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

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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 rodriguezi* (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 subtidally (Bastida et al., 1971). At mid- and low-intertidal levels it co-occurs with the dominant space competitor, the mytilid bivalve *Brachidontes rodriguezi* (d’Orbigny, 1846) (Olivier et al., 1966; Penchaszadeh, 1973). *S. lessoni* feeds mainly on microscopic algae, spores and germinals 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 Penchaszaede, 1968; López Gappa et al., 1996). The reproductive cycle of this species includes dispersal by means of a planktonic larval stage (Olivier and Penchaszaede, 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 Penchaszaede, 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 Notoaclaea 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) (Morronici 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. rodriguezi 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-
quén Harbour. It was the only habitat completely protected from wave action. Rocks and concrete blocks were covered mainly by the seaweed *Entero-
morpha compressa* (Linné) Greville in Harvey, 1849. The most frequent macrofaunal organisms accompanying *S. lessoni*, were the barnacle *Bal-
anus amphitrite* Darwin, 1854 and the decapod *Cy-
tograpsus 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 rodriguezi* 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 rodriguezi* (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-
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.

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

Fig. 2. – *Siphonaria lessoni* in lateral and top view, showing schematically how measurements were taken on the shell.
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 contribu-
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 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). Six limpets from the intertidal level around the outfall (OL) were allocated to the littoral fringe of the same environment (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
phemonen 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 rodriguezi 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 rodriguezi community than at high-intertidal levels (Olivier and Penchasadeh, 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 rodriguezi 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 rodriguezi 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 rodriguezi 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 Ganapat, 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 Notoaecmea (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 morphologic 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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