. 7 Variation in recovery (foot weight as a percent of total weight) for *H. iris*. Least squares regression is shown for pooled data (all localities). Localities with uneven distribution of residuals about the regression are shown: Laura's Leg ((●), Waituna (Nth) (o), and Saddle Point (Nth) ((▲).

neighboring locality, Waituna (Sth). These localities had *H. iris* which varied in recovery (proportion of foot weight relative to total weight): *H. iris* from Waituna (Nth) had lower recovery than those from Waituna (Sth) (Fig. 6), mainly because individuals from Waituna (Nth) had a significantly greater shell weight for a given length than *H. iris* from Waituna (Sth)(by ANCOVA, $P < 0.01$).

For localities with *H. iris* of similar mean length, mean widths were similar (some differences were detected with ANOVA for localities of about 110 mm mean length, but could not be discriminated by SNK tests).

Recovery varied from 0.394 ± 0.001 (Waituna Nth) to 0.487 ± 0.004 (Laura's Leg) but varied independently of sex. Means for recovery varied with shell length (Fig. 7) and between localities (F popn{length} = 26.9, $P < 0.001$). However, SNK tests failed to show significant differences between localities except for Laura's Leg which had *H. iris* of greater mean foot weight than the other localities ($P < 0.05$). The observed differences in recovery can be explained by differences in the mean shell weight (expressed as a proportion of total weight: Laura's Leg 0.329 ± 0.005; Waituna (Nth) 0.400 ± 0.005), but these differences were not significant except for Laura's Leg which had *H. iris* of a lower mean shell weight than the other localities.

The recovery depended on shell weight ($P < 0.001$), but shell weight overall explained only 3.4% of the variation in recovery (n = 2530, r = 0.19). Further variation (2.5%) can be attributed to locality.

The relationship of dry weight with length varied among the 26 localities examined (slopes of log dry weight vs log length were heterogeneous, $P < 0.001$). This was true even for neighboring localities (Cape Young north vs south, localities × ln length, $F_{1,100} = 4.43$, $P < 0.05$). Slopes ranged from 2.92 ± 0.32 (Cape Young (Nth)) to 4.10 ± 0.22 (Sandy Point). Analyses of covariance were therefore not used for dry weight data. Localities contributing to the heterogeneity in the relationship of dry weight with length were Sandy Point, Rangitoto Island, and Moeraki (Fig. 8).

DISCUSSION

In testing assertions by commercial fishers that morphometric variation of *Haliotis iris* occurs between localities, our results showed significant variation in mean shell height, shell width and foot weight. However, the variation observed was mainly due to differences in mean length among localities. Such regional variation in mean size is characteristic of abalone (e.g., Newman 1968; Shepherd & Hearn 1983; Sloan & Breen 1988; McShane et al. 1988, 1994). Even so, additional

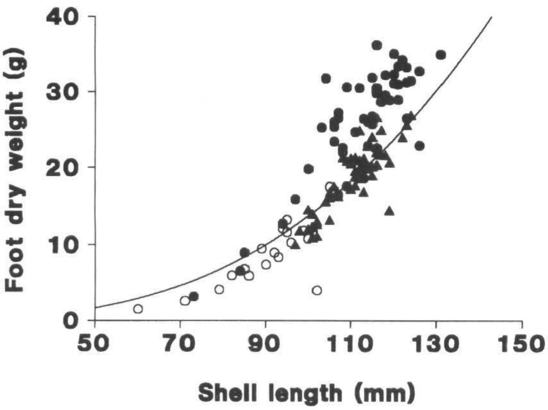

Fig. 8 Variation in dry weight of the foot with the shell length of *H. iris*. Least squares regression is shown for pooled data (all localities). Localities with uneven distribution of residuals about the regression are shown: Stony Creek ((●), Rangitoto Island (o), and Moeraki ((▲).

variation in the relative shell dimensions and weight occurred independently of the shell length among localities of *H. iris*.

Factors operating over large spatial scales, such as latitude and relative wave exposure were significant sources of variation in the mean length of *H. iris*. However, the largest differences occurred over much smaller distances, such as the neighboring localities at Stewart Island. The high residual variation shown for all morphometric parameters within localities is further evidence of small scale variation. This is not surprising, *H. iris* prefer shallow habitats (Sainsbury 1982), and factors which influence growth and morphometrics such as water movement, availability of food and shelter (Shepherd 1973; Shepherd & Hearn 1983; McShane et al. 1988; Day & Fleming 1992; Tissot 1992) will vary over small distances according to topography and depth (Schiel 1993).

In general, the morphometric variation (independent of shell length) among localities of *H. iris*, although statistically significant, was not large. Yet the localities examined spanned more than 10 degrees of latitude, with exposure to summer surface sea temperature maxima differing by about 10°C. Water temperature can affect the growth rate and the mean size of animals from any locality (Atkinson 1994) and can explain the differences in mean length observed among localities of *H. iris*. (Sloan & Breen 1988; Day & Fleming 1992).

In general, our results did not support the suggestion that localities with *H. iris* of small mean length had shells that were higher or wider than those from other localities. However, one sheltered locality, Laura's Leg, had individuals of small mean length but high mean foot weight. Although individuals from Waituna (Nth) were significantly higher and wider than those of greater mean length from a neighboring locality, Waituna (Sth), *H. iris* from Waituna (Nth) had significantly lower mean foot weight than those from Waituna (Sth.). Individuals from Stony Creek were higher and wider than those from other localities but did not show any abnormal deviation in recovery. In contrast, in studies of *H. midae*, Newman (1968) found that recovery varied with shell height. Abalone from slow growing localities can be higher and heavier per unit length than individuals from fast growing localities (Breen & Adkins (1982) for *H. kamschatkana*). We have insufficient information on the growth rate of *H. iris* to test hypotheses of growth-dependent morphometrics. Nonetheless, the variation in the relative weight of *H. iris* (range of 10 g for 100 mm shell length) was small in comparison to that shown for *H. kamschatkana* from different localities (range of 50 g for 100 mm shell length, Breen & Adkins 1982).

In providing these descriptions of morphometric relationships of *H. iris*, we did not consider temporal changes that have been shown to be important in causing seasonal variation in weight yield of other species of abalone (e.g., *H. cracherodii*, Webber 1970; *H. tuberculata*, Hayashi 1983; *H. rubra*, McShane et al. 1988). The dry weight of the foot of *H. iris* varied among localities but the variation was of small magnitude (< 10% of mean values).

Our results indicate that accurate predictions of width ($W = 0.773L$, $r^2 = 0.94$), height ($H = 0.356L$, $r^2 = 0.73$), foot weight ($FW\ g = 7.28 \times 10^{-4} L^{2.47}$, $r^2 = 0.71$), and total weight ($TW\ g = 2.15 \times 10^{-3} L^{2.418}$, $r^2 = 0.72$) can confidently be made for *H. iris*. The recovery (about 42% of the total weight) is similar to that of other species of abalone (McShane et al. 1988; Sloan & Breen 1988). We conclude that the morphometric variation in parameters other than shell length is insufficient to encourage the development of alternative management strategies by shell width rather than shell length.

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