

Morphometric diversity of the pulmonate limpet *Siphonaria lessoni* in different coastal environments*

ALEJANDRO TABLADO and JUAN LÓPEZ GAPPA

Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo 470, Buenos Aires C1405DJR, Argentina. E-mail: tablado@mail.retina.ar, lgappa@mail.retina.ar

SUMMARY: *Siphonaria lessoni* (Blainville, 1824) is the most abundant marine gastropod in the rocky intertidal zone of Buenos Aires Province, Argentina. The morphology of this species was studied in 6 sites near the city of Quequén, differing in intertidal height and degree of exposure to wave action and pollution. Shell length, width, height, and the distance from apex to posterior shell margin were measured, as well as the dry weight of both the shell and limpet body. A data matrix of 600 individuals (100 limpets per site) by 6 variables was analyzed by Principal Component Analysis (PCA) and Discriminant Analysis (DA) in order to compare size and shape differences among sites. As expected, axis I of the PCA explained a very high percentage (87.7 %) of total variance, and can be interpreted as a size factor. Axis II, which summarised 6.9 %, may be regarded as expressing shell shape. Limpets not exposed to wave action within Quequén Harbour showed the highest values in all variables, whereas individuals living within the *Brachidontes rodriguezii* (d'Orbigny, 1846) community were very small and highly variable. Limpets heavily exposed to sewage at mid intertidal levels had a subcentral shell apex and were relatively very low. Classification of individuals by DA showed that the most characteristic morphology corresponded to limpets living at mid intertidal level close to a sewage outfall, or within Quequén Harbour (94 and 97 % correct reallocations, respectively). The influence of different physical and biotic factors on the morphology of *Siphonaria lessoni* is discussed.

Key words: *Siphonaria lessoni*, limpet, size, shape, intertidal, Argentina.

INTRODUCTION

Siphonaria lessoni (Blainville, 1824) is the only pulmonate limpet inhabiting the rocky intertidal zone of Buenos Aires Province, Argentina (Olivier and Penchaszadeh, 1968). In South America, it occurs from Perú to Cape Horn in the Pacific Ocean and along the shores of Argentina and Uruguay and the Malvinas (Falkland) Islands in the Atlantic Ocean (Castellanos *et al.*, 1993). *S. lessoni* is one of the most abundant species at intertidal and littoral fringe levels, although it has also been found subti-

dally (Bastida *et al.*, 1971). At mid- and low-intertidal levels it co-occurs with the dominant space competitor, the mytilid bivalve *Brachidontes rodriguezii* (d'Orbigny, 1846) (Olivier *et al.*, 1966; Penchaszadeh, 1973). *S. lessoni* feeds mainly on microscopic algae, spores and germlings of seaweeds such as *Ulva* and *Enteromorpha* (Bastida *et al.*, 1971) and macroalgae (Godoy and Moreno, 1989; Moreno and Jaramillo, 1983). Its foraging pattern seems to be controlled mainly by substratum humidity. Activity begins when the limpets are exposed by the ebbing tide and ends when the substratum dries up (López Gappa *et al.*, 1996). *S. lessoni* does not show homing behavior in environ-

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ments exposed to wave action (Olivier and Penchaszadeh, 1968; López Gappa *et al.*, 1996). The reproductive cycle of this species includes dispersal by means of a planktonic larval stage (Olivier and Penchaszadeh, 1968), which suggests large scale genetic homogeneity in the pool of individuals recruited each year to the intertidal zone (Johnson and Black, 1984). Therefore, *S. lessoni* may be regarded as an adequate model for the study of environmental influences on morphology.

The influence of vertical distribution and other environmental factors on shell size and morphology have been studied in several intertidal limpets. A remarkable size increase from low- to high-shore levels has been recorded in *S. lessoni* (Olivier and Penchaszadeh, 1968). In Bahía Creek (San Matías Gulf, Argentina), Martín and Estebenet (1993) found that individuals of *S. lessoni* were relatively taller at high- than at low-intertidal levels. In a population of this species growing in a protected environment within Mar del Plata harbour, shell height was relatively greater than in limpets from natural habitats (Bastida *et al.*, 1971).

Based on a comprehensive literature review, Vermeij (1972) concluded that size increases with intertidal height in limpet species inhabiting high shore levels. In *Patella vulgata* Linné, 1758 and *P. aspera* Lamarck, 1822, limpets are relatively taller at high- than at low-intertidal levels (Ebling *et al.*, 1962). Shell heights in *Notoacmea birradiata* (Reeve, 1855) (López, 1995) and *Nacella (Patinigera) macquariensis* Finlay, 1927 (Simpson, 1985) were taller in exposed than in protected areas. The same phenomenon, together with an increase in shell size and volume, was also observed in *N. (P.) deaurata* (Gmelin, 1791) (Morriconi and Calvo, 1993). Greater sizes and growth rates in the vicinity of sewage effluents were observed in *Patella vulgata* (Fischer-Piette, 1948) and *S. lessoni* (Tablado *et al.*, 1994). *Siphonaria pectinata* (Linné, 1758) reached greatest size in habitats where the seaweeds *Ulva* and *Enteromorpha* were present (Voss, 1959). Hobday (1995) showed in *Lottia digitalis* (Rathke, 1833) that body size increases with intertidal height in areas with high or intermediate exposure to wave action. In the tropical limpet *Cellana radiata* (Born, 1780), individuals inhabiting protected environments were relatively larger, more depressed, and with thicker shells than those from exposed habitats, and limpets from high-shore levels were relatively smaller, taller, heavier and with thicker shells than those from low-intertidal levels (Balaparameswara Rao and Ganapati, 1971).

Growth studies in natural habitats and field experiments involving reciprocal translocation of limpets between the *B. rodriguezii* community and areas heavily affected by sewage pollution, showed a remarkable phenotypic plasticity in *S. lessoni* (Tablado *et al.*, 1994). The aim of the present study is to analyze in more detail the relationship between habitat and morphometric diversity in shell size and shape by means of multivariate statistical methods.

MATERIAL AND METHODS

Siphonaria lessoni was sampled in two areas near the city of Quequén, Argentina (38° 34-35'S, 58° 38-42'W): the eastern breakwater of Quequén Harbour and a site known as Carballido, located 4 km eastwards from the harbour (Fig. 1). Two unequal tides occur daily, with mean amplitude of 1.28 m during spring tides and 0.91 m during neap tides.

Quequén Harbour is located at the mouth of Quequén Grande River and is protected by two breakwaters built of granite rocks and concrete blocks. The water within the harbour is typically estuarine. Temperature varies from 8°C in winter to 22.5°C during summer. Salinity values range from 33‰ (a typical value for seawater in the study area) at high tides to 2.5‰ during low tides with strong freshwater input from Quequén Grande River (Bastida and Brankevich, 1980).

The shoreline east of Quequén Harbour consists of a cliff 7-8 m high with a narrow sand strip often present at its base. The intertidal zone is composed of horizontal loess platforms separated by irregular breaks of 40-60 cm height. Grooves lying perpendicular to the shoreline are common at low-intertidal levels. The whole area is exposed to heavy wave action. Salinity ranges from 20 to 33 ‰ due to the influence of estuarine water flowing eastwards from Quequén Grande River, and is also influenced by an outfall discharging *ca.* 14.000 m³.d⁻¹ of untreated sewage from the cities of Necochea and Quequén. Most of the rock surface at the littoral fringe and high intertidal levels is covered by a thin dark layer of crustose lichen (probably *Verrucaria* sp.). A more detailed description of the area and its benthic community structure can be found in López Gappa *et al.* (1990, 1993).

Samples of *S. lessoni* were obtained from six different sites within these two areas (Fig. 1):

Harbour Protected (HP): upper intertidal zone on the inner side of the eastern breakwater, within Que-

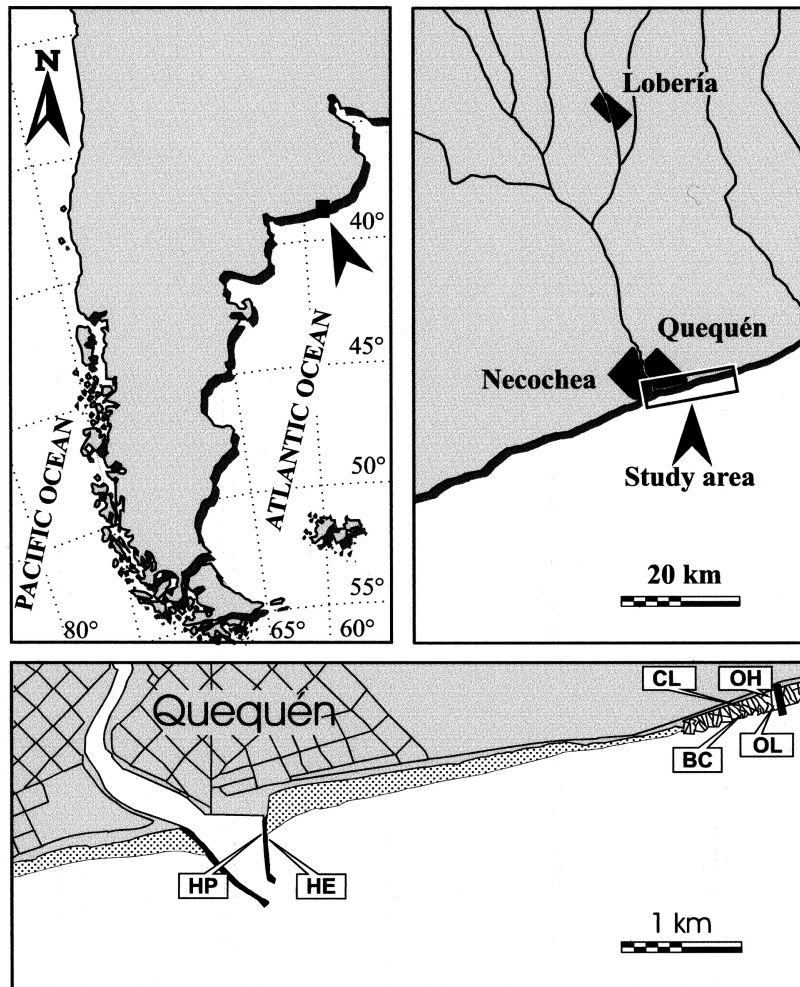


FIG. 1. – Study area showing location of the six sites where samples of *Siphonaria lessoni* were collected. Site codes: OL, Outfall Low; OH, Outfall High; HE, Harbour Exposed; HP, Harbour Protected; CL, Cliff; BC, *Brachidontes* Community.

qué Harbour. It was the only habitat completely protected from wave action. Rocks and concrete blocks were covered mainly by the seaweed *Enteromorpha compressa* (Linné) Greville in Harvey, 1849. The most frequent macrofaunal organisms accompanying *S. lessoni*, were the barnacle *Balanus amphitrite* Darwin, 1854 and the decapod *Cyrtograpsus angulatus* Dana, 1851.

Harbour Exposed (HE): upper intertidal zone on the outer side of the eastern breakwater, a few metres away from HP, but exposed to heavy wave action.

Outfall Low (OL): loess platforms at mid-intertidal levels, close to the sewage outfall. The area is heavily impacted by raw sewage and is dominated by blue-green algae. The *Brachidontes rodriguezii* community is absent (see López Gappa *et al.*, 1990).

Outfall High (OH): similar to OL but on vertical loess walls at the littoral fringe.

Brachidontes Community (BC): mid-intertidal zone, 250 m westwards of the sewage outfall. Samples were taken from the characteristic rocky intertidal community of Buenos Aires Province, dominated by the mytilid *Brachidontes rodriguezii* (see López Gappa *et al.*, 1990).

Cliff (CL): littoral fringe; a few metres away from BC but on vertical walls at the base of the cliff.

The first 100 limpets visible to the naked eye were collected around a randomly determined point at each site on December 12, 1993. Shell length, width, height, and the distance from apex to posterior shell margin were measured to the nearest 0.1 mm with a micrometer eyepiece under a binocular microscope (see Fig. 2). The soft parts and shells were oven dried for 48 h at 60°C and weighed to the nearest 1 mg on an electronic balance. Shell volume was not used as a variable, since a preliminary analysis showed that it provid-

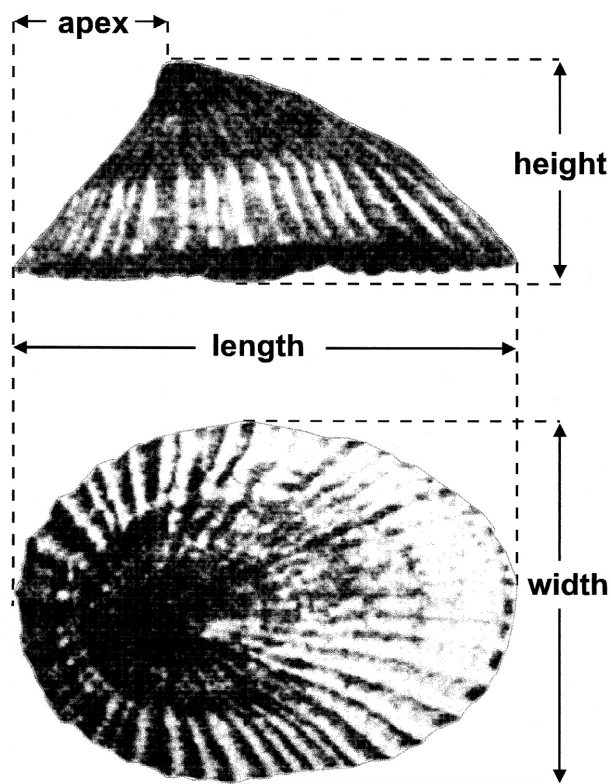


FIG. 2. – *Siphonaria lessoni* in lateral and top view, showing schematically how measurements were taken on the shell.

ed redundant information, highly correlated with length, width and height data.

A basic data matrix containing untransformed data of 6 sites by 6 variables was analyzed by Principal Component Analysis (PCA) using the BMDP statistical package (Dixon, 1981). New orthogonal axes are obtained by this analysis, which are linear combinations of the original variables. PCA was used as a descriptive tool to reduce data dimensionality. As expected (see Results), a high correlation was found among most morphometric variables, with the first PCA axis summarizing a high proportion of the variance among individuals (Somers, 1986). Therefore, individual scores on the first PCA axis were used as a new variable in order to compare “size” differences among sites (see Bookstein, 1989). The non-parametric Kruskal-Wallis test was used for this comparison, since variances remained heterogeneous even after trying several data transformations (Sokal and Rohlf, 1981).

Raw data were also processed by Discriminant Analysis (DA), using the NTSYS-pc package (Rohlf, 1992). Unlike PCA, this analysis maximizes the variance among groups of individuals defined *a priori* (sites). The discriminant functions obtained by this method were then used to reallocate the indi-

TABLE 1. – *Siphonaria lessoni*, descriptive statistics of 6 morphometric variables in samples from 6 intertidal environments at Quequén, Argentina. Apex: distance from apex to posterior margin of the shell.

		Length (mm)	Width (mm)	Height (mm)	Apex (mm)	Dry weight (mg)	Shell weight (mg)
OH	Mean	13.6	10.0	5.5	3.4	45.9	143.7
	Maximum	17.4	13.2	9.2	5.1	86.3	312.5
	Minimum	10.4	7.3	3.2	0.9	15.6	48.0
	S.D.	1.64	1.25	1.08	0.76	18.17	56.52
OL	Mean	14.9	11.3	5.0	4.5	35.3	170.8
	Maximum	18.1	14.0	6.9	6.5	67.3	572.9
	Minimum	12.1	8.4	3.6	3.1	17.8	89.7
	S.D.	1.38	1.20	0.62	0.73	9.59	60.99
CL	Mean	10.1	7.5	4.5	1.8	23.1	68.4
	Maximum	13.7	11.0	7.2	3.5	73.9	205.6
	Minimum	5.7	3.9	2.0	0.1	2.5	8.1
	S.D.	1.63	1.31	1.03	0.70	13.26	37.31
BC	Mean	6.5	4.5	2.5	1.2	8.8	17.4
	Maximum	14.4	10.2	7.3	2.9	74.6	176.5
	Minimum	3.9	2.8	1.5	-0.5	1.3	3.7
	S.D.	2.37	1.59	1.18	0.67	11.57	22.49
HP	Mean	16.1	12.6	8.6	4.9	71.6	271.9
	Maximum	20.2	16.4	11.6	7.2	142.8	541.2
	Minimum	12.2	9.3	5.7	2.4	27.2	105.4
	S.D.	1.67	1.32	1.32	0.95	20.84	107.28
HE	Mean	9.4	6.8	3.8	1.5	12.4	50.7
	Maximum	13.3	9.4	6.3	3.2	30.6	147.8
	Minimum	7.2	4.9	2.5	0.5	5.0	15.2
	S.D.	1.01	0.78	0.61	0.49	4.26	22.98

viduals, showing the degree of overlap among groups. The aim of this analysis is to find out whether limpets of unknown origin can be allocated with a fairly high degree of confidence to a certain habitat, taking into account only their morphological features.

RESULTS

Descriptive statistics of 6 morphometric variables at the 6 sites are shown in Table 1. Site HP had the highest mean values of all 6 variables, while BC showed always a very high variance and lower mean values than the other sites.

Figure 3 shows a graphic summary explaining the morphometric features of the 6 sites sampled in the present study. Limpets collected in HP and CL can be distinguished by their very high shells (height/length relationship: 0.53 and 0.45, respectively), while those heavily exposed to sewage at mid-intertidal levels had very low shells (OL, height/length relationship: 0.34).

Contributions of each of the 6 variables to PCA axes I to III are shown in Table 2. The first and second axes explained together 94.6% of total variance (axis I: 87.7%, axis II: 6.9%). Ordination of limpets on the first two PCA axes is shown in Figure 4. Since axis III explained just 2.2% of the variance, and shows no strong correlations with any of the variables, it has been interpreted as expressing error and will not be discussed hereafter. All variables had positive and very high contributions to axis I, which can be interpreted as a size factor. Moreover, the 6 morphometric variables were positively correlated between each other, and most of the variance among limpets was related to differences in size.

The non-parametric Kruskal-Wallis test of the PCA individual scores on axis I ($H = 496.8$, $p < 0.001$) and *a posteriori* comparisons (Duncan's test, $p < 0.01$ in all cases) showed that size differences among all sites were highly significant: $HP > OL > OH > CL > HE > BC$ (Table 1, Fig. 3).

Axis II of PCA may be interpreted as expressing shell shape. Distance from apex to posterior margin, height and dry weight were the variables contribut-

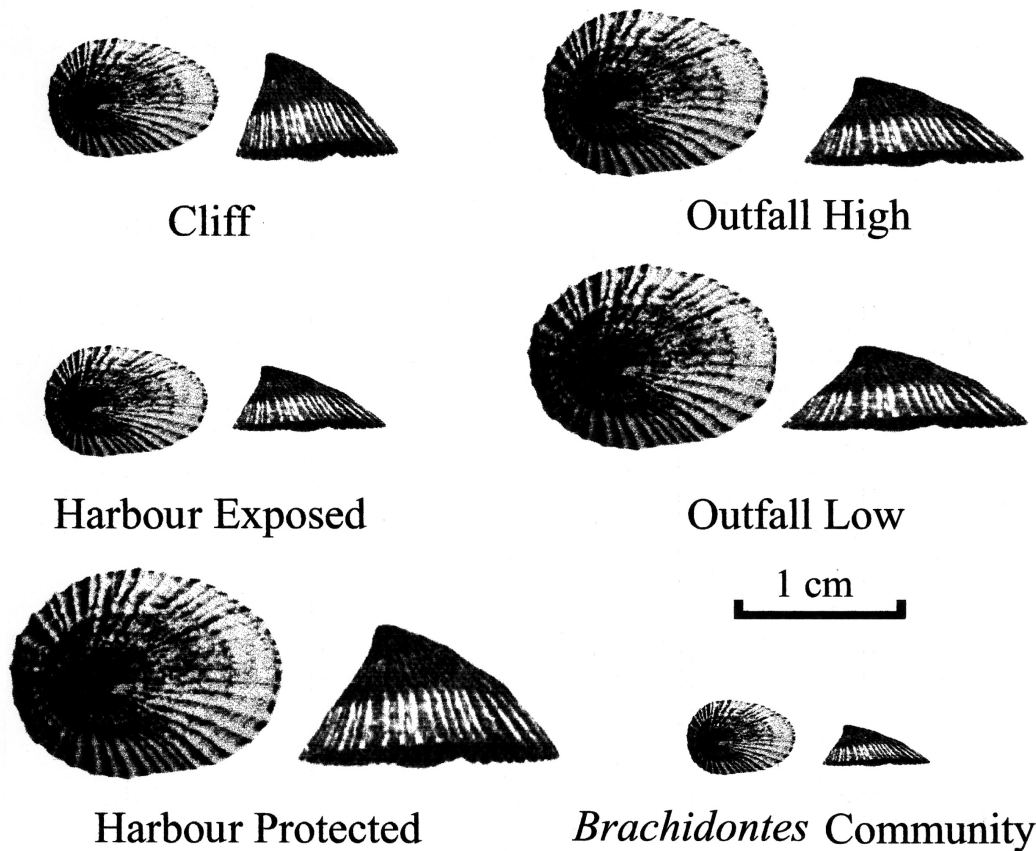


FIG. 3. – *Siphonaria lessoni* in lateral and top view, showing schematically the morphometric variations of the shell in the six sites analyzed in the present study. Each limpet scheme represents mean values for the variables length, width, height and distance from apex to posterior shell margin, taken from Table 1, and was prepared by stretching the same original figure to adequate proportions.

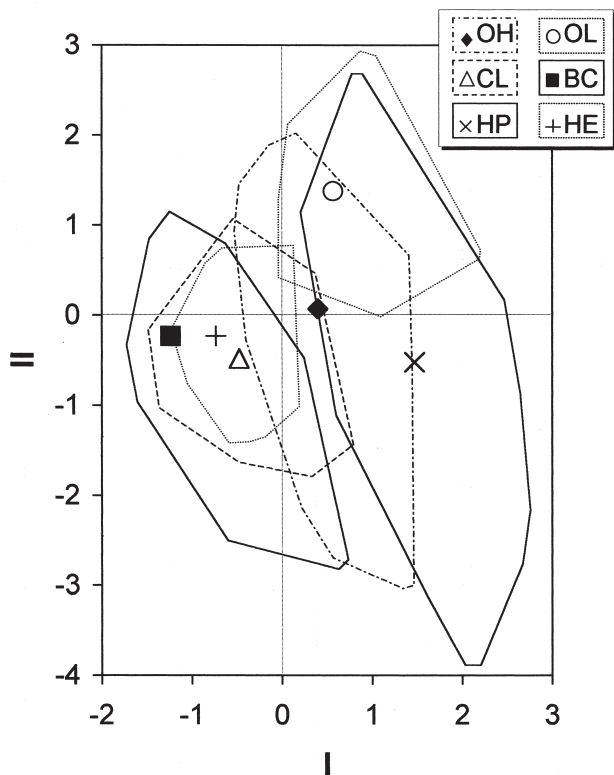


FIG. 4. – Principal Component Analysis of 600 *Siphonaria lessoni* individuals. For clarity, only mean values and lines connecting the most extreme individuals for each site are shown. Site codes as in Figure 1.

TABLE 2. – Principal Component Analysis (PCA). Contribution of each variable to the first three PCA axes. Apex: distance from apex to posterior margin of the shell.

	Axis I	Axis II	Axis III
Length	0.970	0.114	-0.189
Width	0.975	0.110	-0.164
Height	0.934	-0.281	-0.049
Apex	0.859	0.473	0.150
Dry weight	0.933	-0.259	0.077
Shell weight	0.942	-0.129	0.199

ing most to this axis, the latter two negatively (Table 2). Although Figure 4 shows some degree of overlap among different sites, all the limpets from OL had positive values on axis II, indicating low shells with a subcentral apex. HP and HE were the sites showing highest and lowest dispersion of scores on axis II, respectively. Only the plots of CL and OH overlap in part with those of all other habitats.

Analyzing each site separately, a significantly negative correlation ($p < 0.01$) between individual scores on both axes was found in HP ($r = -0.583$), OH ($r = -0.484$), BC ($r = -0.428$) and CL ($r = -0.329$). This correlation is absent, however, in OL

TABLE 3. – Classification of 600 individuals of *Siphonaria lessoni* by Discriminant Analysis. Limpets correctly allocated to their respective sites appear along the diagonal. Site codes as in Figure 1.

	Classification after discriminant analysis						
	OH	OL	CL	BC	HP	HE	
Original classification	OH	79	12	7	0	2	0
OL	6	94	0	0	0	0	
CL	7	0	65	7	2	19	
BC	1	0	7	89	0	3	
HP	1	2	0	0	97	0	
HE	1	0	11	1	0	87	

and HE ($r = 0.139$ and -0.114 respectively, NS). Taking into account that axis I can be regarded as a size factor, this implies that at least in some habitats, shells become relatively higher and with the apex displaced towards the posterior shell margin as limpets grow.

The discriminant function correctly reallocated 85.2% of the limpets (Table 3). Individuals collected within the harbour (HP) and at low-intertidal levels around the outfall (OL) had the most characteristic morphologies, showing 97% and 94% correct reallocations, respectively. The discriminant function assigned three limpets from the harbour environment (HP) to sites affected by sewage pollution (OL and OH). Conversely, most of the wrongly classified limpets (12) from OH were regarded as belonging to OL by the discriminant function. Discrimination was poor for limpets collected at the cliff (CL), with only 65% correct reallocations, 19% limpets classified as HE and most of the remaining individuals classified as OH or BC. Similarly, 25 limpets from other sites were wrongly assigned to CL. While the very small limpets from the *Brachidontes* community (BC) were correctly interpreted as belonging to this site, the largest individuals were wrongly allocated to the cliff (CL) and to the exposed side of the harbour (HE).

DISCUSSION

As expected, the most important morphometric difference among sites was size. The percentage of variance explained by the first PCA axis (87.7%) was remarkably high. It is well known that the littoral fringe individuals of *S. lessoni*, living in areas of low density, have a much greater size than intertidal ones (Olivier and Penchaszadeh, 1968). This

phenomenon could be observed in the present study by comparing sites BC and CL. Wave exposure is similar at both sites, which are separated by just a few metres, but there is an important difference in shore level, since the *Brachidontes rodriguezii* community (BC) is located at mid-intertidal level, and the base of the cliff (CL) at the littoral fringe. Intraspecific competition is also quite different at both sites, since population density is much higher within the *Brachidontes rodriguezii* community than at high-intertidal levels (Olivier and Penchaszadeh, 1968; Tablado *et al.*, 1994). Mean length was 55% higher in CL (10.1 mm) than in BC (6.5 mm) and just 7% of the limpets were misplaced between each other by the discriminant function (Table 3). Studies based on marked and recaptured individuals showed that very small limpets from the *Brachidontes rodriguezii* community grew rapidly when they were presumably swept away by waves to high-intertidal levels with low population density, whereas limpets that remained in the same habitat did not experience significant growth (Tablado *et al.*, 1994).

In addition to differences in shore level, organic enrichment may be another factor contributing to the size differences among sites. Fischer-Piette (1948) recorded high growth rates in limpets living in the vicinity of a sewage outfall, and Tablado *et al.* (1994) observed significantly higher growth rates in limpets translocated from the *Brachidontes rodriguezii* community to a polluted area, than in controls. Interestingly, limpets from the vicinity of the sewage outfall were an exception to the general trend of increasing size toward higher levels (Vermeij, 1972), since limpets in OL were greater in size than in OH (Table 1). This could be related to several factors: (a) Greater foraging space due to the absence of the *Brachidontes rodriguezii* community in areas heavily impacted by organic enrichment (López Gappa *et al.*, 1990), (b) Lower densities of limpets than in natural areas at a similar shore level (Black, 1977; Tablado *et al.*, 1994), and (c) More foraging time at mid- than at high-shore levels (López Gappa *et al.*, 1996).

Size of limpets inhabiting the vicinity of the sewage outfall (OH and OL) was only exceeded by those of limpets living within the harbour (HP) (Table 1, Fig. 3). Harbour environments are usually affected by a wide variety of pollutants (hydrocarbons, heavy metals, organic matter, etc.), and are almost completely protected from wave disturbance. Both factors limit the development of characteristic communities dominating space in natural intertidal

areas. Within Quequén Harbour hard substrata are dominated by highly opportunistic seaweeds (mainly *Enteromorpha* sp.). Tablado *et al.* (1994) showed that *S. lessoni* grows at a much lower rate in an intertidal environment than on an experimental raft moored by Bastida *et al.* (1971) in a neighboring harbour. This phenomenon is related to a remarkable morphometric difference observed in the present study, namely the sharp contrast between the limpet populations sampled inside and outside Quequén Harbour's breakwater (HP, HE). Both groups of limpets were found at a similar intertidal level, separated by just a few metres, but mean shell length was 71% greater within than outside the harbour (Table 1, Fig. 3). As discussed below, it can reasonably be supposed that this difference is mainly related to environmental factors, rather than to age. An increase in size observed when translocating *Lottia digitalis* (= *Colisella digitalis*) and *Colisella scabra* (Gould, 1846) from an exposed to a protected environment was attributed by Brown and Quinn (1988) to the availability of longer foraging periods due to the absence of wave disturbance.

Axis II of PCA explains a relatively small percentage (6.9%) of the total variance. The variables contributing most to this axis were the position of the apex and the height of the shell. Intertidal limpets living close to the sewage outfall and having relatively low shells with the apex located near the center, had the highest scores on this axis. Shell height was relatively greater at the littoral fringe than in intertidal limpets (e.g. CL vs. BC, OH vs. OL; Fig. 3). This fact had been already pointed out both in *S. lessoni* (Martín and Estebenet, 1993) and in other species of limpets (Ebling *et al.*, 1962; Balaparameswara Rao and Ganapati, 1971).

Limpets growing in a protected environment such as Quequén Harbour (HP) also had relatively high shells (Fig. 3). This fact has already been pointed out in *S. lessoni* by Bastida *et al.* (1971). Several authors, however, have observed the opposite trend in some species of prosobranch limpets, where populations exposed to wave action had relatively higher shells than those from protected environments (Balaparameswara Rao and Ganapati, 1971; Simpson, 1985; Morriconi and Calvo, 1993; López, 1995).

The 6 sites sampled in the present study were chosen so as to cover a range of different environments and the most extreme shell morphologies found in this species. As expected, morphometric differences among sites were not absolute and the

multivariate methods (PCA, DA) were of great assistance in showing their degree of overlap (Fig. 4 and Table 3). Some combinations of sites showed no overlap at all in the bivariate PCA plot, and were completely separated (no wrongly reallocated individuals) by the discriminant function (e.g. HP vs. BC, HP vs. HE, OL vs. CL, HE vs. OL, BC vs. OL, Fig. 4). On the other hand, there was complete overlap between sites CL and HE in the bivariate PCA plot, and 11-19 % wrongly reallocated individuals (Table 3), which indicates a similar morphology, as can be seen in Figure 3. In other words, only limpets from sites OL and HP can be allocated with a fairly high degree of confidence to a particular habitat taking into account just their shape (OL) or size (HP). Obviously, overlap would have been greater and morphometric changes much more gradual, had the sites been chosen randomly and in greater number.

In four of the six habitats, a relative increase in shell height and a posterior displacement of shell apex occurred as the limpets became larger. This phenomenon can be seen in Figure 4 by the diagonal outline (stretched towards positive values on axis I and negative values on axis II) of the polygons delimited by limpets with most extreme morphology in sites HP, OH, BC and CL. This is an indication that at least in some sites, *S. lessoni* does not grow isometrically. Bastida *et al.* (1971) pointed out that *S. lessoni* showed a slight allometric growth of width with respect to length in limpets recruited and growing on an experimental raft within a harbour environment. Allometric growth has also been observed in limpets belonging to the genera *Collisella* and *Notoacmea* (Lowell, 1984), and Giesel (1969) found that *Lottia digitalis* (= *Acmaea digitalis*) shows a positive allometry in height under selective pressures limiting lateral growth. According to Simpson (1985) and Morriconi and Calvo (1993) positive allometric growth in height in the prosobranch limpets *Nacella (Patinigera) macquariensis* and *N. (P.) deaurata*, respectively, is influenced by the frequency with which a limpet is obliged to remain firmly clamped to the substratum.

The phenotypic plasticity of *Siphonaria lessoni* was evidenced during field experiments involving reciprocal translocations (Tablado *et al.*, 1994). Black and Johnson (1981) could not find genetic differences explaining the variability of *S. kurracheensis* (Reeve, 1856) along an intertidal gradient in the Australian Southwest. These authors suggested that reciprocal transplants between different environments showing intraspecific differences in morphol-

ogy are the most appropriate tool to discriminate between phenotypic and genotypic causes of morphologic variability.

Since *S. lessoni* has a planktonic larval stage and recruits massively in the intertidal zone during spring (Tablado *et al.*, 1994), and all the study sites were located within a distance of a few kilometers, we can reasonably suppose that most of the limpets analysed in the present study belong to the same annual cohort. Size differences in the population were probably related to microhabitat variation in growth rates, rather than to age. Therefore, low density, organic enrichment, and protected environments (alone or in combination) are factors that may increase the growth rate of *S. lessoni*. Morphometric differences observed in limpets from different habitats are the result of differential growth rates in response to environmental pressures: intertidal level, wave exposure, food availability, and intraspecific competition, among others.

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