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## Age, growth and mortality in four populations of the boring bivalve *Lithophaga patagonica* from Argentina

María Bagur <sup>a,\*</sup>, Christopher A. Richardson <sup>b</sup>, Jorge L. Gutiérrez <sup>c,d</sup>, Lorena P. Arribas <sup>a</sup>, M. Socorro Doldan <sup>e</sup>, M. Gabriela Palomo <sup>a,d</sup>

<sup>a</sup> Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-CONICET), Angel Gallardo 470, Buenos Aires 1405DJR, Argentina

<sup>b</sup> School of Ocean Sciences, College of Natural Sciences, Menai Bridge, Anglesey LL59 5AB, UK

<sup>c</sup> Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, CONICET, Funes 3250, Mar del Plata B7602AYL, Argentina

<sup>d</sup> Grupo de Investigación y Educación en Temas Ambientales (GRIETA), Mar del Plata 7600, Argentina

<sup>e</sup> Instituto de Biología Marina y Pesquera "Almirante Storni", Universidad Nacional del Comahue, CONICET, Güemes 1030, San Antonio Oeste R8520CXV, Río Negro, Argentina

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### ABSTRACT

The boring bivalve *Lithophaga patagonica* (d'Orbigny, 1842) is a locally abundant inhabitant of hard substrata in the coastal waters of the Southwestern Atlantic. In this paper, we describe the growth, age and mortality of three intertidal rock-boring populations of *L. patagonica* and one subtidal oyster shell (*Ostrea puelchana*) boring population. An analysis of acetate peel replicas of shell sections showed that *L. patagonica* slows down its growth during autumn–winter, which leads to changes in the direction and rate of shell deposition and the formation of conspicuous annual (low temperature induced) clefts in the shell margin. Cleft counts and Von Bertalanffy growth analyses indicated that maximum age varies from 4 years in the oyster-boring population to 13 years in a rock-boring one (longevity estimates varied between 6.5 and 15 years, respectively). Maximum asymptotic length ( $L_{\infty}$ ) and Von Bertalanffy growth constant (K) were also variable between populations ( $L_{\infty}$  between 14.76 and 36.95 mm and K from 0.20 to 0.90 yr<sup>-1</sup> respectively). Mortality rates were higher at the two southernmost populations. Type (rock vs. oyster), composition and hardness of the substrata are likely the main factors controlling the observed differences between populations.

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### 1. Introduction

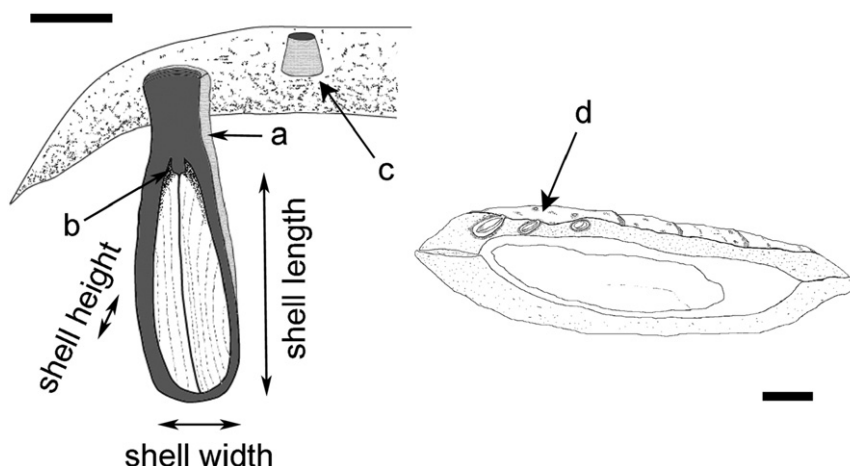
A variety of marine boring bivalves dwell in holes that they make in hard substrata such as sedimentary rock, wood, coral, and other mollusk shells (Ruppert and Barnes, 1994). In adopting this lifestyle these boring bivalves erode hard substrata and, when abundant, can even compromise its structural integrity (e.g., Evans, 1968a; Pinn et al., 2005; Stearley and Ekdale, 1989). Analysis of bioerosion rates are useful for ecological, paleontological and conservation studies (e.g., Bromley, 1978; Stearley and Ekdale, 1989; Toro-Farmer et al., 2004). To evaluate bioerosion rates, demographic parameters such as age structure, growth and mortality rates of the boring organisms are often needed. These parameters can be readily estimated once an age–size relationship has been identified for the species in question (e.g., Pinn et al., 2005; Richardson, 2001; Ridgeway et al., 2012).

Unlike other bivalves that mechanically bore into hard substrata, for example where they use their shells to abrade the substratum or exert pressure on their burrow walls (Ansell, 1970; Ansell and Nair, 1969; Nederlof and Muller, 2012), date mussels (*Lithophaga*, Mytilidae) dissolve calcareous rock, coral, and shells by means of secretions produced by

glands in the mantle margin (Bolognani Fantin and Bolognani, 1979; Hodgkin, 1962; Jaccarini et al., 1968; Kleemann, 1973a; Morton and Scott, 1980). As is commonly the case for boring bivalves, date mussel growth rates and population size structure are likely to vary with substratum type (see Kleemann, 1973a, b, 1996). Nevertheless, to our knowledge there are no studies that compare the age, growth, and mortality of date mussels across populations occurring on different substrata.

*Lithophaga patagonica* (d'Orbigny, 1842) inhabits intertidal and shallow waters in the Southwestern Atlantic from Santa Catarina state (Brazil, 28°S) to Tierra del Fuego Island (Argentina, 55°S) (Pastorino, 1995; Rios, 2009; Rosenberg, 2009). It bores flask-shaped burrows into soft consolidated sediments and oyster shells that, as in other *Lithophaga* species (e.g. *Lithophaga aristata*; Morton, 1993), are partially or completely lined with a layer of calcareous material (Fig. 1). *L. patagonica* is often numerically abundant in benthic communities (e.g. Amor et al., 1991; Olivier et al., 1966; Pastorino, 1995) and is a major borer of oyster, *Ostrea puelchana*, shells (Castellanos and Cabrera, 1957; Mauna et al., 2005; Pascual et al., 2001). While its life-style suggests important geomorphological and ecological effects, there is a dearth of knowledge about the general biology of this species, and particularly, with regard to demographic parameters that may aid in the estimation of bioerosion rates.

\* Corresponding author. Tel.: +54 11 49826595x138.  
E-mail address: [mbagur@macn.gov.ar](mailto:mbagur@macn.gov.ar) (M. Bagur).



**Fig. 1.** Life position of *Lithophaga patagonica* boring into rocks (left) and into *Ostrea puelchana* oysters (right). Shell dimensions (length, width and height) are shown as measured in this study. Ref: a: carbonatic burrow lining, b: posterior calcium-carbonate incrustations, c: prompting tube (lining) from another individual as it is commonly found at some intertidal locations; d: *L. patagonica* living specimens (3) bored into oyster shell. Scale: 1 cm.

In this paper, we estimate the age, growth, and mortality of *L. patagonica* from four locations along the Argentinean coast (37–43°S) that differ in substratum characteristics and other physical, chemical, and biotic variables (Table 1). Age was first estimated using a widely accepted method that has received considerable attention in the last two decades: the analysis of internal growth lines and microbanding patterns in shell sections. This methodology (reviewed in Richardson, 2001) has been successfully used to investigate age and growth rates in many mollusk species (Peharda et al., 2007; Richardson, 1989; Scourse et al., 2006; Wanamaker et al., 2008; including boring piddocks, Pinn et al., 2005), and is particularly suitable for *L. patagonica* where weak surface growth lines and external calcium carbonate incrustations preclude any reliable age estimates by counting the external growth rings (pers. obs.). From these age estimates, shell growth rates in one of the populations were compared for robustness with those obtained from length–frequency distribution analysis (LFDA). Then, longevity and mortality estimates for the four *L. patagonica* populations were obtained from the analysis of age–frequency distributions. Last, variations in growth rates,

longevity and mortality between populations are discussed vis-à-vis differences in the characteristics of the substrata and other environmental variables (wave exposure, water chlorophyll-a concentration, turbidity and temperature).

## 2. Materials and methods

Research was conducted along the Argentinian coastline at Santa Elena (37° 51' S, 57° 30' W, hereafter SE), Quequén (38° 34' S, 58° 39' W, hereafter QQ), Caleta de los Loros (41° 03' S, 64° 07' W, hereafter CL) and Puerto Pirámides (42° 34' S, 64° 17' W, hereafter PP) (Fig. 2). SE, QQ and PP are characterized by active cliffs and intertidal abrasion platforms composed of sedimentary rock (Amor et al., 1991; López Gappa et al., 1990; Scasso and del Río, 1987). Caleta de los Loros is a coastal inlet that stretches ~3 km into the mainland (Escofet et al., 1978). *L. patagonica* were collected from intertidal sedimentary rock (SE, QQ, and PP) and from oyster, *Ostrea puelchana*, beds that occur on areas of sandy-gravel seabed in the subtidal (CL). A summary of the

**Table 1**  
Geographic, oceanographic, and geological data from the four locations under study. Locations: Santa Elena (SE), Quequén (QQ), Caleta de los Loros (CL), Puerto Pirámides (PP). Minerals: Calcite (Cal), Quartz (Qtz), Feldspar (Fsp), Gypsum (Gp). Relative amount: abundant, 26–50% (Ab.), moderate, 16–25% (Mod.), sparse, 6–15% (Sp.), trace, <1% (Tr.). NA: data not available.

Location	SE	QQ	CL	PP	Source
Latitude (°S)	37°51'	38°34'	41°03'	42°34'	GPS data
Depth	Intertidal	Intertidal	Subtidal (12–20 m depth)	Intertidal	Pers. obs.
Maximum tidal amplitude (m)	1.55 (Microtidal)	1.70 (Microtidal)	9.32 (Macrotidal)	5.88 (Macrotidal)	Argentinean Naval Hydrography Service SHN ( <a href="http://www.hidro.gob.ar">www.hidro.gob.ar</a> )
Wave exposure index	8.960	9.158	(Subtidal)	5.157	Calculated from local wind data and nautical charts following Thomas (1986).
Sea surface temperature (°C)	15.61 (1.01)	15.48 (1.19)	15.81 (0.86)	15.10 (1.28)	Mean (SD) annual SST from satellite images of the last 10 years (NOAA; <a href="http://www.oceancolor.gsfc.nasa.gov">www.oceancolor.gsfc.nasa.gov</a> )
Chlorophyll a (mg·m <sup>-3</sup> )	4.47 (0.80)	3.54 (0.63)	2.97 (1.93)	2.13 (1.18)	Mean (SD) annual Chl-a concentrations from satellite images of the last 10 years (NOAA; <a href="http://www.oceancolor.gsfc.nasa.gov">www.oceancolor.gsfc.nasa.gov</a> )
Turbidity (FTU)	42.33 (3.51)	12.66 (2.31)	NA	4.33 (0.58)	Measured in situ using a Colorimeter, n = 5. Values are mean (SD).
Distance to sewage effluent (km)	8	0.5	>10	>10	Calculated from Google Earth
Type of substrate	Sandstone	Calcrete	Oyster shell	Sandstone	Analyzed with an X-ray diffractometer.
Mineral composition	Qtz: Ab.	Cal: Ab.	Cal: 100%	Qtz: Ab.	
	Fsp: Ab.	Qtz: Mod.		Fsp: Ab.	
	Clay: Mod.	Fsp: Mod.		Clay: Sp.	
	Cal: Sp.			Cal: Sp.	
Hardness index	2	12	22	1	Measured in situ as the depth of 10 replicate holes (6 mm diameter) drilled during 10 s with a power drill (see Evans, 1968b; Pinn et al., 2005). The reciprocal of mean hole depth was used as an index of hardness.
	CaCO <sub>3</sub> content (%)	34.36 (18.34)	37.22 (12.39)	≈100	

physicochemical characteristics of each site are shown in Table 1. Rock hardness (hardness index) and turbidity were determined in situ whereas rock samples were collected and carried to the laboratory to determine type, composition of the sediments, and calcium carbonate percentage. Oceanographical data were obtained from satellite images and data bases (see sources in Table 1).

*L. patagonica* was collected seasonally by hand at SE in July 2009, October 2009, January 2010 and May 2010, although only once from the three other locations (QQ: October 2009; CL: December 2010; PP: December 2010). At CL, oysters were obtained by SCUBA diving. Specimens of *L. patagonica* were collected by breaking the substratum (either rock or oyster shell) with a hammer and chisel (725, 355, 519, and 607 specimens collected from SE, QQ, CL, and PP, respectively). They were immediately stored in 70% alcohol, and carried to the laboratory at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina). Shell length, height and width of all individuals were subsequently measured to the nearest 0.01 mm using digital Vernier calipers. Then, their flesh was carefully removed by opening and shucking and dry biomass estimated by drying in an oven at 70 °C for 12 h. Clean, empty shells were set aside for growth line analysis, which was carried out at School of Ocean Sciences, College of Natural Sciences, Menai Bridge, UK. Material collected from the four localities was deposited in the MACN (MACN-In 39036-9).

The age structure of *L. patagonica* from the different populations was determined using shells selected from the length–frequency distributions. Using these data the number of individuals to be aged in each size class from each site was determined as a proportion of the number of shells in each 5 mm size class. The age of 106, 54, 42, and 58 shells were determined from sites SE, QQ, CL, and PP, respectively. Acetate peel replicas of the sectioned shells were prepared by embedding clean, dry shells in resin and sectioning them along the major growth axis (from umbo to posterior shell margin) using a diamond saw. The exposed section of the embedded shell was successively ground on increasingly finer wet and dry paper, polished and etched for 5 min in 0.1 M hydrochloric acid and acetate peel replicas of the polished and etched shell surfaces prepared using the methodology described in Richardson et al. (1979). The dry peels were mounted on a glass slide and viewed through a transmitted light microscope. Timing of the season of formation of the growth lines were assessed in shells collected at Santa Elena (SE). Photomicrographs were created of the margin region of each shell using a Buehler Omnimet software package and the position of the annual growth increments identified and marked. Marginal increment analysis (MIA) was

undertaken by measuring the distance between the most recently deposited growth line and the shell margin in ~10 shells from each season. Estimates of the longevity of the *L. patagonica* shells and the width of the growth increments were determined from peels of sections through the growing margin of the shells ( $n = 96$ ) as the growth series were more clearly defined than those deposited in the shell hinge.

The Von Bertalanffy growth function (VBGF;  $L_t = L_\infty (1 - \exp[-K(t - t_0)])$ ) was fitted to the shell length-at-age data based on measurements of the wide of the growth increments. Growth constants ( $K$ ) and asymptotic maximum shell length ( $L_\infty$ ) were calculated for each population using Fishparm (Prager et al., 1987). The phi-prime ( $\phi'$ ) growth performance index ( $\phi' = \log K + 2 \times \log L_\infty$ ) was used to compare growth amongst populations (Munro and Pauly, 1983). Phi-prime integrates  $K$  and  $L_\infty$  into a single measure and serves better as a growth descriptor than these two, often correlated parameters by themselves. Growth curve estimates were also obtained from the four (seasonal) length–frequency histograms of *L. patagonica* at SE using the ELEFAN routine in FISAT (FAO-ICLARM) – a non-parametric method to fit the VBGF through modes (Gayanilo et al., 1995). The growth parameters ( $L_\infty$  and  $K$ ), for the SE population, obtained from the data generated from the width of the growth increments were compared with the values obtained from the length–frequency histograms. An instantaneous natural mortality rate ( $M$ ) was estimated on the basis of age–frequency distributions (Ricker, 1975; Ridgeway et al., 2012). Since this species is not commercially exploited, total mortality ( $Z$ ) is assumed to be equivalent to natural mortality.  $Z$  was estimated from the slope of the regression between the natural logarithm of the frequency at age data. Longevity was calculated as the x axis intercept of the same regression line. The analysis was restricted to the descending right tail of the age–frequency curve. Finally, we search for differences in allometric relationships at the four *L. patagonica* populations: at each site, Log-transformed shell height, width and dry tissue weight data were regressed against log transformed shell length (Type 1 linear regression models) and significant departures from isometry were evaluated with t-tests (Zar, 2010).

### 3. Results

Obvious black and white lines were observed in the hinge region and along the shell margin. Conspicuous “steps” or clefts representing changes in the direction and rate of shell deposition were consistently observed along the shell margin (Fig. 3, black arrows). In the hinge region the lines were often compacted and partially fused or bifurcated (Fig. 4). A comparison of the counts of growth lines in the shell hinge and margin showed that only 8 out of the 96 shells had the same number of lines in the shell margin and on the hinge plate. To maintain consistency, only estimates of the age of *L. patagonica* were made by counting clefts at the shell margin. Sections of large (adult) shells (30–35 mm length) collected at SE, displayed growth increments during spring and summer close to or at the edge of the shell margin, slow shell growth in autumn (identifiable from changes in the direction of shell deposition), and the virtual cessation of growth in winter (as evidenced by the formation of an obvious cleft along the shell margin, Fig. 5). Seasonal variation in shell growth rates is shown in Fig. 6. High variances were found in shell growth at every season but not in winter, the period when all the shells analyzed slowed or ceased completely their growth and a cleft was deposited in the shell (Fig. 6). The formation of a margin cleft therefore provides a good estimate of the position of the annual winter shell growth cessation, since every cleft represents one winter. Growth lines of unknown periodicity are present in sections of the posterior shell margin of the calcium carbonate shell incrustations (Fig. 5b, white arrows) that surround the burrowed shell (see Fig. 1b).

Counting the margin growth lines (clefts) gave age estimates ranging between 0 and 13 years. The maximum number of annual growth lines were 13 at QQ, 12 at SE, 8 at PP and 4 at CL, the latter site was where *L. patagonica* bored into oyster shells. Von Bertalanffy growth curves from each population are shown in Fig. 7. Asymptotic maximum shell

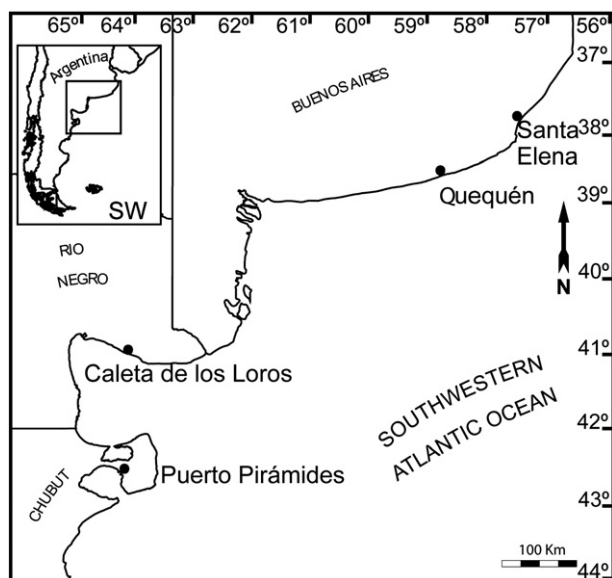
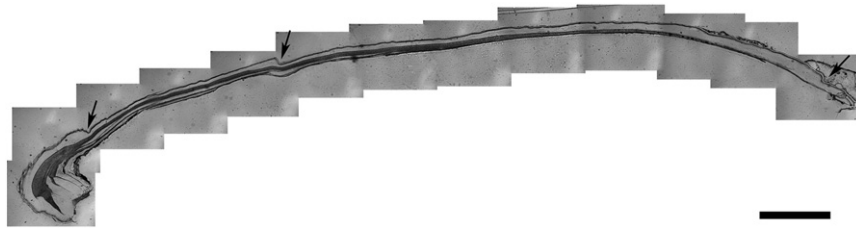


Fig. 2. Location of the four *Lithophaga patagonica* populations under study.



**Fig. 3.** Composite photograph showing the peel of a whole left shell of *Lithophaga patagonica*. Black arrows indicate the 3 margin clefts (indicating 3 winters) present in this shell. Scale: 2 mm.

length and the phi-prime growth performance index were very similar between SE and PP, although average longevity was higher at SE (15 vs. 8.25 years; Table 2). Longevity was similar at SE and QQ (13.3 vs. 15 years), despite slower growth rates and lower asymptotic shell length at QQ (Table 2). The CL population is characterized by a higher growth constant ( $K = 0.90 \text{ yr}^{-1}$ ) and shorter lifespan (longevity estimated at 6.5 years). Mortality rate estimated from the age frequency distributions was 0.23, 0.19, 0.42, and 0.45 for SE, QQ, CL, and PP respectively. The VBGF parameters ( $L_{\infty} = 42.53 \text{ mm}$ ,  $K = 0.270 \text{ yr}^{-1}$ , Table 2) obtained using ELEFAN analysis of the modal progressions at SE approximated those obtained using data from individuals of *L. patagonica* whose age had been determined.

Height–length and width–length relationships of the *L. patagonica* shells were negatively allometric ( $b < 1$ ) for all populations (t-tests:  $p < 0.001$ ; Table 3) indicating that *L. patagonica* grows faster in length than in height or width. Dry weight vs. shell length relationships were isometric, except in the case of *L. patagonica* from QQ where negative allometry was observed, suggesting that the flesh weight of these population is less in larger animals than those from the three other sites.

#### 4. Discussion

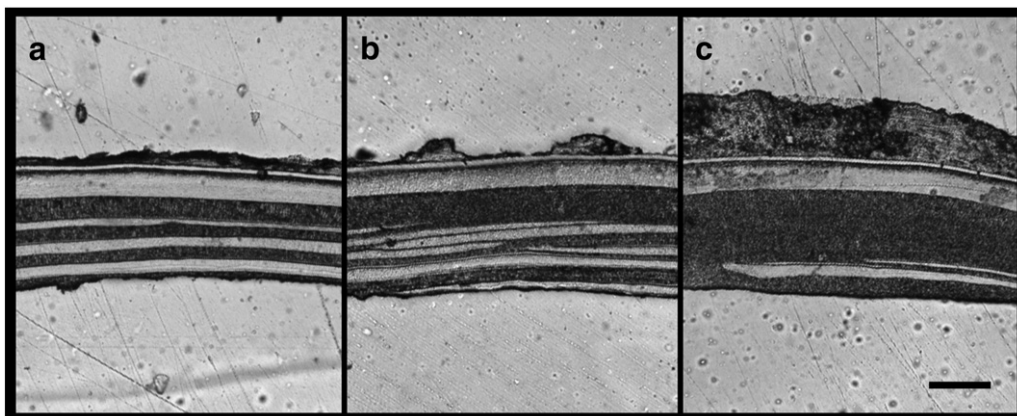
Only growth lines at the shell margin were clearly distinguishable in *L. patagonica*. The analysis of clefts at the shell margin provided estimates of the growth constant (K) at SE that were remarkably similar to those obtained from length–frequency distribution analysis (LFDA; see Table 2). The agreement between these two estimates confirms annual periodicity in the formation of these internal lines. Reproductive lines, although described for *Lithophaga lithophaga* (Galinou-Mitsoudi and Sinis, 1994, 1995), were not observed in this species.

Umbone lines, previously used for age estimations in many bivalve species, including the Mediterranean “date mussel” *L. lithophaga* (Galinou-Mitsoudi and Sinis, 1995) are often bifurcated or compacted, and partially fused in this species. Such barely discernible umbone

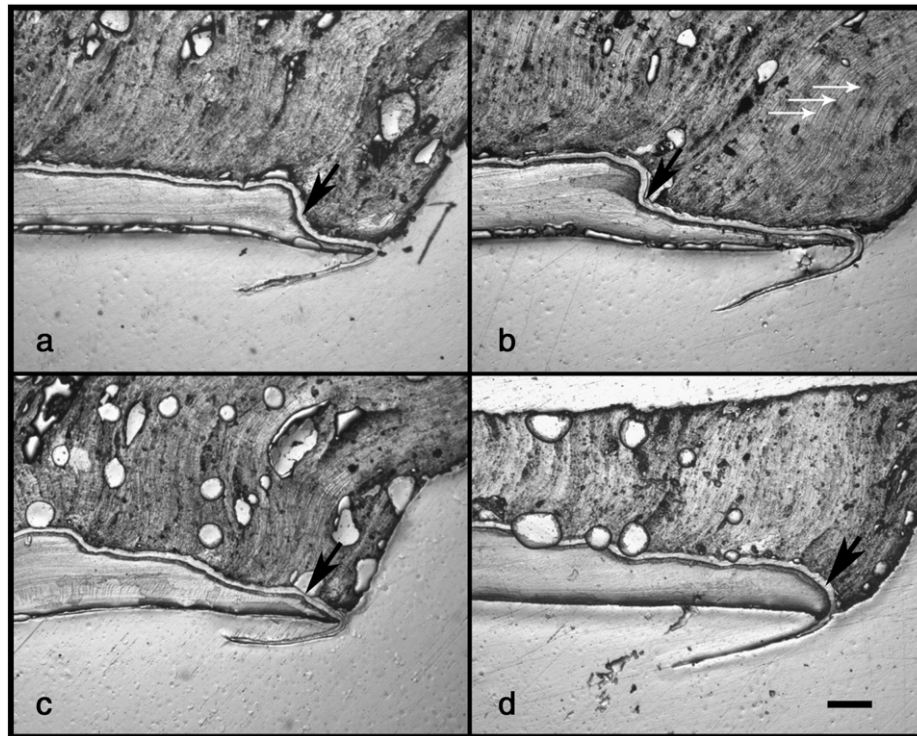
lines might have developed after dissolution of the shell during boring, or periods of anoxia (see Lutz and Clark, 1984). *L. patagonica* exposure to anoxia could occur because of sand burial (pers. obs.) or pulses in sewage disposal in the case of SE and QQ (see Elías et al., 2005; López Gappa et al., 1990). Increased  $\text{CO}_2$  concentrations and decreased pH during anoxic conditions might partly dissolve *L. patagonica* shells leading to fuzzy umbone lines.

Shell deposition in *L. patagonica* was observed to slow down or cease completely in winter. This is likely associated to the withdrawal of the shell-secreting mantle edges from the shell margins (see Richardson, 2001). Decreases in shell growth during autumn–winter have also been reported in other molluscs in the region (Arrighetti et al., 2012; Cledón et al., 2005; Giménez et al., 2004; Herrmann et al., 2009, 2011). As described by Richardson et al. (1990) for other bivalve species, a winter period of growth cessation in *L. patagonica* was preceded by a gradual narrowing of the growth increments. Narrow growth increments then coalesced to form a distinct internal growth line in winter. Larger growth increments were observed again in spring, when temperature and chlorophyll-a concentrations are known to increase (Romero et al., 2006).

Growth accretions were also observed in the calcium carbonate incrustations at the posterior shell margin (Fig. 7, white arrows). These accretions, which are reported for the first time in this study, have an apparent periodicity of deposition that might be associated to variations in boring activity rates. Incrustations at the posterior shell margin in *L. patagonica* can be long (extending up to 1 cm beyond the posterior shell margin) though they are often found broken (pers. obs.). This kind of incrustation is likely generated by the posterior calcium carbonate-secreting glands described by Morton (1993) for *L. aristata* and other Lithophagines. These calcareous incrustations presumably help to occlude the burrow aperture and camouflage the posterior shell by resembling the substratum (Morton, 1993). In the case of *Lithophaga bisulcata*, these long incrustations were postulated to protect the bivalve from predators (Morton, 1990; Scott, 1988), which is also likely in *L. patagonica*.



**Fig. 4.** Photographs of the hinge lines of 3 different shells from Sta. Elena. The black lines (irregular prismatic structures, Carter, 1980) can be distinguished clearly in shell “a”, but in shells “b” and “c” these lines intersection or merge each other and are difficult to distinguish. The hinge section in shell “a” shows distinguishable lines in the same number than those at the shell margin, but hinge sections shown in shells “b” and “c” overestimate and underestimate the number of margin lines, respectively. Scale: 100  $\mu\text{m}$ .

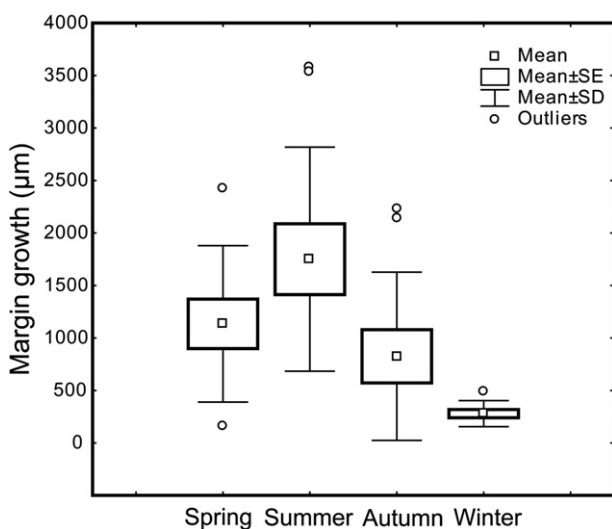


**Fig. 5.** Photomicrographs of acetate peels of the sectioned shell margin of *Lithophaga patagonica* collected from Santa Elena at each four seasons: (a) October (spring), (b) January (summer), (c) May (autumn), (d) July (winter). Black arrows indicate a change in the direction and rate of shell deposition. When the spring begins (a) the shell starts to grow (increment from the black arrow to the end of shell margin); during the whole summer (b) the shell continue growing; in autumn, (c) shell deposition decreases until it ceases completely in winter (d). This process leads to the formation of clefts in the shell margin every winter. White arrows indicate accretions on the shell posterior incrustations, which have an apparent periodicity of deposition. Scale: 200  $\mu\text{m}$ .

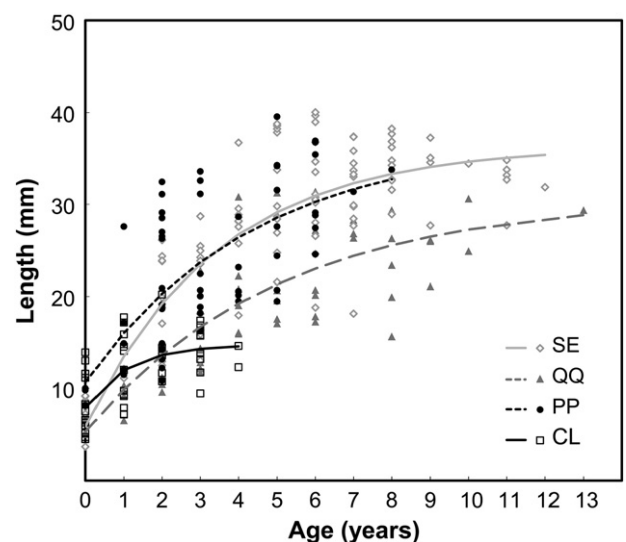
Furthermore, by occluding burrow apertures, these incrustations might protect *L. patagonica* from the extreme environmental variations associated to intertidal life (e.g., excessive air temperatures, desiccation and wave damage). The potential usefulness of these incrustations for growth analyses has yet to be evaluated.

Intertidal rock-boring populations of *L. patagonica* at SE, QQ and PP showed higher asymptotic lengths ( $L_{\infty}$ ) and lower growth constants ( $K$ ) than the subtidal oyster-boring population (Table 2). This indicates that the rock-boring populations slowly approach a larger final size whereas

the oyster-boring population rapidly approaches a smaller final size. Smaller final size in individuals from the oyster-boring population might be due to limitations for growth imposed by the thickness of the oyster shell (generally less than 12 mm). Oyster-boring *L. patagonica* reaches no more than 20 mm length and dwells perpendicularly or nearly perpendicularly to the oyster shell surface (Fig. 1; pers. obs.). Open-ended perforations reaching the internal shell surface were observed in some oysters, but *L. patagonica* individuals were invariably dead in these cases



**Fig. 6.** Growth increments at each season measured on adult shells (30–35 mm) of *Lithophaga patagonica* from Santa Elena. Growth increments were measured from the change in direction and rate of shell deposition (black arrows in Fig. 5) to the end of shell margin ( $n = 10$ ).



**Fig. 7.** Plot of length at age of *Lithophaga patagonica* in the four populations. Growth curves were fitted using the Von Bertalanffy growth equation  $L_t = L_{\infty} (1 - \exp[-K(t - t_0)])$ . Von Bertalanffy parameters for each population are shown in Table 2. Locations: Santa Elena (SE), Quequén (QQ), Caleta de los Loros (CL), Puerto Pirámides (PP).

**Table 2**  
 Von Bertalanffy growth parameters, longevity and mortality of *Lithophaga patagonica* at Santa Elena (SE), Quequén (QQ), Caleta de los Loros (CL), Puerto Pirámides (PP). Growth parameters obtained both from peels and from the length frequency distributions analysis (LFDA) are shown for SE.  $L_{\infty}$ : Asymptotic shell length, K: Von Bertalanffy growth constant,  $t_0$ : Von Bertalanffy growth parameter,  $\psi'$ : phi-prime growth performance index,  $T_{max}$ : estimate of population longevity, and mortality rate. Values of  $L_{\infty}$  and  $t_0$  are mean (SD) except for SE (LFDA).

Location	$L_{\infty}$ (mm)	K ( $yr^{-1}$ )	$t_0$	$\psi'$	$T_{max}$	Mortality rate
SE (peels)	36.34 (1.77)	0.289 (0.05)	-0.60 (0.26)	2.582	15	0.23
SE (LFDA)	42.53	0.270	-	2.689	-	-
QQ	30.78 (4.06)	0.198 (0.07)	-0.95 (0.41)	2.273	13.3	0.19
CL	14.76 (1.56)	0.90 (0.58)	-0.84 (0.49)	2.295	6.5	0.42
PP	36.95 (8.13)	0.228 (0.14)	-1.49 (0.86)	2.493	8.25	0.45

(i.e., only empty shells or linings were found) and a black spot was often observed in the oyster shell around the perforation end. We also observed empty burrows with a thin calcium-carbonate layer at the bottom, possibly due to repair of open-ended perforations by the oysters. It is thus apparent that the oysters trigger an effective defensive reaction once *L. patagonica* bore holes reach the inner shell surface. While the actual mechanism involved in this reaction is still unclear, limits to the final size in oyster-boring *L. patagonica* could clearly result from mortality after individuals grow beyond a size-threshold imposed by oyster shell thickness. Smaller asymptotic length in oyster-boring *L. patagonica* could also be attributed to a higher energetic cost of drilling into an oyster shell relative to boring into a less hard rock; oyster shells appear to be harder than the rock substrate at SE, QQ and PP (Table 1). The higher cost of boring into shells might result in decreased energy allocation to growth.

Despite being a chemical driller, *L. patagonica* was found drilling sediments with remarkably variable calcite content (Table 1). Similar results were found for *L. lithophaga*, which can bore different limestones, including oolitic limestone and dolomite (Kleemann, 1973a,b). Mineral composition and substrate hardness also seem to largely influence the growth parameters in the intertidal rock-boring populations of *L. patagonica*. Both SE and PP abrasion platforms constitute soft sandstone of very similar mineral composition (abundant quartz and feldspar with sparse calcite, Table 1). In QQ, instead, there are hard calcrete rocks with a high amount of calcium-carbonate. Von Bertalanffy growth curves for SE and PP were similar despite a lower longevity at PP, and indicate growth rates (i.e., higher growth constant and asymptotic length; see Table 2) that exceed those at QQ. This is somewhat surprising since SE and PP are the most distant to each other amongst the three populations (ca. 1000 km and 5° latitude) and those showing the most striking differences in climatic or oceanographic variables that can potentially influence growth (see Table 1). The QQ population, in contrast, is located only

100 km away from SE and both locations are quite similar with regard to the magnitude of climatic and oceanographic variables (Table 1). The rock substrate, however, is six to twelve times harder at QQ relative to SE and PP, respectively (Table 1). This suggests that the energetic costs of boring rock would be higher at QQ and that individuals in this population might allocate extra energy to rock boring at the expenses of growth rates. This is also reflected in the low biomass (dry flesh weight) of the QQ population, compared with the other sites (see Table 3). The costs of boring into harder rock could be rewarding in terms of survival since individual detachment from the rock would be hindered due to lower erosion rates. The latter could explain, at least in part, the low mortality rates estimated for the QQ population.

Estimates of longevity and mortality rates also varied between populations but these variations showed no apparent association to substrate type (i.e., oyster or sedimentary rock). Indeed, longevity and mortality rates of the rock-boring population at PP were closer to those of oyster-boring population at CL than to those of the two other rock-boring populations (Table 2). Higher mortality and decreased longevity at PP and CL might be due to regional factors since these are the two southernmost populations in this study. These two populations differ from the northernmost ones in tidal amplitude (higher at PP and CL), mean annual chlorophyll a concentration (lower at PP and CL), exposure to sewage effluents (lower at PP and CL), and perhaps turbidity (presumably lower both at PP and CL, though data is not available for CL; see Table 1). Nonetheless, regional differences in longevity and mortality cannot be simply ascribed to the above environmental differences. Furthermore, differences in asymptotic length and growth constants between these two populations suggest that local factors are evidently important. Longevity and mortality at CL are likely influenced by size thresholds for *L. patagonica* survival related to oyster shell thickness. In the case of PP, physical erosion and concomitant detachment of *L. patagonica* from the sandstone substrate is possibly an important source of mortality, as suggested by the relatively large number of empty burrows present in highly eroded zones of the cliff in this macrotidal area (pers. obs.).

Longevity of *L. patagonica* in this study ranged between 6.5 and 15 years (CL and SE populations, respectively). Blanco et al. (1988) reported a much shorter longevity (5 years) for rock-boring *L. patagonica* at an intertidal location nearby SE. It is uncertain whether that difference reflects small-scale, spatial variations in longevity (the study site in Blanco et al., 1988 is located only a few km apart from SE) or shortcomings in age determination due to the use of surface ring analysis in this previous study (i.e. external lines in *L. patagonica* become hardly distinguishable as the individuals approach its asymptotic length, pers. obs.).

Variations in longevity and growth parameters are remarkable among *Lithophaga* species. For instance, the growth constants reported here for *L. patagonica* are much higher than those reported for *L. lithophaga* at the Northern Evoikos Gulf, Greece ( $K = 0.044 yr^{-1}$ ; see

**Table 3**  
 Allometric relationships in *Lithophaga patagonica* from Santa Elena (SE), Quequén (QQ), Caleta de los Loros (CL), and Puerto Pirámides (PP). Significant p-values after t-tests indicate departures from isometry.

Relationship	Location	Constant (A)	Coefficient (b)	SEb	$\beta$	df	t	Growth
Length vs. Height	SE	-0.35	0.93	0.006	1	664	12.01*	Negative allometric
	QQ	-0.32	0.89	0.010	1	121	10.51*	Negative allometric
	PP	-0.31	0.90	0.009	1	182	10.81*	Negative allometric
	CL	-0.3	0.90	0.013	1	141	7.61*	Negative allometric
Length vs. Width	SE	-0.33	0.88	0.008	1	573	14.63*	Negative allometric
	QQ	-0.34	0.87	0.010	1	119	12.63*	Negative allometric
	PP	-0.32	0.87	0.012	1	179	10.71*	Negative allometric
	CL	-0.33	0.88	0.017	1	135	6.48*	Negative allometric
Length vs. Weight	SE	-5.24	2.96	0.054	3	297	1.16 <sup>NS</sup>	Isometric
	QQ	-4.56	2.30	0.057	3	103	12.45*	Negative allometric
	PP	-5.02	2.90	0.082	3	145	1.15 <sup>NS</sup>	Isometric
	CL	-4.77	2.70	0.345	3	9	0.89 <sup>NS</sup>	Isometric

NS: not significant ( $p > 0.05$ ).

\*  $p < 0.001$ .

Galinou-Mitsoudi and Sinis, 1995). However, *L. lithophaga* has a higher asymptotic length ( $L_{\infty} = 80.14$  mm) and a much longer life span (54 years). Life span was also found to be quite variable among coral boring *Lithophaga* species (e.g. 10–15 years in *L. bisulcata* from the Caribbean; and 6–8 years in *Lithophaga attenuata*, 2.75 years in *Lithophaga plumula*, and 2 years in *L. aristata* from the Eastern Pacific in Panama; Kleemann, 1990). In this study, however, we illustrate that longevity can be equally variable between different populations of a single *Lithophaga* species.

Variations in longevity, mortality, and growth parameters between these populations would be generating differences in the bioerosion rates of intertidal rock substrates. For instance, considering maximum ages of 13 at QQ, 12 at SE, and 8 at PP (this study) and an average burrow volume of 2.4, 2.9, and 2.0 cm<sup>3</sup> for individuals reaching the maximum age respectively at each site (i.e., calculated from individual volume vs. age regressions and assuming burrow volume as similar to individual volume; authors unpublished data), lifetime per capita bioerosion rates would be 0.18, 0.24, and 0.25 cm<sup>3</sup> yr<sup>-1</sup>, respectively. Further research on *L. patagonica* density across the intertidal slope and the maximum depth in the rock at which this species inhabits would be necessary to estimate its overall contribution to coastline erosion rates.

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