



## Variation in density, size, and morphology of the pulmonate limpet *Siphonaria lessonii* along the Southwestern Atlantic



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### ABSTRACT

The density, size, and morphology of coastal invertebrate species often predictably vary with latitude. In this study we evaluate whether the density, size, and morphology of the pulmonate limpet, *Siphonaria lessonii*, in the Southwestern Atlantic varies in agreement to the predictions of the abundance-centre hypothesis (i.e., higher densities by the center of the species range), Bergmann's rule (i.e., increasing body size with latitude), and Allen's rule (i.e., decreasing body surface to volume ratio with latitude). Our results indicate that the upper density bounds of *S. lessonii* decrease with latitude across our study range, which may either contradict expectations of the abundant-centre model (i.e., if assuming a Temperate Southwestern Atlantic/Magellanic distribution; 27°S in the Atlantic to 42°S in the Pacific) or represent a partial trend within a broader scale, abundant-centre pattern (i.e., when considering a panmictic distribution from the Temperate Southwestern Atlantic to the Temperate Southeastern Pacific; 27°S in the Atlantic to 5°S in the Pacific). Limpet shell length (i.e., a surrogate of body size) was not significantly related to latitude (cf. Bergmann's rule). The two principal components of morphological variation in limpet shells – which increased with decreasing shell surface to volume ratio – showed positive and negative relationships with latitude (i.e., contradictory support to Allen's rule). From these analyses, we conclude (a) that the size and morphology of *S. lessonii* are primarily controlled by local conditions rather than broad-scale climatic or environmental gradients and, (b) that geographic marginality does not mean reduced performance in this species at least as it concerns to abundance and maximum size.

### 1. Introduction

The abundance, size and/or morphology of an animal species vary along its distributional range due to ecological and evolutionary processes (Brown, 1995). Several hypotheses were proposed to predict geographic patterns of variation in these species attributes. For instance, the abundant centre hypothesis (ACH, Brown, 1984) predicts that species will show their higher density near its range centre, and decline gradually towards the margins of its geographical distribution because of decreased habitat quality and individual performance near range margins (see also Sagarin and Gaines, 2002; Guo, et al., 2005). As for variation in body size and morphology, Bergmann's rule (in its broadest sense; see Meiri, 2011) predicts increases in body size with latitude meanwhile Allen's rule (Allen, 1877) predicts lower surface to

volume ratio in animal bodies in colder climates. Although Bergmann's and Allen's rules were originally conceived to explain variations in body size and morphology across closely-related endothermic species on the basis of heat exchange relationships (Bergmann, 1847; Allen, 1877), there currently is evidence of Bergmann's- and Allen's-like patterns both at the intraspecific level and in ectotherms (e.g., Ray, 1960; Van Voorhies, 1996; Blanckenhorn and Demont, 2004; Fisher et al., 2010; Berke et al., 2013).

The density, size and morphology of coastal invertebrate species can predictably vary with latitude. As predicted by the ACH, rocky shore gastropods often show higher densities by the center of their linear, latitudinal distributional ranges (e.g., Sagarin and Gaines, 2002; Fenberg and Rivadeneira, 2011; Tam and Scrosati, 2011). Moreover, gastropod size and morphology often varies in agreement with

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predictions of the Bergmann's and Allen's models (e.g., Frank, 1975; Olabarria and Thurston, 2003). Nonetheless, these patterns are far from general. Gastropod densities can also peak by the limits of their distributional ranges or show no clear pattern of variation with latitude (e.g., Sagarin and Gaines, 2002; Gilman, 2005). In the same vein, gastropod size and morphology can show latitudinal gradients that oppose the predictions of Bergmann's and Allen's rules as well as no latitudinal trend at all (e.g., Trussell and Etter, 2001; Conde-Padín et al., 2007; Teso et al., 2011; Malvé et al., 2016). Certainly, variations in gastropod abundance, size and morphology can also occur within locations (e.g., across tidal levels; Olivier et al., 1966; Olivier and Penchaszadeh, 1968; Vermeij, 1972, 1973; Underwood, 1975) or be caused by local environmental factors that vary irrespective of latitude (e.g., coastal morphology, wave exposure, water depth, dissolved oxygen, or substrate type; Giraldo-López and Gómez-Schouben, 1999; McClain and Rex, 2001; Olabarria and Thurston, 2003; Carranza and Norbis, 2005; Teso et al., 2011).

Rocky intertidal invertebrates that show an extensive latitudinal distribution along their one-dimensional ranges are ideal to test whether abundance, size and morphology relates to latitude. The pulmonate limpet *Siphonaria lessonii* Blainville, 1827 (Gastropoda: Siphonariidae) is a good case of study. This species has been reported in the Atlantic coast of South America from Santa Catarina, (Brazil, 27°S) to its southern end (Tierra del Fuego archipelago, Argentina/Chile, 55°S), and on the Pacific coast of South America as north as Paita (Peru, 5°S; Rios, 2009; Güller et al., 2016). Yet, recent molecular studies indicate (a) low genetic differentiation between specimens from the Atlantic (13 sites between 34° and 54°S) and those from a Pacific site at 42°S (Güller et al., 2016) and, (b) noticeable differences between Atlantic specimens (4 sites between 38° and 54°S) and Pacific specimens from sites at 40° and 33°S (Nuñez et al., 2015). These evidences suggest the existence of two clades: one distributed from 27°S in the Atlantic to ca. 42°S in the Pacific (i.e., Temperate Southwestern Atlantic and Magellanic ecoregions; sensu Spalding et al., 2007) and another one that occurs from ca. 42° to 5°S in the Pacific (i.e., Temperate Southeastern Pacific ecoregion, sensu Spalding et al., 2007; see Nuñez et al., 2015; Güller et al., 2016). *S. lessonii* shells are conical with a noticeable apex displaced towards the back (Olivier and Penchaszadeh, 1968). Variations in density, shell size and morphology have been observed to occur across rocky shore levels (e.g., 140 to 3600 ind m<sup>-2</sup>; Olivier et al., 1966; Olivier and Penchaszadeh, 1968), as well as in association to differences in wave exposure, mussel cover, and pollution (Tablado and López Gappa, 2001; Penchaszadeh et al., 2007; Nuñez et al., 2012). However, these comparisons were either local or restricted to a few kilometers along the coastline, which precluded an assessment of latitudinal trends.

In this study we evaluate if the density, size and morphology of *S. lessonii* varies predictably with latitude across an extensive coastal range in the Southwestern Atlantic (Fig. 1, Table 1) and discuss whether the observed patterns fit to the predictions of ACH, Bergmann's rule, and Allen's rule.

## 2. Materials and methods

The density of *Siphonaria lessonii* was quantified at the mid intertidal zone of 23 rocky shores sites distributed along ca. 5075 km of coastline in the Southwestern Atlantic (Punta del Diablo, Rocha, Uruguay to Estancia Moat, Tierra del Fuego, Argentina; 34 to 54°S, Fig. 1, Table 1). The mid intertidal zone of these shores is dominated by mussels. *Brachidontes rodriguezii* is the dominant mussel species north of 41°S (Olivier et al., 1966; Penchaszadeh, 1973; Borthagaray and Carranza, 2007; Penchaszadeh et al., 2007; Arribas et al., 2013). *Perumytilus purpuratus* (also referred in the literature as *Brachidontes purpuratus*) coexist with *B. rodriguezii* between 41 and 43°S and becomes dominant south of 43°S (Adami et al., 2013; Arribas et al., 2013; Trovante et al., 2015). By the southern end of the study range (Tierra del Fuego Island;

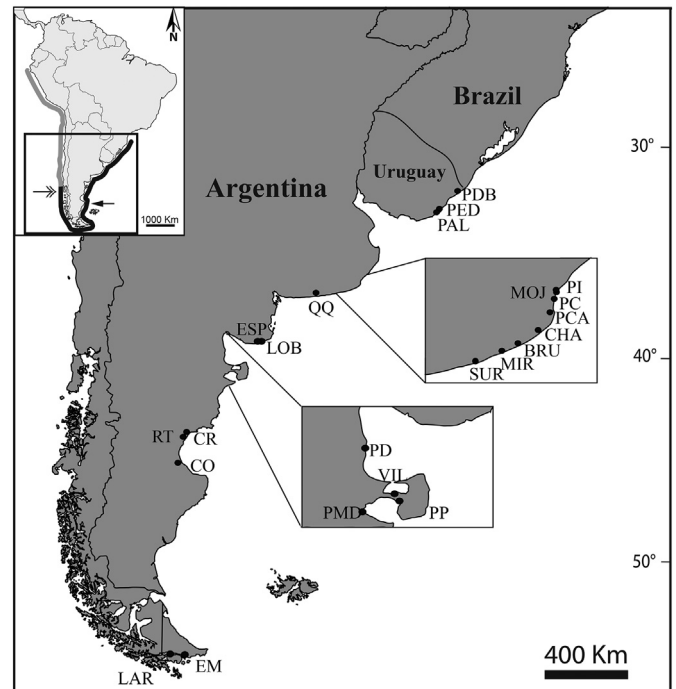


Fig. 1. Location of sampling sites in the Southwestern Atlantic: Punta del Diablo (PDB), La Pedrera (PED), La Paloma (PAL), Punta Iglesia (PI), Torreón del Monje (MOJ), Playa Chica (PC), Punta Cantera (PCA), Chapadmalal (CHA), Las Brusquitas (BRU), Miramar (MIR), Mar del Sur (SUR), Quequén (QQ), El Espigón (ESP), La Lobería (LOB), Playas Doradas (PD), Villarino (VIL), Puerto Pirámides (PP), Puerto Madryn (PMD), Comodoro Rivadavia (CR), Rada Tilly (RT), Caleta Olivia (CO), Playa Larga (LAR), Estancia Moat (EM). The two possible scenario of *Siphonaria lessonii* distributional range; a Temperate Southwestern Atlantic/Magellanic distribution (bold dark gray coastal contour) with a centre at 48°S in the Atlantic (dark gray arrow) and a panmictic distribution (light gray and dark gray contour) with a center at 45°S in the Pacific (double-pointed arrow).

54°S), *P. purpuratus* and *Mytilus chilensis* are co-dominants (see Calcagno et al., 2012). To ensure that comparable tidal levels were sampled at each site, samplings were restricted to the upper edge of the mussel zone, where mussel cover is patchy (cf. continuous cover lower in the intertidal slope) and interspersed by bare rock surface.

Eight squared sampling units (25 cm side) were randomly deployed in the mid intertidal zone at each site and all *S. lessonii* in these units were counted. Furthermore, all the individuals sampled at 8 out of the 23 sites (see Table 1) were collected, fixed in 96% ethanol, and carried to the laboratory. The length of these individuals was measured with Vernier calipers to the nearest 0.01 mm. Length was used as a measure of limpet size as it correlates to body mass (see Bastida et al., 1971). Last, fifteen largest size specimens from each of these 8 sites were selected (6.5–19 mm) and photographed from the right side of the shell with a digital camera (Cannon PowerShot SX150 IS). These pictures were taken against a black background to maximize the contrast of the shell contours.

Quantile regressions were used to evaluate if limpet density and size are related to latitude (see also Olabarria and Thurston, 2003). Least-squares linear regression can be problematic to test these relationships as mean density and body size at each locale may be influenced by the recent history of limpet recruitment. Quantile regression, in contrast, allows choosing a quantile ranging from 0.00 to 1.00 to test for relationships at different regions of the bivariate distribution and is less sensitive to outliers (Cade and Guo, 2000; McClain and Rex, 2001). Significance tests (*t*-tests for slopes) were conducted here on the 10%, 50%, and 90% quantile regression lines using STATA (StataCorp, 2011). Agreement with the predictions of ACH and Bergmann's rule were evaluated from the 90% quantile regression lines as they describe variations in maximum density and size. Relationships with the median

**Table 1**

Coordinates, sampling dates, and variables measured at each sampling site. Measurements were density (D), shell length (L), and shell morphology (M). Abbreviated site names are as in Fig. 1.

Site (abbreviation)	Latitude (S)	Longitude (W)	Sampling date	Measurements
Punta del Diablo (PDB)	34°02'	53°32'	Jun-15	D
La Pedrera (PED)	34°35'	54°07'	Feb-11	D
La Paloma (PAL)	34°39'	54°08'	Jun-15	D, L, M
Punta Iglesia (PI)	37°59'	57°32'	Nov-13	D
Torreón del Monje (MOJ)	38°00'	57°32'	Nov-13	D
Playa Chica (PC)	38°01'	57°31'	Jan-11	D, L, M
Punta Cantera (PCA)	38°05'	57°32'	Jun-13	D
Chapadmalal (CHA)	38°11'	57°39'	Jul-13	D
Las Brusquitas (BRU)	38°14'	57°46'	Nov-13	D
Miramar (MIR)	38°17'	57°50'	Nov-13	D
Mar del Sur (SUR)	38°21'	57°59'	Nov-13	D
Quequén (QQ)	38°34'	58°40'	Jan-11	D, L, M
El Espigón (ESP)	41°08'	63°02'	Mar-11	D, L, M
La Lobería (LOB)	41°09'	63°07'	Mar-11	D, L, M
Playas Doradas (PD)	41°38'	65°01'	Mar-11	D
Villarino (VIL)	42°24'	64°15'	Sep-12	D, L, M
Puerto Pirámides (PP)	42°34'	64°17'	Mar-11	D
Puerto Madryn (PMD)	42°47'	64°57'	Mar-11	D, L, M
Comodoro Rivadavia (CR)	45°52'	67°30'	Dec-12	D, L, M
Rada Tilly (RT)	45°56'	67°33'	Dec-12	D
Caleta Olivia (CO)	46°26'	67°30'	Dec-12	D
Playa Larga (LAR)	54°49'	68°11'	Oct-12	D
Estancia Moat (EM)	54°58'	66°44'	Apr-14	D

and the 10% quantile were included here to depict variations in density and size distributions with latitude.

Additionally, the abundance distribution patterns of *S. lessonii* were evaluated by means of non-parametric constraint space analysis following procedures developed by [Enquist et al. \(1995\)](#) and [Sagarin and Gaines \(2002\)](#). This approach examines the bounds on abundances in different parts of the species range and has become extensively used to characterize the shape of abundance distributions (e.g., [Samis and Eckert, 2007](#); [Rivadeneira et al., 2010](#); [Fenberg and Rivadeneira, 2011](#); [Baldanzi et al., 2013](#)). To evaluate the abundance distribution of *S. lessonii*, densities were first converted to relative abundance (RA) values by dividing the mean densities for each site by the maximum mean density observed along the range. Then, range locations were standardized to range index (RI) values:

$$RI = 2(L - S)/R$$

where *L* is the location of the sampling site in degrees latitude, *S* is the latitudinal centre of the sampled range, and *R* is the latitudinal extent of the range. RI ranges between  $-1$  and  $1$ , so that sites with values close to  $0$  are considered to be near the centre of distribution and values close to  $-1$  and  $1$  are near the distributional edges (in our case, Atlantic and Pacific edges, respectively). Here we considered two alternative distributional scenarios for *S. lessonii*: (a) a Temperate Southwestern Atlantic/Magellanic distribution (from  $27^{\circ}\text{S}$  in the Atlantic to ca.  $42^{\circ}\text{S}$  in the Pacific, with a centre at  $48^{\circ}\text{S}$  in the Atlantic) as suggested by molecular analyses (see [Nuñez et al., 2015](#); [Güller et al., 2016](#)) and, (b) a panmictic distribution across the whole range where this species has been reported (i.e., from  $27^{\circ}\text{S}$  in the Atlantic to  $5^{\circ}\text{S}$  in the Pacific, with a centre at  $45^{\circ}\text{S}$  in the Pacific; see [Rios, 2009](#); [Güller et al., 2016](#)). As our study range covered just 25% of the putative distributional range of this species under the second scenario (i.e.,  $20^{\circ}$  out of  $80^{\circ}$  latitude), abundance distribution patterns in this case were evaluated after supplementing our data with literature records of *S. lessonii* density at a series of Pacific sites ([Table 2](#)). In both cases, bounds in the cloud of points RA vs. RI plots were tested against normal and linear constraint functions –i.e., abundant-centre and ramped patterns, respectively (Abundant-edge patterns were disregarded after visual inspection of plotted data). The degree of fit of the data to each constraint space was evaluated by calculating the sum of squared deviations (SS) for sites exceeding the constraint boundary. The fit of the

model was considered significant when the observed SS value was lower than the 5th percentile of the distribution of SS values obtained from 10,000 randomized datasets. All calculations were carried out using Microsoft Excel. Randomized datasets and SS values were obtained using Poptools 3.2 (i.e. a Microsoft Excel add-in for the analysis of matrix population models and simulation of stochastic processes; [Hood, 2010](#)).

A geometric morphometric technique was used to characterize the morphology of limpet shells. Digital shell images were processed using the SHAPE software ([Iwata and Ukai, 2002](#)) and variation in shell morphology across study sites was evaluated using Elliptic Fourier analysis (EFA) on the outline coordinates ([Kuhl and Giardina, 1982](#)). Elliptic Fourier coefficients were mathematically normalized to avoid biases caused by location, size, rotation, and starting position of shell ([Rohlf and Archie, 1984](#)). The closed curve of each shell contour was decomposed into 15 harmonics, which represented 99.99% of the total Fourier power spectrum (see also [Nuñez et al., 2012](#)). Principal component analysis (PCA) in the variance-covariance matrix of the normalized elliptic Fourier coefficients was used to detect patterns of morphological variation across locations ([Rohlf and Archie, 1984](#)). Differences in shell morphology across sites were evaluated with a multivariate analysis of variance (MANOVA) using PAST ([Hammer et al., 2001](#)). As in the case of density and size, quantile regressions were used to test if variations of the two principal components obtained from PCA are associated with latitude.

### 3. Results and discussion

The density of *Siphonaria lessonii* decreased significantly with latitude for the 90% and 50% quantile lines (but not for the 10% quantile line; [Table 3](#), [Fig. 2a](#)). This indicates a decrease in median density and upper density bounds with latitude. In agreement, non-parametric constraint space analysis indicates that the abundance distribution pattern of this species best fits to a linear, ramped pattern (i.e., overall Atlantic to Pacific decrease) when assuming a Southwestern Atlantic/Magellanic distribution ([Table 4](#), [Fig. 3a](#)). However, the abundant-centre pattern is the best fitting one when assuming a panmictic distribution across the whole range where this species has been reported, and after published density estimates from the Pacific are included in our analysis ([Table 4](#), [Fig. 3b](#)). Thus, the observed decrease in *S. lessonii*,

**Table 2**  
Published values of mean *Siphonaria lessonii* density at Southeastern Pacific sites.

Site	Latitude (°S)	Density (ind 0.0625 m <sup>-2</sup> )	Reference
Lima	10	14.5 <sup>d</sup>	Paredes and Tarazona, 1980
Bahía de Ancón	11	1.4 <sup>b</sup>	Reyes-Turumanya, 2015
Islay	17	2.4 <sup>b</sup>	Tejada-Pérez, 2014
Península Cavanca	20	3.1 <sup>a</sup>	Aguilera et al., 2014
Bahía Antofagasta	23	1.5 <sup>b</sup>	Cerda and Castilla, 2001
Las Cruces	33	30.0 <sup>c</sup>	Aguilera and Navarrete, 2007
Bahía Mehuín	39	82.3 <sup>c</sup>	Jara and Moreno, 1984
Calhuco	40	190.0 <sup>c</sup>	Tejada-Martinez et al., 2016

<sup>a</sup> Mean density at a particular place and time (i.e., snapshot).  
<sup>b</sup> Maximum average density in data from neighboring places located within the same site and sampled at a single time.  
<sup>c</sup> Maximum average density in temporal series of data obtained from a single place.

**Table 3**  
Summary of quantile regression analyses evaluating the potential linear relationships of density, shell length, and the two principal components of morphological variation in *Siphonaria lessonii* (PC1 and PC2) with latitude at the 10, 50, and 90% quantiles.

Dependent variable	Intercept (b <sub>0</sub> )	Slope (b <sub>1</sub> )	t (b <sub>1</sub> )	Pseudo-r <sup>2</sup>
Density				
10%	0.4771	0	0	0.0000
50%	2.5158	- 0.0304	- 3.54**	0.0308
90%	3.1253	- 0.0335	- 4.73**	0.0508
Shell length				
10%	- 0.0073	0.0194	16.29**	0.0915
50%	0.2466	0.016	9.68**	0.0603
90%	0.9464	0.0027	0.72	0.0053
PC1				
10%	- 0.1697	0.002	0.6	0.0154
50%	- 0.3034	0.0071	1.94	0.0525
90%	- 0.6205	0.0178	5.80**	0.1322
PC2				
10%	0.0689	- 0.003	- 3.30**	0.0135
50%	0.0608	- 0.0014	- 1.01	0.0063
90%	0.0799	- 0.0006	- 0.22	0.0033

\*\* p < 0.01.

density with latitude along the Southwestern Atlantic may either contradict expectations of the abundant-centre model (i.e., if assuming a Temperate Southwestern Atlantic-Magellanic distribution) or represent a partial trend within a broad scale, abundant-centre pattern (i.e., when considering a panmictic distribution from the Temperate Southwestern

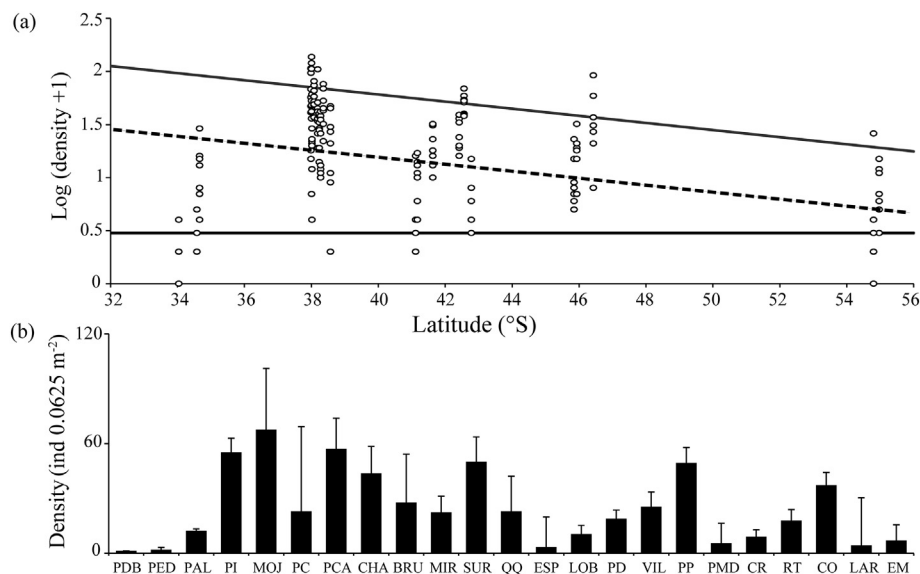
**Table 4**  
Summary of non-parametric constraint space analysis testing the fit of *Siphonaria lessonii* abundance bounds to linear and normal constraint functions (i.e., ramped and abundant-centre patterns, respectively) under two alternative distributional scenarios, a Temperate Southwestern Atlantic/Magellanic distribution (27°S in the Atlantic to 42°S in the Pacific) and a panmictic distribution from the Temperate Southwestern Atlantic to the Temperate Southeastern Pacific; (27°S in the Atlantic to 5°S in the Pacific). The sum of squared deviations for sites exceeding the constraint boundary (SS<sub>obs</sub>) and the 5th percentile of the distribution of SS values obtained from 10,000 randomized datasets (SS<sub>(0.05)</sub>) are shown.

Distributional scenario	Model	SS <sub>obs</sub>	SS <sub>(0.05)</sub>
Temperate Southwestern Atlantic/Magellanic	Linear (Ramped pattern)	0.082*	0.083
	Normal (Abundant-centre pattern)	2.23	1.04
Temperate Southwestern Atlantic to Temperate Southeastern Pacific	Linear (Ramped pattern)	0.30	0.02
	Normal (Abundant-centre pattern)	3 × 10 <sup>-4</sup>	2 × 10 <sup>-3</sup>

\* p < 0.05.

Atlantic to the Temperate Southeastern Pacific). Certainly, additional research on the genetics and phylogeography of this species along the Pacific coastline is still necessary to establish its actual distributional range and reach a definitive conclusion on its geographic abundance distribution pattern. Furthermore, it would also be desirable to obtain density data from the Pacific following the protocol used here in order to rule out potential artifacts due to methodological differences across studies (e.g., samples taken from different tidal levels).

Although we have sampled our sites at different times of the year,



**Fig. 2.** (a) Relationship between *Siphonaria lessonii* density and latitude at the 10, 50, and 90% quantiles. (b) Mean (SD) density of *S. lessonii* across sites.



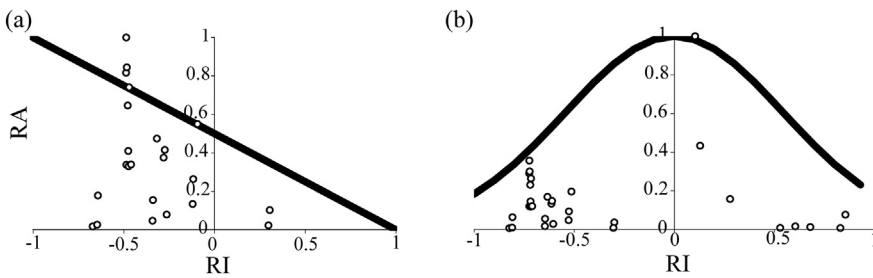


Fig. 3. Relative abundance (RA) of *Siphonaria lessonii* under two alternative distributional scenarios, (a) a Temperate Southwestern Atlantic/Magellanic distribution (27°S in the Atlantic to 42°S in the Pacific) and, (b) a panmictic distribution from the Temperate Southwestern Atlantic to the Temperate Southeastern Pacific (27°S in the Atlantic to 5°S in the Pacific). RI ranges between -1 and 1, which respectively represent Atlantic and Pacific distribution edges, and equals zero at the centre of the distribution. Curves represent the best fitting model in each case. Data from this study and literature data (see Table 2) are shown as filled and open symbols, respectively.

sampling date is unlikely to confound the observed negative relationships between limpet density (i.e., median and upper bounds; see above) and latitude. While local density values will clearly be influenced by the timing of sampling in relation to recruitment and mortality pulses, here we have circumvented potentially confounding influences of sampling date by sampling nearby sites on different months to the extent that logistics allowed. The negligible confounding influence of sampling date on the observed density-latitude relationship can be illustrated here by two facts. First, peak densities within our study range were observed at a handful of sites located within 38°S latitude that were sampled on different sampling dates – i.e., Nov-2013 (Torreón del Monje, Punta Iglesia, Mar del Sur), Jun-2013 (Punta Cantera), and Jul-2013 (Chapadmalal) (see Table 1 and Fig. 2b). Secondly, minimum densities were registered at the two southernmost locations, Estancia Moat and Playa Larga (54°S), which were sampled in Apr-2014 and Oct-2012, respectively (see Table 1 and Fig. 2b). This means that maximum and minimum densities across our study range were detected irrespective of sampling date and suggests that a decrease in limpet densities with latitude occurs independently of any potential influence of recruitment and mortality pulses. Unfortunately, the temporal dynamics of *S. lessonii* recruitment and mortality are largely unknown throughout this study range (but see Tablado et al., 1994) and expected to differ even between nearby locations (Tablado et al., 1994; Lagos et al., 2007), which precludes to assess their realized influence on our local density measures.

Shell length in *S. lessonii* increased significantly with latitude for the 10% and 50% quantile lines, but not for the 90% quantile line (Table 3, Fig. 4). The non-significant 90% quantile line suggests that latitudinal clines in maximum body size – such as the positive relationships between size and latitude predicted by Bergmann's rule – do not occur in this species across our study range. Similar results were found for other gastropod species along the south-western Atlantic coast (e.g., *Olivancillaria carcellesi*; Teso et al., 2011; *Trophon geversianus*, Malvé et al., 2016). Mechanistic explanations of Bergmann's or converse-Bergmann's clines generally relate to variations in temperature or other environmental variables that are highly correlated with latitude (e.g., Bergmann, 1847; Blackburn et al., 1999; Malvé et al., 2016). Nevertheless, size in *S. lessonii* and other species in the genus *Siphonaria* have been observed to vary in association to local habitat conditions that are

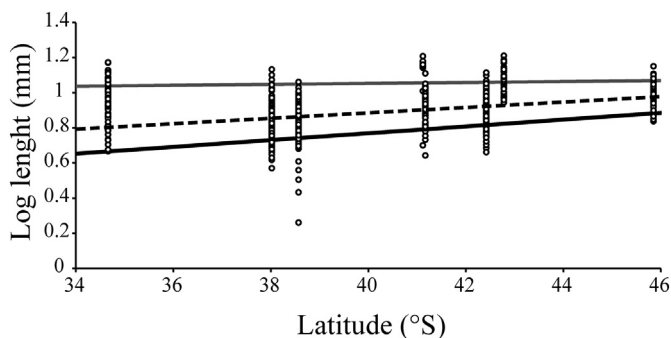


Fig. 4. Relationship between the shell length of *Siphonaria lessonii* and latitude at the 10, 50, and 90% quantiles.

usually uncorrelated to latitude (e.g., phytobenthic production, algal community composition, organic pollution, wave exposure, habitat complexity, substratum type and slope; see Liu, 1994; Tablado et al., 1994; Ocaña, 2003; Boukhicha et al., 2015). In addition, size variations may also be influenced by the history of local colonization and extinction through evolutionary time, which might not necessarily relate to latitude (see Berke et al., 2013; Nuñez et al., 2015). Consequently, the lack of a significant latitudinal size cline in *S. lessonii* would be a reasonable result.

The first two components of PCA explained 75% of the morphological variation of *S. lessonii* across the study range, with 59% of variation explained by PC1 alone (Fig. 5a). MANOVA indicated significant morphological differences in *S. lessonii* between sites (Pillai trace = 1.012,  $F_{(14, 224)} = 16.37$ ,  $p < 0.001$ ). PC1 increased with latitude for the 90% quantile lines, but not for the 10 and 50% quantile lines (Table 3, Fig. 5b). This result suggests that the pattern of morphological variation in *S. lessonii* conforms to Allen's rule, at least to

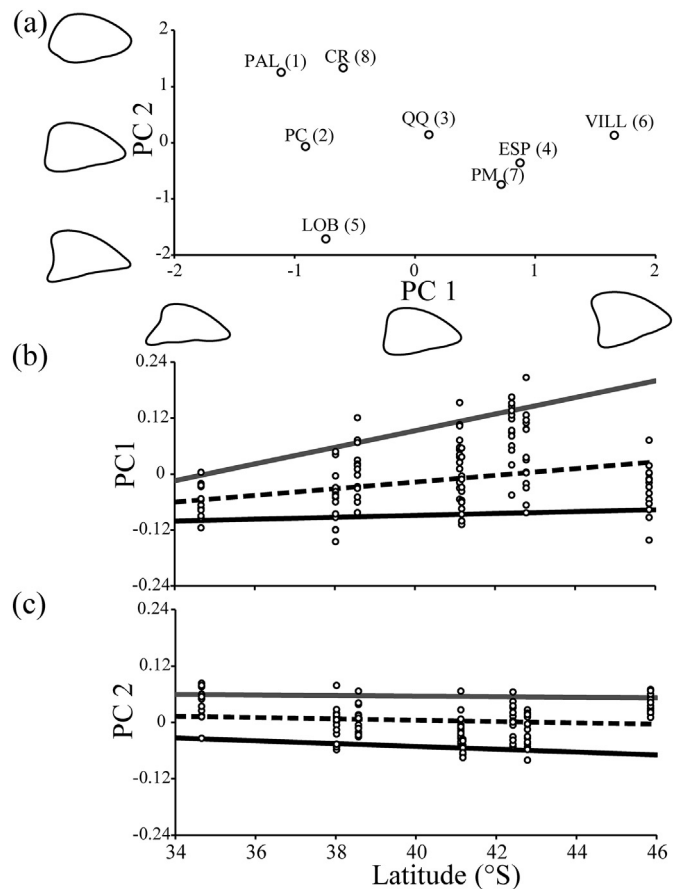


Fig. 5. (a) Principal components analysis of shell shape variation in *Siphonaria lessonii*. Points represent the averages at each site. Site codes are as in Table 1. Shell shape contours represent the kind of morphological variation represented by each axis. (b) Relationship between PC1 and latitude. (c) Relationship between PC2 and latitude.

some degree. Indeed, PC1 describes variation in the position and height of the apex relative to the base of the shell, with PC1 values increasing as shells become less flat and their surface to volume ratio decreases (PC1 is inversely proportional to surface to volume ratio; Fig. 5a). According to Allen's rule, lower surface to volume ratios in animal bodies should be favored in colder climates as this would reduce heat losses (Allen 1877). In agreement, an increase in the 90% quantile of PC1 with latitude indicates that the proportion of individuals with tall shells and low surface-to volume ratios increases as climate becomes colder.

On the other hand, PC2 decreased significantly with latitude for the 10% quantile lines, but not for the 50 and 90% quantile lines (Table 3, Fig. 5b). This apparently contradicts Allen's rule since PC2 describes whether the posterior end of the shell is pointed or truncated, with PC2 values decreasing as the posterior shell end becomes more pointed and shell surface-to-volume ratios increase (PC2 inversely proportional to surface to volume ratio; Fig. 5a). A decrease in the 10% quantile of PC2 with latitude indicates that the proportion of individuals with pointed shells and high surface-to volume ratios increases as climate becomes colder. Hence, it is likely that other factors than temperature favor the occurrence of pointed posterior shell ends in *S. lessonii*.

Summing up, we found (a) negative relationships between density and latitude, (b) no evidence of Bergmann's size clines and, (c) contradictory support to Allen's rule in *S. lessonii* along the Southwestern Atlantic. This suggests that the size and morphology of this species along our study range is controlled by local abiotic and biotic conditions (see also Tablado et al., 1994; Tablado and López Gappa, 2001; Nuñez et al., 2012) rather than broad-scale climatic or environmental gradients. Furthermore, our findings also challenge the 'centre-periphery hypothesis', which states that genetic variation and the demographic performance of a species decrease from the centre to the edge of its geographic range because environmental conditions become harsher towards range limits (see Pironon et al., 2016). Here, a typical measure of demographic performance, such as size, does not decrease towards the Atlantic distributional edge of *S. lessonii* (see Fig. 4) and similar considerations might apply to abundance if a Temperate Southwestern Atlantic/Magellanic distribution proves to be real for this species (see Fig. 3a). Moreover, although the morphology of *S. lessonii* shells seems to become less variable as we move towards its Atlantic distributional edge (see 10 and 90% quantile lines for PC1 in Fig. 5b), this might reflect reduced variation in environmentally-induced phenotypic plasticity rather than decreased genetic variation (noteworthy, the latter is commonly the case in intertidal gastropods; e.g., Trussell and Etter, 2001; Hollander et al., 2006; see Bourdeau et al., 2015 for a review). Hence, we cannot assert from our data that factors acting as selective forces and affecting the demographic performance of *S. lessonii* increase in severity towards its Atlantic distributional edge. Rather, our study adds to an enlarging list of examples illustrating mismatches between geographic and ecological marginality gradients (see Pironon et al., 2016 for a review).

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