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Endolithic invertebrate communities and bioerosion rates in southwestern Atlantic intertidal consolidated sediments

María Bagur · Jorge L. Gutiérrez · Lorena P. Arribas · M. Gabriela Palomo

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Abstract Organisms boring into intertidal consolidated sediments generate bioerosion. It is generally unknown, however, whether they can significantly contribute to coastline retraction. In this paper, we describe endolithic communities and estimate bioerosion and physical erosion rates at three southwestern Atlantic intertidal sites (37, 38, and 42°S; Argentina). In the northernmost site, we have also analyzed spatial variation in species richness and abundance as a function of height within the tidal slope, orientation of the rock surface in relation to breaking waves (i.e., facing or not), and rock hardness. The number of species and the combined abundance of individuals from the different species were larger at the low intertidal level but did not differ between surface orientations. The density of chemically boring organisms increased with increasing rock hardness and calcium carbonate content. In contrast, no correlation was found between rock hardness and the abundance of organisms that bore by mechanical means. Endolithic community composition and bioerosion rates differed among the three sites, the latter being higher at the site with the softer substrate. Bioerosion estimates were two orders of magnitude lower than physical erosion estimates at each site. The bivalve *Lithophaga patagonica* was the species that contributed the most to bioerosion at all these locations. While results suggest that bioerosion contributes little to overall coastal erosion at the three study sites, boring organisms might still facilitate physical erosion by weakening the rock either via chemical or mechanical means. Besides, their apparently inconsequential direct action as bioeroders can have positive consequences for biodiversity via increased habitat complexity.

Introduction

To thrive in rocky intertidal shores, organisms have to withstand substantial variations in physical factors such as temperature, air exposure, or the mechanical impact of waves (Little and Kitching 1996). Typical examples of organismal adaptations to this habitat include clamping down in limpets, attachment threads in mussels, and folding inward in sea anemones (Levinton 2009). Additionally, some organisms have developed the ability to live inside rocks. Species from different taxonomic groups—such as sponges, bivalves, polychaetes, echinoids, barnacles, sipunculans, bryozoans, phoronids, coralliophilid gastropods, and alphaeid, and callianassid shrimps—can erode hard substrates either mechanically, chemically, or via the combination of both mechanisms (Yonge 1963; Kleemann 2005). As it is general for intertidal organisms, the abundance of these *endolithic* species varies across the intertidal slope in response to physical factors such as temperature, air exposure, or sand burial (Evans 1968a;

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M. Bagur (✉) · L. P. Arribas · M. G. Palomo
Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-CONICET), Av. Ángel Gallardo 470, 3er Piso Lab. 57, C1405DJR Buenos Aires, Argentina
e-mail: mbagur@macn.gov.ar

J. L. Gutiérrez · M. G. Palomo
Grupo de Investigación y Educación en Temas Ambientales (GrIETA), San Eduardo del Mar, Argentina

J. L. Gutiérrez
Facultad de Ciencias Exactas y Naturales and CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

J. L. Gutiérrez
Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA

Stearley and Ekdale 1989; Galinou-Mitsoudi and Sinis 1997). In addition, the distribution of boring organisms is also influenced by rock properties, such as hardness and composition (Yonge 1963; Evans 1968a, Kleemann 1973, 1996; Amor et al. 1991).

When evaluating species composition and relative abundance in boring invertebrate communities, it is necessary to obtain reliable estimates of bioerosion rates. Bioerosion is the destruction and removal of consolidated minerals or lithic substrate by the direct action of organisms (Neumann 1966). When abundant, the bioeroders themselves can severely compromise the structural stability of their substrate (e.g., when infesting the holdfast region of corals; see MacGeachy and Stearn 1976; Hutchings 1986). In other cases, substrate instability and erosion result from the interaction between bioeroders and physical forces. For instance, boring organisms often weaken the substrate making it more susceptible to physical erosion (e.g., facilitation of rock "undercutting"; Evans 1968a). The reverse situation can also occur; i.e., damage caused by physical or chemical erosion can facilitate subsequent bioerosion (Hutchings 1986).

Intertidal sedimentary rock outcrops are common along most of the Argentinean coast. They usually occur in the form of abrasion platforms associated with inactive or active cliffs (Kokot et al. 2004; Isla and Bértola 2005). Despite 29 large accretion zones identified along the Argentinean coastline, most of its length is cliff-dominated and shows evidence of erosion to a higher or lesser degree (Kokot 2004). Physical erosion along the Argentinean coastline is caused by storms and rising sea levels (Schillizzi et al. 2004; Kokot 2004) but also by human activities that alter sand supplies such as sand extraction (Marcomini and López 1999), dune afforestation (Isla et al. 1998), or the construction of breakwaters and poorly planned coastal structures (López and Marcomini 2005; Marcomini et al. 2007). Despite the widespread distribution of cliff-dominated coastlines along the Argentinean coast and the important scientific and public concern about their retreat (more than 1 m year^{-1} at certain sites; see Isla and Bértola 2005), boring organisms in sedimentary rock outcrops were rarely subject of research (but see Amor et al. 1991) and no estimate of bioerosion rates was available to date.

In this paper, we describe the endolithic communities and estimate rates of bioerosion and physical erosion in intertidal consolidated sediments of three southwestern Atlantic sites (37, 38, and 42°S). In the case of the northernmost site (SE, see Fig. 1), within-site variation in the abundance of the different species was also analyzed as a function of (a) height within the tidal slope, (b) orientation of the rock surface with regard to breaking waves (i.e., facing or not), and (c) rock hardness.

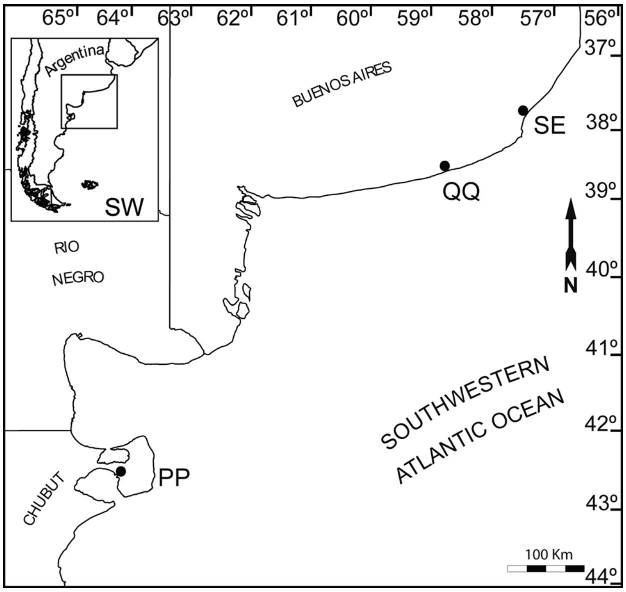

Fig. 1 Location of the three sites under study. *SE* Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides

Materials and methods

Study sites

The study was conducted in three intertidal sites in the Argentinean coast: Santa Elena (37°51′S, 57°30′W; hereafter SE), Quequén (38°34′S, 58°39′W, hereafter QQ), and Puerto Pirámides (42°34′S, 64°17′W, hereafter PP) (Fig. 1). The three sites are characterized by extensive abrasion platforms that lie at the base of active cliffs and are crossed by drainage channels more or less perpendicular to the shoreline. SE and QQ are characterized by microtidal regimes (maximum amplitude 1.55 and 1.70 m, respectively), while PP is a macrotidal site (maximum amplitude 5.88 m). The abrasion platforms at SE are composed of compact sedimentary rock, sometimes cemented by crystalline calcium carbonate, with variable color and hardness (Amor et al. 1991). Platforms at QQ are composed of loess with abundant calcretes that confer high hardness to the rock (Bagur et al. 2013). The same three intertidal zones can be visually distinguished at both sites; i.e., a low intertidal zone dominated by the alga *Corallina officinalis*, a mid-intertidal zone dominated by the mussel *Brachidontes rodriguezii*, and a sand-influenced high intertidal zone characterized by bare rock with low cover of *Enteromorpha* spp. and other green algae. PP is characterized by packstone platforms that often contain marine fossils (mainly oyster and pectinid shells) and carbonatic cement (Scasso and del Río 1987). The seaweed *C. officinalis* also dominates the low intertidal zone at this site, while the mid-intertidal zone is dominated by the mussel *Brachidontes purpuratus*, and the high intertidal zone is characterized by the presence of barnacles, *Balanus glandula*, and pulmonate limpets, *Siphonaria lessoni*, in relatively large numbers.

Local distribution of endolithic species and physical variables

The local abundance of endolithic species with regard to physical variables was analyzed at SE. Rock samples (ca. 2,000 cm^3, i.e., equivalent to 3,700 ± 790 g of rock, $n = 16$) were collected in July 2009, October 2009, January 2010, and May 2010 in the low and mid-intertidal level (the high intertidal zone was covered by sand in most sampling dates and, thus, was excluded from the analysis) and from rock surfaces oriented seaward (i.e., facing to breaking waves) and landward (i.e., facing to return flows). Rock pieces were removed by means of hammer and chisel, and sample volume was measured by displacement of water in a graduated bucket. A total of 64 samples were collected (i.e., four replicates for each combination of orientation, tidal height, and sampling date). Every rock sample was carefully fragmented into small pieces (1 cm^3 or less), and all endolithic animals were removed, stored in 70 % alcohol, and taken to the laboratory, where they were identified to the lowest possible taxonomic level and counted. The specimens collected here and throughout this study were stored at Museo Argentino de Ciencias Naturales (MACN-In 39497-514).

To evaluate whether our sampling effort sufficed to obtain reliable estimates of species richness at each intertidal level (i.e., mid vs. low) and substrate orientation (i.e., seaward vs. landward), we constructed species accumulation curves using rarefaction techniques (Gotelli and Colwell 2001) and compared observed species richness values (S_{obs}) with the Chao 2 estimate of the total number of species likely to be observed in the community (Chao 1984). The Chao 2 richness estimate uses the ratio of the number of species observed only once in a dataset to the number of species observed twice to approximate the actual number of species present in a habitat type (Colwell and Coddington 1994). The degree to which the Chao 2 estimate matches S_{obs} provides an indication of how thoroughly the community has been sampled (Badano et al. 2006). Confidence intervals (95 %; hereafter CIs) for S_{obs} were calculated based on the unconditional variance estimate developed by Colwell et al. (2004). EstimateS 8.2.0 (Colwell 2005) was used to construct species accumulation curves and to calculate CIs and the Chao 2 estimate.

Three-way ANOVA was used to test the null hypotheses of no difference in the combined abundance of all species and the abundance of each numerically dominant species between sampling dates, tidal heights, and substrate orientations. Data were previously tested for homogeneity of variances using Cochran's test and transformed when needed in order to meet this assumption. Student–Newman–Keuls' (SNK) post hoc test was used to test for differences between factor levels after significant ANOVA.

Rock hardness (estimated as perforability) was measured in each sample as the mean depth of 3 holes (6 mm diameter) drilled during 10 s with a power drill (see Evans 1968b; Pinn et al. 2005). The drill was always operated by the same person who exerted no force on it. Differences in rock hardness between tidal heights and substrate orientations were tested with two-way ANOVA. The calcium carbonate ($CaCO_3$) content of the rock samples was calculated as weight loss after treatment with concentrated HCl (Carver 1971). Correlation analysis was used to test for linear association between rock hardness and $CaCO_3$ content. Correlation analysis was also used to test for linear association between rock hardness and the abundance of chemically and mechanically boring organisms. Abundance data from the mid- and low intertidal zones were separately analyzed to factor out differences in community composition and rock hardness. In both cases, data were log-transformed to meet the linearity assumption. Species were classified either as mechanical or chemical borers based on previous research on the species or genus (see Table 1).

The relative strength of wave forces on seaward- and landward-oriented rock surfaces at the mid- and low intertidal zone was estimated from the dissolution of chlorine tablets (see Bartol et al. 1999). Both in September 2009 and September 2010, eight pre-weighed tablets (commonly used for swimming pool disinfection) were placed into mesh bags (5 mm mesh size) and attached to the rock surface with U-shaped iron stakes. After 2 tidal cycles (24 h), the tablets were collected, dried, and weighed. Tablet dissolution (i.e., the difference between initial and final dry weight) was used as a surrogate of flow exposure. Differences in flow exposure between tidal heights and substrate orientations were analyzed by means of two-way ANOVA. Data from both years were pooled after detecting no differences between years.

Geographic variations in endolithic communities and bioerosion rates

To compare endolithic communities and bioerosion rates among sites, five rock samples (2,000 cm^3) were collected in the low intertidal level each at SE, QQ, and PP between November 2009 and January 2010, and all endolithic invertebrates were removed, identified, and counted (see methods above). Specimens from numerically dominant species (i.e., species comprising at least 25 % of the total number of individuals in the samples) were measured in length to the nearest 0.01 mm using digital vernier calipers (shell length in the case of bivalves and body length in the case

Table 1 Mean (±SD) density of intertidal endolithic species in the pooled samples taken seasonally from Santa Elena (SE), and proportional numerical contribution of each species to the total number of individuals

Taxonomy	Species	Density	% of fauna	Intertidal distribution	Life mode	Other locations
Mollusca						
Cl. Bivalvia						
Mytilidae	*Lithophaga patagonica* (d'Orbigny 1842)	10.06 (10.60)	27.18	MI, LI	Chemical borer (Kleemann 1996; Mikkelsen and Bieler 2008)	QQ, PP
Pholadidae	*Barnea lamellosa* (d'Orbigny 1846)	1.20 (2.36)	3.25	MI, LI	Mechanical borer (Turner 1954; Yonge 1963; Mikkelsen and Bieler 2008)	–
Pholadidae	*Netastoma darwinii* (G.B. Sowerby II 1849)	0.17 (0.55)	0.46	MI, LI	Mechanical borer (Turner 1954; Mikkelsen and Bieler 2008)	QQ, PP
Veneridae	*Petricola dactylus* G.B. Sowerby I 1823	0.17 (0.42)	0.46	MI, LI	Mechanical borer (Yonge 1963; Ansell and Nair 1969; Mikkelsen and Bieler 2008)	–
Veneridae	*Petricola lapicida* (Gmelin 1791)	0.05 (0.21)	0.13	LI	Mechanical borer (Yonge 1963; Ansell and Nair 1969; Mikkelsen and Bieler 2008)	–
Hiatellidae	*Hiatella* cf. *meridionalis* d'Orbigny 1846	0.91 (1.37)	2.45	MI, LI	Mechanical borer or nestler (Hunter 1949; Mikkelsen and Bieler 2008)	PP
Myidae	*Sphenia fragilis* (H Adams and A Adams 1854)	1.25 (2.05)	3.38	MI, LI	Nestler (Yonge 1951; Mikkelsen and Bieler 2008)	–
Lyonsiidae	*Entodesma patagonica* (d'Orbigny 1846)	0.02 (0.13)	0.04	LI	Nestler (Mikkelsen and Bieler 2008)	–
Annelida						
Cl. Polychaeta						
Flabelligeridae	*Pherusa* sp. Oken 1807	11.88 (14.64)	32.08	MI, LI	Chemical borer (Amor et al. 1991; Amor 1994; Beesley et al. 2000)	QQ
Cirratulidae	*Dodecaceria meridiana* Elías and Rivero 2009	0.83 (1.77)	2.24	MI, LI	Chemical borer (Elías and Rivero 2009; Beesley et al. 2000)	–
Sipunculida						
O. Golfingiiformes						
Themistidae	*Themiste alutacea* (Grube and Oersted 1858)	10.48 (16.36)	28.32	MI, LI	Chemical borer (Williams and Margolis 1974; Cutler and Cutler 1988)	QQ

Density is expressed as number of individuals per sample (2,000 cm^3 of rock; ca. 270 cm^2 area). The main boring mechanism of each species, their distribution in the intertidal zone (*MI* mid-intertidal level, *LI* low intertidal level), and their occurrence in samples from other locations covered in this study (*QQ* Quequén, *PP* Puerto Pirámides) are also reported

Table 2 Age estimates of the numerically dominant species considered in bioerosion calculations at the three sites covered in this study

Species	Taxon	Age estimation method	Maximum age (years)		
			SE	QQ	PP
Lithophaga patagonica	Bivalvia	Annual lines counted in acetate peel replicas of the sectioned shell surfaces (Bagur et al. 2013)	12	13	8
Barnea lamellosa	Bivalvia	Counting of external growth rings	31	–	–
Themiste alutacea	Sipunculida	Age classes assumed as modes in the size-frequency distribution as detected by the Battacharya's method	2	2	–
Pherusa sp.	Polychaeta	Age classes assumed as modes in the size-frequency distribution as detected by the Battacharya's method	3	2	–

SE Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides

of sipunculans and polychaetes). Individual volume was estimated from length measurements using volume-length regression models constructed for each dominant species at each location. To construct each of these models, the volume of nearly 100 pre-measured individuals was determined by water displacement in a graduated cylinder (precision 0.01 ml). Although not so abundant (i.e., <25 % of the total number of individuals in the samples), the bivalve *Barnea lamellosa* was also included in the analysis because of its potentially important contribution to rock erosion by virtue of its large size (up to 7.5 cm length and 10.39 cm^3 volume). Bioerosion by small-sized species found at low densities (7, 1, and 2 species at SE, QQ, and PP, respectively) was expected to be negligible and therefore not included in the analysis. Additionally, rock hardness was estimated at each site by means of the drilling method explained above (10 holes drilled per site). One-way ANOVA was used to test for differences among sites in the joint abundance of all species, the abundance of the dominant species, and rock hardness.

Annual bioerosion rates (B) by each numerically dominant endolithic species at each site were estimated as follows:

$$B = \sum_{a=1}^{a=\max} (v_a - v_{a-1}) d_a$$

where v_a is mean burrow volume for individuals at age a (in years) and d_a is their mean density.

Mean burrow volume at age a (v_a) was calculated from individual volume versus length regressions after assuming burrow volume as similar to individual volume (severe underestimation of burrow volume owing to this assumption is highly unlikely because numerically dominant species in this study tightly fit into their burrows; pers. obs). The density (d) of each species as individuals per area unit was estimated from original data on individuals per volume unit after dividing sample volume by the maximum perforation depth observed in the samples (7.5 cm for *Barnea lamellosa* at SE; perforation depth estimated from individual body length). This was done because it was not viable to directly measure the exposed area of the rock samples. Sample removal unavoidably caused fragmentation into several rock pieces of irregular contour and shape, and thus, it was virtually impossible either to predict the actual contour and shape of the sample before its collection or to rearrange the collected rock fragments into the original form. Sample depth was assumed as the depth of the deeper known burrow because the irregular surface and bottom fragmentation of chiseled out rock samples precluded us to accurately control for sample depth. In spite of the irregular profile of the samples, in all cases, we targeted for a maximum depth of 10–12 cm and ensured that they were deep enough to comprise all organisms present in a portion of rock surface. Therefore, actual sample depth is expected to exceed maximum perforation depth, and, concomitantly, our areal density estimates and areal bioerosion estimates are likely small underestimates of actual density and bioerosion rates.

Age estimates of *Barnea lamellosa* and the numerically dominant species considered in this analysis (i.e., the bivalve *Lithophaga patagonica*, the sipunculan *Themiste alutacea*, and the polychaete *Pherusa* sp.) were based on distinct sources and approaches (summarized in Table 2).

Physical and total erosion rates

Physical erosion rates and the relative contribution of wave climate and rock properties to physical erosion rates at each site were evaluated with a rock transplant experiment. Twenty-four pieces of rock were collected each at SE, QQ, and PP and then carefully molded with chisel to a nearly cylindrical shape (ca. 8 cm radius and 6 cm height; average weight 915 ± 121 g; i.e., between half and a third of their original size). Careful molding of the original rock pieces into smaller ones of similar size and shape was necessary to eliminate differences in the amount of rock surface exposed to water flows as well as any damage caused during removal of the original rock piece. Each rock cylinder was placed into a separate net bag (10-mm mesh size). Rock pieces from SE, QQ, and PP were randomly distributed in the low intertidal zone at each site ($n = 8$) and tightly attached to the intertidal rock from their net bags by means of *U*-shaped iron stakes. After 6 months, the experimental rock transplants were collected and dried, and their final weight and volume measured in order to calculate weight and volume loss. The experiment was conducted twice at each site (March 2012–September 2012, September 2012–March 2013). Two-way ANOVA was used to test the null hypothesis of no differences in physical erosion rates between shores and rock types. Bioerosion and physical erosion rates were summed to calculate total erosion rates at each shore. Since a high number of replicates were lost, sample sizes for these analyses were 3 and 5 for the first and second experimental period, respectively. Since no replicate was recovered from SE at the end of the second experimental period, this site was not included in the analysis. Annual physical erosion rates at QQ and PP (as percentage of rock eroded) were calculated by summing the percentage of weight loss in local rock pieces during both 6-month experimental periods. In the case of SE, annual physical erosion rates were estimated after multiplying by the percentage of weight loss of rock observed during the March–September 2012 period. Total erosion rates at each site (as percent volume loss) were estimated as the sum of annual physical erosion rates and annual bioerosion rates.

Results

Physical variables

Rock hardness (measured as rock perforability) and flow exposure (measured as weight loss in chlorine tablets) varied locally at SE. They both were higher in the low intertidal level but did not significantly differ between seaward- and landward-oriented rock surfaces (Table 3). Rock perforability (i.e., the inverse of hardness) was negatively correlated with the $CaCO_3$ content of the rocks (Spearman rank correlation, $r_s = -0.81$, $n = 28$, $P < 0.01$, Fig. 2). There was a large variance in hardness and $CaCO_3$ content between rocks (16–72 % $CaCO_3$). There were also a few soft rocks with <10 % $CaCO_3$, which were uninhabited by endolithic species.

Rock hardness also varied between sites. Mean rock perforability was 11.40 ± 9.40 mm at SE, 1.85 ± 1.20 mm at QQ, and 22.1 ± 7.55 at PP (ANOVA, $F_{(2,27)} = 20.98$, $P < 0.01$, SNK: QQ < SE < PP).

Local distribution of endolithic species

Eleven endolithic macrofaunal species were found at SE (Table 1). The most abundant species were the sipunculan *Themiste alutacea,* the bivalve *Lithophaga patagonica,* and the polychaete *Pherusa sp.* (Table 1). The bivalves *Petricola lapicida* and *Entodesma patagonica* were rare species only found at the low intertidal level (3 and 1 individuals, respectively).

Eleven and nine species were found in the low and the mid-intertidal level, respectively (Fig. 3a); meanwhile, ten species were found both at seaward- and landward-oriented rock surfaces (Fig. 3b). Species–area curves approached an asymptote before 32 samples (i.e., our sample size) in all cases (Fig. 3a, b), indicating that the sampling effort was sufficient to fully capture the richness of the assemblages. In agreement, the values of Chao 2 estimate were the same or close to the observed species richness at each intertidal level (Fig. 3a) and substrate orientation (Fig. 3b). Combined abundance of all endolithic organisms was higher in autumn (but no differences were found in SNK test) and in the low intertidal level (Table 4a). The three numerically dominant species and the large bivalve *Barnea lamellosa* are unevenly distributed across the intertidal platform. *L. patagonica* was abundant in all samples, and as *B.*

Table 3 Results of two-way ANOVA testing the effect of tidal height and substrate orientation on (a) rock hardness and, (b) flow exposure

Source	*df*	MS	*F*	*P*
(a) Rock hardness				
Height	1	1,008.51	9.66	**<0.01**
Orientation	1	78.96	0.76	0.38
Height × Orientation	1	59.53	0.57	0.45
Error	60	104.42		
(b) Flow exposure				
Height	1	13,764.10	10.89	**<0.01**
Orientation	1	180.62	0.14	0.71
Height × Orientation	1	0.40	0.00	0.95
Error	12	1,263.38		

Significant differences ($P < 0.05$) are marked in bold

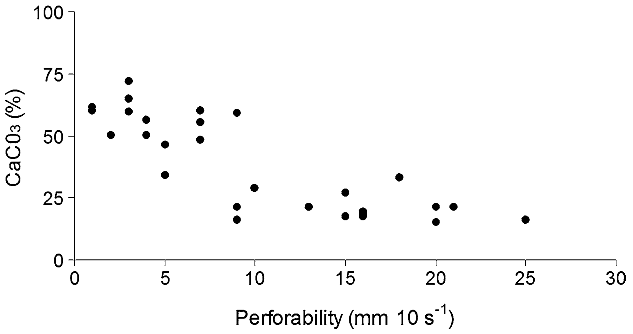

Fig. 2 Relationship between rock hardness (measured as mm of perforability using a power drill) and the calcium carbonate content of the rocks

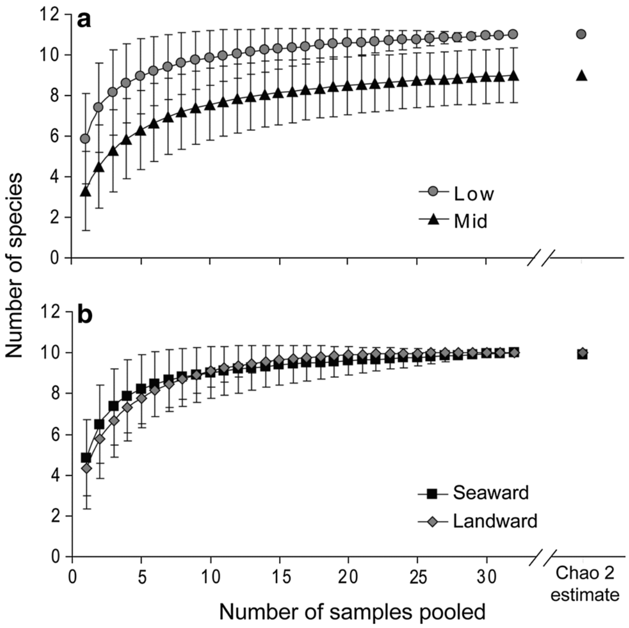

Fig. 3 Species accumulation curves (±95 % confidence intervals) comparing species richness between **a** mid- and low intertidal height and **b** seaward- versus landward- oriented rock surfaces. *Separate symbols* at the *right of the curves* are the values of the Chao 2 estimate

lamellosa, significantly more abundant at the low intertidal level (Table 4b, e). Although *T. alutacea* abundance varied largely between samples (0–77 ind. per sample; absent in 28 % of samples), higher abundance was found in spring at the mid-intertidal zone (i.e., significant season by tidal level interaction; see Table 4c). The polychaete *Pherusa* sp. was present in 89 % of the samples, and its abundance differed between seasons (but no differences found in SNK test), tidal heights (higher at the low intertidal zone), and substrate orientations (higher in seaward-oriented rock surfaces; Table 4d).

The density of chemical borers was negatively correlated with rock perforability both at mid- and low intertidal levels (Fig. 4a, b; Table 5). There was no correlation between rock hardness and the abundance of mechanical borers at both intertidal levels (Fig 4c, d; Table 5).

Geographic variations in endolithic communities

From the 10 endolithic species found at the low intertidal zone of SE in January 2010 (*Entodesma patagonica* was not found in this sampling date), only 4 and 3 were found at QQ and PP, respectively, in November 2009 and December 2009 (Table 1). The three dominant species at SE (*L. patagonica*, *T. alutacea,* and *Pherusa* sp.) were also present and dominant in QQ (>25 % of the total individuals), but only *L. patagonica* was present at PP, in high densities (Fig. 5). *Netastoma darwinii* was scarce (<1 ind. per 2,000 cm^3 rock in average) at the three sites. *Hiatella* cf. *meridionalis* occurred in low numbers at SE and PP. No differences were found between sites in the joint abundance of all species (ANOVA, $F_{(2,12)} = 0.42$, $P = 0.66$).

Erosion estimates

Rates of bioerosion by the dominant species at each site are summarized in Table 6. *L. patagonica* contributed the most to bioerosion at all locations. The highest and lowest bioerosion rates (as the sum of all dominant species contributions) were observed at PP and QQ, respectively.

The effects of site and rock type on physical erosion rates varied between study periods. A significant interaction between rock type and site was observed in March 2012–September 2012 (ANOVA, $F_{(4,18)} = 12.44$, $P < 0.01$). PP sandstone was significantly more eroded than the two other rock types both at SE and QQ but not at PP (all rock types were similarly eroded at this site). Erosion of SE sandstone and PP sandstone was significantly lower at PP relative to the two other sites, while QQ calcrete was similarly eroded at all the sites (Fig. 6a). In contrast, only significant effects of rock type were observed during September 2012–March 2013, with higher erosion of PP sandstone relative to the two other rock types both at QQ and PP (ANOVA, $F_{(2,24)} = 9.49$, $P < 0.01$, Fig. 6b).

Estimates of total annual erosion (as the sum of the percentage of weight losses due to physical and biological erosion) were 33.79, 23.44, and 35.38 % at SE, QQ, and PP, respectively. Annual volume losses in local rock types due to physical erosion were two orders of magnitude higher than bioerosion estimates (Table 7).

Discussion

Local distribution of endolithic species

From the 11 endolithic species found at SE, three of them were not reported in an earlier study at the site—i.e., the bivalves *Sphenia fragilis, Entodesma patagonica,* and *Petricola lapicida* (see Amor et al. 1991). Furthermore, the finding of the nestler bivalve *S. fragilis* represented a Southward expansion of its distribution range (Pastorino and Bagur 2011). The low intertidal level showed a larger number of species than the mid-intertidal zone. The same was observed for the combined abundance of individuals from the distinct endolithic species. This is likely associated with lower desiccation at the low intertidal level due to decreased emersion time, as is general for rocky shores (Little and Kitching 1996). On the other hand, richness and combined abundance of endolithic species did not differ

Table 4 Results of three-way ANOVA testing the effect of season (se), tidal level (le), and substrate orientation (or) on combined abundance of all species and abundance of the numerically dominant species (or with large size, e.g., *Barnea lamellosa*)

Source	*df*	MS	*F*	*P*	Difference
(a) Combined abundance					
se	3	3,241.64	3.62	**0.02**	Wi = Au = Su = Sp
le	1	7,203.77	8.04	**0.01**	Mid < Low
or	1	2,197.27	2.45	0.12	
seXle	3	1,844.64	2.06	0.12	
seXor	3	586.39	0.65	0.58	
leXor	1	185.64	0.21	0.65	
seXleXor	3	979.35	1.09	0.36	
Error	48	896.09			
(b) *Lithophaga patagonica*					
se	3	2.53	1.44	0.24	
le	1	7.12	4.05	**0.04**	Mid < Low
or	1	4.70	2.68	0.11	
seXle	3	1.96	1.11	0.35	
seXor	3	1.02	0.58	0.63	
leXor	1	1.79	1.02	0.32	
seXleXor	3	1.33	0.76	0.52	
Error	48	1.76			
(c) *Themiste alutacea*					
se	3	17.83	6.62	<0.01	
le	1	7.87	2.92	0.09	
or	1	0.10	0.04	0.85	
seXle	3	14.40	5.35	**<0.01**	Mid: Wi = Su = Au < Sp
seXor	3	0.13	0.05	0.99	
leXor	1	2.20	0.82	0.37	
seXleXor	3	3.08	1.14	0.34	
Error	48	2.69			
(d) *Pherusa* sp.					
se	3	5.18	5.99	**<0.01**	Wi = Au = Su = Sp
le	1	8.32	9.61	**<0.01**	Mid < Low
or	1	5.39	6.22	**0.02**	Lan < Sea
seXle	3	2.11	2.43	0.08	
seXor	3	0.32	0.37	0.77	
leXor	1	0.17	0.2	0.66	
seXleXor	3	0.67	0.78	0.51	
Error	48	0.87			
(e) *Barnea lamellosa*					
se	3	46.82	0.86	0.46	
le	1	345.15	6.33	**0.01**	Mid < Low
or	1	26.40	0.48	0.48	
seXle	3	61.40	1.13	0.34	
seXor	3	44.32	0.81	0.49	
leXor	1	0.39	0.07	0.79	
seXleXor	3	17.65	0.32	0.80	
Error	48	54.53			

Significant differences ($P < 0.05$) are marked in bold. Differences between the levels of each factor after significant factor effects are shown in the far right column. These differences were established after ANOVA results for factors including two levels (tidal level: mid vs. low; substrate orientation: landward vs. seaward). In the case of season (i.e., four levels), post hoc SNK tests were used after significant factor effects. *Wi* winter, *Sp* spring, *Su* summer, *Au* autumn, *Mid* mid-intertidal, *Low* low intertidal, *Lan* landward, *Sea* seaward

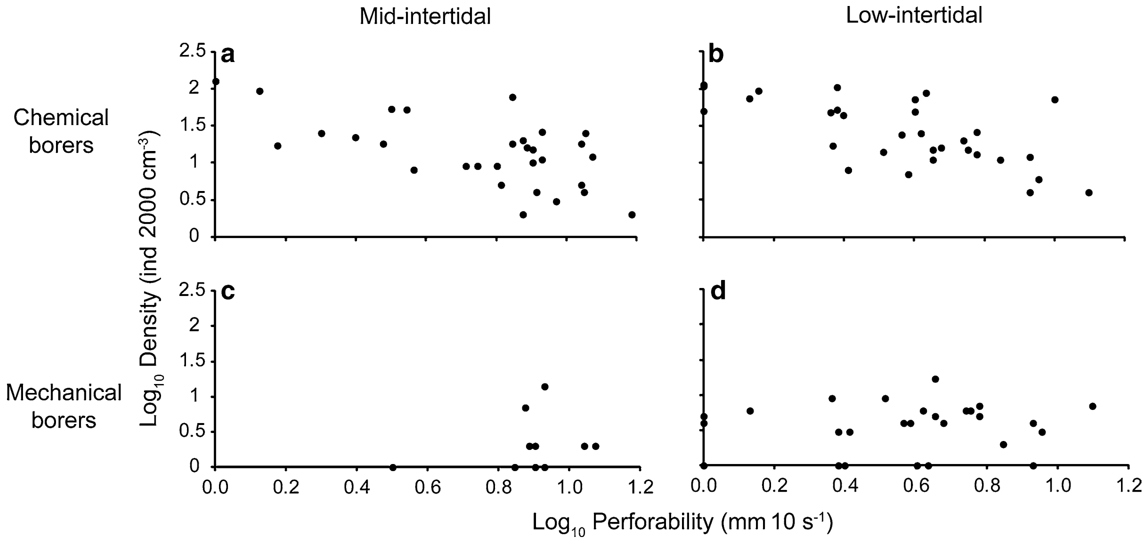

Fig. 4 Relationships between rock hardness (measured as mm of perforability using a power drill) and the density of chemical (**a**, **b**) and mechanical borers (**c**, **d**; measured as individuals per 2,000 cm^3 rock), at the mid (**a**, **c**)- and low intertidal zone (**b**, **d**)

Table 5 Correlation between *endolithic* invertebrate densities (ind 2,000 cm^{-3}) and rock perforability (mm 10 s^{-1}) (both variables transformed to Log_{10}) at the mid- and low intertidal level

	Mid-intertidal			Low intertidal		
	r	*n*	*P*	*r*	*n*	*P*
Chemical borers (Pooled)	−0.63	32	**<0.01**	−0.69	32	**<0.01**
Mechanical borers (Pooled)	0.26	10	0.47	0.19	29	0.34
Lithophaga patagonica (Ch)	−0.09	32	0.59	−0.67	32	**<0.01**
Themiste alutacea (Ch)	−0.75	17	**<0.01**	−0.49	29	**<0.01**
Pherusa sp. (Ch)	−0.43	26	**0.02**	−0.52	31	**<0.01**
Dodecaceria meridiana (Ch)	−0.06	6	0.90	−0.47	14	0.08
Barnea lamellosa (Me)	0.24	7	0.58	0.22	20	0.33
Netastoma darwinii (Me)	–	2	–	0.51	5	0.37
Petricola dactylus (Me)	–	1	–	0.41	9	0.26
Hiatella cf. *meridionalis* (Me)	0.36	5	0.54	−0.20	22	0.36
Petricola lapicida (Me)	–	0	–	–	3	–
Sphenia fragilis (Ne)	0.23	10	0.50	−0.16	22	0.45
Entodesma patagonica (Ne)	–	0	–	–	1	–

Correlation coefficients (*r*), sample sizes (*n*), and significance levels (*P*) are shown. *Ch* chemical borer, *Me* mechanical borer, *Ne* nestler. Correlation analysis was not performed for species with $n < 5$, but their densities where included in the joint abundance analysis. Significant differences ($P < 0.05$) are marked in bold

between seaward- and landward-oriented rock surfaces. In agreement, flow exposure (estimated from the dissolution of chlorine tablets) did not vary between seaward- and landward-oriented surfaces. The combined abundance of all species peaked in autumn, which is reasonable since summer is the reproductive season of many coastal marine invertebrate species in the southwestern Atlantic (e.g., Penchaszadeh and Olivier 1975; Herrmann et al. 2009) and peaks in larval recruitment frequently occur in late summer and autumn (e.g., Gutiérrez et al. 2000; Adami et al. 2008).

The three numerically dominant species at SE (*Lithophaga patagonica*, *Themiste alutacea* and *Pherusa* sp.) are chemical drillers. These three species, however, differed in seasonal abundance and habitat use. *Lithophaga patagonica* was abundant during the four seasons and very versatile in terms of habitat use. It inhabits rocks of varying hardness and occurs both at the mid- and low intertidal levels, although at a higher density in the latter. It was observed mostly in vertical surfaces and drainage channels. The sipunculan *T. alutacea* was more abundant in spring and at the mid-intertidal zone, occurring at very high densities in a few samples (more than 70 ind. 2,000 cm^3 rock). It is associated with hard rock and seems to have high tolerance to sand burial events. Subtidal sand ridges are frequently eroded at SE during storms (see Elías et al. 2005), which leads to periodic sand deposition and removal at

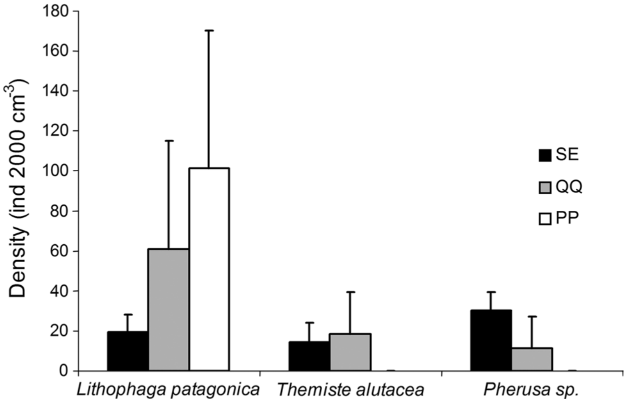

Fig. 5 Mean (±SD) density of the three dominant species present at the three study sites. *SE* Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides

Table 6 Average rates of bioerosion by the dominant endolithic species in the three sites covered in this study

Species	Bioerosion rates ($cm^3\ m^{-2}\ year^{-1}$)		
	SE	QQ	PP
Lithophaga patagonica	162.98	215.14	738.43
Themiste alutacea	36.37	37.54	
Pherusa sp.	104.13	12.10	
Barnea lamellosa	44.80		
Total	348.28	264.78	738.43

SE Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides

intertidal sandstone platforms (pers obs). During our spring sampling—conducted shortly after rocks were uncovered from sand burial—we observed recently dead (decaying) individuals of *L. patagonica*, *Pherusa* sp., and *Barnea lamellosa* while all *T. alutacea* individuals were found alive. This likely explains its numerical dominance in the mid-intertidal level, which is more frequently affected by sand burial events than the low intertidal zone.

Pherusa sp. varied in abundances between seasons, showing higher densities in summer and lower in winter (although due to high variability, no differences between seasons were detected with the SNK test). It occurred at higher abundance at the low intertidal zone and seaward-oriented rock surfaces. Differences in *Pherusa* sp. abundance between seaward- and landward-oriented rock surfaces suggest that flow exposure may differ between them when wave conditions are different from those of the measurement dates or, alternatively, that physical or biotic influences other than flow exposure may differ between both surface orientations (e.g., predation, sedimentation). This latter alternative is likely if we consider that sand accumulation tends to be higher at landward-oriented rock surfaces (pers obs). Increased sand deposition and resuspension in landward-oriented rock surfaces may clog up the filter feeding system of *Pherusa* sp. (formed by the chaetae and branchiae; see Amor 1994). *Pherusa* sp. predation by crabs (which are common at SE; pers obs) might also be higher at the landward-oriented rock surfaces (see Leonard et al. 1998).

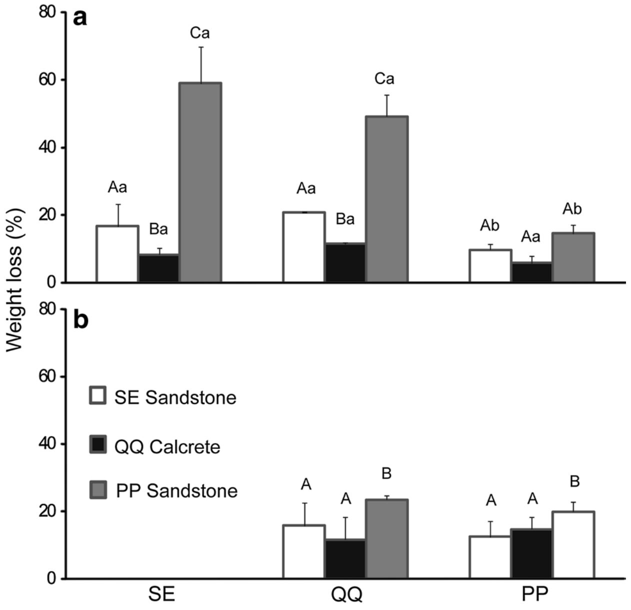

Fig. 6 Percent weight loss in rock transplants in the low intertidal zone of three sites (*SE* Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides) during **a** March 2012–September 2012 and, **b** September 2012–March 2013. SE data from September 2012–March 2013 are not available due to considerable loss of replicates. The *capital letters above bars* indicate differences in rock erosion within the same site, and *lowercase letters* indicate differences in the erosion of a particular rock type between different sites

Table 7 Estimates of annual percent weight losses of rock due to physical erosion, bioerosion, and both combined for the three sites covered in this study

Source	Annual erosion (%)		
	SE	QQ	PP
Physical	33.34	23.10	34.42
Biological	0.45	0.34	0.96
Total	33.79	23.44	35.38

SE Santa Elena, *QQ* Quequén, *PP* Puerto Pirámides

In general, mechanically boring organisms inhabit the softer rocks whereas chemically boring ones are also able to drill into very hard ones (Yonge 1963; Evans 1968a; Amor et al. 1991; Kleemann 1996). In this study, chemical borers occurred at higher abundance in the harder rocks (i.e., rocks rich in calcium carbonate). *T. alutacea* was the chemical borer whose abundance was most correlated with rock hardness (Table 5). However, the chemically boring polychaete *Dodecaceria meridiana* was found boring into hard rocks as previously reported by Elías and Rivero (2009), but also into the softer rocks and the calcite linings of *L. patagonica* burrows. In addition—and contrary to the above expectations—mechanical borers in this study were not restricted to the softer rocks but occurred in rocks of variable hardness (1.35- to 15.3-mm perforability, minimum and maximum perforability recorded in SE:1 and 25 mm, respectively). Among mechanical borers, the species dwelling into the hardest rocks was *Hiatella* cf. *meridionalis*. Nonetheless, some *Hiatella* species can either nestle into crevices or dig their own burrow, depending on the type of substratum onto which the larvae settle (Hunter 1949). This might also be the case for *H.* cf. *meridionalis* at SE. *Sphenia fragilis* has often been found sharing crevices with *H.* cf. *meridionalis*, or even occupying their burrows. *Sphenia fragilis* is clearly a nestler, which attaches into crevices with its byssus and molds its shells to the form of the crevice (though it is also fairly common among seaweed, *Corallina officinalis*, thalli or mussel, *Brachidontes rodriguezii*, byssal threads; see Pastorino and Bagur 2011). As a nestler species, *S. fragilis* can occupy crevices in different kinds of rock (Mikkelsen and Bieler 2008) and, therefore, its abundance does not correlate with rock hardness. Associations between *Hiatella* and *Sphenia* species seem to be common elsewhere (see Yonge 1951).

The low density of chemical borers in soft rocks suggests larval preference for rocks with high calcium carbonate content and/or lower post-settlement mortality therein. Hard rocks rich in calcium carbonate are expected to favor chemical boring since it generally proceeds via the secretion of acidic compounds (Kleemann 1973). Increased predation in softer rock is unlikely since this should affect the densities of both chemically and mechanically boring species. In contrast, our results indicate that the density of mechanically boring organisms does not vary with rock hardness (i.e., only the density of chemically boring organisms decreases with decreasing hardness). In advance, we found no apparent reason why chemically boring species should be more affected by predation than mechanically boring ones.

Geographic variations in endolithic communities

Preliminary comparisons of endolithic communities between SE, QQ, and PP can be made by comparing the five samples taken at each site during November 2009–January 2010. In the case of SE, these five samples had 10 out of the 11 endolithic species found in the seasonal sampling (i.e., 64 samples). Although QQ is only 120 km away from SE and both sites are located within the same biogeographic province, their endolithic communities seem to differ. Most species found at QQ were chemical drillers capable to bore the very hard calcrete rocks that characterize this site. From the six mechanical borers/nestlers found at SE, only *Netastoma darwinii* was found at QQ (few individuals in a rock sample that was softer than the average). Physical and oceanographic features other than rock hardness are similar between SE and QQ (Bagur et al. 2013), which suggests that rock hardness and mineral composition are the main factors explaining the differences between their endolithic communities.

In the case of PP, only three endolithic species were found, with a noticeable numerical dominance of *L. patagonica*. This site is characterized by soft sandstones similar in mineral composition to those at SE but is located 1,000 km away. Oceanographical features are quite different between both sites (e.g., tidal range, wave exposure, productivity, turbidity; see Bagur et al. 2013). Furthermore, PP is located in a different biogeographic province than SE and QQ. In spite of similar rock properties at SE and PP, seven of the species found at SE were absent at PP. Geographic barriers to dispersal (e.g., due to coastal circulation) and oceanographic factors such as temperature and productivity (which are lower at PP) may be limiting the range distribution of many of these species.

Lithophaga patagonica was abundant at the three sites. Local scale analysis at SE indicates that its abundance positively correlates with rock hardness (and $CaCO_3$ content). When considering SE and QQ (i.e., the two sites that are the closest to each other), *L. patagonica* abundance at each site also seems positively related to rock hardness (i.e. higher abundance and hardness at QQ). A similar positive association between abundance and rock hardness at a small spatial scale (sites separated by less than 2 km) was observed for *Lithophaga lithophaga* in the Adriatic Sea (Kleemann 1973). Nevertheless, no relationship between abundance and rock hardness becomes apparent when considering a larger scale, since PP shows the softest rock and the highest *L. patagonica* densities.

Erosion estimates

Bioerosion rates differed between the three sites, and *Lithophaga patagonica* was the organism that contributed the most to bioerosion at the three sites. The lower bioerosion rates were observed at QQ, which is associated with lower organismal growth rates in the relatively hard rock that characterizes this site (see Bagur et al. 2013). Based on the annual bioerosion estimates reported in Table 6, we can predict that the complete erosion of a rock of 1 m^2 area by 7.5 cm depth (maximum burrow depth in this study) would take 222, 294, and 104 years at SE, QQ, and PP, respectively. These bioerosion estimates (see Table 6) are low if compared with those reported by Pinn et al. (2005) for a chalk and clay substrate at Lyme Regis, Southern England. These authors estimated that piddocks (*Pholas dactylus, Barnea candida*, and *B. parva*) erode the substrate at a rate of 2,909 cm^3 m^{-2} $year^{-1}$. This is equivalent to a volume loss of 3.42 % per year and 41.1 % along the lifespan of piddocks (ca. 12 years). This means that a 1 m^2 quadrate of 8.5 cm depth (the maximum burrow depth in piddocks) would just take 29.21 years to be completely eroded. Piddocks play a significant role as bioeroders in many English sites because of their high abundance and large size. Indeed, a single adult individual of *Pholas dactylus* can remove 10.1 cm^3 of substratum in 12 years (Pinn et al. 2005). The only endolithic species in our study that can potentially reach a similar volume of substratum removal during its lifetime is *Barnea lamellosa* (10.39 cm^3). However, this bivalve occurs at low abundance and presumably takes longer than *P. dactylus* in removing that amount of rock (maximum age is estimated here in 31 years).

Variations in substrate properties can also contribute to differences between our bioerosion estimates and those in Pinn et al. (2005). The clay–chalk substrate at Lyme Regis is presumably softer and more erodible (at least by mechanical means) than the sandstone or calcrete found at our study sites. In agreement, our bioerosion estimates are comparable to those obtained from substrates that are evidently harder than those in Pinn et al. (2005). For instance, bioerosion caused by a diverse endolithic assemblage (including representatives of the genera *Lithophaga* and *Themiste*) in the northern Gulf of California, USA, was estimated to occur at rates of 148.3 cm^3 m^{-2} $year^{-1}$ at a site with a calcarenite and sandy coquina substrate and 303.3 cm^3 m^{-2} $year^{-1}$ at a site with a substrate of molluscan coquina with pebbles and sand (Stearley and Ekdale 1989). These rates resemble our estimates for QQ and SE, respectively. Furthermore, our estimates are also comparable to some estimates of coral bioerosion rates when presented as mass per area unit per year (i.e., considering an average rock density of 1.85 g cm^{-3} based on SE samples). This includes cases where *Lithophaga* spp. are the main boring organisms (0.76–2.03 kg m^{-2} in Gorgona Island, Tropical Eastern Pacific, Colombia; Cantera et al. 2003, Londoño-Cruz et al. 2003) as well as reefs dominated bioeroders such as sponges and grazers (0.76 kg m^{-2} $year^{-1}$ in a Barbados reef, MacGeachy and Stearn 1976; 0.07–1.96 kg m^{-2} $year^{-1}$ in Lizard Island, Great Barrier Reef, Australia; Kiene and Hutchings 1994).

Physical erosion rates in coastal areas are a function of wave exposure and rock hardness. In agreement, our results show that both rock type and site affect physical erosion rates on rock transplants. The hard calcrete rocks from QQ are more resistant to physical erosion compared to the other types of rocks, and irrespective of site. On the contrary, the soft sandstones from PP are easily eroded at all sites. QQ is the site with the highest wave exposure (see Isla and Bértola 2005; Bagur et al. 2013) but the lowest annual physical erosion rates, likely because its lower rock erodability. Conversely, PP is located in a Gulf and is little exposed to waves (Bagur et al. 2013) but shows the highest physical erosion rates in this study, presumably because its soft sandstone substrate and tidal currents associated with macrotidal conditions. SE shows annual physical erosion rates similar to those at PP, but associated with high wave exposure (Bagur et al. 2013) and relatively harder rocks (intermediate between QQ and PP).

Our estimates of physical erosion rates were two orders of magnitude higher than those of bioerosion. Nonetheless, bioerosion can still be of geomorphic significance. Dense patches of bioeroders—such as the remarkably dense aggregations of *Themiste alutacea* in hard rocks of the mid-intertidal zone at SE—might be contributing to the irregular modeling of the rock substrate at small scales (e.g., centimeters to a few decimeters). Furthermore, bioeroders can also facilitate larger-scale physical erosion by weakening the rock either via chemical or mechanical means (Donn and Boardman 1988). In spite that bioerosion per se is low relative to purely physical erosion at our study sites, their multiplicative effects (e.g., facilitation of physical erosion by bioeroders) might substantially contribute to overall coastal erosion. Last, low rates of bioerosion relative to physical erosion do not curtail the possible importance of endolithic invertebrates as elements of biodiversity in the often biotically depauperate intertidal consolidated sediments of the Argentinean coast (see Adami et al. 2004; Arribas et al. 2013) nor their potential, physical ecosystem engineering impacts (sensu Jones et al. 1994) on other organisms via burrowing and the concomitant creation of three-dimensional habitat in the form of vacant burrows (Pinn et al. 2008; see also Gutiérrez et al. 2003).

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