

Relationship between Allometric Growth, with Respect to Shell Height, and Habitats for Two Patellid Limpets, *Nacella (Patinigera) macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holten, 1802)

by

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Abstract. The relationship between allometric growth of the shell (with respect to height:length) and environmental influences of water turbulence and desiccation were examined in two patellid limpet species, *Nacella (Patinigera) macquariensis* Finlay, 1927, and *Cellana tramoserica* (Holten, 1802), from two widely different climatic regimes. The allometric intensity of increase of shell height in relation to length and increases in the relative shell heights (comparisons of height:length ratios in different allometric groupings) were found to be correlated with increasing water turbulence, especially in *N. (P.) macquariensis*. This contrasted with suggestions that the major environmental influence on the height of limpet shells is from desiccation. The results supported an existing hypothesis that the height:length ratio of the shells of limpets is influenced by the frequency with which a limpet is obliged to adhere strongly to the substrate. Other possible influences on the allometric growth, with respect to shell height, are discussed. Different shell forms in predation middens of Dominican gulls (*Larus dominicanus* Lichtenstein) were used to interpret the selection of limpets by the gulls.

INTRODUCTION

RELATIONSHIPS BETWEEN THE shell heights of intertidal limpets and their environment have been examined in a number of studies (RUSSELL, 1907; ORTON, 1932; EBLING *et al.*, 1962; BALAPARAMESWARA RAO & GANAPATI, 1971; WALKER, 1972; VERMEIJ, 1973, 1980; BRANCH, 1975; BANNISTER, 1975; WARBURTON, 1976; BRANCH & MARSH, 1978; LOWELL, 1984). In order to determine whether the shells of some limpets are relatively higher or lower than others, some form of standardization of the height is necessary. Usually shell height has been standardized against shell length, although other ratios have been employed, for example, shell height:geometrical mean of the major and minor diameters of the shell base (VERMEIJ, 1973). Early studies simply compared ratios of shell height:shell length over a range of lengths (RUSSELL, 1907; ORTON, 1932).

Limpets usually exhibit allometric growth, resulting in changing proportions between shell height and length; the height:length ratio increases with increasing size, al-

though an isometric pattern with increasing size has been recorded in some species (BRANCH, 1975). Consequently, in later studies, more complete comparisons between groups of limpets employ comparisons between regressions of shell height versus shell length over a range of limpet sizes.

Different methods, objectives, and descriptive terms used in previous studies can lead to confusion in comparisons across them. Consequently, I will use the following terms: (1) *allometric intensity* of shell-height increase—the continuum of shell height regressed against shell length for a range of lengths (*i.e.*, the slope of a regression equation), (2) *relative shell height*—height:length proportions of shells in comparisons between allometric continuums, (3) *height ratio* of shells—height:length proportions of shells where allometry has not been considered.

In previous studies, comparisons between limpets using the above criteria have attributed larger height ratios and relative shell heights to stress from desiccation (ORTON, 1932; DAVIES, 1969; BALAPARAMESWARA RAO & GANAPATI, 1971; VERMEIJ, 1973, 1978; BANNISTER, 1975; BRANCH, 1975), increased water turbulence (EBLING *et*

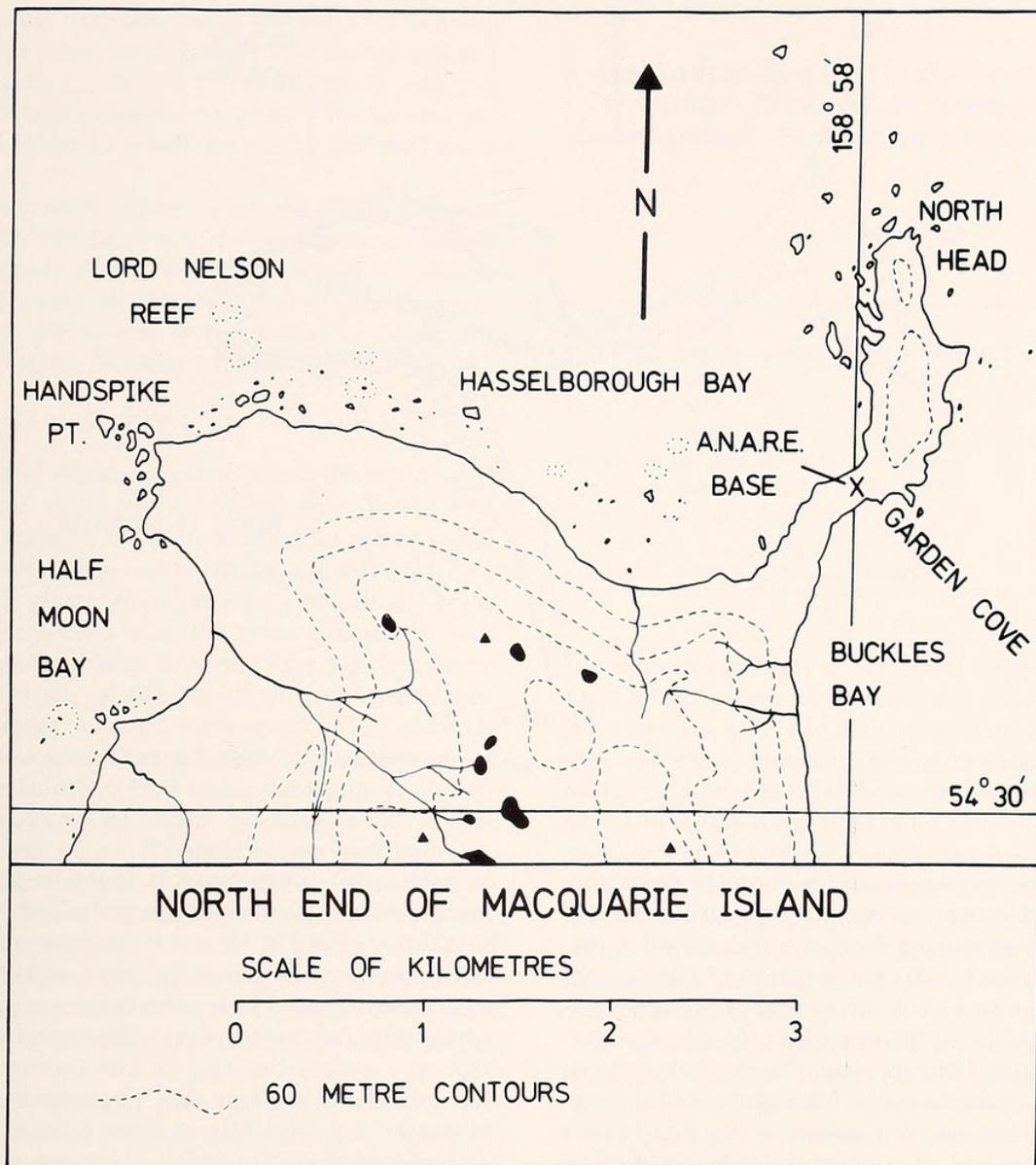


Figure 1

North end of Macquarie Island. Collections of *Nacella (P.) macquariensis* were made in the vicinity of the ANARE base.

al., 1962; WALKER, 1972), and slower growth rates (VERMEIJ, 1980).

The aim of the present study was to investigate the associations of desiccation and water turbulence with the allometric growth of shell height of limpets from two widely separated localities in different climatic regimes. On sub-Antarctic Macquarie Island (54°38'S, 158°53'E) *Nacella (Patinigera) macquariensis* Finlay, 1927, was the study animal. Variations in the height ratios of shells of *N. (P.) macquariensis* were noted in previous collections examined by DELL (1964). The other species, *Cellana tramoserica* (Holten, 1802), was collected at Arrawarra, northern New South Wales (30°3'S, 153°12'E).

The heavy predation on *Nacella (P.) macquariensis* by

Dominican gulls (*Larus dominicanus* Lichtenstein) and the resultant availability of shells from gull middens, nest sites, and roosts gave rise to a connected, subsidiary aim to the study. If limpet shell shape proved to be correlated with habitat, then shell characters of a predation sample could indicate that part of the limpet population particularly susceptible to predation by the gulls.

SITES, MATERIALS, AND METHODS

Specimens of *Nacella (P.) macquariensis* were collected from six habitats in the region of the isthmus at the northern end of Macquarie Island (Figure 1): (1) rock surfaces in the eulittoral zone on the west coast exposed to the

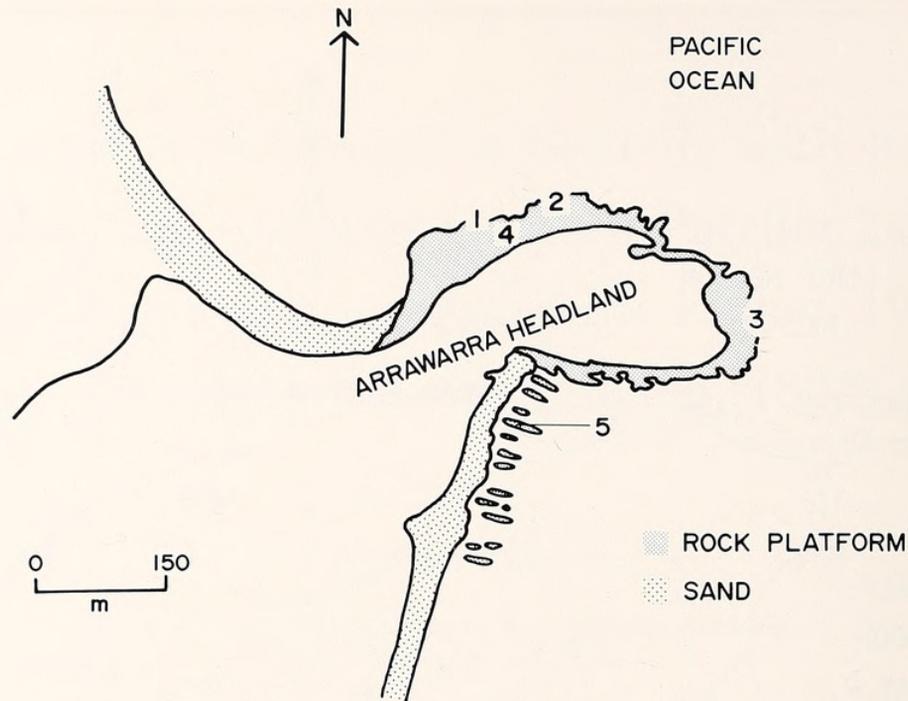


Figure 2

Arrawarra Headland. The numbers on the figure correspond to the collection localities for *Cellana tramoserica*, outlined in the text.

open sea; (2) rock surfaces in the eulittoral zone on the east coast exposed to the open sea; (3) rock surfaces at the top of the sublittoral zone on the east coast exposed to the open sea; (4) deep rock pools in the eulittoral zone on the east coast; (5) high rock pools situated approximately 3.5 m above the waterline on the east coast; (6) at a depth of 6 m on the east coast ("diving station"). Shells of limpets preyed upon by Dominican gulls (*Larus dominicanus*) were collected and divided into two categories: (a) shells from Dominican gull feeding sites where the gulls pecked out the flesh and left the shell behind and (b) shells from nest sites and roosting areas where the gulls regurgitated the remains, having swallowed the limpets whole. Two feeding sites were sampled in the "pecked out" predation category.

Limpets in habitats (1) and (2) were exposed to a high degree of turbulence from breaking waves and were subjected to potential desiccation only during emersion in windy and/or sunny conditions, the latter condition being very rare on Macquarie Island (the prevailing winds are from the west and, consequently, wave action is usually more severe on the west coast; however, for some months the turbulence on the east coast, estimated by a combination of wave height and wave frequency, is comparable to that of the west coast [SIMPSON, 1976]). Limpets in habitat (3) were also exposed to a high degree of turbulence both from breaking waves and water flow; stress from desiccation was virtually nonexistent. Habitats (4), (5), and (6) presented no desiccation problems for limpets.

At habitat (6) water currents could be strong, but the forces would be much less than that of wave action in the littoral zone. Habitat (4) was subjected to very little water movement, from flow into the pools at high water. The pools from habitat (5) represented a rare situation and, hence, provided limited data. These pools were located high on a steeply sloping face that received wave splash during moderate to heavy seas. The steep aspect prevented fouling by deposited kelp or from seals, as was the case for high rock pools (in which no limpets were found) on more gently sloping rock platforms. The effect of turbulence in these latter two habitats was negligible.

The headland from where *Cellana tramoserica* was collected is shown in Figure 2. The prevailing seas are from the southeast, causing the eastern and southern side of the headland to be exposed to heavier wave action than the northern side. There were five collection sites: (1) the bottom of the range of the limpets (lower part of the eulittoral zone) on the northern shore of the headland in an area partly sheltered by a fringing reef; (2) rock surfaces exposed to heavy wave action in the barnacle zone (*Tessieropora rosea* [Krauss]) on the northern shores of the headland; (3) rock surfaces in the barnacle (*T. rosea*) zone on the eastern point of the headland; (4) a gently sloping rock platform in the upper eulittoral zone on the northern shore of the headland; and (5) rock outcrops in the upper eulittoral zone on the beach immediately south of the headland. The above habitats were classed as follows: (1) little influence from either desiccation or wave action, (2)

moderate influence from desiccation and subjected to heavy wave action, (3) moderate influence from desiccation and heavier wave action than for (2), (4) frequently subjected to air exposure and desiccation with only moderate wave action, and (5) subjected to both desiccation and very heavy wave action.

If limpets regularly moved from one habitat type to another, possible effects on shell form from particular environmental factors of any one habitat would be masked. Consequently, specimens of both *Nacella (P.) macquariensis* and *Cellana tramoserica* were marked to record the amount of movement between habitats.

RESULTS

The movement of marked specimens in different habitats over a one year study period showed that *Nacella (P.) macquariensis* tends to live in fixed areas. In the eulittoral zone, individuals mostly remained in a small area (<1 m²); movements greater than 3 m were rare, usually being horizontal movements within the zone. Limpets in rock pools in the eulittoral zone showed a very high constancy of location. Limpets at the top of the sublittoral zone showed the greatest amount of movement. They were always in the same general area, but individuals sometimes moved into the eulittoral zone above the region of *Durvillea antarctica* (Chamisso) Hariot holdfasts, which represents a sublittoral fringe. Transect counts over one year showed seasonal variations in numbers, but there were no seasonal migrations of populations between eulittoral and sublittoral zones, such as shown by WALKER (1972) for the Antarctic limpet *Nacella (Patinigera) concinna* (Strebels) where migration down the shore was correlated with low temperatures and the formation of an ice film on the shore.

Specimens of *Nacella (P.) macquariensis* at diving stations were not marked for studies of movement. However, the heavy and normal encrustation of coralline algae on specimens indicated that they had been continuously submerged at the depth of collection. Limpets from the top of the sublittoral zone had a sparser covering of coralline algae, and limpets from the eulittoral zone either had no, a poor, or (when in shallow pools) a gnarled growth of coralline algae on the shells. The only coralline algal cover on the shells, similar to that for diving station limpets, was found on specimens from deep pools in the lower littoral and sublittoral zones. Encrustations of the tubeworm *Spirorbis aggregatus* Caullery & Mesnil were frequently but not always found on limpets in eulittoral rock pools, and provided some indication of type of habitat. The constancy of location exhibited by *N. (P.) macquariensis* was sufficient to ensure that the samples represented populations from the selected sites.

For *Cellana tramoserica*, marked specimens were found to remain within the habitat areas selected over a period of nine months. In addition, the encrustations of living algae and living barnacles indicated that the limpets were

Table 1

Regression analysis of shell height (y) on shell length (x) for *Nacella (P.) macquariensis* from all categories.

Category	Size range (lengths, mm)	n	Regression equation (log y = log a + b log x)	
			log a	b
High rock pools	17.9-47.2	16	-0.771	1.063
Predation (regurgitated)	16.2-47.5	126	-0.720	1.128
Diving station	18.0-45.1	131	-0.807	1.166
Deep rock pools	29.1-42.0	34	-0.933	1.194
Eulittoral, east coast	20.2-49.0	102	-0.974	1.322
Predation (pecked out #1)	18.5-44.8	58	-1.039	1.336
Predation (pecked out #2)	25.7-49.5	95	-1.039	1.371
Top of sublittoral, east coast	22.6-42.1	41	-1.369	1.541
Eulittoral, west coast	20.6-60.7	66	-1.430	1.583

long-term inhabitants of the lower littoral and the barnacle zones, respectively. Conversely, limpets from the upper eulittoral zone had no encrustations, indicating that at least they had not recently come from the other two habitats. In studies of *C. tramoserica* near Sydney over a period of 20 months, FLETCHER (1984) also found that marked limpets had not moved between four shore subdivisions: high, mid, and low intertidal and subtidal (there were no subtidal populations at the headland in the present study). As well, MACKAY & UNDERWOOD (1977) have shown that a proportion of *C. tramoserica* populations exhibits homing behavior.

Two models of the allometric relationship between shell height (y) and shell length (x) were fitted for all sets of data using the Minitab statistical package (RYAN *et al.*, 1981): (1) a linear regression model ($y = a + bx$) and (2) the linear regression form ($\log_{10}y = \log_{10}a + b \log_{10}x$) of the power relationship $y = ax^b$. For both species and all sites, the power relationship proved to be a better fit to the data, where b = slope and $\log_{10}a$ = intercept for each line.

For each species, particular models, ranging from a single regression for all data to separate regressions for each habitat/category, were fitted using the generalized linear interactive model computer program, GLIM (BAKER & NELDER, 1978). Mean deviances were compared to test the fit of particular models. Variance ratios were determined as (difference of deviances)/(mean deviance of the fuller model) on $m:(n - m - 1)$ degrees of freedom, with m being the number of coefficients (slopes and intercepts) in the model and n being the total number of data considered.

For the nine sites from which *Nacella (P.) macquariensis* was collected, the relationships between shell height and shell length are given by the regressions in Table 1. To determine the most appropriate combination of regressions, the following models were tested:

Table 2

Combination of categories of *Nacella (P.) macquariensis* into separate groups on the basis of slope.

Group	Intercepts (log a)	Common slope (b)
(1) High rock pools	-0.885	1.139
Deep rock pools	-0.848	
Diving station	-0.767	
Predation (regurgitated)	-0.737	
(2) Predation (pecked out #1 + pecked out #2)	-1.049	1.344
Eulittoral, east coast	-1.008	
(3) Eulittoral, west coast + top of sublittoral, east coast	-1.430	1.582

- Model I: 1 slope, 1 intercept (a single regression);
- Model II: 1 slope, 9 intercepts;
- Model III: 9 slopes, 1 intercept;
- Model IV: 3 slopes, 9 intercepts;
- Model V: 9 slopes, 9 intercepts.

Model II was found to be a more appropriate model than Model I ($F = 49.33$ on 8,659 d.f.; $P < 0.001$). Model IV was found to be more appropriate than both Model II ($F = 24.05$ on 2,657 d.f.; $P < 0.001$) and Model III ($F = 21.40$ on 2,657 d.f.; $P < 0.001$). The fullest model, Model V, was found not to be more appropriate than Model IV ($F = 0.20$ on 6,651 d.f.; $P > 0.50$).

Model IV separated out three groups on the basis of significantly different slopes. Within two of these groups two data sets could be combined in terms of no significant difference between intercepts, resulting in Model VI (3 slopes and 7 intercepts). Model VI was tested against Model IV and it was found that the fuller model, Model IV, did not give a significant reduction in mean deviance and was, therefore, not more appropriate than Model VI ($F = 0.20$ on 2,257 d.f.; $P > 0.50$). Hence, the most appropriate combination of regressions was that represented by Model VI, and this is shown in Table 2 and Figure 3.

The total variability in shell height attributable to the dependence of shell height on shell length in a particular model is given by the unbiased estimator $\hat{\rho}^2$, the adjusted coefficient of variation (ZAR, 1974). For Model VI, $\hat{\rho}^2$ was 0.88.

In group 1 (Table 2, Figure 3), all the limpets came from continuously submersed habitats except for one set—the predation (regurgitated) category. Group 2 included limpets from the east coast—from eulittoral rock surfaces and from both the predation (pecked out) categories. Group 3 was made up of limpets from the eulittoral zone on the west coast and from the top of the sublittoral zone on the east coast. In group 2, the height:length proportions of the shells at both the predation (pecked out) sites were

not significantly different in terms of either slope or intercept and, hence, could be combined. The shells of limpets from the top of the sublittoral zone on the east coast were not significantly different, in terms of either slope or intercept, from those of the west coast eulittoral zone. These were combined in group 3.

For the five sites from which *Cellana tramoserica* was collected, the relationships between shell height and shell length are given in Table 3. In determining the most appropriate combinations of linear regressions in this case, the following models were tested:

- Model I: 1 slope, 1 intercept;
- Model II: 1 slope, 5 intercepts;
- Model III: 5 slopes, 1 intercept;
- Model IV: 2 slopes, 5 intercepts;
- Model V: 5 slopes, 5 intercepts.

Model II was found to be more appropriate than Model I ($F = 57.46$ on 4,390 d.f.; $P < 0.001$). Model IV was found to be more appropriate than both Model II ($F = 10.97$ on 1,389 d.f.; $P < 0.01$) and Model III ($F = 10.86$ on 1,389 d.f.; $P < 0.01$). The fullest model, Model V, was

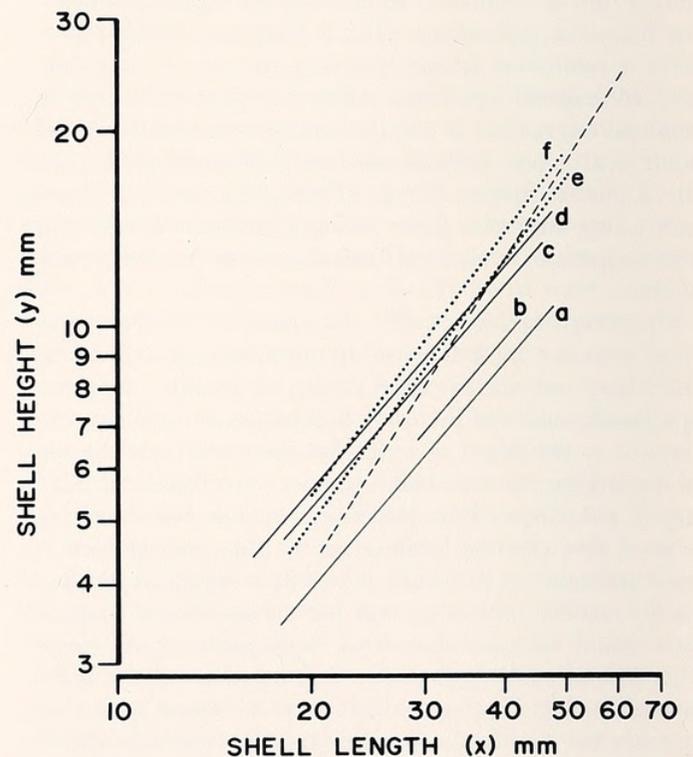


Figure 3

Regressions of height on length of categories within groups of *Nacella (P.) macquariensis*, plotted on log axes. Solid lines = group 1 where a = "high rock pools," b = "deep rock pools," c = "diving station," and d = "predation regurgitated." Dotted lines = group 2 where e = "predation (pecked out #1 + pecked out #2)" and f = "eulittoral, east coast." Dashed line = group 3 ("eulittoral, west coast" + "top of sublittoral, east coast").

Table 3

Regression analysis of shell height (y) on shell length (x) for *Cellana tramoserica* from all categories.

Category	Size range (lengths, mm)	n	Regression equation (log y = log a + b log x)	
			log a	b
Upper eulittoral zone	15.6–42.4	81	–1.110	1.429
Barnacle zone, northern side	17.2–42.0	93	–1.101	1.435
Lower eulittoral zone	15.7–44.6	98	–1.181	1.435
Barnacle zone, eastern side	16.1–38.4	71	–1.106	1.443
Upper eulittoral, southern rocks	15.0–52.7	53	–1.377	1.615

found not to be more appropriate than Model IV ($F = 0.05$ on 3,386 d.f.; $P > 0.50$).

Model IV separated out two groups on the basis of significantly different slopes. Within one of these groups two data sets could be combined in terms of no significant difference between intercepts, resulting in Model VI (2 slopes, 4 intercepts). Model VI was tested against Model IV, and it was found that the fuller model, Model IV, did not give a significant reduction in mean deviance and was, therefore, not more appropriate than Model VI ($F = 0.25$ on 4,386 d.f.; $P > 0.50$). The most appropriate combination of regressions is that represented by Model VI and shown in Table 4 and Figure 4. For Model VI, the adjusted coefficient of variation, $\hat{\rho}^2$, was 0.93.

Group 1 (Table 4, Figure 4) included limpets from both the upper and lower eulittoral zone on the northern side of the headland, and the limpets from the barnacle zone areas. Both sets of limpets from the two barnacle-zone areas could be combined, as there was no significant difference between the intercepts. The limpets comprising group 2 (upper eulittoral, southern rocks) were significantly different from the others on the basis of slope of the regression.

There are two components to the allometric growth of the limpet shells of *Nacella (P.) macquariensis* and *Cellana tramoserica*, as shown by the regressions of height on length—slopes and intercepts. The slopes show the rate of increase of height with increasing length. When the slopes are significantly different, there is a difference in allometric intensity of height increase in relation to length during growth. If possible influence from some environmental factor during the growth of the limpet shell through adulthood is being examined, then consideration of slopes is the prime concern. Within a group having nonsignificantly different slopes, significantly different intercepts indicate differences in relative shell heights; that is, limpets from different sites had different “starts” to their relative shell heights, and maintained the same allometric inten-

sity of height increase throughout growth. Comparing relative shell heights between groups with significantly different slopes will give different answers depending on the selected value of length. This emphasizes the futility of comparing shell heights among groups of limpets for some standard length of shell, if allometric growth is not considered.

DISCUSSION

The climate of Macquarie Island (with precipitation occurring over approximately 330 days in each year, a mean relative humidity of 88%, and persistent cloud cover—see SIMPSON [1976]) poses very few desiccation problems for intertidal limpets. Desiccation stress would be encountered by intertidal animals only on the occasional sunny day in summer with calm seas. COURTNEY (1972) identified wind as a desiccating factor for intertidal mollusks, but the persistent precipitation, high humidity, and heavy seas would greatly reduce any desiccating effect of the wind on Macquarie Island shores. Thus, with minimal influence from desiccation, the habitats selected on Macquarie Island shores effectively represent a gradation of water turbulence.

A number of authors have suggested that water turbulence has either a negligible or no effect on increasing the height of limpet shells (ORTON, 1932; BALAPARAMESWARA RAO & GANAPATI, 1971; BERRY & RUDGE, 1973; BRANCH & MARSH, 1978). Further, it could be argued from the equations of drag forces on limpet shell shape (WARBURTON, 1976; BRANCH & MARSH, 1978) that a lower-spined shell should reduce drag and, hence, be more favorable for an environment with a high degree of water movement. If the above were generally true, shells of *Nacella (P.) macquariensis* could be expected to show either no difference in allometric growth with respect to shell height or even a decrease in height across a gradient of increasing water turbulence.

For *Nacella (P.) macquariensis* there were three groupings on the basis of allometric intensity of height increase. These groups had significantly different slopes to their combined regressions, in ascending order from group 1

Table 4

Combination of categories of *Cellana tramoserica* into separate groups on the basis of slope.

Group	Intercepts (log a)	Common slope (b)
(1) Lower eulittoral zone	–1.178	
Upper eulittoral zone	–1.116	1.433
Barnacle zone (northern + eastern sides)	–1.095	
(2) Upper eulittoral, southern rocks	–1.377	1.615

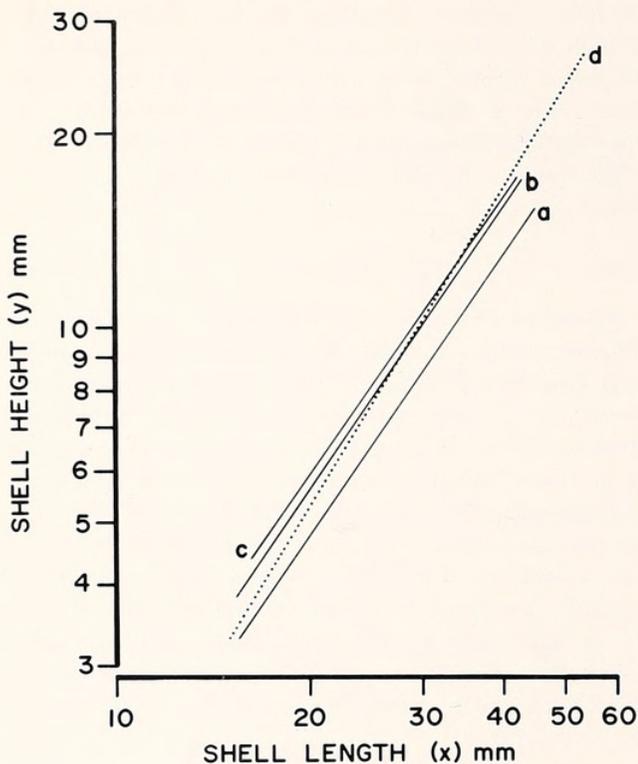


Figure 4

Regressions of height on length of categories within groups of *Cellana tramoserica*, plotted on log axes. Solid lines = group 1 where a = "lower eulittoral zone," b = "upper eulittoral zone," and c = "barnacle zone (northern and eastern sides)." Dotted lines (d) = group 2 ("upper eulittoral, southern rocks").

through group 3 (Table 2, Figure 3). This order matched the increasing degree of water turbulence impinging on the habitat categories within the groups, with the apparent exception of the "top of the sublittoral, east coast" category which was combined with the category subjected to the heaviest wave action of all ("eulittoral, west coast") in group 3. However, the longer period of lower intensity wave action at the top of the sublittoral zone on the east coast may have the same degree of impact as a shorter period of higher intensity wave action in the eulittoral zone on the west coast.

For *Cellana tramoserica*, collections from four sites were combined on the basis of no significant difference between slopes of their regressions (group 1). Thus, in group 1 the differential effects from either wave action or desiccation could not be identified as influencing the allometric intensity of height increase. Group 1 limpets had a significantly lower slope for the combined regression than that of group 2 (Table 4, Figure 4). The limpets in group 2 were subject to stress from both heavy wave action and desiccation. Further, parts of the rocks in the group 2 habitat were occasionally covered by shifting sands that could encroach on the areas occupied by the limpets, thus presenting a further stress.

For both species, there were significant differences in intercepts among categories comprising some of the groups. That is, although some categories showed the same allometric intensity of shell height increase, there were significant differences in relative shell heights for limpets from different habitats. In group 1 for *Nacella (P.) macquariensis*, limpets in high rock pools had the lowest relative shell height followed by, in ascending order, limpets from deep rock pools, diving station, and predation (regurgitated). The increase in relative shell height of the three habitat categories followed a sequence of increasing water turbulence. For *Cellana tramoserica*, the significantly different intercepts for limpet populations in group 1 followed a sequence that could be associated with both increasing desiccation stress and water turbulence, with the relatively highest shells occurring in the area of greatest wave action.

Thus, for *Nacella (P.) macquariensis* the allometric intensity of shell-height increase and the increase in relative shell heights were clearly correlated with increasing water turbulence. For *Cellana tramoserica* allometric intensity of shell-height increase was greater only where wave action was constant and very strong. Desiccation stress was not correlated with allometric intensity of shell-height increase. Both increasing water turbulence and desiccation stress were correlated with an increase in relative shell heights, with evidence of the most effect being associated with increasing water turbulence.

The data for both species showed that, if there is a significantly greater slope for a group, then members of that group will eventually reach a greater relative shell height (Figures 3, 4). What is curious is that in those groups that have the significantly greatest slopes, the smaller (by length) shells should have such low relative shell heights, *i.e.*, group 3 for *Nacella (P.) macquariensis* (Figure 3) and group 2 for *Cellana tramoserica* (Figure 4). Perhaps the smaller limpets in such areas of greater environmental stress occupy some form of protected microhabitat and move out onto more open rock surfaces as they grow.

A number of factors have been previously suggested as influencing the shell height of limpets and these require examination here.

Variation in shell-height ratios of *Patella vulgata* Linnaeus on English shores formed the basis of the earliest studies on this topic in intertidal limpets. RUSSELL (1907) observed that specimens from localities that were exposed to heavy wave action were lower-spired than those from sheltered localities. ORTON (1932) found that the shells of adult limpets living on the upper shore were taller than those of individuals near the low water level or in rock pools. Orton correlated higher shell types with desiccation. He suggested that limpets inhabiting higher levels would hold their shells closer to the substrate to prevent drying out. The consequently strong grip would pull in the mantle margin, the site of secretion of new shell. Hence, a smaller peripheral increment of growth would be made

and continued growth would result in a steeper shell. ORTON (1932) further suggested that wave action would have a negligible influence on shell shape of *P. vulgata*, although he recognized that wave action would also cause a limpet to adhere more firmly. MOORE (1934) found that specimens of *P. vulgata*, with large height ratios, developed a shelf of flatter shell growth when transferred from the shore into a fish-hatching pond. Moore attributed this to the removal of desiccation stress, but the experimental design could not entirely discount decrease in water turbulence as an effect. Curiously, nearly all the "shelved" limpets returned to the initial angle of shell growth while still in the pond.

EBLING *et al.* (1962), working on *Patella* species in Ireland, found significantly greater relative shell heights for *P. aspersa* Röding where they were permanently submerged and subjected to strong currents. Ebling *et al.* suggested that water turbulence could also cause greater relative shell heights by obliging the limpets to adhere firmly. In a study on the tropical limpet *Cellana radiata radiata* (Born), taken from different habitats and zonal levels, BALAPARAMESWARA RAO & GANAPATI (1971) concluded that desiccation was more important than wave action in influencing shell characters.

From shell measurements of a number of limpet species, VERMEIJ (1973, 1978) found that the shell-height ratio increased in an upshore direction and suggested that this was an adaptation to desiccation stress. VERMEIJ (1973) argued that a taller shell would increase the water reservoir and decrease the region of water loss, *i.e.*, the area and perimeter of the base. BANNISTER (1975) recorded greater desiccation tolerance in the taller-shelled *Patella lusitanica* (Gmelin) of the upper eulittoral zone to that of the lower-shelled *Patella caerulea* (Linnaeus) of the lower eulittoral zone of Mediterranean shores. In comparisons across seven species of *Patella* on South African shores, BRANCH (1975) found a strong correlation between zonal position on the shore and tolerance to water loss; however, there was no close correlation between zonation and relative shell heights.

In a review of limpet biology, BRANCH (1981) noted that many authors have recorded greater height ratios and relative shell heights in drier habitats for a number of species. Also, BRANCH (1981) observed that an intraspecific increase in relative shell height usually occurs in limpets from higher on the shore but the same pattern is not always true when different species are compared. Results from interspecific comparisons will always embody wide genotypic options for morphological strategies. Consequently, it is perhaps not surprising that general hypotheses will be confounded when pooling results from a number of species.

On the coasts of North America, there have been a number of studies on the possible effects of desiccation on the morphology of acmaeid limpets. On the east coast, WALLACE (1972) found that, in *Acmaea testudinalis* (Müller), tolerance of desiccation was related to size and that

limpets in a habitat with increased desiccation stress (intertidal rock face versus tide pools and subtidal area) did not have greater shell height ratios. On the west coast, WOLCOTT (1973) reported no correlation between either size or shell shape and desiccation rates or tolerances in interspecific comparisons among five species of limpets (although no quantitative details of shell shape were presented). Wolcott determined that the ability to form a mucus sheet between the shell margin and the substrate was the most important adaptation to desiccation. Aware that interspecific comparisons may confuse the issue, LOWELL (1984) undertook intraspecific investigations for four species of acmaeid limpets. Lowell determined that increasing size significantly reduced water loss but that variation in shell shape (as measured by volume/circumference) had no effect on water loss. Lowell suggested that variation in shell shape might be partially or primarily due to factors other than resistance to desiccation.

In Britain, DAVIES (1969) recorded a greater desiccation tolerance in specimens of *Patella vulgata* from high levels of the shore compared to that of specimens from low levels. While Davies speculated that this may be partly attributable to shell shape, his results primarily showed that desiccation tolerance was inversely related to body size.

As shown here for *Nacella (P.) macquariensis*, one factor associated with allometric intensity of shell-height increase and greater relative shell heights is an increase in water turbulence. As previously mentioned, some authors have discounted wave action as having an influence on the shell height of limpets. However, EBLING *et al.* (1962) and WALKER (1972) found associations between increased water turbulence and relative shell height. DURRANT (1975) found significantly different height:width ratios in the freshwater limpet *Ancylus fluviatilis* Müller from river and lake populations, where there was no exposure to desiccation. The river populations (with greater water flow) had taller shells. BRANCH (1981) has noted the contrasting arguments for influences on shell height in areas of strong water movement: (a) flatter shells are adaptive where wave action is strong because they cause less drag, versus (b) strong water currents cause a limpet to clamp down tightly and thereby deposit shell in a tall conical form—in the manner as postulated by ORTON (1932). Further, BRANCH (1975) and BRANCH & MARSH (1978) have reasoned that higher-domed shells will allow greater muscle development and insertion that, in turn, would strengthen tenacity.

GRENON & WALKER (1981) found no significant differences between the tenacity of low and high shore level *Patella vulgata* on both exposed and sheltered shores. Thus, the taller-shelled populations (from the upper shore) did not display a greater tenacity. BRANCH & MARSH (1978) reported that relative shell height was not correlated with tenacity in six *Patella* species. However, in the two species with strong allometric intensity of height increase against length (*P. argenvillei* Krauss and *P. granatina* Linnaeus),

relative shell height was significantly correlated with tenacity per unit area of the foot.

VERMEIJ (1978) noted that a pattern in allometric growth intensity of mollusks for different parts of the shore may be a function of an adaptive trend or a by-product of variation in growth rate. VERMEIJ (1980) went on to state "Various lines of evidence have led me to believe that many instances of gradual changes in shell allometry (especially doming) are geometrically tied to growth rate." In experimental manipulations of *Collisella* limpets in California, HAVEN (1973) noted that rapid growth in *C. scabra* resulted in new shell being deposited at a flatter angle. Growth rates of intertidal limpets have often been found to decline in an upshore direction (BRANCH, 1974; LEWIS & BOWMAN, 1975; PHILLIPS, 1981) and this corresponds with the previously mentioned trend for relative shell heights of limpets to increase in an upshore direction. Presumably, the slower growth rates are related to lesser abundance of food or time available for grazing. LEWIS & BOWMAN (1975) showed that *Patella vulgata* had different growth rates in different habitats. Growth rates were higher at low tidal levels compared to high tidal levels, and superimposed on this was the biological influence of growth rates being lower in sites inhabited by barnacles and/or mussels, whose presence reduced the surface area that could be easily grazed. In five of these habitats, Lewis & Bowman recorded a matching sequence between decrease in growth rate and increasing allometric intensity of shell-height increase. This presents strong evidence for shell allometry being a function of growth rate. THOMPSON (1980) also found growth rates of *P. vulgata* to be highest on bare rock and lowest on areas with a dense population of barnacles.

Of particular relevance to the present study, FLETCHER (1984) found that a mid-tidal population of *Cellana tramoserica* had a lower growth rate, a higher density, and a significantly greater allometric intensity of shell-height increase than that for a subtidal population. However, the correlation with growth rate did not hold true for all of the study sites investigated by Fletcher (high, mid-, and low intertidal and subtidal). The order of allometric intensity of shell height increase across the four populations was "high" = "mid-" > "low" > "sub," while that for the growth rates was "mid-" < "high" = "low" < "sub." A reverse trend of higher growth rates at upper levels has been found where densities of limpets at higher levels are lower, which would result in more food being available (SUTHERLAND, 1970; CREESE, 1980). Unfortunately, there are no corresponding data on shell heights in these cases.

Water turbulence and desiccation could be acting with different emphases upon intertidal limpets in different climatic regions and different parts of the shore. The data from the present study and the mixed findings from other works show that no one environmental factor has a universal relationship with allometric growth of shell height. If, as ORTON (1932) suggests, an obligation to adhere

firmly increases the steepness of shell formation, then any factor (*e.g.*, water turbulence or desiccation) that causes a limpet to clamp down frequently enough will have such an ultimate effect. Although alternative explanations have been put forward in seeking relationships between relative shell height and tenacity (BRANCH, 1975; BRANCH & MARSH, 1978), Orton's argument would apply, whatever the tenacity capability of a species. The assigning of adaptive trends to allometric growth in limpets relies almost entirely on correlative evidence. Indeed, correlations between such features as allometric intensity of shell-height increase and degree of stress from water turbulence and desiccation may simply be because such stresses reduce growth rates rather than because of any adaptive advantage. Experimental proof for time-related features such as shell growth is difficult to obtain. Field manipulation of animals, for example, between habitats of differing intensities of desiccation and water turbulence would also have to account for possible differences in food availability, grazing capabilities, or densities, which, in turn, would affect growth rates. A useful addition to the present data would be to apply an immediate aging technique (*i.e.*, from shell growth lines) to limpets from several habitats, and this will form the subject of further studies.

The predation categories of *Nacella (P.) macquariensis* present an interesting result, subsidiary to the central aim of the study. The similarity in the shells of limpets from the two predation (pecked out) sites on the east coast showed that gulls feeding in this way were selectively taking limpets with respect to shell shape in terms of height: length proportion. The similarity in slope to that for limpets in the eulittoral zone indicated that the gulls were taking the limpets from that region, but they were selecting limpets that had lower relative shell heights, as indicated by the significantly different lower intercept for the predation category. Limpets taken by gulls and later regurgitated were combined with limpets from pools and the diving station into the one group, on the basis of slope. This implies that the gulls took limpets that they could swallow from pools. As they floated among intertidal rocks during calm seas, Dominican gulls were observed diving their heads under water to pick off limpets. A similar situation was reported for Dominican gulls feeding on *Nacella (P.) delesserti* (Philippi) on Marion Island by BLANKLEY (1981). However, in regard to rock pools at Macquarie Island, Dominican gulls were observed taking limpets only from the edges of pools. Also, it is highly unlikely that pool populations could supply the number of limpets swallowed whole by gulls—not only in the area covered in this study but also for the whole island. It is more likely that the inclusion of the predation (regurgitated) category in group 1 is an artifact from the gulls' selection of limpets. That is, their selection of smaller limpets for swallowing (the majority of the limpets in this category were in the lower end of the length range) biased the result, placing these limpets in with group 1.

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