

Shape and growth in European Atlantic *Patella limpets* (Gastropoda, Mollusca). Ecological implications for survival

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Specimens of *Patella intermedia*, *Patella rustica*, *Patella ulysiponensis*, and *Patella vulgata* were analyzed for shell and radula characteristics. Shell growth in *P. rustica* and *P. ulysiponensis* was basically isometric, indicating that shell shape was constant during growth. On the contrary, shell growth in *P. intermedia* and *P. vulgata* was positively allometric, indicating that as shells increased in size, the base became more circular and the cone more centred and relatively higher. Radula relative size increased in the order *P. ulysiponensis*, *P. vulgata*, *P. intermedia* and *P. rustica*, and had negative allometric growth in all species, indicating that radula grew less as shell increased in size. Data reported in the literature estimated that the lowest risk of dislodgment for a limpet is associated with a centred apex, and a (shell height)/(shell length) or (shell height)/(shell width) ratio of ca 0.53. However, as reported for other limpets, in all four studied *Patella* species, shells were more eccentric and flat than this theoretical optimum. Data reported in the literature indicated that, in limpets, decreasing the (shell base perimeter)/(shell volume) or (shell surface area)/(shell volume) ratios by increasing size results in lower soft body temperature and desiccation. In the present study, *P. rustica* shells displayed the lowest ratios, and *P. ulysiponensis* shells, the highest. Considering that the former species lives at high shore levels, and the latter species at low levels, it appeared that shell shape in European Atlantic limpets can be directly related to resistance to desiccation and high temperature stresses. Radula relative size (in relation to shell height) also increased with increasing level in the shore, suggesting that this might be due to a decreasing abundance of algae with increasing shore level.

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Limpets are one of the most abundant molluscs in rocky shores. However, the rocky shore is a harsh environment, considering the huge force and impact of waves against the rocks. Additionally, at each tidal cycle, limpets are out of water for considerable period of time, being therefore exposed to high temperature and desiccation stresses.

Each limpet has its permanent place to live attached to the substratum in a slight depression in the rocks (home)

(Hyman 1967, Fretter and Graham 1994). After an excursion for feeding on algae, the animal commonly returns to its home. Foraging can occur at low tide, when the animal is emerged, or at high tide, during submersion, and can vary with the period of the day (Williams et al. 1999). Limpets are strongly adherent to the substratum, even while moving. Adhesion to the substratum during inactivity is accomplished by the secretion of a pedal mucus, with

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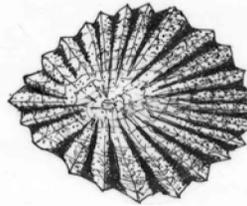
glue-like properties (Smith et al. 1999). While moving, limpets remain adhered due to suction (Ellem et al. 2002). Limpets “clump” or “hunker down” when disturbed. Shell clumping brings the lower rim of the shell into direct contact with the substratum; this creates friction between the shell and substratum that provides increased resistance to horizontal shear and prevents dislodgement (Ellem et al. 2002). Strong adhesion to the substratum reduces water loss, since there is a close fit between the shell and the substratum.

The four *Patella* species found in European Atlantic seawaters occupy different positions in the shore (Evans 1957, Fischer-Piette and Gaillard 1959, Ibañez 1982, Guerra and Gaudencio 1986). *P. ulyssiponensis* is a low-shore species, being out of water only at low tide. *P. intermedia* and *P. vulgata* occur at most levels, and can be ex-

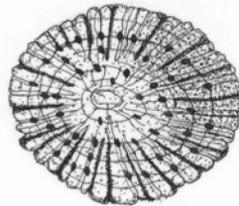
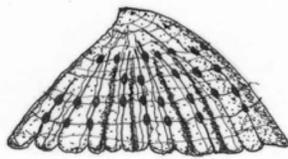
posed to air for considerable periods of time each tidal cycle. *P. rustica* Linné 1758 is restricted to high shore levels, being submerged at high tide, or only humidified by water splashes. Since the exact position of the animal in the shore directly influences the time to air exposure, these *Patella* species can exhibit different adaptations to the rocky shore environment.

This work was aimed to study shell shape and radula size in *P. intermedia*, *P. rustica*, *P. ulyssiponensis* and *P. vulgata*, and to correlate these parameters with their habitat. In particular the following questions were raised: Have these species different shell shape and radula size?, Do shell shape and radula size change with growth?, and Can the morphological characteristics of each species be related to its survival under the dominant ecological conditions?

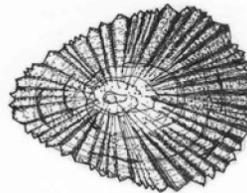
Patella intermedia



Patella rustica



Patella ulyssiponensis



Patella vulgata

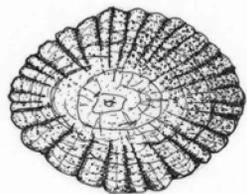


Fig. 1. Lateral (left), top (central) and interior (right) views of *P. intermedia*, *P. rustica*, *P. ulyssiponensis* and *P. vulgata* shells.

Materials and methods

The specimens

Specimens were collected at the following rocky shores along the Portuguese continental coast (coordinates, °W, °N): Afife (−8.8754, 41.7798), Aguçadoura (−8.7821, 41.4319), Amoreira (−8.8434, 37.3553), Baleal (−9.3382, 39.3742), Carcavelos (−9.3249, 38.6747), Foz do Arelho (−9.2253, 39.4383), Luz (−8.7250, 37.0879), Marinha (−8.4109, 37.0912), Monte Estoril (−9.3991, 38.7039), São João do Estoril (−9.3662, 38.6936), and Telheiro (−8.9781, 37.0478). *P. intermedia* and *P. vulgata* were collected at mid-shore, *P. rustica* at high-shore, and *P. ulysiponensis* at low-shore levels. The total number of collected specimens were 726 for *P. intermedia*, 113 for *P. rustica*, 413 for *P. ulysiponensis*, and 381 for *P. vulgata*. In the laboratory, the specimens were immersed for a few minutes in boiling water to separate the shell from the soft part. The radula

was removed from the visceral mass by dissection, immersed in household bleach to remove mucilaginous substances and washed in distilled water. Radula length (RL) was measured to the nearest one mm using a ruler. After air-drying, pluricuspid teeth were observed using a binocular microscope, with 80 × final magnification. The external and internal shell surfaces were examined and their characteristics were recorded (Fig. 1). Shell length (SL), shell width (SW), shell width at the apex (SWA), shell height (SH), and shell length from apex to anterior end (SAA) (Fig. 2 for the definition of these measures) were then measured directly to the nearest 0.01 mm using a digital calliper (Mitutoyo, model CD-15DC).

Identification of the specimens at the species level was based on the morphology of the radula pluricuspid teeth and of the shell (Fig. 1), by comparison with data reported in the literature (Evans 1947, 1953, Fischer-Piette and Gaillard 1959, Christiaens 1973, Fretter and Graham 1994), as previously described (Cabral 2003).

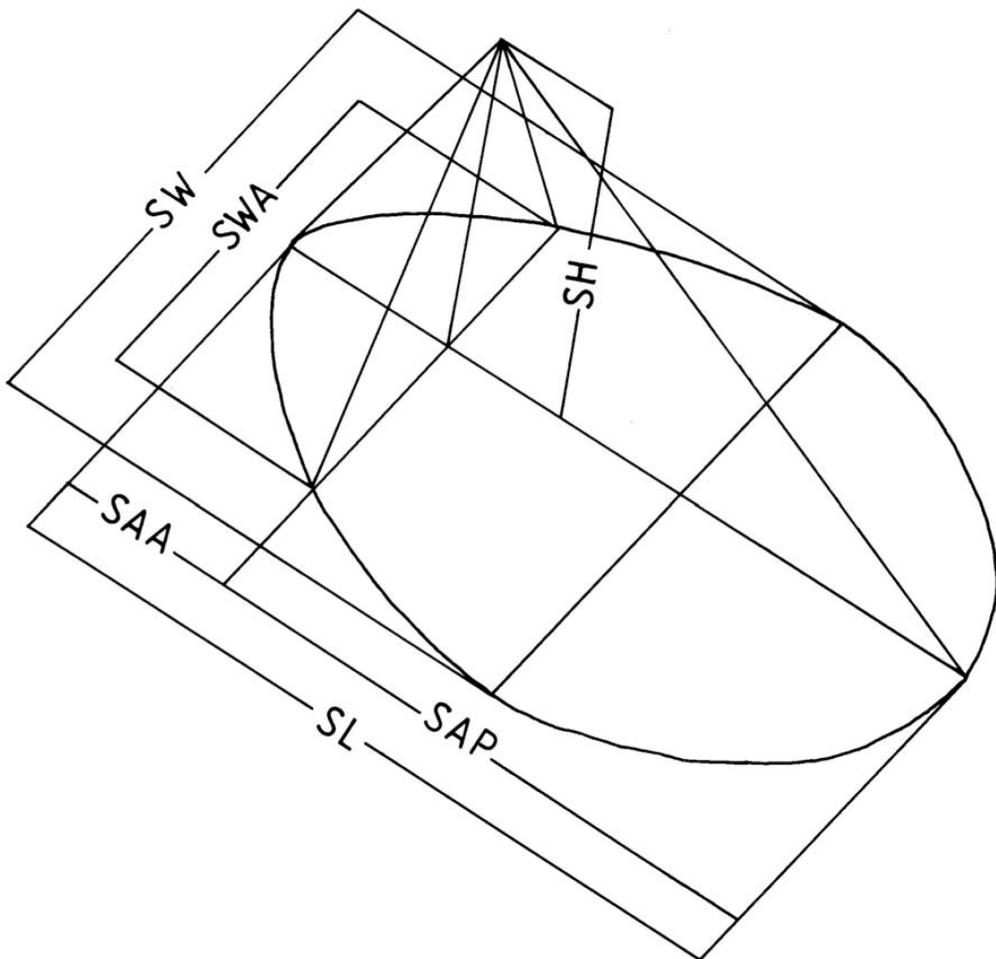


Fig. 2. Distances measured in the shells (description of the variables in the text).

Shape analysis

Shell length from apex to posterior end (SAP) was estimated as SL-SAA. Shell base radius (BR) was calculated as $(SL+SW)/4$, shell conicity as the SH/SL ratio, shell cone eccentricity as SAA/SAP, and shell base ellipticity as SW/SL (Table 1). The base perimeter was calculated as $2\pi \times BR$. The base surface area (BS) was calculated as $\pi \times BR^2$. The shell surface area (SS) was determined using the formula of the surface area of a parabolic cone, $3.6 \times BR \times \sqrt{BR^2 + ((4/3) \times SH)}$. The total surface area of exposure was calculated as BS + SS. The shell volume was determined using the formula of the volume of a parabolic cone $[(\pi \times BR^2 \times SH) / 2]$.

The shape of the limpet shell was decomposed in four parameters: base ellipticity and eccentricity, conicity and cone eccentricity (Table 1). Each one of these parameters was quantified by calculating one or several variables (ratios) (Table 1). Radula relative size was assessed by calculating ratios between radula length and distances measured in the shells. Shape change during growth was assessed by plotting each variable describing shell shape and radula size (ratios variables) against shell length, and by plotting the logarithm of each variable describing shell and radula absolute sizes against the logarithm of shell length. The significance of shell shape change was assessed by testing if the slope of these regressions lines was significantly different from zero (ratio variables) or one (log transformed variables), respectively. All collected specimens were used in shape analysis.

Statistics

Comparisons of the means of the variables describing shell shape and radula relative size was carried out by ANOVA. The relationship between the variables was assessed by calculating the Pearson linear correlation coefficient. All regressions used the least-squares method. Normality plots of residuals revealed only a few data pairs outside the 95% envelope range. To test if the slope was significantly different from zero or one, a t test was carried out according to

Zar (1984). Comparisons of the slopes and intercepts of the regressions were carried out by a t test (comparison of two regressions) or by ANCOVA (comparison of three or four regressions), as described by Zar (1984). In the ANCOVA, slopes were compared firstly, and if found to be significantly different, the procedure stopped and regression lines declared significantly different. If slopes were not significantly different, intercepts were then compared. Significance level was set at 0.05.

Results

Shell shape and radula relative size

Shell shape and radula size in the studied *Patella* species were first evaluated by comparison of the means or medians of the variables used in the analyses of these parameters (Table 2). Similar conclusions were obtained using the mean or median values. Shell base ellipticity was lower than one in all species. It increased from *P. ulyssiponensis* to *P. rustica* and *P. intermedia*, indicating that these shells have an ellipsoidal/oval/parabolic or ovule-shaped base, narrower in *P. ulyssiponensis* and broader in *P. rustica* and *P. intermedia* (Fig. 1). Shell base eccentricity was highest in *P. ulyssiponensis* and lowest in *P. rustica*. Shell conicity also increased in this order. *P. ulyssiponensis* and *P. rustica* shells were therefore opposite in shape, from the flat cone with a narrow ovule-shaped base in the former species, to the tall cone with a wide ellipsoidal/oval/parabolic base in the latter species (Fig. 1). Shell cone eccentricity was much far <1 in all species. It was lowest in *P. intermedia* and highest in *P. ulyssiponensis* and *P. rustica*, indicating a very asymmetrical cone in the former species, and a more centred apex in the later two species (Fig. 1). Radula relative size increased in the order *P. ulyssiponensis*, *P. vulgata*, *P. intermedia*, and *P. rustica*. Radula size in *P. intermedia* and *P. vulgata* was similar if expressed as ratios to SL, but different as ratios to SH. For each variable, all means were significantly different according to ANOVA (Table 2).

Table 1. Variables used in the analyses of shell shape.

Shape parameter	Variable	Trends
Base ellipticity	SW/SL	▶ =1 Circle ▶ <1 Ellipse/Oval/Parabola/Ovule ▶ <1, ratio increases with decreasing ellipticity
Base eccentricity	SWA/SW	▶ ≈1 Circle/Ellipse/Oval/Parabola ▶ <1 Ovule ▶ <1, ratio increases with transition from ovule to ellipse
Conicity	SH/SL	▶ Increases with increasing conicity
Cone eccentricity	SAA/SAP	▶ =1 Centred apex/Symmetrical cone ▶ <1 Apex near the anterior end ▶ <1, ratio increases with decreasing eccentricity

Table 2. Descriptive statistics for the variables describing shell shape and radula relative size.

	<i>P. intermedia</i>			<i>P. rustica</i>			<i>P. ulyssiponensis</i>			<i>P. vulgata</i>			ANOVA	
	Mean	Median	CV %	Mean	Median	CV %	Mean	Median	CV %	Mean	Median	CV %	F	p
SW/SL	0.831	0.831	5.0	0.826	0.820	4.1	0.769	0.768	5.5	0.799	0.801	5.2	213	< 0.00001
SWA/SW	0.869	0.873	5.5	0.930	0.931	2.8	0.864	0.868	5.4	0.900	0.899	7.2	82	< 0.00001
SH/SL	0.316	0.308	23.2	0.439	0.441	12.6	0.303	0.301	14.9	0.356	0.352	16.6	174	< 0.00001
SAA/SAP	0.606	0.601	31.3	0.743	0.744	14.3	0.679	0.678	22.8	0.634	0.587	25.4	31	< 0.00001
RL/SL	1.66	1.64	17.9	3.01	2.97	21.6	0.96	0.94	15.8	1.60	1.59	19.5	1364	< 0.00001
RL/SH	5.47	5.26	25.6	6.87	6.62	20.3	3.20	3.14	18.6	4.57	4.47	20.2	485	< 0.00001

Shape change during growth

Shape change during growth was first assessed by plotting each variable describing shell shape and radula size (ratio variables) against shell length (Fig. 3, Table 3). In *P. rustica*, all variables describing shell shape were not significantly correlated with shell length, indicating that shells of this species maintain a constant shape during growth. In *P. ulyssiponensis*, variables related to base ellipticity and conicity were uncorrelated with shell length. However, variables describing base and cone eccentricity significantly increased with shell size, indicating that shells of this species acquired a more elliptical base and a more centred apex as size increases, but maintained the relative height. In *P. intermedia* and *P. vulgata*, most of the variables describing shell shape were significantly positively correlated with shell length; that is, as shells increased in size, the base became more circular and the cone more centred and relatively taller. In all four *Patella* species, radula relative size decreased during growth. *P. intermedia*, *P. ulyssiponensis* and *P. vulgata* displayed similar low negative slopes, but *P. rustica* showed a steeper line. Intercepts decreased in the order *P. rustica*, *P. intermedia*, *P. vulgata* and *P. ulyssiponensis*.

During growth, *P. rustica* and *P. ulyssiponensis* shells maintained their opposite morphologies (Fig. 3). *P. rustica* shells displayed the most circular shell base (higher SW/SL and SWA/SW ratios), and the most conical and centred shells (higher SH/SL and SAA/SAP ratios) of the four species. However, big *P. intermedia* shells had the most circular base and centred apex. On the opposite side, *P. ulyssiponensis* was the species with narrowest and more ovule-shaped shell base (lowest SW/SL and SWA/SW ratios), and the flattest (lowest SH/SL ratio) shells. *P. intermedia* and *P. vulgata* shells displayed intermediate morphologies between these two extremes.

Plotting the variables describing shell and radula sizes against shell length, both log transformed, resulted in highly significant linear correlations (Fig. 4 and 5, Table 4). Regression analysis of the log-log plots confirmed pre-

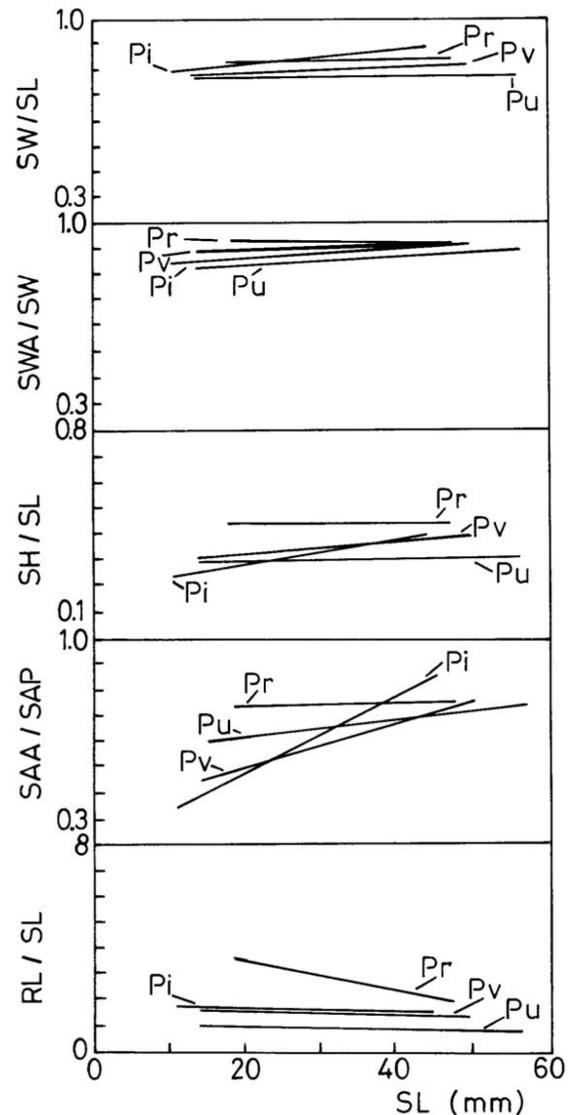


Fig. 3. Plots of ratios describing shell shape or radula relative size changes during growth against shell length. Only the regression lines are displayed (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulyssiponensis*, Pv = *P. vulgata*).

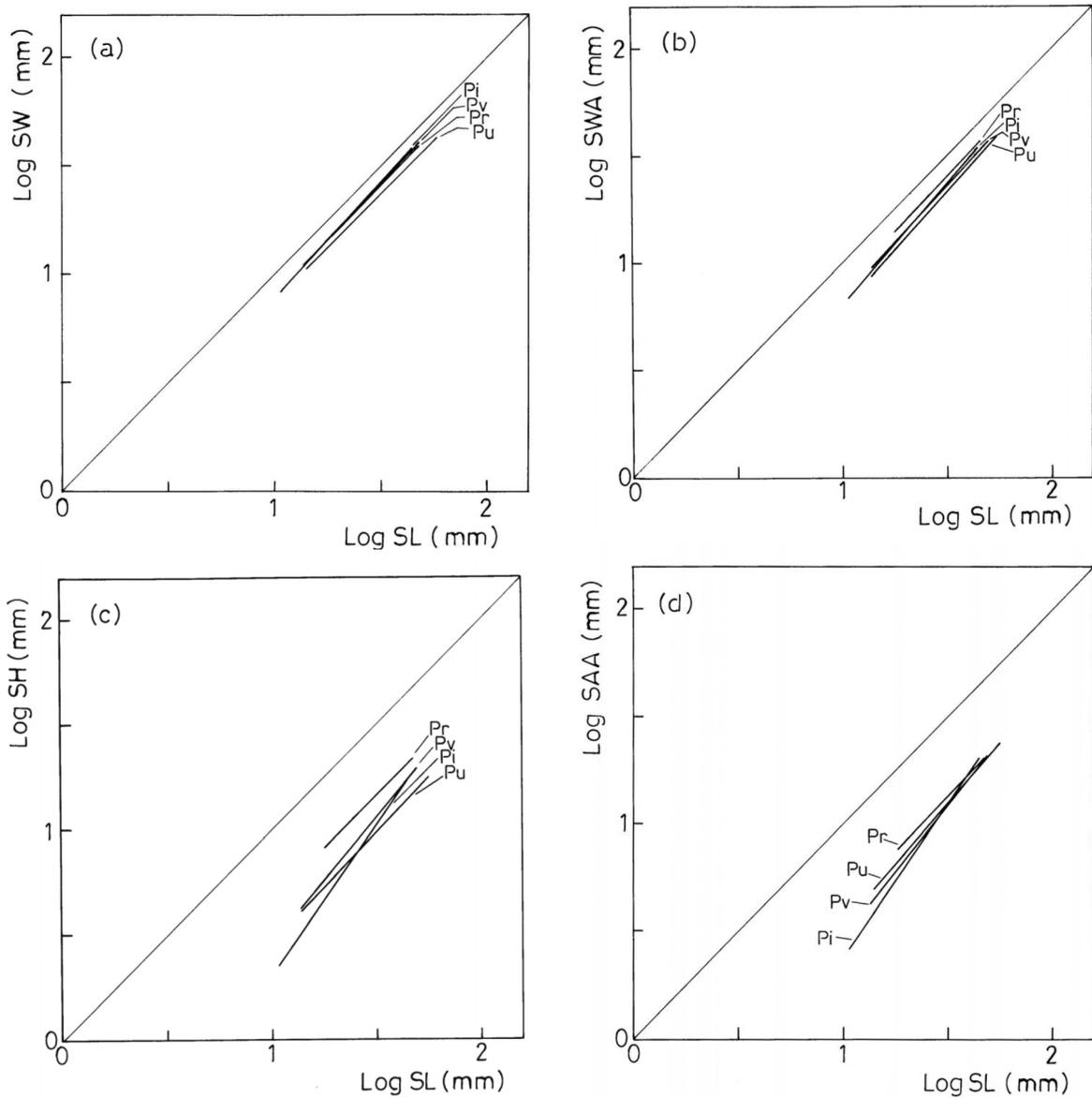


Fig. 4. Plots of the logarithm of shell measures against the logarithm of shell length. (A) Shell width (SW). (B) Shell width at the apex (SWA). (C) Shell height (SH). (D) Shell length from apex to anterior end (SAA) (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulysiponensis*, Pv = *P. vulgata*).

vious analyses using ratio variables. In *P. rustica*, the slopes of all regressions were not significantly different from one, indicating isometric growth, i.e. shell shape was constant as size increased (Huxley 1924, Huxley and Teissier 1936, Gould 1966, Huxley 1993). In *P. ulysiponensis*, shell growth was essentially isometric, except for base and cone eccentricity, which increased more than shell length. In *P. intermedia* and *P. vulgata*, shell growth was positively allometric (Huxley 1924, Huxley and Teissier 1936, Gould 1966, Huxley 1993), the shells being more conical and centred with a less elliptical base as size increased. In the four *Patella* species, the slope of log RL vs log SL was <1,

indicating negative allometry (Huxley 1924, Huxley and Teissier 1936, Gould 1966, Huxley 1993).

The comparison of the regressions of the log-log plots indicated that most slopes and all intercepts were significantly different (Table 5). This suggests different shell and radula shapes and growing patterns among the four studied *Patella* species, in accordance with results from previous analyses. When the four species were simultaneously compared, the most significantly different slopes were those of regressions describing shell conicity (log SH vs log SL), cone eccentricity (log SAA vs log SL), and radula relative size (log RL vs log SL); the least significantly different

Table 3. Parameters of the regression lines (ratios) for evaluating shape change during growth.

Species	Variable vs SL	Pearson r	Intercept	Slope			p slope \neq 0
				Value	95% Confidence limits		
<i>P. intermedia</i>	SW/SL	0.269	0.778	0.0019	0.0014	0.0024	< 0.001
	SWA/SW	0.246	0.814	0.0020	0.0014	0.0025	< 0.001
	SH/SL	0.380	0.185	0.0047	0.0039	0.0055	< 0.001
	SAA/SAP	0.469	0.188	0.0150	0.0130	0.0171	< 0.001
	RL/SL	-0.136	1.85	-0.0007	-0.0003	-0.0010	< 0.001
<i>P. rustica</i>	SW/SL	0.103	0.808	0.00062	-0.0005	0.0018	> 0.20
	SWA/SW	0.0184	0.928	0.000086	-0.00078	0.00096	> 0.50
	SH/SL	-0.0202	0.445	-0.00020	-0.0021	0.0017	> 0.50
	SAA/SAP	0.043	0.719	0.00082	-0.0028	0.0044	> 0.50
	RL/SL	-0.515	4.74	-0.0060	-0.0078	-0.0041	< 0.001
<i>P. ulyssiponensis</i>	SW/SL	0.053	0.755	0.00036	-0.0003	0.0010	> 0.20
	SWA/SW	0.220	0.803	0.0017	0.00095	0.0024	< 0.001
	SH/SL	0.051	0.289	0.00037	-0.00033	0.0011	> 0.20
	SAA/SAP	0.137	0.553	0.0034	0.0010	0.0058	< 0.01
	RL/SL	-0.189	1.13	-0.00046	-0.00023	-0.00069	< 0.001
<i>P. vulgata</i>	SW/SL	0.182	0.762	0.0011	0.0005	0.0017	< 0.005
	SWA/SW	0.105	0.867	0.0010	0.00004	0.0019	0.02–0.05
	SH/SL	0.276	0.276	0.0024	0.0015	0.0032	< 0.001
	SAA/SAP	0.373	0.339	0.0087	0.0065	0.0108	< 0.001
	RL/SL	-0.150	1.83	-0.00068	-0.00023	-0.0011	< 0.005

slopes were those of the regressions related to base ellipticity and eccentricity. The most differentiating morphological traits among the four studied limpet species were the shell cone height and centring and radula relative size.

Plots of the ratios shell base perimeter/shell volume, shell surface area/shell volume and total surface area/shell

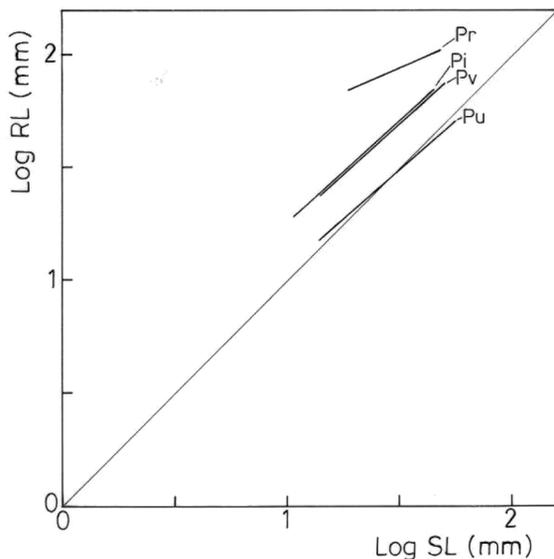


Fig. 5. Plots of the logarithm of radula length against the logarithm of shell length (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulyssiponensis*, Pv = *P. vulgata*).

volume, against shell length, are shown in Fig. 6 to 8. For all four species, increasing shell length corresponded to decreasing ratios. Except for small shells, *P. rustica* and *P. ulyssiponensis* displayed the lowest and highest ratios at a given shell length, respectively, in accordance with the highest and lowest mean conicities, respectively, exhibited by these two species. *P. intermedia* and *P. vulgata* shells exhibited intermediate features. *P. ulyssiponensis* shells exhibited the lowest slope, in accordance with the isometric increase in height with length. *P. intermedia* and *P. vulgata* shells exhibited the highest slopes due to the allometric increase in shell height with shell length.

Discussion

The shells of *P. intermedia*, *P. rustica*, *P. ulyssiponensis* and *P. vulgata* exhibited characteristic shapes and growing patterns. However, whereas *P. rustica* and *P. ulyssiponensis* shells exhibited opposite morphological traits, *P. intermedia* and *P. vulgata* shells shared some characteristics. *P. rustica* shells were tall and centred cones, with almost circular base. Shell shape was maintained during growth. On the contrary, *P. ulyssiponensis* shells were flat cones, with an ovule-shaped base. Shell shape was basically constant during growth, except that shells became more centred as size increased. *P. intermedia* and *P. vulgata* shells displayed intermediate shell shapes between these two extremes morphologies, but both displayed pronounced

Table 4. Parameters of the regression lines (log transformed) for evaluating shape change during growth and testing isometric vs allometric growth.

Species	Variable vs Log SL	Pearson r	Intercept	Slope			p slope \neq 1	Isometry vs Allometry at 0.05 level
				Value	95% Confidence limits			
<i>P. intermedia</i>	Log SW	0.981	-0.173	1.064	1.049	1.080	< 0.001	Allometry
	Log SWA	0.971	-0.323	1.126	1.106	1.146	< 0.001	Allometry
	Log SH	0.853	-1.115	1.421	1.358	1.484	< 0.001	Allometry
	Log SAA	0.906	-1.063	1.436	1.387	1.485	< 0.001	Allometry
	Log RL	0.753	0.349	0.906	0.848	0.963	< 0.001	Allometry
<i>P. rustica</i>	Log SW	0.980	-0.122	1.026	0.987	1.065	0.20–0.50	Isometry
	Log SWA	0.973	-0.164	1.033	0.987	1.080	0.10–0.20	Isometry
	Log SH	0.833	-0.371	1.007	0.882	1.133	> 0.50	Isometry
	Log SAA	0.918	-0.421	1.032	0.948	1.116	0.20–0.50	Isometry
	Log RL	0.395	1.289	0.435	0.245	0.626	< 0.001	Allometry
<i>P. ulysiponensis</i>	Log SW	0.958	-0.149	1.022	0.992	1.051	0.10–0.20	Isometry
	Log SWA	0.955	-0.318	1.089	1.056	1.122	< 0.001	Allometry
	Log SH	0.786	-0.615	1.059	0.978	1.139	> 0.50	Isometry
	Log SAA	0.865	-0.608	1.133	1.070	1.197	0.02–0.05	Allometry
	Log RL	0.710	0.173	0.872	0.790	0.950	< 0.005	Allometry
<i>P. vulgata</i>	Log SW	0.970	-0.163	1.042	1.016	1.068	< 0.001	Allometry
	Log SWA	0.974	-0.264	1.078	1.053	1.103	< 0.001	Allometry
	Log SH	0.869	-0.782	1.216	1.146	1.285	< 0.001	Allometry
	Log SAA	0.894	-0.821	1.261	1.198	1.325	< 0.001	Allometry
	Log RL	0.719	0.329	0.873	0.792	0.955	< 0.001	Allometry

shell shape changes during growth. Small *P. intermedia* shells were flat, with a very anterior apex, but as size increased they became more conical and centred. *P. vulgata* shells displayed similar but less marked shell growing trends. In the current identification schemes for the European Atlantic *Patella* species, the most used characteristics of the shell are the texture and pigmentation of the internal and external surfaces. The results reported in the present work indicated that shell shape, mainly conicity and cone eccentricity, should be taken into account in the identification of specimens.

Limpets are one of the most abundant groups of molluscs in the intertidal rocks of sea-shores. At high tide, waves crash on the shore and impose intense hydrodynamic forces (Denny and Blanchette 2000). Organisms living

on the surf zone are subjected to water flow of very high velocity and acceleration. In this environment, molluscs face the problem of being swept away (Vermeij 1993). It has been estimated that the lowest risk of dislodgment for a limpet is associated with a centred apex, and a SH/SL or SH/SW ratio of ca 0.53 (Denny 2000, Denny and Blanchette 2000). Displacement of the apex away from the centre of the shell, and/or lower or higher SH/SL ratios should result in increasing tensile stress and concomitant higher probability of being swept away (Denny 1988, 2000, Denny and Blanchette 2000). However, limpets overall the world do not conform to these patterns. Vermeij (1973) studied shell shape in several species collected in different sites of Latin America, the West Indies, West Africa, and the Middle East. Conicity was evaluated by the SH

Table 5. Comparison of the regression lines for evaluating shape change during growth in the studied *Patella* species.

Variable vs Log SL	Comparison of slopes		Comparison of intercepts	
	F/t	p	F/t	p
Log SW	3.20	0.05–0.02	Not tested	–
Log SWA	1.17	> 0.50	168.1	< 0.001
Log SH	20.4	< 0.001	Not tested	–
Log SAA	18.5	< 0.001	Not tested	–
Log RL	8.85	< 0.001	Not tested	–

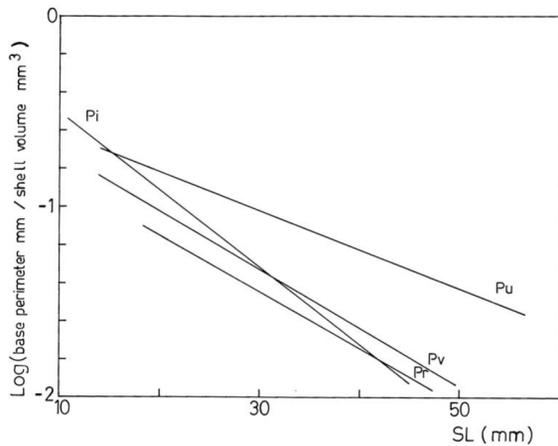


Fig. 6. Plots of the ratio between the base perimeter and shell volume, against shell length (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulysiponensis*, Pv = *P. vulgata*).

$1/\sqrt{(SL \times SW)}$ ratio, which is ca the mean of SH/SL and SH/SW ratios. Mean conicity for the studied *Acmaea*, *Celana*, *Patella* and *Scurria* species (ten, three, three and one species) was very uniform, and ranged between 0.334 and 0.386. Denny (1989) presented shell ratio measurements for 14 limpet species from South Africa and the west coast of North America. Mean SAA/SL and SH/SL ratios for these species were in the 0.190–0.500 and 0.185–0.665 ranges, respectively. Denny (2000) compiled data for 79 species of 12 genera of limpets from all over the world, mostly outside Europe. Overall mean SAA/SL, SH/SL and SH/SW ratios for these species were 0.35, 0.34 and 0.42, respectively. Branch and Marsh (1978) studied shell shape in six *Patella* species from the South Africa coast. Mean SAA/SAP and SH/SL ratios ranged between 0.64–0.81 and 0.22–0.43. In the present work, mean SAA/SL, SH/SL and SH/SW ratios for *P. intermedia*, *P. rustica*, *P. ulysiponensis* and *P. vulgata* were 0.370–0.424, 0.303–0.439, and 0.380–0.532, respectively (Table 2), indicating that European Atlantic limpets also display an under theoretical optimum shell shape in relation to dislodgment by wave action.

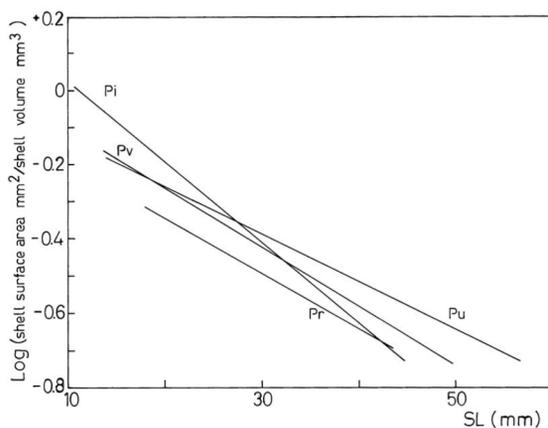


Fig. 7. Plots of the ratio between shell surface area and shell volume, against shell length (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulysiponensis*, Pv = *P. vulgata*).

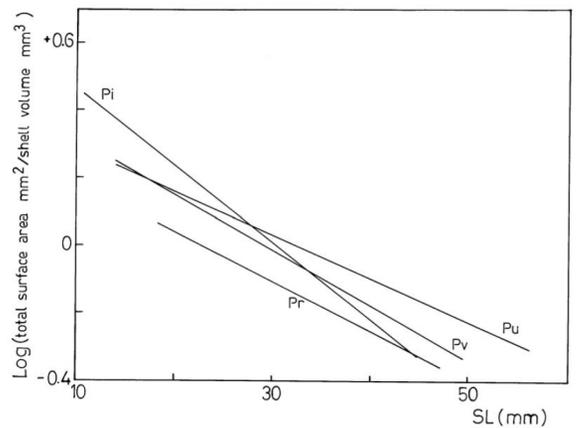


Fig. 8. Plots of the ratio between total surface area and shell volume, against shell length (Pi = *P. intermedia*, Pr = *P. rustica*, Pu = *P. ulysiponensis*, Pv = *P. vulgata*).

An explanation for the observed difference between the theoretical optimum shell shape and the observed limpet shapes is that tenacity is very important, or even dominant, in the resistance of the limpets to being swept away in the seashore environment. Indeed, limpets are known to exhibit huge strengths of adhesion to the substratum. Branch and Marsh (1978) compared tenacity in six *Patella* species from the South Africa coast. Tenacity increased in the order *P. oculus*, *P. granatina*, *P. granularis*, *P. longicosta*, *P. argenvillei*, and *P. cochlear*, corresponding to increasing exposure to wave action in the shore.

Limpets are subjected to wetting and drying each tidal cycle (Branch 1981). Ability to resist desiccation is therefore of primary importance for intertidal limpets, since the loss of body water can be the direct cause of death due to desiccation (Hyman 1967, Davies 1969). Moreover, limpets are probably more prone to heating than other organisms, since a large surface area is exposed to sun and little shadow is cast (Branch 1975). When immersed, limpets rapidly equilibrate with seawater temperature, but when exposed to sunlight and air temperatures, the temperature of the soft body can exceed the atmospheric temperatures (Davies 1970, Branch 1981). The primary site of evaporation from a limpet's body is at the shell periphery (Davies 1969, Vermeij 1973, Denny 2000). Over the course of a sunny low tide, limpets firmly attached to the home scar lose less water than limpets out of the home scar or than limpets allowed to elevate shell margins (Garrity 1984). With direct sunlight, the amount of heat energy absorbed depends on the surface area of the shell perpendicular to the sun's rays (Vermeij 1973, 1993). Heat loss, however,

depends on the total surface area, including surfaces that are not at right angles to the incoming rays, and cooling by the loss of water from the foot and from the space between the foot and the shell (Vermeij 1973, 1993). Desiccation and temperature of the animal body are therefore directly dependent on the perimeter of the base (and the strength of attachment to the home scar), the surface area of exposure and the mass of the soft body. Since limpets have fundamentally a conic shell, and the soft body size and the reservoir of water are determined by the shell volume, with increasing shell size, the ratios perimeter or surface area/soft body mass decrease, resulting in lower desiccation and soft body temperature (Hyman 1967, Davies 1969, 1970, Branch 1975, 1981, Vermeij 1973, 1993, Fretter and Graham 1994). These facts have been experimentally confirmed (Vermeij 1973, Branch 1975, Garrity 1984).

In the present study of European Atlantic limpets, shell conicity increased in the order, *P. ulyssiponensis*, *P. intermedia*, *P. vulgata*, and *P. rustica* (Table 2). This order corresponded to an increasingly higher level in the shore, suggesting that shell shape in European Atlantic limpets can be directly related to resistance to desiccation and high temperature stresses, as reported for other limpet species. This hypothesis was confirmed by plotting the ratios in Fig. 6 to 8. All these results favour the interpretation that shell shape in European Atlantic limpets can be related, at least partially, to the avoidance of desiccation and heat stresses. Except for small shells, *P. ulyssiponensis* shells were the flattest, and therefore, the most prone to water loss and heating this species is out of water only at low tide. *P. rustica* shells were the tallest, and except for very big shells, the least prone to lose water and heat this species is out of water for most of the day. The high slope exhibited by *P. intermedia* and *P. vulgata* suggested that as the animal increases in size it is less prone to desiccation and heating stresses. However, some characteristics of the shells of these species might also influence the amplitude of desiccation and heating. *P. ulyssiponensis* shells are usually covered by algae, and this can further decrease heating. On the contrary, *P. rustica* shells are dark coloured, and this can antagonize the advantage of pronounced shell conicity exhibited by this species (Vermeij 1971).

The radula of the studied *Patella* species displayed negative allometric growth. Branch (1975) reported growth functions for seven *Patella* species of the South Africa coasts. Whilst in four species the slope of the log shell height vs log shell length plot was ≈ 1 , indicating isometric growth in height, it was >1.3 in three other species, indicating allometric growth. However, no statistical tests were reported for these data. The length of the radula in European Atlantic limpets increased in the order *P. ulyssiponensis*, *P. vulgata*, *P. intermedia*, and *P. rustica*, corresponding to an increasing water level in the shore. Limpets are grazers, and feed on algae and detritus found on the substratum. The overall abundance of algae in the intertidal zone shows a general decreasing trend from the lowest to the highest

levels of the shore, since most species do not tolerate drying for long periods. According to Fretter and Graham (1994), the length of the radula increase with increasing usage and wear. The results presented here are compatible with this view, and suggested that the very long radula of *P. rustica* can be related to the low density of algae in the higher shore levels, with concomitant higher usage of the radula in order to scratch the amount of food necessary for survival.

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