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Microgeographical shell variation in *Littorina striata,* a planktonic developing periwinkle

Abstract *Littorina striata* is a strictly Macaronesian, intertidal periwinkle with planktonic development. The species produces both nodulose and smooth shells, which co-occur at Ilheu de Vila Franca do Campo, a drowned crater situated about 1000 m off the south coast of São Miguel, Azores. The present work describes and analyzes the shell variation, temporal change and ecological distribution of the two shell types at this crater over a 3-year period. Nodulose shells were more common in the sheltered lagoon inside the crater, while smooth specimens dominated the outside of the wave-exposed crater. Moreover, nodulose specimens were smaller and weighed less compared to smooth ones. However, regardless of morphotype, shells from the lagoon had a smaller aperture and were less globose than those from the outside. Within an exposure regime, smooth specimens had a larger aperture. These patterns remained constant over time. They are tentatively interpreted as functional adaptations to thermal stress and wave exposure. The mechanisms that maintain these patterns are still unknown. Yet, aperture height of specimens transplanted from the lagoon to the outside increased markedly over a period of 5 months, whereas no comparable changes were observed in other experimental groups (i.e. transplanted from the outside into the lagoon, transplanted within the outside and transplanted within the lagoon; the latter two transplant groups being the blancos). This suggests that at least the aperture size in *L. striata* may be an ecophenotypically plastic trait.

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Introduction

Many prosobranch gastropods show intraspecific variability involving shell shape, size, colour, sculpture and weight (e.g. Struhsaker 1968; Crothers 1981, 1992; Sergievsky 1992; Boulding and Van Alstyne 1993; Chapman 1995; Johannesson 1995; Johannesson and Johannesson 1996; Hull et al. 1996). This variation occurs on both macro- (e.g. between distant regions) and microgeographic scales (e.g. over distances of a few metres or between different shore levels at the same site). The differential distribution of shell morphologies in prosobranchs lacking planktonic development is usually explained as a result of natural selection (Seeley 1986; Chapman 1995; Johannesson and Johannesson 1996). Wave action in exposed habitats, for example, selects for small, relatively smooth and light shells with a large aperture, whereas sheltered habitats with strong crab predation favour elongated, strongly sculptured and heavy shells with small apertures (Vermeij 1978; Reimchen 1981; Sundberg 1988; Boulding and Van Alstyne 1993; Frid and Fordham 1994; Chapman 1995; Preston et al. 1996). Shell differences between shore levels, in turn, are usually attributed to selection by desiccation and heat stress (Vermeij 1978; McMahon 1990). In this situation, high-shore specimens have a small aperture and tend to be sculptured and high-spired compared to low-shore specimens. Although selection is thought to be the main driving force behind morphological differentiation, phenotypic plasticity sometimes also accounts for shell variation in prosobranchs without planktonic development (Chapman 1995). In *Nucella lapillus,* for example, shell morphology is regulated by chemical cues released by foraging crabs and damaged conspecifics (Palmer 1990), affecting shell weight, apertural tooth height and thickness of the peristome. Similarly, Etter

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(1988) showed that *N. lapillus* transplanted from sheltered to wave-exposed areas develop a larger foot. *Littorina sitkana* appears to be highly plastic for shell ornamentation (Boulding et al. 1993). In *L. obtusata* the shell thickness is affected by the presence of crabs (Trussel 1996). Evidently, shell variation does not only reflect differential adaptive responses in heterogeneous environments, but may also be due to the dependency of metabolic rates on temperature or other external factors (Vermeij 1978).

Species with planktonic development usually have greater dispersal abilities than species without planktonic development (Scheltema 1995). Since local population differentiation in planktonic developers will be counteracted by gene flow, morphological differentiation between spatially separated populations will be inversely related to the intensity of larval dispersal (Scheltema 1971). Thus, morphological differences among local populations of planktonic developing species are more likely to reflect environmental variables acting on the phenotype, rather than on the genotype (McMahon and Whitehead 1987).

Hitherto, adaptive shell variation has mainly been studied in prosobranchs without planktonic development, whereas little attention has been given to macro- and microgeographical shell variation in planktonic developers. Probably because planktonic developers often display less shell variability, compared to non-planktonic developers, as shown in several studies of the planktonic developing periwinkle *Littorina littorea* (Janson 1987; Johannesson 1992) and in other planktonic developing littorinids (McMahon 1992; Chapman 1995). Moreover, the temporal stability of morphological patterns has rarely been addressed. Therefore, the present study aims at describing and analyzing the spatio-temporal microgeographic distribution of shell variation in the planktonic developing periwinkle *Littorina striata* King and Broderip, 1832.

Littorina striata is a periwinkle that only occurs in the Macaronesian islands (Azores, Canary Islands, Madeira and Cape Verde), where it is common on bare rocks in the upper eulittoral and littoral fringe (Reid 1996). Its lower limit is amongst the uppermost barnacles and it extends up into the splash zone (Reid 1996). *L. striata* displays a high degree of shell variation, particularly with respect to shell sculpture, which is rather unique, given its planktonic development, though similar sculptural variation has been described by Struhsaker (1968) in another planktonic developing littorinid, *L. picta* [now *Nodilittorina hawaiiensis*]. Superficially, the nodulose shell of *L. striata* (nodulose form; see Fig. 2), often known as "var. *affinis*", looks quite distinct from typical *L. striata*, which has only a spiral granulose appearance (smooth form; see Fig. 2). Many early authors, therefore, retained *L. affinis* as a separate species (Reid 1996 and references therein). However, no anatomical or radular differences have been found between the nodulose and the smooth forms (Reid 1996). Preliminary population genetic results suggest that both forms share

a common gene pool (De Wolf et al. 1994). They exhibit similar heat coma temperatures (Vedel and Depledge 1995) and are both extremely capable of controlling evaporative water loss (Britton 1995). There is, however, still some controversy about the description and interpretation of this sculptural variation in *L. striata*. While some authors (Rosewater 1981; Britton 1995) regard nodulation as a juvenile characteristic disappearing in adult stages, others doubt its age determination (Reid 1996), and several authors have given different interpretations with regard to its functionality (see "Discussion"). Although the sculptural variation is likely to be of functional significance, it is not known how this variation is determined, or how the distribution of sculptural types on the shore is achieved (Reid 1996).

Both shell forms occur microsympatrically on Ilheu de Vila Franca do Campo, a drowned volcanic crater about 1000 m off the south coast of São Miguel (Azores). This crater consists of two small islands, surrounding a circular lagoon, which is connected with the ocean by a small channel and six narrow fissures (Fig. 1) (Martins 1976; Morton 1990). As a result, wave action on the outside of the crater is much stronger than in the lagoon, which is extremely sheltered. Environmental conditions will therefore tend to be very heterogeneous between the lagoon and the outside. This situation thus provides an excellent setting for studying the ecological correlates of the aforementioned microgeographic shell variation in a planktonic developing prosobranch, while at the same time contributes to the debate concerning sculptural variation in *Littorina striata*.

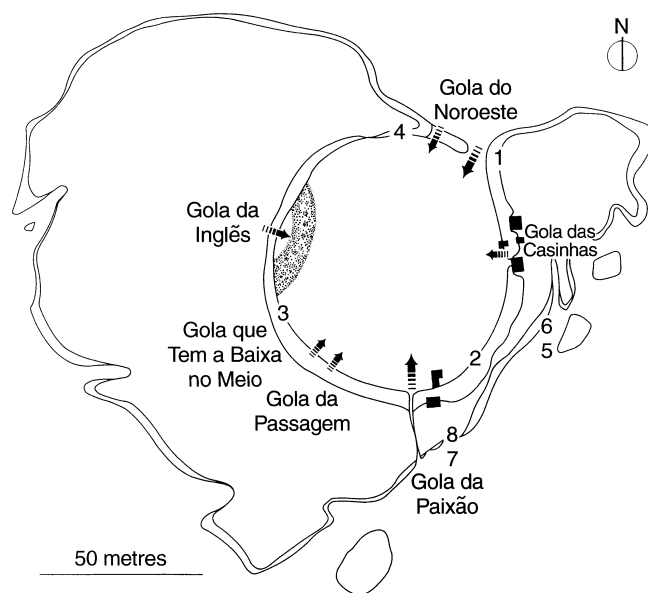**Fig. 1** Ilheu de Vila Franca do Campo (37°42′N; 25°26′W). Locations of sampled populations of *Littorina striata* (*1–4* lagoon; *5–8* outside). *Arrows* indicate water influx areas, *stippled area* in front of the "Gola da Ingles" represents a sand bench

Materials and methods

Sampling

Littorina striata was collected annually (August 1992, July 1993 and July 1994) at eight sites in Ilheu de Vila Franca do Campo (here further referred to as Ilheu) (Fig. 1). Sites 1, 2, 3 and 4 were located in the lagoon, where the periwinkles occur in the upper shore and splash zone along a narrow strip of algae (*Bangia fuscopurpurea*) just above the barnacle belt (*Chthamalus stellatus*) (Morton 1990). The four other sites were located outside the lagoon, with Sites 6 and 8 situated in the splash zone, and Sites 5 and 7 situated lower in the barnacle belt at the upper edge of the middle shore level. Thus, the paired sites, 5/6 and 7/8, represented two vertical transects.

Periwinkles were sampled randomly during 15 min over a surface of a few square metres. In this way a total of 1078 specimens was collected.

Morphometric analysis

Specimens were divided into nodulose and smooth categories (Fig. 2). Subsequently, five shell traits (Fig. 3) were measured with a calliper to the nearest 0.05 mm: height (HS), width (WS), aperture height (HA), aperture width (WA) and height of the spire (HT). In addition, total weight (TW, shell plus soft parts) and body weight (BW, soft parts alone) were determined to the nearest milligram.

The distribution of the nodulose and smooth shells between the lagoon and the outside of the crater or between high and low shore
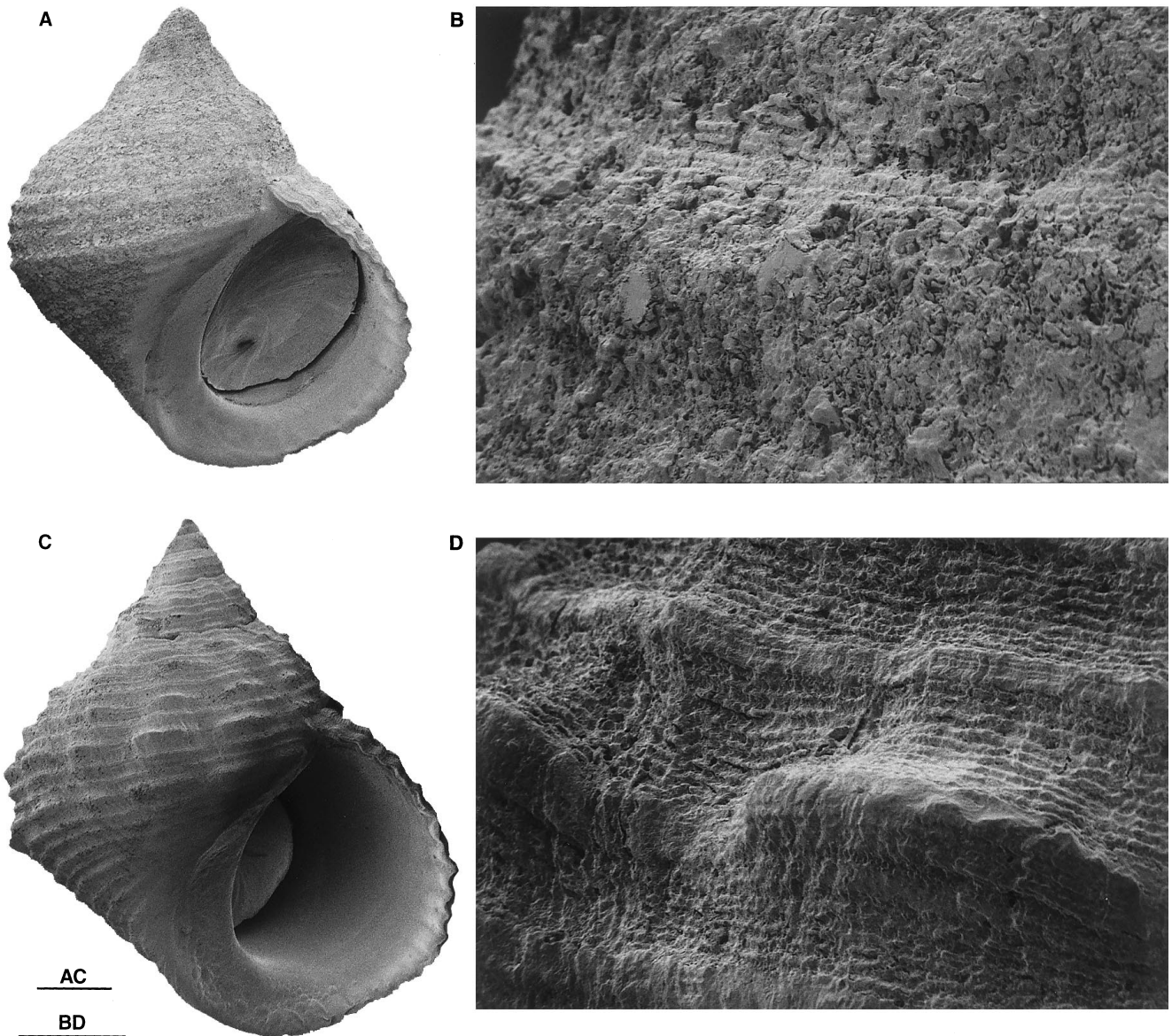

Fig. 2 *Littorina striata*. **A** Smooth and **C** nodulose shell forms; **B** and **D** detail of their respective shell surfaces. *Scale bars:* 1 mm (A, C); 100 μm (B, D)
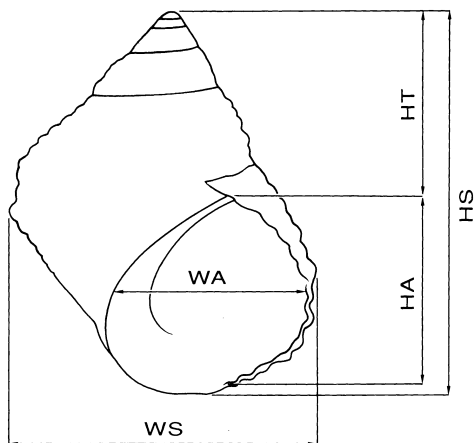
Fig. 3 Shell variables measured in this study (*HS* shell height; *WS* shell width *HA* aperture height; *WA* aperture width; *HT* height of shell top)

sampling sites was analyzed per sampling year with 2×2 contingency tables and Fisher exact tests. Morphometric patterns were investigated by means of a three-way multivariate analysis of variance (MANOVA), involving all seven measured variables (i.e. HS, WS, HA, WA, HT, TW and BW), contrasting the factors "year" (1992, 1993 and 1994), "wave exposure" (lagoon, i.e. sheltered, vs outside, i.e. exposed) and "morphotype" (nodulose vs smooth). Weights were log-transformed to make them normally distributed. The effects of the three factors contrasted in the MANOVA were further inspected by means of a standard canonical discriminant analysis (CDA) of all morphometric data. Because there was a consistent year effect (see "Results"), each year was analyzed separately. Two sets of CDAs were performed: one contrasting the eight sites, the other contrasting the four shell groups nodulose/lagoon, nodulose/outside, smooth/lagoon and smooth/outside. For each year, the mean values of the first two canonical variables (CVs) of the first CDA were used to plot the eight sites. The mean values of the first two CVs of the latter analysis were used to plot morphometric changes in the four groups as a function of time. Null hypotheses were rejected at $p < 0.05$.

Fisher exact tests were implemented by the program STAT-EXACT v. 2.11 (Cytel Software Corporation, Cambridge, Massachusetts). MANOVA and CDA evaluations were performed with the STATISTICA v. 5.0 package (Statsoft, Tulsa, Oklahoma).

Transplantation experiment

A total of 240 specimens of comparable size (see Table 6) were collected in the lagoon and at the outside of the crater (August 1994). Four measurements were taken: HS, WS, HA and HT. The specimens were then divided into four groups: 60 specimens were transplanted from the lagoon to the outside (A), 60 specimens were transplanted within the lagoon (B) (= blanco lagoon), 60 specimens from the outside into the lagoon (C), and 60 were transplanted at the outside (D) (= blanco outside). Each individual was marked by a group specific colour dot, using water-resistant paint. Individuals were recaptured every month and measured.

After 5 months, a two-way MANOVA was performed contrasting the factors "transplantation group" and "month". Scheffé's post hoc test was used to compare means. Subsequently, a CDA was performed. The mean values of CV1 were used to plot morphometric changes in the four groups as a function of time. All tests were performed with the STATISTICA v. 5.0 package (Statsoft, Tulsa, Oklahoma) and interpreted at a 5% significance level.

## Results

Spatial and temporal patterns

The relative morphotype abundance per sampling site (Fig. 4) showed a statistically significant difference between the lagoon, where the nodulose specimens were more frequent, and the outside, where the smooth shells predominated (Table 1). This pattern was consistent over the three sampling years (Table 1). At the outside of the crater there was also a tendency for splash zone specimens to be more frequently nodulose than the specimens from lower shore levels (Fig. 4). However, this pattern was in most cases statistically not significant (Table 1).

Mean values of the morphometric data (i.e. HS, WS, HA, WA, HT, TW and BW) are summarized per year, sampling site and morphotype in Table 2. A three-way MANOVA showed that the three contrasted factors significantly contributed to the observed morphometric

Table 1 *Littorina striata*. Exact *p*-values for distributional differences of nodulose versus smooth individuals between lagoon and outside, and high (6,8) and low (5,7) shore sampling sites per year

Sites	1992	1993	1994
Lagoon vs Outside	0.0001	0.0001	0.0001
5 vs 6	0.1752	0.0310	0.0011
7 vs 8	0.0113	0.3848	0.5000

Fig. 4 *Littorina striata*. Distribution of the nodulose and smooth morphotypes in the lagoon (*1–4* sheltered sites) and in the outside (*5–8* exposed sites) of the crater
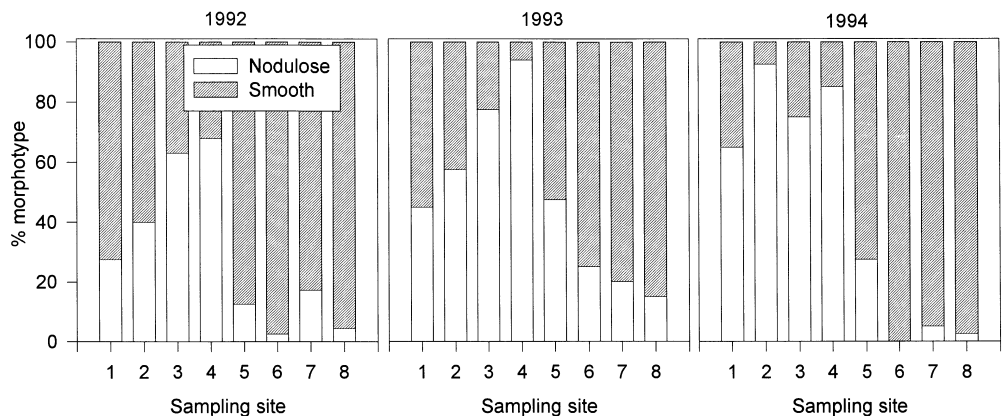
variation, with regard to HS, WS, HA, WA, HT, TW and BW. Nodulose specimens were smaller and weighed less than smooth individuals. In the same way, specimens from the lagoon were smaller and weighed less than specimens from the outside (Table 2). This was, of course, consistent with the fact that nodulose shells are more abundant in the lagoon (Fig. 4). The interactions between the factors "year" and "wave exposure" and

Table 2 *Littorina striata*. Annual mean values (*HS* shell height; *WS* shell width; *HA* aperture height; *WA* aperture width; *HT* height shell top; *TW* total weight; *BW* body weight) and standard deviations for the smooth (*S*) and nodulose (*N*) morphotypes in each of the eight sampling sites for each of the seven measured variables (in 10^{-2} mm)

Site, mor- photype		HS Mean	SD	WS Mean	SD	HA Mean	SD	WA Mean	SD	HT Mean	SD	TW Mean	SD	BW Mean	SD	N
1992																
1	S	760.17	125.28	622.41	110.34	524.13	81.13	373.27	56.75	381.89	62.14	135.38	66.65	51.03	19.66	29
1	N	717.91	137.93	586.25	107.47	490.41	95.21	339.58	74.72	362.50	65.28	113.42	71.32	47.08	18.67	12
2	S	814.00	122.02	682.33	96.31	569.16	86.64	393.00	60.38	392.83	69.45	155.20	59.16	59.63	22.98	30
2	N	675.00	130.05	548.50	111.78	459.75	99.90	309.00	62.17	321.75	59.19	87.40	50.91	37.05	17.51	20
3	S	778.42	100.94	647.63	80.97	529.73	73.46	347.36	39.24	362.89	54.50	130.05	55.94	44.95	16.49	19
3	N	713.97	77.60	594.85	68.60	489.70	59.27	320.29	46.15	334.85	42.02	96.50	29.13	35.12	10.78	34
4	S	877.14	114.27	700.23	100.70	549.28	83.02	396.90	58.28	440.95	53.96	182.57	75.35	63.29	23.29	21
4	N	735.35	122.77	581.07	101.18	451.90	81.28	323.69	66.26	371.78	64.16	106.98	58.43	38.64	19.37	42
5	S	825.28	166.44	705.57	123.38	582.14	103.04	436.42	76.53	407.86	121.91	178.46	101.03	61.17	32.19	35
5	N	663.00	126.52	562.00	85.56	479.00	79.09	353.00	60.48	335.00	74.41	92.40	41.03	33.20	13.97	5
6	S	824.36	130.33	712.05	102.24	589.74	75.83	445.89	75.84	377.95	68.26	200.97	81.58	69.74	26.38	39
6	N	660.00	0.00	590.00	0.00	500.00	0.00	330.00	0.00	270.00	0.00	104.00	0.00	30.00	0.00	1
7	S	1085.47	148.40	907.73	119.92	753.92	97.14	506.90	70.62	496.07	82.27	400.36	166.33	129.29	50.23	42
7	N	910.00	149.23	747.22	121.50	646.66	108.68	419.44	71.96	405.55	79.23	220.11	120.20	76.56	35.20	9
8	S	947.15	139.46	780.56	113.14	638.69	88.57	454.71	76.69	426.91	68.19	292.63	122.75	85.11	33.27	89
8	N	731.25	32.75	600.00	46.55	485.00	54.92	357.50	37.08	308.75	9.46	112.25	20.89	37.25	10.90	4
Total		842.14	173.80	697.79	144.97	573.37	121.12	403.74	90.44	397.85	84.55	198.86	134.44	66.07	39.14	431
1993																
1	S	838.41	126.13	695.23	111.83	539.09	73.67	390.91	73.01	392.04	64.45	175.32	76.63	72.32	26.71	22
1	N	656.39	175.46	534.17	160.33	409.72	116.95	282.78	87.16	301.67	91.83	96.50	102.52	42.94	31.30	18
2	S	812.35	153.27	675.29	138.53	524.12	103.11	377.65	82.79	366.47	91.41	147.65	72.94	65.94	35.19	17
2	N	613.48	136.32	499.13	110.77	375.42	87.46	254.78	77.39	284.78	72.59	65.87	42.11	34.35	20.31	23
3	S	773.33	90.66	652.22	71.81	490.55	58.12	349.44	51.63	360.00	45.89	130.33	40.10	54.33	14.32	9
3	N	672.58	141.98	551.61	121.44	418.39	99.21	294.19	73.06	307.74	70.73	82.23	56.96	37.87	20.38	31
4	S	1027.50	10.61	815.00	7.07	627.50	17.68	482.50	38.89	502.50	3.53	241.50	3.53	91.50	17.68	2
4	N	654.33	144.43	515.33	117.48	398.00	106.44	279.83	74.05	313.83	65.08	72.23	55.09	36.40	21.23	30
5	S	932.86	169.33	741.43	129.23	630.95	106.78	441.90	97.59	445.00	84.41	201.76	99.72	93.00	44.59	21
5	N	873.95	117.20	697.10	91.67	589.21	74.78	439.47	70.25	420.79	63.12	159.05	60.49	73.21	26.43	19
6	S	855.50	166.19	724.83	135.44	603.50	109.81	449.50	85.03	404.83	82.53	199.10	138.62	69.53	40.48	30
6	N	667.50	67.87	553.50	60.83	461.50	42.03	341.50	43.40	326.00	40.61	79.00	26.20	33.90	11.54	10
7	S	941.56	160.64	783.91	132.25	639.22	107.25	481.09	87.53	426.87	89.18	252.16	136.26	100.37	45.77	32
7	N	790.00	169.87	632.50	151.11	528.75	98.70	382.50	79.91	353.12	87.17	173.25	140.90	65.12	39.09	8
8	S	1007.97	154.59	873.24	130.33	691.89	100.25	517.30	82.95	455.27	82.03	352.78	162.39	117.49	50.05	37
8	N	778.33	67.14	661.67	56.86	518.33	27.54	370.00	26.46	346.67	28.87	138.00	33.42	54.67	10.02	3
Total		808.62	195.38	668.16	170.56	533.22	143.58	387.28	117.17	375.48	95.61	169.66	134.32	68.03	44.06	312
1994																
1	S	809.67	93.40	705.33	79.97	555.33	68.54	418.67	49.84	403.00	48.17	146.27	48.80	58.33	16.00	15
1	N	628.27	83.26	521.54	77.02	415.00	52.23	305.77	39.99	311.54	39.57	65.19	24.93	29.46	12.02	26
2	S	743.33	141.80	651.67	176.16	478.33	28.43	381.67	89.63	341.67	53.46	124.33	97.57	61.00	39.95	3
2	N	590.42	112.19	483.47	79.02	392.64	61.51	286.11	56.21	285.14	45.46	49.11	23.39	28.61	11.76	36
3	S	845.00	137.46	671.00	143.29	564.00	89.00	422.00	76.46	401.50	59.63	159.10	77.14	68.50	27.22	10
3	N	742.00	126.29	625.17	110.94	500.50	89.51	368.17	70.07	353.17	56.19	103.30	52.33	52.07	20.75	30
4	S	611.67	215.42	567.50	167.95	452.50	141.48	330.00	104.31	339.17	88.74	93.17	72.00	43.00	28.54	6
4	N	559.71	123.32	452.65	103.82	363.53	85.36	255.44	64.52	284.27	61.29	43.94	38.36	24.94	15.63	34
5	S	781.71	86.81	657.56	78.78	536.71	64.20	385.85	43.31	359.76	42.56	125.15	42.75	61.76	17.54	41
5	N	686.79	104.67	584.64	106.53	476.43	84.02	341.07	68.45	316.07	45.92	87.50	41.38	48.93	20.11	14
6	S	804.75	80.82	703.62	72.64	564.87	56.48	421.37	51.91	375.50	41.10	156.75	47.66	60.15	18.26	40
6	N	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
7	S	805.13	117.54	692.50	103.55	553.55	77.42	415.00	60.92	371.84	59.19	147.82	67.73	64.71	28.28	38
7	N	640.00	14.14	515.00	42.43	425.00	7.07	295.00	0.00	292.50	24.75	56.00	4.24	35.00	14.14	2
8	S	865.13	89.42	769.61	79.77	614.23	57.36	458.59	45.98	401.54	51.26	197.03	58.06	77.54	21.51	39
8	N	900.00	0.00	765.00	0.00	640.00	0.00	440.00	0.00	395.00	0.00	161.00	0.00	76.00	0.00	1
Total		733.57	147.39	624.40	137.28	502.00	107.46	369.37	85.70	348.39	65.08	116.34	69.35	52.12	26.00	335

Table 3 *Littorina striata*. Results of a three-way multivariate analysis of variance testing for differences between sampling year (Factor 1), exposure regime (Factor 2), morphotype (Factor 3) and their interactions

Source	Wilks' λ	Rao's R	df 1,2	p-level
1	0.679178	32.22519	14,2114	0.000001
2	0.783444	41.73874	7,1057	0.000001
3	0.785956	41.12280	7,1057	0.000001
1 × 2	0.889282	9.12432	14,2114	0.000001
1 × 3	0.969947	2.32147	14,2114	0.003578
2 × 3	0.985566	2.21139	7,1057	0.031158
1 × 2 × 3	0.979873	1.54290	14,2114	0.088303

between "year" and "morphotype" were significant (Table 3) too, such that the mean value of each variable decreased annually in both morphotypes (nodulose and smooth), as well as in both wave-exposure regimes (lagoon and outside). The interaction between "wave exposure" and "morphotype" was also significant, though less so than both other two-way interactions, indicating

the effect of wave exposure on morphometric differences between both shell forms as shown below in the CDA.

The CDAs provided more detail about the morphometric differences. In the first CDA (Table 4), CV1 accounted for 49.2, 59.6 and 66.2% of the total variation in 1992, 1993 and 1994, respectively. CV1 in the second CDA (Table 5) explained 85% of the total variation. CV1 is, in both analyses, mainly an expression of the aperture height (HA). Since this root consistently separated the lagoon populations from those of the outside (Fig. 5), it suggests a relationship between aperture size and wave exposure in a way that, regardless of morphotype, specimens from the wave-exposed outside have a larger aperture than specimens from the sheltered lagoon (Fig. 6). Yet, within each wave-exposure regime, nodulose specimens have a smaller aperture than smooth ones (Fig. 6). CV2 explained a further 24.7, 30.3 and 22.4% respectively in 1992, 1993 and 1994, while in CDA2 (Table 5) it accounted for an additional 25.8% of the total variation. CV2 appeared to reflect shell shape as expressed by HS, WS and HT (Tables 4, 5). However,

Table 4 *Littorina striata*. Standardized coefficients of the canonical variables in the CDA of the eight sampling sites per year (*HS* shell height; *WS* shell width; *HA* aperture height; *WA* aperture width; *HT* height of shell top; *TW* total weight; *BW* body weight; *Cum.%* cummulative percentage explained variation; *CAN R* canonical correlation coefficient)

	Root 1	Root 2	Root 3	Root 4	Root 5	Root 6	Root 7
1992							
HS	−0.352325	2.57191	0.71988	−0.16291	0.67512	−0.57532	2.92616
WS	−0.347809	−0.13375	0.14275	−0.52789	−3.90923	−0.68701	−1.77769
HA	1.356424	−1.00798	−2.14520	−1.02442	1.41576	0.66569	0.63887
WA	−0.038911	−1.52707	1.65240	0.63535	0.26669	−0.21815	0.55375
HT	−0.861237	−0.26789	−0.24575	1.04920	−0.09210	0.28997	−0.67416
TW	0.906726	0.92811	1.81838	−0.92422	1.40145	0.65734	−1.67148
BW	0.040700	−0.49280	−1.81387	1.64410	0.01610	−1.78230	0.04407
Eigen value	1.086674	0.54660	0.35414	0.14512	0.04335	0.03079	0.00117
Cum.%	0.492189	0.73976	0.90016	0.96589	0.98553	0.99947	1.00000
CAN R	0.721643	0.594493	0.51139	0.35598	0.20383	0.17282	0.03420
p	0.000001	0.000001	0.00001	0.00001	0.00027	0.00988	0.48194
1993							
HS	4.14438	1.50845	4.06251	−1.67792	1.30856	−4.19913	2.26536
WS	1.47712	−3.91611	−1.32790	3.16097	−1.36296	0.05784	−2.24597
HA	−4.13543	1.85073	−1.00048	1.26288	−0.54775	1.79223	2.41350
WA	−1.15395	−0.07935	−0.25351	−1.26670	1.82345	−0.65925	−1.57861
HT	−0.86926	1.42570	−1.72533	−0.51986	−1.94625	1.02213	−1.28181
TW	−0.18000	−1.86321	−0.80170	−1.97580	−0.31145	−0.18157	1.29091
BW	0.10620	0.85476	1.59597	0.80832	0.52791	2.06115	−1.17609
Eigen value	1.91557	0.97402	0.24051	0.03812	0.03554	0.00760	0.00030
Cum.%	0.59644	0.89972	0.97461	0.98647	0.99754	0.99991	1.00000
CAN R	0.81056	0.70243	0.44032	0.19162	0.18526	0.08685	0.01727
p	0.00001	0.00001	0.00001	0.08237	0.16131	0.66467	0.76344
1994							
HS	0.26564	1.24005	−0.78523	−1.16326	−0.23410	0.61717	2.79558
WS	0.32850	−0.25336	−0.31093	−0.01431	0.22234	−2.92472	0.40782
HA	0.95355	0.89193	0.92488	1.11489	2.82537	1.40947	−1.1513
WA	0.58851	−0.61173	−1.43125	−1.66060	−1.60667	0.39386	−1.55779
HT	−1.07906	−0.93396	−0.87933	1.93986	−0.29777	0.00649	−0.83576
TW	0.52710	−2.51999	1.62617	−0.19444	−0.18549	0.85910	1.12585
BW	−0.84025	2.27876	0.76023	0.54997	−1.17947	−0.38215	−0.70671
Eigen value	1.29522	0.43882	0.13160	0.06020	0.02464	0.00443	0.00032
Cum.%	0.66244	0.88688	0.95418	0.98497	0.99757	0.99984	1.00000
CAN R	0.75120	0.55335	0.34102	0.23828	0.15507	0.06637	0.01779
p	0.00001	0.00001	0.00001	0.02698	0.39309	0.81864	0.74782

Table 5 *Littorina striata*. Standardized coefficients of the canonical variables in the CDA, contrasting four shell groups (nodulose outside, nodulose lagoon, smooth outside, smooth lagoon) per year (*abbreviations* see Table 4)

	Root 1	Root 2	Root 3	Root 4	Root 5	Root 6	Root 7
HS	0.76496	−1.69170	1.13680	3.35429	1.12246	0.71747	−0.07559
WS	−0.89827	1.14552	1.55546	−2.43382	0.34268	2.57128	−0.85766
HA	1.51789	0.05055	−2.63626	−0.37054	1.16842	−1.57529	−1.63858
WA	0.49185	1.66807	−0.29092	1.01728	−0.38426	0.50878	1.48883
HT	−0.31953	−0.12542	−1.16406	−0.72462	−1.85831	0.14902	−0.24784
TW	0.98650	−1.79924	0.32775	−0.78335	−0.13129	−0.57122	1.64597
BW	−0.20585	0.72564	1.28530	0.07007	−0.79634	−1.56535	−0.61408
Eigen value	1.10369	0.31480	0.20324	0.04985	0.03566	0.02231	0.00439
Cum.%	0.63652	0.81808	0.93529	0.96404	0.98460	0.99747	1.00000
CAN R	0.72432	0.48931	0.41098	0.21789	0.18556	0.14772	0.06608
p	0.00001	0.00001	0.00001	0.00001	0.00001	0.00528	0.45898

Fig. 5 *Littorina striata*. Graphical representation of the first two CVs, representing the sheltered (*1–4*) and exposed (*5–8*) populations collected in 1992, 1993 and 1994 on Ilheu
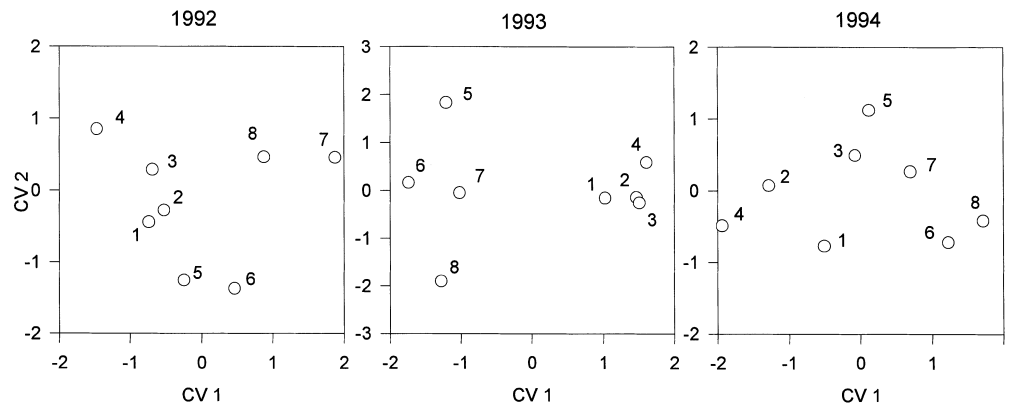
this root did not show a clear pattern at the population level (Fig. 5), but did suggest an annual shape change when the four shell groups were considered (Fig. 7). Whereas in 1992 shells tended to be more elongate and high-spired, they became more and more globose and low-spired in 1993 and 1994 (Fig. 7). Once again there was an exposure effect whereby, regardless of morphotype, specimens from the outside were more globose than specimens from the lagoon (Fig. 7). Although some of the remaining CVs still accounted for a significant
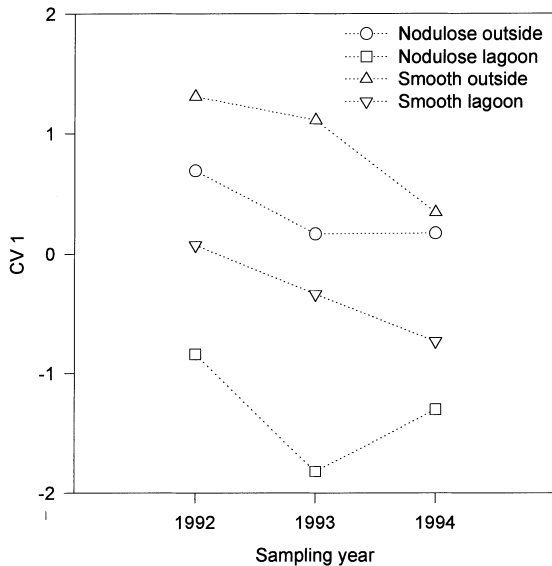
Fig. 6 *Littorina striata*. Graphical representation of CV1 as a function of sampling year for nodulose versus smooth groups outside versus inside the lagoon
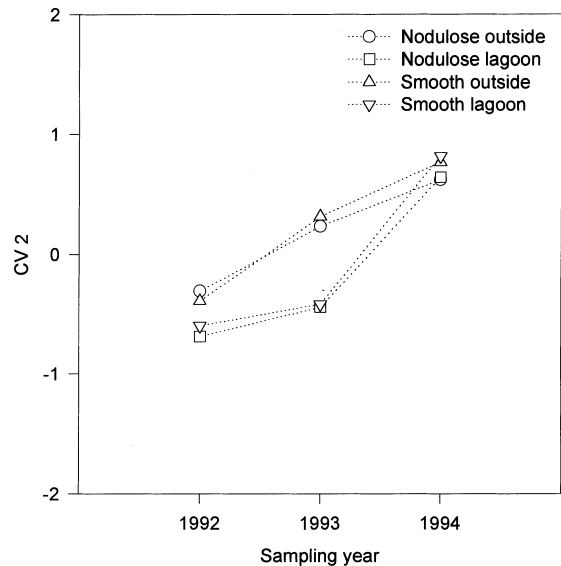
Fig. 7 *Littorina striata*. Graphical representation of CV2 as a function of sampling year for nodulose versus smooth groups outside versus inside the lagoon

Table 6 *Littorina striata*. Mean values and standard deviations of the four transplantation groups (*A* transplant to outside; *B* blanco lagoon; *C* transplant to lagoon; *D* blanco outside) from start and end of the experiment (*S* start; *E* end) for each of the four measured variables (in 10^{-2} mm) (*other abbreviations* see Table 4)

	HS		WS		HA		HT		Recapture %
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
SA	795.67	46.12	664.33	41.68	509.67	31.95	380.17	28.66	100
SB	820.00	60.17	694.17	47.69	534.83	37.29	385.33	33.63	100
SC	939.50	62.72	814.17	48.73	642.50	54.80	423.83	40.78	100
SD	943.33	70.52	833.17	54.34	646.67	39.25	426.67	7.72	100
EA	980.77	69.70	809.61	47.85	693.08	40.18	428.46	42.05	21.66
EB	880.60	55.06	736.87	49.64	617.50	44.48	401.87	32.83	13.33
EC	933.33	53.93	845.00	26.46	685.00	56.79	400.00	32.79	5
ED	925.00	43.01	810.38	38.05	685.77	42.32	415.77	30.61	21.66

part of the total variation, none of them revealed clear morphometric patterns or allowed a straightforward interpretation (Tables 4, 5). Sex-linked morphometric differences were also observed, however they did not alter the results and will be discussed in a forthcoming article.

Transplantation experiment

A summary of the measurements is given in Table 6. The two-way MANOVA showed that both contrasted factors ("transplantation group" and "month") and their interaction contributed significantly to the observed shell variation (Table 7). The results of Scheffé's tests of the differences for aperture height (HA) between the four transplantation groups at the start and the end of the experiment are shown in Table 8. As expected, at the start of the experiment (August), there were no significant differences between groups from the same wave-exposure regime, yet both groups from the outside had a significantly larger aperture than those from the lagoon. Similar significant differences between the groups from the lagoon and the outside were also observed for the

three other measures (not shown, data available upon request). After 5 months (December), however, the differences between the lagoon and the outside groups were no longer significant. Yet, in December, the specimens transplanted from the lagoon to the outside (Group A) had a significantly larger aperture than in August before their transplantation, while the three other experimental groups (i.e. B, C and D) did not reveal significant morphometric differences between the start and the end of the experiment.

A more detailed picture of the transplantation results was obtained with a CDA (Table 9) and subsequent plotting of the mean values for CV1 as a function of time (Fig. 8). As in the previous CDAs, CV1 mainly reflected aperture height (Table 9), thus discriminating between lagoon and outside groups in August (Fig. 8). Starting from the second month (September), the value of CV1 decreased drastically for the specimens transplanted from the lagoon to the outside and became negative in November and December. It thus assumed a value comparable to that of specimens that originated from the outside. In contrast, CV1 did not change markedly in any of the other three transplantation groups, even though in all cases its value decreased consistently and more or less proportionally (Fig. 8). Unfortunately, after 5 months the experiment had to be stopped because of insufficient recapture numbers (A = 21.7%; B = 13.3%; C = 5%; D = 21.6%) in December.

Table 7 *Littorina striata*. Results of a two-way multivariate analysis of variance testing for differences between transplantation group (Factor 1), month (Factor 2) and their interaction in the transplantation experiment

Source	Wilks' λ	Rao's R	df 1,2	p-level
1	0.329280	34.51419	16,1259	0.000001
2	0.421675	35.06732	12,1090	0.000001
1 × 2	0.577573	5.07029	48,1589	0.000001

Discussion

Our results show that: (1) nodulose shells are more common in the sheltered lagoon, whereas smooth specimens predominate on the wave-exposed outside of the

Table 8 *Littorina striata*. Results of Sheffé's tests, for differences in aperture height among populations between start and end of the transplantation experiment (*S* start; *E* end) for experimental and blanco groups (*A* transplant to outside; *B* blanco lagoon; *C* transplant to lagoon; *D* blanco outside)

	SA	SB	SC	SD	EA	EB	EC	ED
SA								
SB	0.99823							
SC	0.00001	0.00001						
SD	0.00001	0.00001	1.0000					
EA	0.00001	0.00001	0.77322	0.88692				
EB	0.00116	0.13004	0.99999	0.99997	0.57472			
EC	0.00017	0.00893	0.99998	0.99999	1.0000	0.99759		
ED	0.00001	0.00001	0.94172	0.98047	1.0000	0.77746	1.0000	

Table 9 *Littorina striata*. Standardized coefficients of the canonical variables in a CDA of the eight populations involved in a transplantation experiment in August (start experiment) and December (end experiment) (*abbreviations* see Table 4)

	Root 1	Root 2	Root 3	Root 4
HS	0.87901	0.24919	−2.94150	−1.32687
WS	−0.78020	−1.96589	0.57690	−0.14328
HA	−0.91596	1.71808	1.02805	0.47583
HT	−0.06822	0.00420	1.10980	1.78360
Eigen value	2.75408	1.07440	0.24102	0.08076
Cum.%	0.66359	0.92247	0.98054	1.00000
CAN *R*	0.85651	0.71967	0.44069	0.27336
p	0.00001	0.00001	0.00001	0.00793
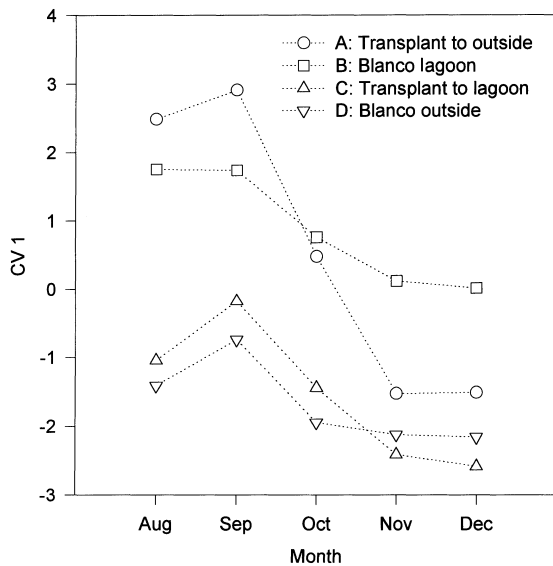
Fig. 8 *Littorina striata*. Transplantation experiment: graphical representation of CV1 as a function of time

crater; (2) on the outside there is a tendency for nodulose shells to be more common higher up the shore, while smooth shells dominate at lower shore levels; (3) nodulose specimens are smaller and weigh less than smooth ones; (4) regardless of morphotype, specimens from the lagoon are less globose, smaller and have a smaller aperture than those from the outside; (5) within the lagoon or the outside, nodulose specimens have a smaller aperture than smooth ones; and (6) overall shell size decreased gradually over the 3 years, and over the same period shell shape changed from rather elongate to more globose.

Considering the heterogeneous environmental microgeographical conditions at Ilheu, we expect that the nonrandom distribution of morphotypes and the overall morphometric differentiation of *Littorina striata* reflect alternative functional strategies. There is some controversy about the description and interpretation of the sculptural polymorphism in *L. striata* (Reid 1996). According to some authors (Rosewater 1981; Britton 1995) nodules on the shell surface can be regarded as a juvenile characteristic, as nodules on the spire whorls are re-

placed on subsequent whorls by spiral striae. However, Reid (1996) has shown that the degree of nodulation does not normally change appreciably during growth. Instead he found nodulose shells to attain smaller sizes than smooth shells (Reid 1996). Our data confirm his results. Moreover, nodulose specimens have fully developed adult genitalia just as often as smooth specimens (DeWolf personal observations). Hence, nodulosity does not seem to be a strictly age-related trait.

Alternatively the development of nodules could be regarded as a method of shell reinforcement improving protection against predation. This is however unlikely since there was no indication of intense crab or fish predation at Ilheu (De Wolf personal observations). Therefore, we tentatively interpret the presence of nodules as having a thermoregulatory function (Vermeij 1973; McMahon 1990), because littorinids are supposed to reduce heat stress by minimizing the contact between shell and substrate, and by maximizing reflectance and convection from the shell surface (Vermeij 1973). The presence of nodules would then imply an increase of the reflectance and convection surface of the shell, while the area for solar heat absorption would remain the same (Vermeij 1973). Nodulose shells should therefore have a functional advantage over smooth ones on shores experiencing higher thermal loadings (Britton 1995). This could provide a functional explanation for the abundance of nodulose shells in the lagoon, where the (near) absence of wave action may provoke higher thermal stress. Outside the lagoon, on the contrary, shells may be cooled by evaporation of the water that is repeatedly splashed on the shell surface. This scenario is consistent with the tendency of smooth shells to be more abundant at the lower shore levels on the outside, where wave exposure is much stronger and more permanent. Similarly Britton (1995) found nodulose shells to be more abundant on a black basaltic shore heated by the sun, and less common on shores with paler rocks. Conversely, on wave-exposed shores we expect nodulose specimens to be disadvantageous. As shown by Denny (1988), surface irregularities increase drag. Nodulose specimens are therefore less favoured on wave-exposed shores compared to smooth specimens, particularly as they have a smaller aperture and thus have a less efficient holdfast onto the substrate.

Besides evaporation of water at the shell surface, littorinids may also regulate their thermal regime by evaporative tissue water loss. Britton (1995) suggested that in this respect both morphotypes of *Littorina striata* do not differ significantly. Yet, these results are not unequivocal because Britton (1995) determined total dry weights as the sum of shell and body weight. Given the differences in weight and in aperture morphology between nodulose and smooth *L. striata*, we suggest that both morphotypes may in fact show differential evaporative tissue water loss. Similarly, Vedel and Depledge (1995) found that the heat coma tolerances of nodulose and smooth *L. striata* do not differ significantly (nodulose: 44.52 °C; smooth: 44.63 °C). Yet, these results also

require further testing since they were determined on animals that were kept permanently in water, an artifical thermal situation not encountered in the lagoon or the upper shore levels, where the periwinkles rarely remain submerged. Given the assumption that the nodules may function as reflectance surface in open air, we suggest that thermoregulation should be determined under these conditions too.

Aperture size in many gastropod species has been shown to vary with the degree of wave exposure (Vermeij 1978). Generally specimens from wave-exposed shores tend to have a larger aperture size, compared to wave-sheltered specimens, enabling them to develop a larger foot which in turn provides a better holdfast onto the substrate (Heller 1976; Vermeij 1980; Raffaelli 1982; Grahame and Mill 1986; Gibbs 1993). This is clearly advantageous on wave-exposed shores, such as the outside of Ilheu, because a better holdfast reduces the probability for dislodgement by waves. Aperture size differences between outside and lagoon specimens have been shown on many occasions (Tables 4, 5, 7), and its functional significance is supported by the transplantation experiment, which showed that specimens removed from the lagoon to the outside changed their aperture size accordingly. Similar apertural size variations in relation to wave exposure have been reported for *Littorina obtusata*, *L. mariae* [now *L. fabalis*] (Reimchen 1974), *L. nigrolineata* [now *L. compressa*] (Naylor and Begon 1981), *L. saxatilis* (Raffaelli 1982), *Nucella lapillus* (Crothers 1985) and *Gibbula cineraria* (Frid and Fordham 1994). Conversely, the smaller aperture size of specimens from the lagoon may be advantageous because it reduces the contact between shell, foot and substrate, thus further minimizing heat stress. The aperture size difference between nodulose and smooth specimens of the same exposure regime may also be functional, the larger weight of the smooth shells requiring a better holdfast and hence a larger foot.

Big, smooth specimens with large apertures thus predominate on wave-exposed shores where the probability for dislodgement is high, whereas small, nodulose shells predominate on dark rocks heated by the sun (Britton 1995), at wave-sheltered shores and at the highest tidal levels, i.e., those situations were heat and desiccation stress are likely to be the most severe (Reid 1996). Aperture size and the presence or absence of nodules may therefore have a functional value, though further experimental evidence is needed. Although wave and heat stress suggest a possible function for the observed shell variation, it does not explain the underlying mechanism responsible for it. An ecophenotypic effect, for example arising from differential growth rates between lagoon and outside specimens, could account for the observed shell patterns, as suggested by Reid (1996). As shown in other *Littorina* species (Gaillard 1965; Boulding et al. 1993), sculpture could be a function of growth rate, while the influence of growth rate upon shape may possibly be a consequence of geometrical constraints (Vermeij 1980), though there are conflicting reports on the connection between growth rate and shape (i.e. Spight 1973; Kemp and Bertness 1984). Specimens occupying shores where algal food is less abundant and/or opportunities for feeding limited should grow more slowly and attain smaller sizes (Reid 1996). As a consequence and possibly due to a continuous calcium deposit, nodules could be developed. The fact that lagoon specimens are smaller than outside specimens could suggest a differential growth rate between the outside and the lagoon. The slower-growing lagoon specimens might more often develop nodules, whereas, the faster-growing outside specimens remain smooth and develop a larger aperture size due to allometric growth. Alternatively the shell variation could also be the result of natural selection. Concerning the aperture size variation, the results of the transplantation experiment were compatible with both alternatives, as it was not possible to decide unequivocally whether the aperture size increase of the specimens transferred from the lagoon to the outside was due to an increased growth rate or to selection against specimens with smaller apertures. Yet, as the recapture percentage of the specimens transferred from the lagoon to the outside was high compared to that of the other transplantation groups, and since these three other groups also showed a steady, but much less pronounced apertural size increase over the same period (i.e. reflecting normal growth), we tentatively suspect that aperture size may be an ecophenotypically plastic feature produced by allometric growth. This situation would be similar to that observed in *Nucella lapillus* (Etter 1988). For the other features discussed here (sculpture and overall shell size and shape), the underlying mechanisms are more obscure, though other authors (Etter 1988; Reid 1996), with the exception of Struhsaker (1968), opted to explain intraspecific shell variability in planktonic developing prosobranchs in terms of ecophenotypic plasticity too. Yet, if natural selection is responsible for the morphological heterogeneity, then one should expect population genetic differentiation. If phenotypic plasticity is at work, no population genetic differentiation is to be expected. This latter strategy is probably more advantageous for a widely distributed species with planktonic development. Nevertheless, given the solid nature and irreversible growth of shells, it must be clear that plasticity, if it occurs, cannot work in all directions (e.g. large shells cannot become small again). Hence it seems possible that the microgeographic morphological heterogeneity in *Littorina striata* at Ilheu is the result of combined effects of plasticity and selection.

Altogether, in contrast to the expectations for a planktonic developing species, *Littorina striata* displays a considerable, well-structured and consistent degree of microgeographic morphological heterogeneity, which is to a large extent comparable with morphological patterns described in intertidal prosobranchs that do not have a planktonic development. Although the morphological heterogeneity in *L. striata* at Ilheu can be interpreted in functional terms, it remains to be decided

which mechanisms, i.e. natural selection or phenotypic plasticity, are responsible for the observed patterns. Therefore, in a forthcoming study we will use allozymes to evaluate whether the morphological heterogeneity reported here is accompanied by a population genetic differentiation and whether the smooth and nodulose morphs share a common gene pool.

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