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Shell Shape Variation of Tropical Limpet *Cellana testudinaria* (Class: Gastropoda, Family: Patellidae) Living on the Rocky Shore in Relation to Their Zonal Distribution

Abraham Seumel Khouw
Faculty of Fisheries and Marine Sciences, Pattimura University, Ambon – Indonesia,
Phone: 0911-351727, HP: 081343044295, E-mail: askhouw@web.de

Abstrak

Pengujian terhadap dimensi tubuh dari limpet C. testudinaria mengindikasikan bahwa sampel yang dikoleksi dari tiga tingkatan zona pantai adalah berbeda nyata dalam panjang, lebar, tinggi, jarak antara puncak cangkang dari anterior, dan jarak antara puncak cangkang dari posterior. Keseluruhan hubungan antara panjang cangkang terhadap dimensi tubuh lainnya adalah alometrik negatif. Hubungan antara panjang cangkang dengan jarak apex-anterior dan apex-posterior mengindikasikan bahwa bentuk cangkang untuk limpet berukuran panjang 18 mm yang hidup pada zona bawah cenderung agak ke belakang sedangkan ukuran yang lebih besar cenderung agak ke depan. Studi morfometri pada rasio panjang cangkang terhadap lebar dan tinggi cangkang serta rasio keliling terhadap volume cangkang menunjukkan hasil yang sama dengan analisa pada dimensi tubuh yang mengindikasikan bahwa limpet yang menempati zona bawah adalah lebih lebar, tinggi dan lebih lancip dari limpet yang menempati zona atas dan tengah dari pantai.

Kata kunci: *Limpet, Cellana testudinaria, dimensi tubuh, zona pantai, allometri.*

Abstract

An examination of the body dimensions of C. testudinaria indicated that specimens collected from the three different shore levels were significantly different in shell length (L), width (B), height (H), distance from apex to anterior margin (AA), and distance from apex to posterior margin (AP). The overall relationships between body dimensions and shell length were negatively allometric. The relationships of shell length to AA and AP indicated that the apex of limpets living at the low shore level are shifted backward in individuals less than 18 mm in shell length, while it is shifted forward in larger limpets. Morphometric studies on the ratio of shell length to shell width and shell height and the ratio of shell circumference to volume provided similar results as the analyses of the body dimensions, indicating that limpets inhabiting the low shore level were broader and taller and had more acute, backward shifted apex than those living at the high and middle shore levels.

Key words: *Limpet, Cellana testudinaria, body dimensions, shore levels, allometric.*

Introduction

Many limpets are characteristic inhabitants of the intertidal zone of wave-tide-swept rocky shores, and thus occupy one of the most physically stressful environments on earth. This extended distribution subjects them to an alternating wetting and drying due to the wave exposure and the tidal cycle. At low tide, those limpets are exposed to terrestrial conditions and the concomitant heat and desiccation stresses, while at high tide as waves crash on the shore, water impose large hydrodynamic forces (Hobday, 1995; Denny & Blanchette, 2000), and can push and pull a limpet and threaten to lift it from the rock surface. Not surprisingly biologist and ecologists have speculated that these challenges must have been important in the evolution of these creatures. Surely, they argued, natural selection must have favoured – at least in part – limpets with shells shaped to resist the assault of the deep. Bannister (1975) said that the general structure, decoration and sculpture of a gastropod shell are not entirely unrelated to the environment in which the gastropod lives.

A variety of functional interpretations and evolutionary scenario have been assigned to the differences among limpet shell shape (for reviews, see Branch, 1981; Vermeij, 1993). These include the possibility of the shell shape in response to thermal and desiccation stress in the intertidal zone (Denny,

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2000), predation on limpets by crabs (Lowell, 1985; 1986) and birds (Hahn & Denny, 1988), and foraging and territorial behaviour by the limpets itself (Stimson, 1970). An analysis of the shell form in several families of intertidal limpets has revealed the existence of morphological gradients (Russell, 1909; Orton, 1928; Das & Seshappa, 1947; Balaparameswara Rao & Ganapati, 1971; Breen, 1972; Bannister, 1975; see review by Branch, 1981; Lowell, 1984; Hobday, 1995). These gradients are also evident from temperate to tropical latitudes, and may be modified or overridden by exposure to wave action and other factors (Vermeij, 1973). To verify the relationship between dryness of the environment and height of the shells by transplanting the animals from dry rocks to pools, Moore (1934) found that the shells developed shelves and new growth resulted in a flattening of the shell. Although Orton (1928) found that wave action plays only a minor and secondary role in controlling shell height in limpets, he correlated differences in shell height with differences in the degree of exposure to desiccation. Since then, several authors have shown this trend for taller shells to be linked with drier habitats in many species (Balaparameswara Rao & Ganapati, 1971; Bannister, 1975). However, measurements made by Denny (2000) suggest that the evolved shape of limpet shells has not been "fine-tuned" to the flow environment. In addition, several studies have addressed the role of shell shape in determining the hydrodynamic force to which a limpet will be subjected (Warburton, 1976; Branch & Marsh, 1978; Denny, 1985; 1995; Denny & Blanchette, 2000).

Authors (Russell, 1909; Orton, 1928; Moore, 1934; Das & Seshappa, 1947; Evans, 1953; Southward & Orton, 1954; Ebling et al., 1962) have already drawn attention to the variations in the shape of *Patella vulgata* shells induced by different ecological factors. They had a well marked that inter-specific increase in relative shell height with increasing shore levels. *P. vulgata* from high levels have taller and more domed shell, because in dry desiccation habitats the limpet has to clamp down more tightly, pulling in its mantle so that if the mantle glands deposit the shell while in this position, the shell circumference will be reduced and the shell taller (Russell, 1909; Orton, 1933). Among tropical limpet *Cellana radiata* (Balaparameswara Rao & Ganapati, 1971) and *Cellana toreuma* (Ino, 1935), relative acute height and degree of development of external sculpture generally increase inter-specifically, and often intra-specifically, from low to high shore levels. Vermeij (1993) pointed out that because of the coiling characteristic of most gastropod shells, which is greatly reduced in limpets, results in a conical shell with a large aperture (Denny, 2000). Therefore, some limpets' shells are very high-acute, with a height-to-length ratio that exceeds of 0.2 – 0.6 and mean ratio of 0.53 (Denny & Blanchete, 2000). Furthermore, it is also widely acknowledged that limpets "clamp" or "hunker down" when disturbed in an effort to prevent dislodgement (McAlister & Fisher, 1968; Cook et al., 1969), although no attempt has been done to quantify the clamping response (Ellem et al., 2002). Shell clamping brings the lower rim of the conical shell of a limpet into direct contact with the substratum.

Materials and Methods

Study site

The study was carried out on the intertidal rocky shore of Ohoiwait (latitude $5^0 45'15"$ S, longitude $132^0 57'20"$ E), Big Kai Island, Southeast Mollucas, Indonesia (Fig. 1) from October 2001 to September 2002. The intertidal region investigated is about 0.25 km^2 (1 km long and 0.25 km wide). Thus, it is small enough that atmospheric conditions may be assumed, for most purposes, to be uniform over the whole area. The shore consisted of shingles, pebbles, medium and big boulders. The physical conditions in the tidal zones are quite different; the higher shore is wetted almost exclusively by tidal sea level rise, but the lower shore receives considerable wave action.

Sampling

Fieldwork was undertaken at the intertidal rocky shore of Ohoiwait between October 2001 and September 2002. Three different tide levels (from the extreme high water spring tide EHWST to the extreme low water spring tide ELWST) parallel to the shoreline were defined in relation to heights above the mean low water level predicted by local tide tables (Dinas Hidro-Oseanografi TNI AL, 2001; 2002). These zones were identified using staffs and a spirit-level during calm days. In the following, they are high (1 – 1.5 m), middle (0.5 – 1 m) and low (0 – 0.5 m) shore levels. The width of each shore level ranges from 80 m to 85 m.

As pure random sampling was not feasible due to pronounced environmental heterogeneity within the shore levels, a systematic sampling design was chosen. At each shore level, 6 sampling squares (1 m^2), 25 m apart, were installed along a line parallel to the shoreline. Hence, a total of 18 permanent quadrates were placed between the EHWST and the water edge, the first square being randomly defined. Heights of the quadrates above ELWST and the distances between quadrates were calculated from the profiles obtained.

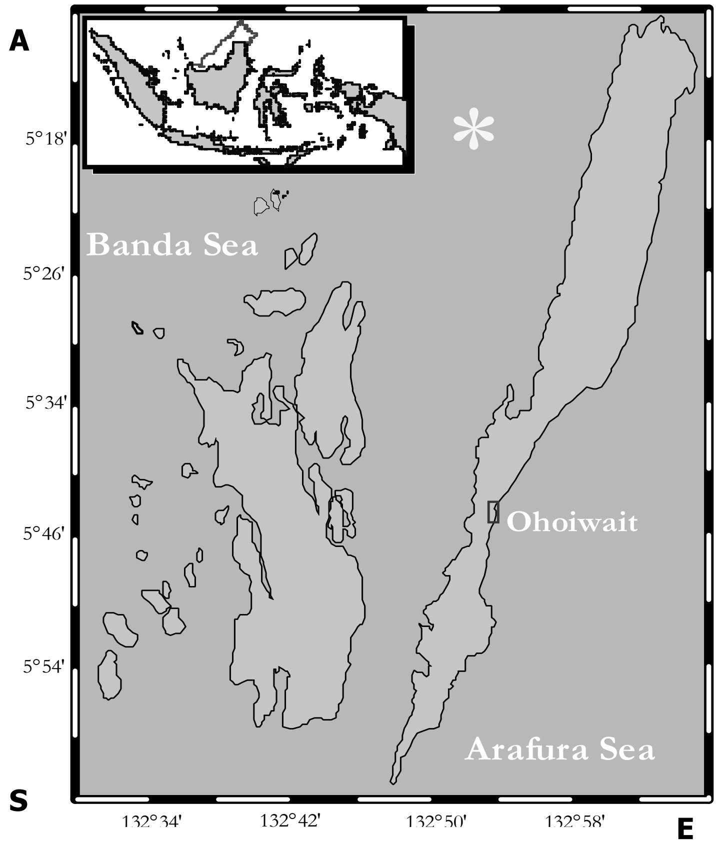

Figure 1. Map of study site of Ohoiwait located at the Big Kai Island (A) and profile of the rocky shore intertidal (B).

In each quadrate, specimens were collected by hand picking or dug out with a spade, and the shells were cleaned from the material covered. Sampled specimens were counted and measured for their shell dimensions using vernier calliper to the nearest 0.1 mm, as this allowed limpets to be measured *in situ* on the shore. In some cases, the juvenile limpets could not be dug out because of their soft and brittle shell. Therefore, their shell was measured directly by placing the vernier calliper to the shell. After measurements, limpets were released back to their habitats.

Most of *C. testudinaria* live attached to the surface of the substratum, although some of them were also found hiding below the boulders, pebbles, and shingles. Rocks lying within the quadrates, which were movable, were turned over and removed down to bedrock, and the undersides of rocks were searched as far as possible, so that concealed limpets were included in the count. Loose small gravel, a habitat sometimes favoured by small individuals, was also carefully searched.

Shell measurements

Five main characteristics of the shell: length (L), width (W), height (H), distance from apex to anterior margin (AA) and distance from apex to posterior margin (AP) were measured using vernier calipers to the nearest 0.1 mm. The dimensions utilized in shell measurements are shown in Figure 2.

Data analyses

Length of the limpet shell was taken as the main parameter to study the variations of the other 5 variables of the body dimensions. Linear regression equations were calculated separately by the method of least square (Sokal and Rohlf, 1995), to examine the relationship between the width and length, the height and length, distance from the apex to the anterior margin and length, distance from the apex to the posterior margin and length. Regression lines were drawn separately for the above 4 relations at the three shore levels, and the mean values were plotted above them. Using the position of the regression lines, the body dimensions of limpets living at different shore levels were compared.

Multivariate analysis of variance MANOVA was applied to study interrelations between the 5 characteristics of the shell, and to determine if the

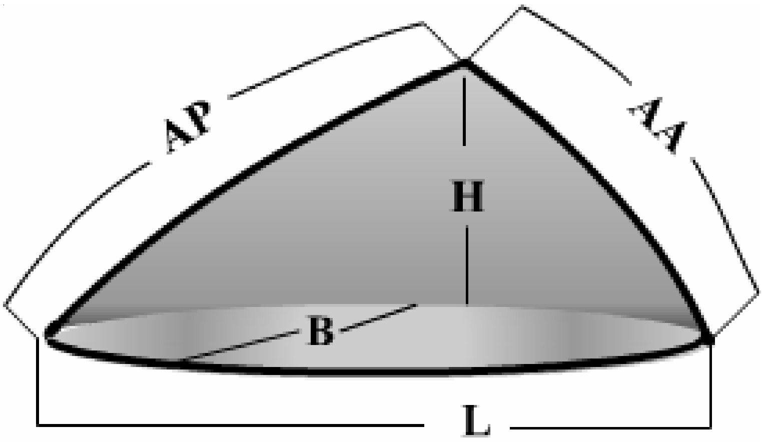

Figure 2. Dimensions utilized for shell measure-ments. AA-distance from apex to anterior margin; AP-distance from apex to posterior margin; H-height; B-width; L-length.

mean size differed in each shore levels. The Barlett's test of homogeneity of variances was used to test the differences of regression (Snedecor & Cochran, 1967), while the students' *t*-test was used to calculate the deviation of the shell allometry from the isometric *b*-value through the equation of $y = b\,x^{á}$ where *y* is body dimensions, *x* is shell length, *b* and á are constants, in which for any value of á different from 1, an increase of shell dimensions was considered allometrical.

The additional models of height-to-length (H/(L/2)) and height-to-width (H/(W/2)) ratios, and proportional location of shell apex (E = AA/(L/2)) formulated by Denny (2000), and the means of the ratios L/B, (L+W)/2, (L+W)/2H and BW/L^3 formulated by Bannister (1975), were calculated in each shore levels, since morphological gradient can best be described in terms of relative shell height over the geometrical mean of length and width of the base (Ward, 1967; Vermeij, 1973). The influence of changing shell shape can be quantified further by the function: $W = c\,L^{á}$ and $H = c\,L^{á}$ where W is shell width, H is shell height, L is shell length, c and á are constants. If á (the constant of allometry) = 1, then the two factors change proportionally, but á > 1 if the shell width or shell height increases faster than length during growth.

The allometric relationship between circumference (CF) and volume (V) of limpet shells was also calculated. The shell was treated as an elliptical cone, thus volume and circumference were estimated by the formula from Lowell (1984): $V = p.L.W.H / 12$ and $CF = 2p\,(L^2/8 + W^2/8)^{0.5}$ where V is volume, CF is circumference, L is shell length, W is shell width, and H is shell height. The allometric change in circumference relative to volume was determined by regressing natural logarithm (ln) *CF* against ln *V* using the major axis method. This method is preferred in morphological analyses when neither variable can be regarded as independent (Gould, 1966). Taking antilogarithms of the ln-ln linear functions yielded power functions of the form: $CF = b.V^{a}$ where b and a are constants. a is significantly < 0.33 using a Model II comparison (Clarke, 1980), indicating an average change in shape with increasing size; i.e. volume exhibits positive allometry relative to circumference because the shell becomes more domed as the limpet grows (Lowell, 1984). To separate the effects of shape from the effects of size, a measure of size should be independent from shape. This measure can be obtained by rearranging the power function to obtain $V^a/CF = 1/b$. 1/b is approximately equal to the allometric values of V^a/CF for limpets of all size within a species (Lowell, 1984). Individuals for which $V^a/CF > 1/b$ are more highly acute than average for the species, whereas those for which $V^a/CF < 1/b$ are flatter than average.

Results and Discussion

Body dimensions

An examination of 5 variables of body dimensions in the specimen of *C. testudinaria* collected at the three different shore levels and the result of an analysis using the analysis of variance (ANOVA) are summarized in Table 1 and are presented as an average of body dimensions in Figure 3.

The comparison of the overall body dimensions due to different shore levels show that limpets living at the low shore level are significantly longer, broader, and taller than those living at the high and middle shore levels (Fig. 3). Two-way without replication of ANOVA test on the body dimensions for the three shore levels shows highly significant differences between the shore levels (Table 1).

Table 1. The analysis of variance (ANOVA) on the shell dimensions of *Cellana testudinaria*. SS-Sum of Square; df-degrees of freedom; MS-Mean Square; P-Probability; ** highly significant; ns-not significant.

Source of Variation	SS	df	M S	F	P-value	F crit
Shore levels	151.97	2	75.98	22.62	0.05**	3.04
Body dimensions	9034.92	5	1806.98	537.95	0.05**	2.25
Interaction	43.99	10	4.39	1.30	0.05 *ns*	1.87
Within	665.07	198	3.35			
Total	9895.96	215				

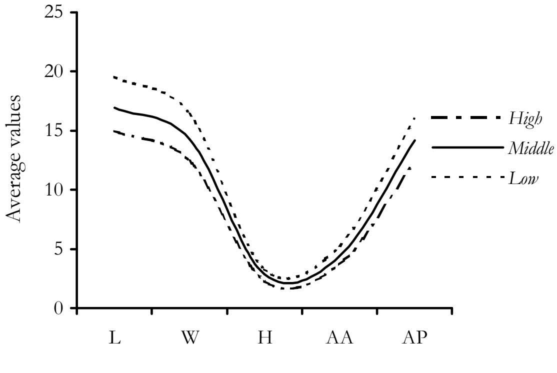

Figure 3. Average of body dimension for limpets of *Cellana testudinaria* living at the three different shore level. L-length; W-width; H-height; AA-apex to anterior; AP-apex to posterior.

Table 2. Test for deviation from isometry ($b = 1$) on the 95 % confidence limits of b together with the Bartlett's test of *Cellana testudinaria*. *df*-degrees of freedom; S^2-variance of samples; *-negatively allometric. $M = 2.3026*[[(Ó\ df * \ln(n\ df * S^2/n\ df)] - (n\ df * \ln S^2)]$. therefore $M_{AA} = 197.19$ and $M_{AP} = 101.07$

Apex to anterior margin with M = 197.19			
Shore levels	b at 95 %	t-test	P
High	± 0.0078	70	< 0.05*
Middle	± 0.0101	61	< 0.05*
Low	± 0.0304	16	< 0.05*
Apex to posterior margin with M=101.07			
High	± 0.0099	179	< 0.05*
Middle	± 0.0123	150	< 0.05*
Low	± 0.0368	51	< 0.05*

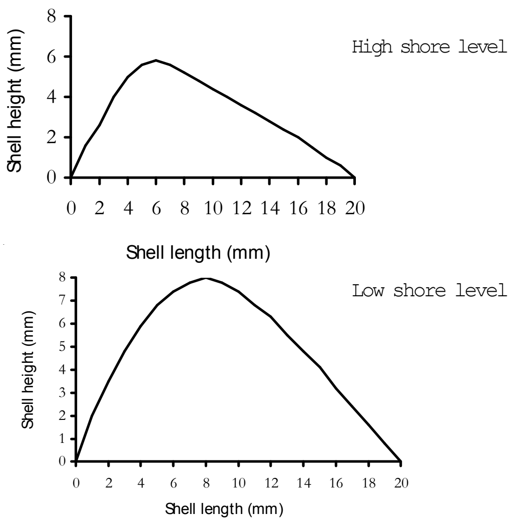

Figure 4. Limpet's shell shape inhabiting high and low shore levels

Position of the apex

t-test on the deviation of the shell allometry from isometric showed that the relationships between both variables for the three different shore levels were negatively allometric (Table 2), indicating that an increase in the distance from apex to anterior and posterior margins were slower than an increase in length when limpets grew in size. The Bartletts' tests clearly show that there is a high significant difference on the slopes of regression lines for the three different shore levels.

The above observations indicate that the apex of the shell is shifted more backwards in individual *C. testudinaria* of less than 18 mm in shell length living at the low shore level and more forward in limpets living at the high and the middle shore levels. However, when limpets grow bigger and the shell length increases longer than 18 mm, then the apex of those limpets living at the high shore level is shifted more backwards. A diagrammatic representation of the shape of the shell of the limpets inhabiting the high and low shore levels is shown in Figure 4.

The results of the present study have shown that the shell characteristics vary with the habitat of *C. testudinaria*. Two extreme forms have been described: high shells with a remarkable apex curvature, and flat shells only slightly curved. Those limpets inhabit the low shore level are generally larger in size (Fig. 3), with a high acute and with the apex of the shell shifted more towards to the posterior margin (Fig. 4).

Previous workers found that the average shell length of *Patella vulgata* (Brian & Owen, 1952), and

Table 3. Means of body dimensional ratios of *Cellana testudinaria* at the three shore levels.

Shell dimensional ratio	High shore level	Middle shore level	Low shore level	F
L/W	1.2164 ± 0.0791	1.2084 ± 0.0886	1.2141 ± 0.1424	*ns*
(L+W)/2	13.7053 ± 4.5620	15.6038 ± 5.3331	17.9591 ± 5.3273	P < 0.001
(L+W)/2H	6.8384 ± 2.3475	6.3019 ± 1.9177	5.9930 ± 1.5165	P < 0.001
H/(L/2)	0.2898 ± 0.0755	0.3163 ± 0.0975	0.3245 ± 0.0805	P < 0.001
H/(W/2)	0.3500 ± 0.0842	0.3774 ± 0.1001	0.3914 ± 0.0971	P < 0.001
E = AA/(L/2)	0.4936 ± 0.0815	0.5077 ± 0.0977	0.5471 ± 0.1426	P < 0.001

L : length (mm); *W* : width (mm); *H* : height (mm); *BW* : total body wet weight (mg); *AA* : apex to anterior (mm). *F*-Statistical significant differences between means (one way – ANOVA test); *ns*- not significant.

Table 4. Analysis of variance on the mean of the shell circumference (CF) and the shell volume (V) for the three shore levels during the study periods. *SS*-sum of squares; *df*-degrees of freedom; *MS*-mean square; *P*-probability.

Shore level	SS		df	MS		F		P	F crit
	CF	V		CF	V	CF	V		
Between Groups	630.2	89656.2	2	315.1	44828.1	6.16*	3.03 *ns*	0.005	3.28
Within Groups	1688.7	488056.6	33	51.2	14789.6				
Total	2318.9	577712.8	35						

Note: * significant.; *ns* not significant.

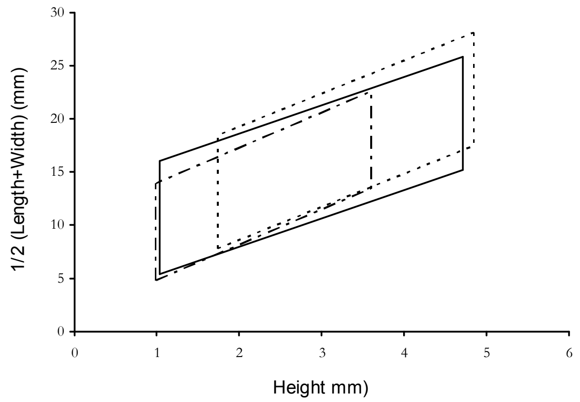

Figure 5. Statistical domain of regression (L+B)/2 on H in limpet shells of *Cellana testudinaria* living at high shore level (.—.), middle shore level (—), and low shore level (…). Slopes have been drawn to standard deviations of estimate on either side of regression line, and vertical boundaries to standard deviations on either side of mean height.

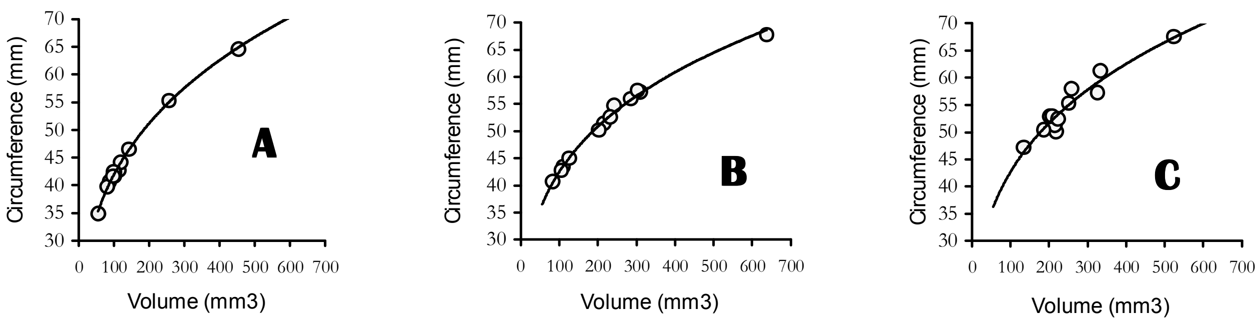

Figure 6. *Cellana testudinaria*. Monthly circumference (CF) of shell aperture versus monthly shell volume (V): curves drawn from power functions derived from reduced major axis regressions of ln CF against ln V; A, the high shore level, CF = 11.062$V^{0.2892}$, r = 0.99, n = 12; B, the middle shore level, CF = 12.929$V^{0.2585}$, r = 0.99, n = 12; C, the low shore level, CF = 12.013$V^{0.2754}$, r = 0.96, n = 12; r, correlation coefficient; n, sample size.

Lottia digitalis (Wootton, 1993) at lower shore level is greater than those limpets at higher levels. They attempted to explain that limpets live to the lower shore levels, which inhabit damp locations, reduce their activity of the shell muscle, and so the consequent absence of any constraint on the extension of the shell. Segal (1956) observed that shells of high intertidal *Acmaea limatula* have a smaller volume than shells of low intertidal individuals. Khouw (2002) independently reported that several species of limpets such as *Cellana radiata* and *Colisella striata* inhabiting the lower shore levels are generally larger in size, with a high acute and wide based shells. The similar patterns were also found for *Patella* living at low-level, in which *Patella oculus*, *Patella argenvillei*, and *Patella barbara*, have very tall shells (Branch, 1975). In contrast to the pattern found in this study, a greater shell of limpets in a high shore level than in a damp habitat has been found by Orton (1928) in *Patella vulgata*, by Sutherland (1970) in *Macclintockia scabra*, by Balaparameswara Rao & Ganapati (1971) in *Cellana radiata*, and by Bannister (1975) in *Patella lusitanica*. Davies (1969) has shown that in British and Mediterranean *Patella* species, the shell is tall and conical in upper shore species and progressively flatter in lower shore and subtidal species. Orton (1928) and Branch (1975) attributed the higher acute and narrow based shells at the limpets living at higher shore levels as the result of the attempt on the part of the limpets to contract the shell down more tightly to the substrate in order to avoid desiccation under exposed conditions. Whereas, several authors (Lowell, 1984; Denny & Blanchette, 2000) concluded that the flat shell of limpets is an adaptation to the lower shore levels due to the high degree of water turbulence. It is, therefore, usually thought that, in *Cellana*, as in other patelliform molluscs, the type with a high shell is found where the limpets are exposed to drought and slight water movements, whereas the flat varieties occur where there is a high degree humidity and water turbulence (Orton, 1933; Moore, 1934; Lowell, 1986; Denny, 2000; Denny & Blanchette, 2000).

The limpet shell measurements may also be used for interspecific differentiation. The ratio of the distance from the apex to the posterior margin (AP) to the distance from the apex to the anterior margin (AA) of the present specimen *C. testudinaria* were 3.32 for the high shore level, 3.24 for the middle shore level, and 3.02 for the low shore level with the mean of 3.19, which appeared higher than those reported by Saad (1997) for *Cellana eucosmia* (1.50), by Emam (1994) for *Cellana karachiensis* (1.21), and by Khouw (2002) for *Cellana radiata* (1.16) and *Colisella striata* (1.79). This indicates that the shell of *C. testudinaria* found in the present study is more acute than those reported by previous researchers. In general this ratio decreased slightly as the animal grew in size (Emam, 1994). Although the shell of limpets living at the low shore level are more shifted backwards than those living at the other shore levels, the overall pattern showed that it was more shifted forwards compared to the other species reported by Russell (1909) and Orton (1928) for *Patella vulgata*, by Balaparameswara Rao & Ganapati (1971) for *Cellana radiata*, by Emam (1994) for *Cellana karachiensis*, and by Saad (1997) for *Cellana eucosmia*.

Although shell morphometrics of *C. testudinaria* from the intertidal rocky shore are slightly different from those of *Cellana radiata* from India (Balaparameswara Rao & Ganapati, 1971) and from the Gulf of Agaba, *Cellana eucosmia* from the Gulf of Suez (Saad, 1997), patterns of the changes in the shell shape with growth are generally similar. The relationships of shell length to shell width, height, apex to anterior, and apex to posterior are linear, while the relationships of shell length to shell weight are curvilinear. Similar results were reported for *Cellana karachiensis* from the Arabian Gulf and Gulf of Oman (Emam, 1994), and for *Cellana radia* and *Colisella striata* from the intertidal of Ohoiwait (Khouw, 2002). The shell of *C. testudinaria* was proportional during growth as the relationships of length to width and height were isometric.

Changing in shell dimension

Means of the 6-ratios of the body dimensions and the significant differences among them (one-way ANOVA test) are given in Table 3. Ratio of L/W indicates that the shells are slightly broader in limpets living at the middle shore level than those at the other levels, although, one-way ANOVA test shows that there is no significant differences among shore levels. In addition, the other ratio of (L+W)/2 indicates that the "mean" of length and width is significantly higher in the shells of limpets living at the low shore level than the other levels. The result of ANOVA test also showed that there was highly significant difference among shore levels ($P < 0.001$). The ratio (L+W)/2H indicates that the shells of limpets living at the low shore level are higher than the others living at the high and the middle shore levels, since ANOVA test showed highly significant difference on that ratio among shore levels (Table 3). The mean ponderousness indices of BW/L^3 give further evidence of the significant difference in total body wet weight of limpets living at the three shore levels, since the mean ponderousness index of 0.1673 was observed for limpets at the high shore level to be differ significantly from the mean values of 0.1197 and 0.1179 of limpets at the middle and low shore levels ($P < 0.001$). The significantly lower ponderousness indices of limpets living at the middle and low levels seem to be a reflection of significantly greater length in these shells compared with those living at the high shore level (Fig. 3).

The models of H/(L/2), H/(W/2), and E = AA/(L/2) ratios developed by Denny (2000) show that there are also highly significant differences (one-way ANOVA test, $P < 0.001$) on the mean values of shell among shore levels. The á-values of the three ratios are higher for the limpets living at the low shore level than those at the other shore level, indicating that limpets living to the lower shore levels are taller, broader, and the apex of the shell are shifted more backwards (Fig. 4). In addition, the proportional location of the shell apex values (E-value) for limpets at the three different shore levels are less than 1, implies that the apex is upstream of the centre of the shell form (Denny, 2000).

An analysis on the relationships between shell width (W) and shell height (H) on shell length (L) using the function of changing shell shape, gives the mean constant of allometry á-values of less than 1 (á < 1) for the three shore levels, indicates that shell width or shell height changes improportionally to the shell length. Thus, an increase in both factors is slower than an increase in the shell length during growth.

The statistical domains of the regressions of (L+W)/2 on H in the limpets living at the three shore levels have been plotted in Fig. 5 to include 95 % (mean ± SD) of the sample populations in terms of (L+W)/2 and H values. The domains show some overlap: 67 % of the domain of the limpets at the high shore level is overlapped by that of limpets at low shore level, and almost the whole domain (98 %) by limpets at the middle level. Further, those limpets at the middle shore level approximately overlap 95 % of the domain of limpets at the low shore level.

The statistical domains as are shown in Fig. 5 relate to shell shape. If the differences in shell shape between the limpets live at the different shore levels are regarded due to morphologically adaptation, then it could be considered to reflect the differences and overlap in their distribution on the shore.

Changing in shell circumference and volume

The allometric relationships between circumference (CF) and volume (V) for the three different shore levels are shown in Figure 6. The regression equations are:

- *High shore level:* $\ln CF = 2.4035 + 0.2892 \ln V$
- *Middle shore level:* $\ln CF = 2.5595 + 0.2585 \ln V$
- *Low shore level:* $\ln CF = 2.4860 + 0.2754 \ln V$

Shell volume increases as the cube of linear morphological measurements of shell circumference for an isometrically growing limpet, due to simple geometric considerations.

The result of *t*-test on the deviations from isometry (á < 0.33) shows that shell volume of limpets living at the three shore levels exhibits highly significant positive allometry relative to the shell circumference ($P < 0.001$, *t*-test), as is the case described above, volume increases even more rapidly relative to circumference as the animals grows. In addition, á is significantly smaller for limpets living at the low shore level than for those living at the high shore level. Thus, limpets living at the low shore level show a greater average change in shape with increasing size.

One-way ANOVA tests on the mean shell circumference and volume for the three different shore levels show that there is significant difference in the shell circumference, but no significant difference is obtained for the shell volume (Table 4). The mean circumference of limpets living at the low shore level (54.7269 ± 5.6025 mm) is higher than at the high (44.7136 ± 7.8626 mm) and the middle (51.6117 ± 7.7658 mm) shore levels. This may indicate that when limpets exhibiting the same shell volume are compared, those limpets living at low shore level are taller than those living to the higher level, otherwise the shell of limpets living at the high shore levels becomes more domed as the limpets grow.

The results of separating the effects of shape from the effects of size by rearranging the power function to obtain the ratio: $V^a/CF = 1/b$, give the ratio values of (0.090405 : 0.0904) for the high shore level, (0.077351 : 0.077346) for the middle shore level, and (0.083269 : 0.083243) for the low shore level, indicating that limpets live at the low shore level are more highly acute than those living to the higher shore levels. Regression of $V^á/C$ against V yielded non-significant correlation coefficients ($r < 0.30$, $P > 0.05$), demonstrating that this measure of shape is indeed independent of size. In general, the results of this study on actual limpet shells reinforce the conclusion on the basis of conical models. For the symmetrical models, Denny (2000) found that the lowest risk of dislodgement by wave action for a limpet is associated with a shell having a central apex (roughly one to one; 1.06) and a height-to-length ratio of approximately

0.53. The average ratio of shell height to radius (H/(L/2)) for a selection of limpets that Denny (2000) chose at random from every continent was 0.68 with the span ratios among these animals fairly evenly distributed in a range from 0.37 to 1.27. However, *C. testudinaria* limpets rarely have shells with these dimensions. The ratios calculated for those limpets from the three shore levels were 0.49 and 0.35 for the high shore level, 0.51 and 0.38 for the middle shore level, and 0.55 and 0.39 for the low shore level, with the mean ratio of 0.52 and 0.37, respectively. This indicates that most limpets have an apex that is well anterior of the centre of the shell, and slightly domed. These values are slightly lower than those found in *Patella vulgata* from Europe (0.75 and 0.92), *Notoacmea schrenkii* from Japan (0.39 and 0.78), *Cellana tramoserica* from Australia (0.95 and 0.75), and *Patella argenvillei* from South Africa (0.95 and 0.85), reported by Denny (2000). Variation in shape about the allometric average in the terms of the shell circumference and the shell volume may be compared with variation in shape among limpets live at different shore levels. In *C. testudinaria* live at the intertidal rocky shore, known to fit the power function of $CF = 11.062V^{0.2892}$, $CF = 12.929V^{0.2585}$, and $CF = 12.013V^{0.2754}$, ranges from the high to the lower shore levels. Standardising allometrically average limpets from their shell volume to one size yields a circumference difference of 15.8% for the high shore level, 17.58% for the middle shore level, and 16.86% for the low shore level, respectively. Tentatively, the ratio of $V^{â}/C$ to 1/â can suggest that lower limpets are more acute than average for those higher limpets. Clearly those limpets conform to the results obtained by analysing the shell dimension. Therefore, the average change in shape due to allometry could potentially have at least as great an effect on variation in shape about the allometric average. This potential effect may be primarily or partially related to developmental responses to the variation in environmental conditions. For instance, development differences may be an adaptational response to selective pressure such as hydrodynamic forces (Hobday, 1995; Denny & Blanchette, 2000), desiccation (for review see Branch, 1981), predation (Lowell, 1986; Hahn & Denny, 1988), or the behaviour by the limpet itself (Stimson, 1970). Possible morphological constraints on the shell shape can also be affected by the muscle attachment (Branch & Marsh, 1978), or may be due to the genetic factors as has been shown to be the case in other gastropods (Struhsaker, 1968). It can be, therefore, concluded that the shell form of *C. testudinaria* occupies the rocky shore, exhibiting a significant tendency for basal dimensions of the shell to decrease interspecifically from low to high shore levels.

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