Differences in Density, Shell Allometry and Growth Between Two Populations of *Limnoperna fortunei* (Mytilidae) from the Río De La Plata Basin, Argentina

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DIFFERENCES IN DENSITY, SHELL ALLOMETRY AND GROWTH BETWEEN TWO POPULATIONS OF *LIMNOPERNA FORTUNEI* (MYTILIDAE) FROM THE RÍO DE LA PLATA BASIN, ARGENTINA

Nicolás Bonel[1*, 3], Lía C. Solari[2] & Julio Lorda[4]

ABSTRACT

The invasive freshwater mussel, the mytilid *Limnoperna fortunei* (Dunker, 1857), has a great capacity for colonizing a wide range of aquatic environments because of its dispersal ability, high fecundity and wide range of physiological tolerances. Most of the biological and ecological studies of *L. fortunei*, having been restricted to specific locations, lack comparative analyses among different habitats. In this investigation, we examined the differences in larval density, density in settlement plates, shell allometry, and growth between two populations from the Río de la Plata basin, Argentina. One of the populations inhabited a heavily polluted area, whereas the other a moderately polluted area. We predicted that the density and growth of the golden mussel would be lower in the heavily polluted environment, expecting therefore to find variations in shell allometry as a consequence of differences in density and environmental conditions between the sites investigated. We accordingly found that the larval density, the density of settled individuals, and the growth were lower in the more polluted environment. We also observed allometric differences because the individuals from the moderately polluted area with higher population densities were more elongated (i.e., with a higher shell length-to-width ratio). The golden mussel tolerates a wide range of environmental conditions and can survive in many polluted water bodies where other invasive species cannot. The findings presented here support the idea that *L. fortunei* can inhabit heavily polluted environments, but at the expense of a significant decrease in its biologic potential.

Key words: invasive species, freshwater mussel, population dynamics, growth rate, water pollution.

INTRODUCTION

Population size – one of the key parameters determining the economic and ecologic impacts of an invasive species – may vary over space and time (Strayer & Malcom, 2006). Information concerning the influence of environmental conditions on growth, survival and fecundity of aquatic species is necessary for making predictions about the potential for populations to expand and exploit new habitats (Garton & Johnson, 2000).

The freshwater bivalve *Limnoperna fortunei* (Dunker, 1857) is native to Southeast Asia and has been introduced into other regions of Asia and South America (Boltovskoy et al., 2009a). Known as the golden mussel, *L. fortunei* has become a pest species of global concern over the last few decades because of its major economic impacts on the industrial and power plants that use raw river or lake water for their processes (Ricciardi, 1998; Boltovskoy et al., 2009b), and as a result of its ecological impacts upon the native communities of mollusks and crustaceans (Lopes et al., 2009). In Argentina, *L. fortunei* was first detected in 1991 in the brackish waters of the Río de la Plata estuary (Pastorino et al., 1993). Shortly thereafter, this mytilid expanded its range of settlement throughout more than 3,000 km of the Río

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de la Plata-Paraná-Paraguay river system (reviewed in Boltovskoy et al., 2009a). The geographical dispersion of *L. fortunei* is largely facilitated by its planktonic larvae (Cataldo & Boltovskoy, 2000). This freshwater mytilid shares several biologic and ecologic features with the European and North American invasive pest mollusk, the zebra mussel, *Dreissena polymorpha* (Pallas) (Karatayev et al., 2007). Like *D. polymorpha*, the golden mussel possesses many of the characteristics attributed to successful invaders, that is, a short generation time, phenotypic plasticity, gregariousness, abundance in its native habitat, wide environmental tolerance and commensal association with human activity, all of which characteristics make its potential spread and establishment in North American waters very likely (Ricciardi, 1998; Oliveira, 2010a).

The population dynamics of the bivalves depends on the successful settlement and recruitment of dispersed larvae (Martel et al., 1994). During the reproductive period of *L. fortunei* (September through April), the density of the settled individuals can exceed 200,000 mussels/m^2 because of the high abundance of recently settled juveniles, whereas the density of the subadult and adult individuals usually ranges between 5,000 and 10,000 mussels/m^2 (Sardiña et al., 2009). High population density promotes changes in shell allometry as the result of a regulation in food intake, some form of physical interference, or an interaction between the two (Alunno-Bruscia et al., 2001). In spite of the high densities and extensive conglomerations that are characteristic of *L. fortunei*, no studies have as yet looked at the shell allometry and analyzed its relationship to population density. Only Morton (1977) in Hong Kong has estimated the ratios of shell width to height to length in *L. fortunei*, but he did not perform a comparative analysis of shell allometry among different populations.

Variations in growth often are habitat-specific and directly related to the local environmental conditions (Alfaro et al., 2008). An analysis of growth rates under natural conditions is a necessary first step in understanding the growth dynamics and energy balance of a given bivalve population (Dorgelo, 1992). Previous studies have estimated the growth of *L. fortunei* individuals in the Neotropical Region and in Asia through different methods; those investigations, however, were limited to only one location per study (Boltovskoy & Cataldo, 1999; Maroñas et al., 2003; dos Santos et al., 2008; Belz et al., 2010; Darrigran et al., 2011; Nakano et al., 2011). Magara et al. (2001) analyzed the growth of *L. fortunei* in two Japanese water systems, but they performed no comparative analyses of the growth between the two environments. Oliveira et al. (2011) compared the growth of two populations in Brazil but found no differences.

Most of the biological and ecological studies of *L. fortunei* were restricted to specific locations and therefore lacked comparative analyses (Boltovskoy et al., 2009a). Moreover, virtually no information is available on the ecological preferences of *L. fortunei*, and our knowledge of its limnologic and biologic traits within the enormous and very complex South American river system is still limited (Boltovskoy et al., 2006). In this study, we investigated the differences in larval density, density on settlement plates, shell allometry, and growth between two populations of *L. fortunei* from two river systems from the Río de la Plata basin. Since this species can inhabit ecosystems with widely differing environmental characteristics, we predicted that the density and growth of *L. fortunei* would be lower in heavily polluted environments. Furthermore, as a consequence of such differences in population densities and environmental conditions, we expected that individuals from high densities and moderately polluted habitats would have elongated shells.

Information on the spatial variability in the ecological aspects related to the life-history of *L. fortunei* in response to different environmental conditions would contribute to the existing data garnered from specific locations. A more comprehensive understanding of the biologic parameters of this invasive freshwater mussel in the face of potentially stressful conditions would help us to predict the effect scenarios such as climate change and eutrophication might have on this mytilid's life-history traits and subsequently its impact on native invaded ecosystems.

METHODS

Study Sites

To perform this study, we selected two water bodies from the Río de la Plata basin, Argentina. The first site was in the Coronda River, a secondary course of the Paraná River (31°41'26.88"S, 60°44'34.08"W). The Coronda is close to two urban centers with approximately 600,000 inhabitants who release various urban and industrial discharges as well as rural run-

offs constituting major sources of organic matter (Devercelli & Peruchet, 2008). The second site was the Santiago River (34°51'5.76"S, 57°53'29.76"W) located 350 km southeast of the first sampling point. This river is an 8 km-long tributary of the Río de la Plata estuary and is close to two extensive urban centers with more than 11 million inhabitants that, in turn, are located along the first 80 km of the south shore of the Río de la Plata estuary (Colombo et al., 1989).

Environmental Parameters

We measured water temperature (T), pH, dissolved oxygen (DO), and conductivity with a digital multimeter (Sper Scientific 850081). Water clarity was measured with a Secchi-disk. The calcium concentration was determined in the laboratory by a volumetric method involving a Na_2EDTA solution and a murexide indicator (APHA, 1998). For photosynthetic-pigment analyses, we sampled 1–2 L of water, transferred the water samples to dark plastic bottles, and transported them to the laboratory in a cooler with ice to avoid chlorophyll photo-oxidation. The techniques, procedures, and assessments of chlorophyll concentration per cubic meter were carried out according to APHA (1998). We took weekly and monthly measurements of environmental parameters in the Santiago and Coronda rivers, respectively. To stabilize the variances and improve normality, we used the natural logarithm to transform all environmental data. To compare physicochemical and biologic parameters from both sites, we used two-tail pairwise *t*-tests. A discriminant analysis was applied to the quantitative data. Environmental variables were used in the multivariate analysis as explanatory parameters with respect to differences between two levels of an *a-priori* defined categorical variable (i.e., the study sites).

Larval Density

At both study sites, we filtered 400–500 L of water through a Wisconsin net (47 µm mesh size) using a water pump to obtain a total of 15 samples in the Coronda River from April 2007 through February 2009 and 14 samples in the Santiago River from March 2007 through March 2009. The particulate material retained by the net in a 0.5 L was placed in a receptacle and preserved in 40% (v/v) aqueous ethanol. We analyzed three to four 1 mL aliquots (subsamples) from each sample. Each subsample was placed in a 1 mL Sedgwick-Rafter chamber and observed with a stereoscopic microscope. To compare larval densities, we calculated the total density per cubic meter and then performed two-tail pairwise *t*-tests. The larval densities were squared-root transformed to meet the assumptions of normality and homoscedasticity. To evaluate associations between environmental variables and larval densities, we used Pearson's correlation coefficient.

Density on Settlement Plates

In order to calculate field densities, we deployed 36 settlement plates per river. We grouped the settlement plates – 10 x 10 cm square frames with 1 mm plastic mesh screens – in 12 blocks with three plates on each block and placed the settlement plates 1 m below the surface. At each study site, we regarded the sampling date prior to the first evidence of settlement as the initial date in the study. We collected data in the Santiago River from December 2007 through April 2009. In the Coronda River, we had to divide the study into two stages because six groups of collectors were lost. We collected data from October 2007 through June 2008 and then from September 2008 through February 2009. Once we collected the settlement plates, we transported the samples immediately to the laboratory in plastic bags. The individuals were gently detached from the collectors, washed over a sieve (1 mm pore size), and preserved in 70% (v/v) aqueous ethanol (Nakano et al., 2011).

To evaluate the relationship between density and larval settlement with the environmental parameters, we used Pearson's correlation coefficient. To meet normality and homoscedastic conditions, we transformed the density values to square roots, the percentage data to arcsine square roots, and calculated the natural logarithms of the environmental parameters. To compare densities from both study sites, we used a two-tail pairwise *t*-test.

Shell Allometry

We measured the length (L: mm, maximum anteroposterior axis) of all individuals collected from the settlement plates. To analyze and compare shell allometry between individuals from each site, we used only mussels longer than three millimeters. For these mussels we also measured the height (H: mm, maximum dorsoventral axis) and width (W: mm, maximum lateral axis; Alunno-Bruscia et al., 2001). We

used a Mitutoyo digital caliper (precision, 0.01 mm) for all measurements.

For each block, sampling date, and study site, we calculated the means of the morphometric variables and examined the allometric relationships of height and width as a function of length. We tested each pair of size variables with the allometric equation $y = ax^b$, where a and b are the coefficients of the equation. The correspondence of allometric curves fitted to mussels from the two rivers was tested through the use of the sum of the squares from the F test. A nonsignificant F-statistics indicated that a single allometric curve was sufficient to describe the populations being compared (Blanchard & Feder, 2000). We also analyzed the effect of spatial variation on morphometric variables using two independent ANCOVAs with height and width as dependent variables, length as a covariable, and sites as factors. Shell dimensions were transformed by the natural logarithm to homogenize variances.

To investigate changes in shell morphology, we calculated the morphometric ratios between the linear shell dimensions, length-to-width (L/W), length-to-height (L/H), and height-to-width (H/W) (Alunno-Bruscia et al., 2001). We transformed the ratios to arc-sine square roots to meet normality and homoscedastic conditions, and used two-tail t-tests to make comparisons between the groups. To analyze the relationship between population density and changes in morphometric ratios, we used Pearson's correlation coefficient.

Growth

To assess growth, we used length-frequency distributions with reference to the average shell length. We calculated the range of each length-frequency distribution as the difference between the maximum and minimum value of the frequency data. The equation to calculate the number of the classes is:

$$k = 1 + \log_2 n$$

where k is the number of the class interval and n is the sample size. The equation for class interval of width (h) is:

$$h = (\text{range} + \varepsilon) / k$$

where ε = 10% difference from the range of values (i.e., minima and maxima values) (Sturges, 1926).

To identify cohorts by means of the length-frequency distributions, we applied the Bhattacharya (1967) method available in FISAT II software (Version 1.1.2, FAO-ICLARM Fish Assessment Tools; Gayanilo et al., 1996). To confirm each modal progression, we used the NORMSEP method also available in the FISAT II software (Pauly & Caddy, 1985). Depending on shell length, we defined two categories of individuals: (1) juveniles (length < 5 mm, the minimum size for sexual differentiation; Darrigran et al., 1999); (2) subadults and adults (length > 5 mm).

To describe and compare the growth between both sites, we fitted linear and nonlinear regression models (quadratic and cubic) (Smit et al., 1992). Each fit was tested according to the sum of the squares from the F test. The null hypothesis was that the simpler model (the one with fewer parameters) was correct. If $P < 0.05$, the null hypothesis is rejected (i.e., the simpler model is discarded), and the conclusion becomes that the more complex model fits the data group significantly better. Likewise, we used this test to compare the parameters from each growth curve of the two populations from the two rivers. A nonsignificant F-statistics indicated that a single allometric curve was sufficient to describe the populations being compared (Blanchard & Feder, 2000). All statistical analyses were performed by means of the SPSS 17.0 statistical package, JMP statistical software (v9.0 SAS Institute), and GraphPad Prism 5 (www.graphpad.com).

RESULTS

Environmental Variables

Table 1 summarizes the descriptive statistics of the environmental variables measured at both study sites. Pairwise comparisons showed significant differences in water temperature between the two study sites ($t_{(17)} = -3.38$, $P = 0.0036$). On the average, the Coronda River was warmer than the Santiago by 1.2°C. The dissolved oxygen was significantly different between the Coronda and Santiago rivers ($t_{(16)} = -7.99$, $P < 0.0001$). The Coronda River exhibited, on the average, a 3.4 mg/L higher concentration of dissolved oxygen than the Santiago. Conversely, the conductivity, at an increment of 0.209 mS/cm, was significantly higher in the Santiago River ($t_{(17)} = 6.49$, $P < 0.0001$). Both sites were characterized by slightly alkaline water, but the pairwise comparisons revealed that the pH was nevertheless significantly different ($t_{(17)} = -3.04$, $P = 0.0074$) between the two rivers, with the Coronda River being an average of 0.14 units more alkaline than the Santiago. Although at both sites the

TABLE 1. Mean value ± standard deviation (minimum-maximum; n, number of samples) of the environmental variables measured at both study sites and the pairwise *t*-test results. T, water temperature (°C); DO, dissolved oxygen (mg/L); Cond, conductivity (mS/cm); Secchi, transparency (m); Ca, calcium concentration (mg/L); Chl a, chlorophyll *a* (mg/m^3); Chl b, chlorophyll *b* (mg/m^3); Chl c, chlorophyll *c* (mg/m^3).

	Coronda River	Santiago River	Paired *t*-test
T	20.7 ± 5.8 (10.1–29.5) n = 18	19.5 ± 5.7 (9.5–27.6) n = 23	$t_{(17)}$ = -3.38, P = 0.0036
pH	7.55 ± 0.22 (7.16–8.0) n = 18	7.41 ± 0.12 (7.17–7.54) n = 23	$t_{(17)}$ = -3.04, P = 0.0074
DO	8.6 ± 2.4 (6.0–14.8) n = 18	5.2 ± 1.7 (2.8–10.3) n = 22	$t_{(16)}$ = -7.99, P < 0.0001
Cond	0.223 ± 0.144 (0.081–0.655) n = 18	0.432 ± 0.050 (0.327–0.509) n = 23	$t_{(17)}$ = 6.49, P < 0.0001
Secchi	0.3 ± 0.1 (0.1–0.5) n = 15	0.5 ± 0.1 (0.3–0.8) n = 21	$t_{(14)}$ = 4.13, P = 0.001
Ca	48 ± 46 (6–180) n = 13	53 ± 27 (13–88) n = 17	$t_{(11)}$ = 1.32, P = 0.2111
Chl a	6.9 ± 5.6 (2.6–22.9) n = 13	17.2 ± 12.7 (0.9–45) n = 20	$t_{(12)}$ = 3.01, P = 0.0109
Chl b	3.0 ± 5.6 (0–21.1) n = 13	10.8 ± 18.3 (0–82.1) n = 20	$t_{(12)}$ = 3.17, P = 0.008
Chl c	2.8 ± 3.5 (0–12.9) n = 13	4.2 ± 4.6 (0.1–18.4) n = 20	$t_{(12)}$ = 0.22, P = 0.8316

water clarity was low, the Coronda River being 0.2 m less transparent than the Santiago, exhibited a significant difference in turbidity ($t_{(14)}$ = 4.13, P = 0.001). The calcium concentration was comparable between the two sites ($t_{(11)}$ = 1.32, P = 0.2111). The Santiago River had an average of 10.3 and 7.8 mg/m^3 higher concentrations of chlorophyll *a* ($t_{(12)}$ = 3.01, P = 0.0109) and *b*, respectively, than the Coronda ($t_{(12)}$ = 3.17, P = 0.008), while the chlorophyll *c* was equivalent ($t_{(12)}$ = 0.22, P = 0.8316).

Discriminant analysis gave a 95.1% correct classification. The canonic correlation coefficient from discriminant function 1 was 0.962 – that is, the proportion of variance resulting from the difference between groups (the coefficient^2 x 100) was 92.5%. The score values for the Santiago River (centroid at -2.837 on the discriminant eigenvector) ranged from -6.10 to -0.232, but for the Coronda River (centroid at 4.019) from -2.011 to 5.541. Based on a 0.30 cut-off discriminant loading criterion, from all variables entered into discriminant analysis, the structure matrix revealed only two physicochemical variables that significantly loaded on the discriminant function: conductivity (-0.557) and dissolved oxygen (0.319; Fig. 1).

Larval Density

A pairwise comparison revealed that the larval density (LD) was significantly higher in

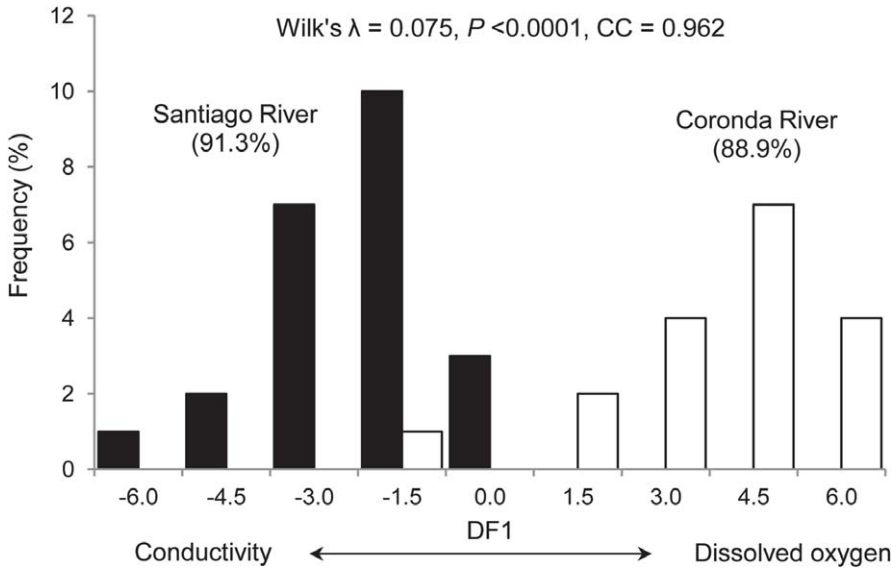

FIG. 1. Frequency histogram of discriminant function 1 (DF1) corresponding to the discriminant analysis through the use of biotic and abiotic parameters from the Coronda and Santiago rivers. The correct classification percentages, Wilks's λ, and canonical correlation (CC) are indicated.

the Coronda River than in the Santiago ($t_{(6)}$ = -3.402, P = 0.0145; Fig. 2a). Notwithstanding, the difference estimated could have been heavily influenced by a single sample in December 2007 in the Coronda River (Fig. 2a). We therefore performed a pairwise comparison excluding the paired data, but the difference in the larval densities between the two rivers still remained significant ($t_{(5)}$ = -3.985, P = 0.0105). In the Coronda River, the density attained the highest values in December 2007 (20,240 ± 7,825 ind/m^3). During 2008, we observed two main density peaks, in April (5,320 ± 1,773 ind/m^3) and in December (4,800 ± 462 ind/m^3), but in each instance the density values were fourfold lower than in December 2007. We found the lowest densities, < 500 ind/m^3, when temperature was below 15°C (Fig. 2a). We found a positive correlation between larval density and temperature (LD = -230.77 + 92.70 T, r = 0.784, P < 0.0001) and a negative correlation with dissolved oxygen (LD = 271.46 – 106.34 DO, r = -0.7576, P < 0.001). The remaining environmental variables showed no significant correlation with density.

In the Santiago River, we observed two main larval density peaks during 2007, one in May (3,000 ± 265 ind/m^3) and another in December (2,600 ± 902 ind/m^3). A single peak occurred in April 2008 (3,420 ± 570 ind/m^3), while in 2009 the peak was recorded in March (2,625 ± 573 ind/m^3). The larval density in the water column was also lower than 500 ind/m^3 when water temperatures were below 15–16°C (Fig. 2a). We found a positive correlation between larval density and temperature (LD = -125.91 + 50.93 T, r = 0.589, P = 0.0265). Contrary to what we observed in the Coronda River, we found no significant correlation between the dissolved oxygen levels and the larval density.

Density on Settlement Plates

A pairwise comparison revealed that the total density (TD) of settled mussels was significantly lower in the Santiago River than in the Coronda River ($t_{(6)}$ = -3.056, P = 0.0223; Fig. 2c). In the Santiago River, the highest density occurred in April 2007 (31,900 ± 13,323 ind/m^2), when 90% of the individuals sampled were juveniles (Juv; Fig. 2b). The lowest density (1,167 ± 551 ind/m^2) was observed in December, with juveniles representing 46% of the total individuals. In 2009, the highest peak was recorded in March (13,200 ± 8,728 ind/m^2), with 60% being juveniles (Fig. 2b). We found both a positive correlation between the total density and the percentage of juveniles (Juv =

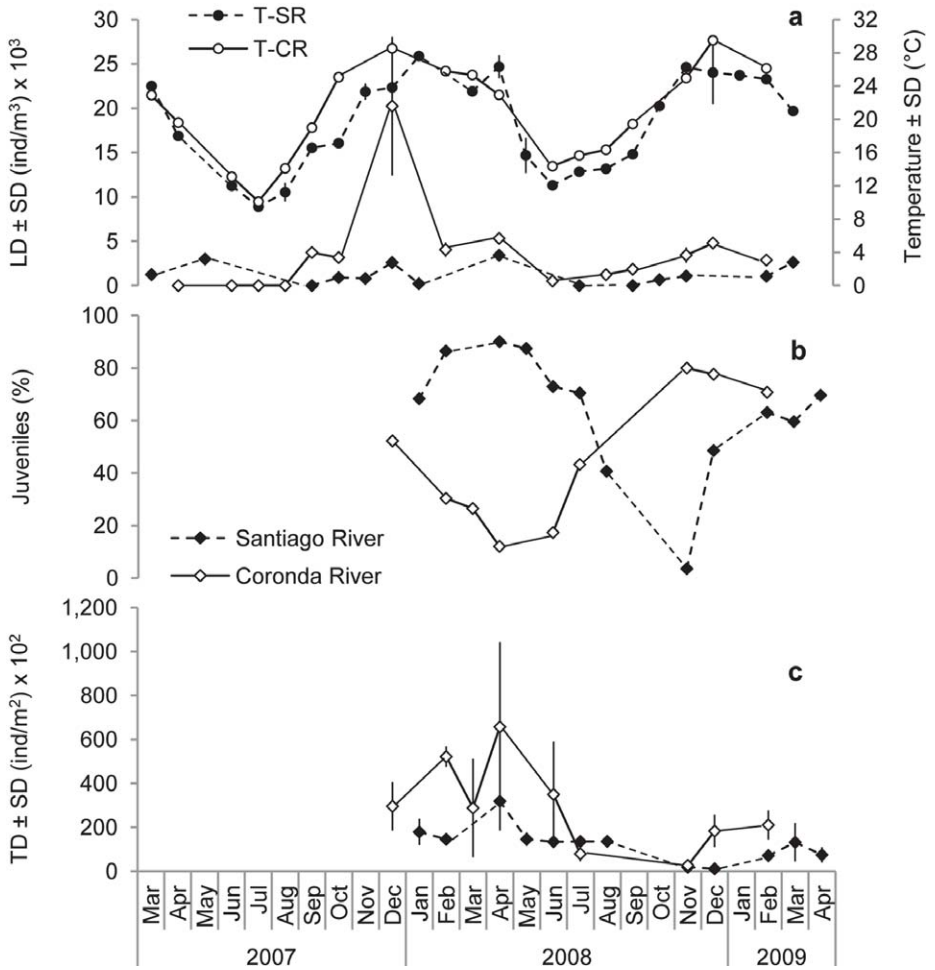

FIG. 2. Seasonal variation of *Limnoperna fortunei* and water temperature (T) ± standard deviation (SD) from the Coronda (CR) and Santiago (SR) rivers with respect to a: Larval density, LD ± SD; b: Percentage of juveniles (%); c: Total density of settled individuals, TD ± SD.

1.909 + 0.0071 TD, $r = 0.6077$, $P = 0.0361$) and a negative correlation between the total density and the pH (TD = 4,169.65 – 544.54 pH, $r = -0.6679$, $P = 0.0247$). The remaining biotic and abiotic variables showed no significant correlation with density.

In the Coronda River, the highest density was found in April 2008 (65,700 ± 38,466 ind/m²) during the first stage of the study. Contrary to what we observed in the Santiago River, the juveniles represented only 12.1% of the total individuals. The lowest density (7,933 ± 3,347 ind/m²) occurred at the beginning of winter (July), but at this time the juveniles had increased to 43%. In the second stage, the first block contained 2,768 ± 321 ind/m², and 80% were juveniles (Fig. 2b–c). The highest mean density occurred in February 2009 (21,100 ± 6,630 ind/m²), at which time the juveniles represented 71% of the total. The average density in the first stage (36,528 ± 20,117 ind/m²) was higher than in the second (14,033 ± 9,941 ind/m²), but the mean percentage of juveniles was lower (30 ± 15 and 76 ± 4%, respectively; Fig. 2b–c). We found a negative correlation between the total density and the percentage of juveniles (Juv = 3.161 + 0.0041 TD, $r = -0.7612$, $P = 0.0172$). As the density increased, the fraction of juveniles

TABLE 2. Coefficients of allometry from the least-square potential regression ($y = ax^b$) and the linearized model ($\ln y = a + b \ln x$) based on values of height (H) and width (W) as functions of length (L) from the Coronda and Santiago rivers. R^2, coefficient of determination; ln, natural logarithm.

	Coronda River			Santiago River		
Model	*a*	*b*	R^2	*a*	*b*	R^2
$H = aL^b$	0.636	0.895	0.99	0.614	0.900	0.99
$W = aL^b$	0.377	0.996	0.99	0.312	1.110	0.99
$\ln H = a + b \ln L$	-0.466	0.902	0.99	-0.490	0.901	0.99
$\ln W = a + b \ln L$	-1.008	1.012	0.99	-1.140	1.097	0.98

decreased. Finally, we observed a negative correlation between the total density and the water clarity (TD = 257.11 – 407.42 Secchi, r = -0.7030, P = 0.0347), but no significant correlation between the total density and any of the remaining biotic or abiotic variables.

Shell Allometry

We measured the shell dimensions of 1,850 individuals from the Santiago River and 5,281 from the Coronda. The measurements on the mussels from the Santiago River showed that

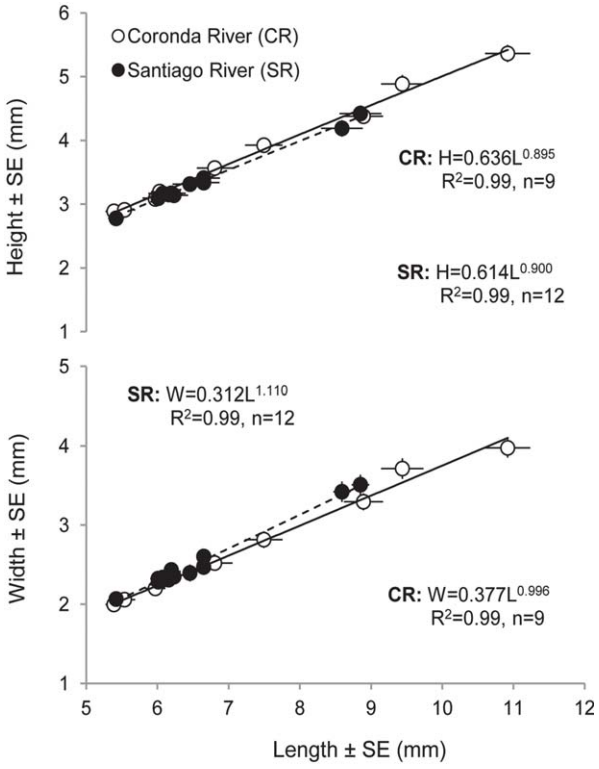

FIG. 3. Allometric regressions ($y = ax^b$) of mean values ± standard error (SE) of height (H) and width (W) as functions of length (L). Solid line: Coronda River; dashed line: Santiago River.

TABLE 3. Results of an analysis of covariance (ANCOVA) testing the spatial variability on ln-transformed shell dimensions (height: H and width: W) of *Limnoperna fortunei* as a function of sites (the Coronda and Santiago rivers) with the natural logarithm of shell-length as covariable.

Source	*d.f.*	MS	F	*P*
lnH				
Sites	1	0.0031	14.31	0.0014
lnL	1	0.6068	2778.78	< 0.0001
Error	18	0.0002		
lnW				
Sites	1	0.0044	8.47	0.0093
lnL	1	0.8045	1534.29	< 0.0001
Error	18	0.0005		

the shell length was 1.33 ± 0.05 and 2.61 ± 0.05 times greater than the height and the width, respectively; while the mussels from the Coronda River had shells of length 1.38 ± 0.04 and 2.68 ± 0.01 times greater than the height and the width, respectively. The shell length-to-height allometric relationships of the mussels from the Coronda and Santiago rivers were significantly different between the two sites ($F_{(2,17)}$ = 5.623, P = 0.0133), but in both instances the models indicated a slight negative allometry (Table 2; Fig. 3). The shell length-to-width relationships for mussels from the Coronda River were consistent with isometry, while for individuals from the Santiago River the model showed a positive allometry (Table 2; Fig. 3). The allometric curves were significantly different between the two rivers ($F_{(2,17)}$ = 6.704, P = 0.0071).

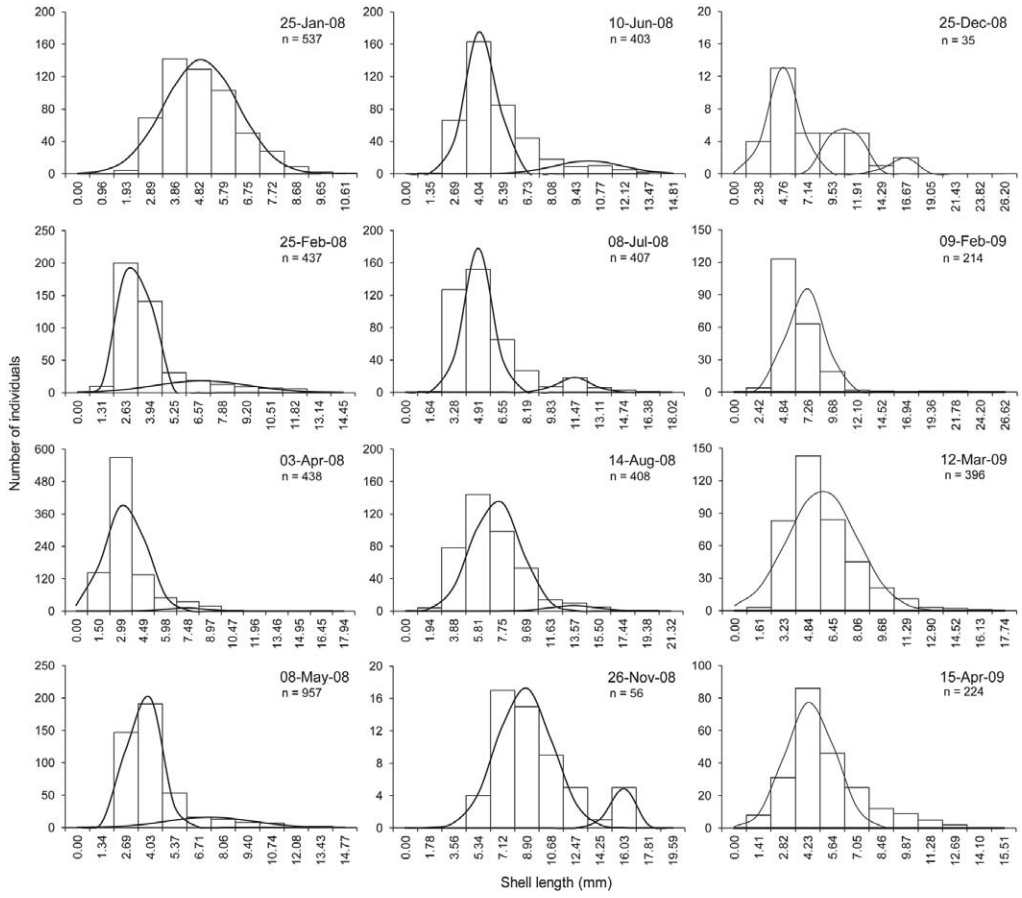

FIG. 4. Length-frequency distribution of *Limnoperna fortunei* from the Santiago River between January 2008 and April 2009; n: number of mussels measured.

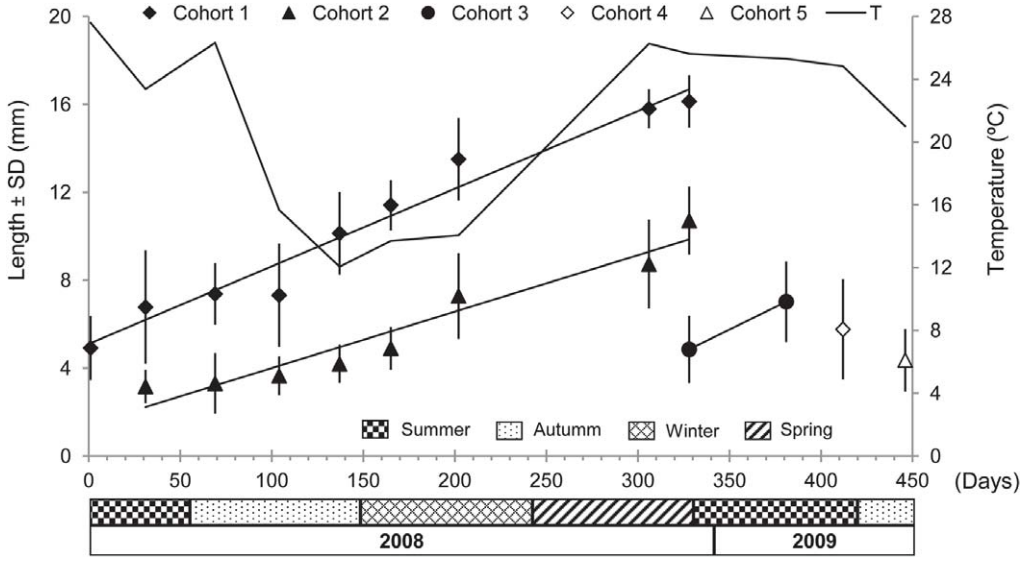

FIG. 5. Growth models fitted to the mean shell-lengths ± standard deviation (SD) of cohorts identified throughout the period of study in the Santiago River. T: water temperature.

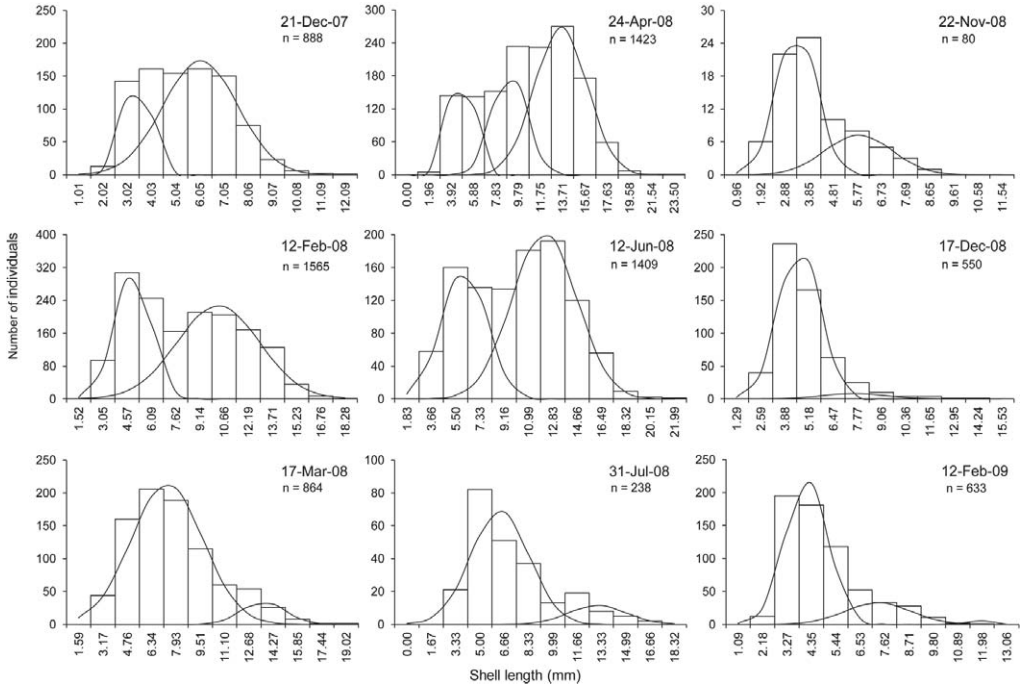

FIG. 6. Length-frequency distribution of *Limnoperna fortunei* from the Coronda River between December 2007 and February 2009; n: number of mussels measured.

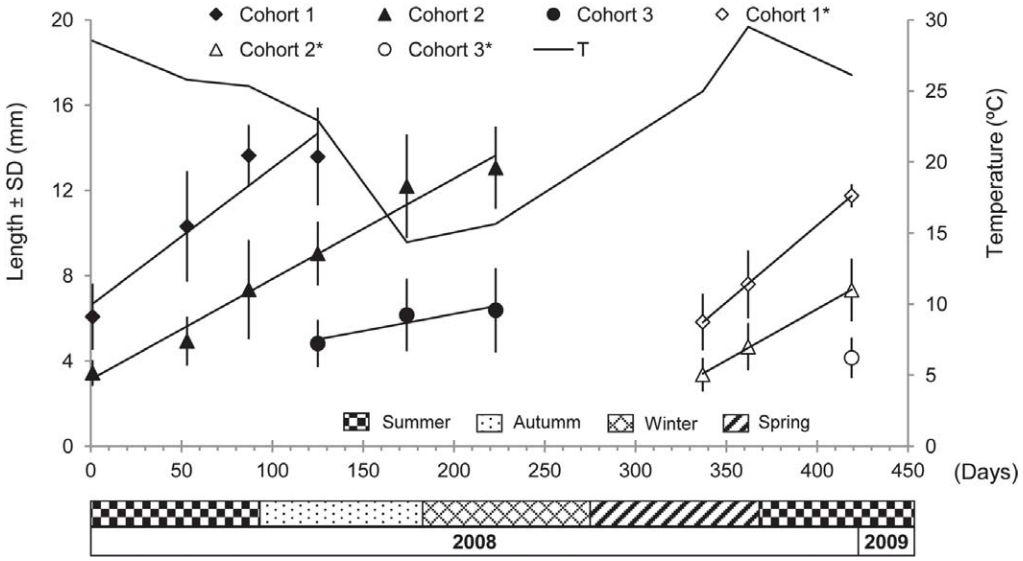

FIG. 7. Growth models fitted to the mean shell-lengths ± standard deviation (SD) of cohorts identified throughout the period of the first and second stage (*) of the study in the Coronda River. T: water temperature.

The sites had a significant effect on shell dimensions: mussels from the Coronda River exhibited a higher height and a lower width than individuals from the Santiago River (Table 3). In both instances no significant interaction occurred between the sites and the covariable shell length ($F_{(1,17)}$ = 0.0007, P = 0.979, and $F_{(1,17)}$ = 2.3826, P = 0.141; respectively). The *t*-test for the morphometric ratios indicated that the length-to-width was significantly higher – that is, individuals were more elongated – in the Coronda River than in the Santiago ($t_{(19)}$ = -2.576, P = 0.0092). We found no significant correlation between density and shell length-to-width values in the Coronda River, but the pooled density and shell length-to-width ratios from both study sites gave a positive correlation between the total density of settled individuals and the length-to-width ratio (L/W = 1.0482 + 0.000135 TD, r = 0.4512, P = 0.0401).

TABLE 4. Results of the *F*-test performed to fit the best-growth model for each cohort. Parameters of the growth model (y = a + bx) fitted to each cohort of mussels from each site. R^2: coefficient of determination, NA: data not available, (*): cohorts identified in the second stage.

Sites	Cohort	*F* test	Model	R^2
Santiago River (SR)	1	$F_{(1,6)}$ = 0.432, P = 0.536	y = 0.0353x + 5.10	0.96
	2	$F_{(1,5)}$ = 2.651, P = 0.165	y = 0.0257x + 2.22	0.93
	3	NA	y = 1.573x + 1.41	1.00
Coronda River (CR)	1	$F_{(1,1)}$ = 2.487, P = 0.360	y = 0.0645x + 6.61	0.90
	2	$F_{(1,3)}$ = 0.102, P = 0.771	y = 0.0471x + 3.13	0.98
	3	NA	y = 0.0159x + 3.02	0.85
	1*	NA	y = 0.0723x – 18.55	1.00
	2*	NA	y = 0.0481x – 12.81	1.00
SR *vs.* CR	1 *vs.* 1	$F_{(2,9)}$ = 20.33, P < 0.001	Different curve for each data set	NA
	2 *vs.* 2	$F_{(2,10)}$ = 66.38, P < 0.001	Different curve for each data set	NA

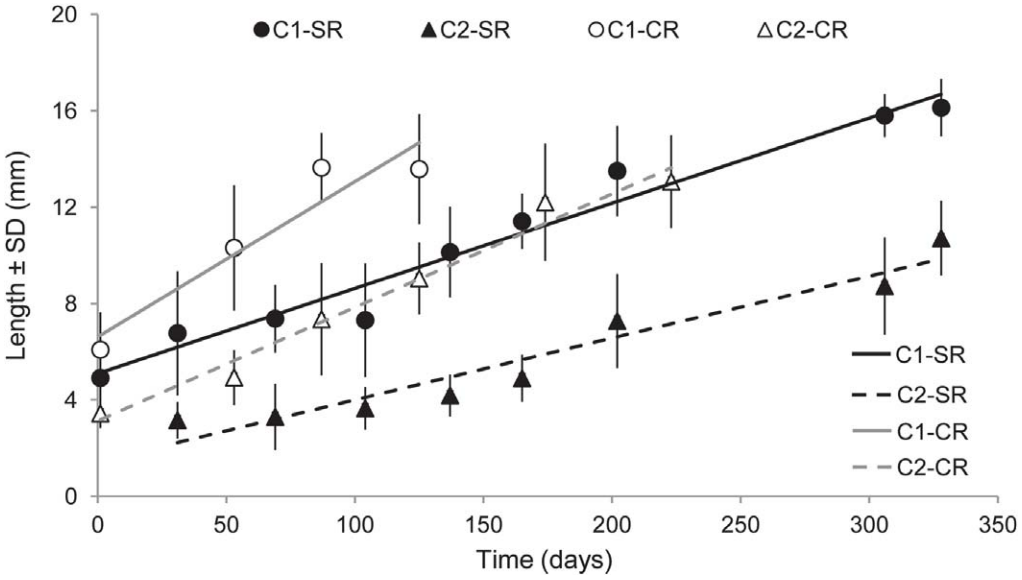

FIG. 8. Differences between the slopes of each growth model fitted to mean shell lengths ± standard deviation (SD) of cohorts 1 (C1) and 2 (C2) of *Limnoperna fortunei* from the Coronda and Santiago rivers.

Growth

We constructed length-frequency distributions based on the length values of 4,512 mussels from the Santiago River (Fig. 4). Polymodal decomposition identified five cohorts throughout the study period (Fig. 5). The *F* test did not reject the null hypothesis: cohorts 1 and 2 were better described by a linear model (Table 4). By contrast, cohort 3 was defined by two modal components, while cohorts 4 and 5 by a single one. Therefore, for all three of these cohorts, we were unable to apply the *F* test, and a straight-line was accordingly fitted by default (Table 4; Fig. 5).

In the Coronda River, we constructed the length-frequency distributions using 7,290 mussels (Fig. 6). We identified three cohorts in each experimental stage (Fig. 7). The better model to describe the growth of cohorts 1 and 2 in the first stage was the linear one (Table 4). A straight-line was fitted by default to Cohort 3 and to the cohorts in the second stage since an *F* test could not be performed because of the low number of modal components (Table 4; Fig. 7).

The *F* test of the sum of squares between the linear models of growth fitted to the cohorts 1 and 2 of each study site gave significant differences ($F_{(2,9)}$ = 20.33, $P < 0.001$ and $F_{(2,10)}$ = 66.38, $P < 0.001$; respectively). In both instances, the mussels from the Coronda River grew faster than those from the Santiago (Table 4; Fig. 8).

DISCUSSION

The present work constitutes the first comprehensive study analyzing and comparing the density, shell allometry, and growth of *L. fortunei* in dissimilar environmental conditions. Consistent with our predictions, the larval density, the density in settlement plates, and the growth of *L. fortunei* were significantly lower in the more polluted environment, the Santiago River. We also found significant differences in the shell allometry between the two populations of mussels. The individuals who exhibited a higher shell-growth rate and a higher population density in the less polluted environment were also more elongated (i.e., higher length-to-width ratio) than those from the more polluted habitat and lower density.

We observed a positive correlation between water temperature and larval density at both study sites. The larval density was very low or even nil at the end of autumn and the middle of winter, when the water temperature dropped

below 15–16°C at both locations. These results coincide with those of previous studies and would support the idea of a water-temperature threshold that modulated *L. fortunei* spawning events (Cataldo & Boltovskoy, 2000; Magara et al., 2001; Rojas Molina & José de Paggi, 2008; Boltovskoy et al., 2009a; Nakano et al., 2010). Moreover, the dissolved oxygen levels have been suggested to have a negative influence on the spawning and larval survival of this mollusk (Morton, 1977; Nakano et al., 2010; Oliveira et al., 2010b). We accordingly observed a strong negative correlation between the dissolved oxygen and the larval density in the Coronda River, but for reasons still unclear found no corresponding relationship in the Santiago River. We believe that this discrepancy might be associated with the low concentration and seasonal fluctuation in the dissolved oxygen that occurred mostly throughout the second year of the study.

The Santiago River has a higher average biological oxygen demand (9.2 mg/L; data provided by Engineering Department, La Plata Port Management Consortium) than the Coronda (4.3 mg/L and 2.3 mg/L during low and high water periods, respectively; Devercelli & Peruchet, 2008). These differing values of biological oxygen demand are fully consistent with the differences in dissolved oxygen estimated in this work, as the Santiago River's dissolved-oxygen concentrations were significantly lower than those of the Coronda River. The Santiago River exhibits heavy-metal concentrations some twenty- to fifty-fold above the recommended maximum levels for the protection of aquatic life (Steciow, 1998). The Río de La Plata estuary contains more than 300 point sources of pollution; and the anthropic input from domestic, industrial, and urban discharges have been identified as the primary cause of the eutrophication of this area (Kurucz et al., 1998). The level of pollution in the Santiago River, for its part, along with surrounding region, is significantly higher than in the Coronda River as a result of the input of hydrocarbon and heavy metals from nearby oil industries, the Río-Santiago shipyard, and the surrounding large urban centers (Colombo et al., 1989; Kurucz et al., 1998).

High concentrations of water pollutants and heavy metals can play a major role as stressors for aquatic animals and even have deleterious effects (Widdows & Donkin, 1992). *Limnoperna fortunei*, when exposed to heavy metals, manifests fertility disorders and a subsequent reduction in fecundity (Belaich et al., 2006). Our results indicated that the larval density in the Santiago River, as the more polluted environment, was significantly lower than in the Coronda. Previous studies have looked at differences in *L. fortunei* larval densities in different aquatic ecosystems in the middle region of the Río de la Plata basin. For example, Rojas Molina & José de Paggi (2008) found differences between the Colastiné and the Santa Fe rivers (17,200 ± 3,200 ind/m^3 *vs*. 2,900 ± 900 ind/m^3), but the authors provided no explanation for those regional differences. Boltovskoy et al. (2009a) also reported larval densities from different sites from the Río de la Plata basin and found that the densities from water bodies located close to the Coronda and Santiago rivers showed a variation ranging between about 4,000 and 7,000 ind/m^3. These authors mentioned, however, that in other aquatic ecosystems, also from the Río de la Plata basin, the larval densities were far lower (450–729 ind/m^3). They suggested that differences in larval densities were most probably a result of the size of the reproductive population settled at each site. In addition, Nakano et al. (2010) concluded that spatial differences in the larval density of *L. fortunei* between two lakes in Japan were the result of differences in the physicochemical environments of the two lakes. We believe that, despite a possible difference in the size of the reproductive population settled, the primary cause for the lower larval density observed in the Santiago River would be a biological response of mussels exposed to the higher level of pollutants at that site.

Variations in environmental conditions among sites clearly result in differences in mussel settlement, growth, and condition index (Dorgelo, 1992; Alfaro et al., 2008; Oliveira et al., 2011). Higher levels of pollution lead to higher larval-mortality rates and affect the settlement process by inhibiting the production of byssal threads (Widdows & Donkin, 1992). We accordingly found that the density of the settled individuals was significantly lower in the Santiago River – it being a more polluted environment than the Coronda. This result would corroborate the difference we observed in the larval densities. Indeed, the lower larval densities and higher levels of pollution in the Santiago River could have fully accounted for the decrement in the number of individuals in the settlement plates there. The population structure of the mussels in the Santiago River was best represented by individuals that were smaller than 6 mm in length, in contrast to the Coronda River, where the most representa-

tive individuals were larger than that value. Those structural differences were very likely related to differing growth rates *per se*, as the mussels in the Coronda River grew faster and reached larger sizes than the individuals in the Santiago.

Mollusks, like most organisms, exhibit progressive changes in their relative proportions with increasing body size as a response to high conspecific density dependence, as an ontogenetic process, or as a flexible consequence of environmental conditions (Alunno-Bruscia et al., 2001). Laterally compressed mussels grown at high densities would encounter fewer restrictions in valve opening than those compressed dorsoventrally (Lauzon-Guay et al., 2005). We found evidence that the mussels at higher population density in the less polluted environment of the Coronda River were significantly more elongated – that is, had a higher length-to-width ratio – than those at lower density in the more polluted environment of the Santiago. Nonetheless, we found no significant correlation between the density and the length-to-width values of the individuals in the Coronda River. When, however, we pooled the data from both sites, we found a positive relationship. We therefore favor the concept that mussels from high population densities tend to be more elongated – that is, longer – relative to individuals from low population densities (Lauzon-Guay et al., 2005). Based on these allometric relationships, we suggest that the observed differences in shell allometry could have also been related to a lower shell-growth rate in mussels from the more polluted environment.

Previous studies found similar growth rates of *L. fortunei* in Brazil (dos Santos et al*.,* 2008), Asia (Morton, 1977; Iwasaki & Uryu, 1998; Magara et al., 2001), and in the Río de la Plata basin (Boltovskoy & Cataldo, 1999; Maroñas et al., 2003; Darrigran et al., 2011), but most of those investigations were restricted to specific locations and therefore lacked comparative analyses. Mussels living under different environmental conditions are likely to have different growth rates (Anthony et al., 2001). Bivalves exposed to habitats that are heavily polluted tend to bioaccumulate inorganic and organic contaminants (Widdows & Donkin, 1992). Consequently, such individuals exhibit poor growth and a decline in body weight that can negatively impact reproduction (Widdows & Donkin, 1992; Alfaro et al., 2008). Although a number of factors can affect growth, we hypothesized that the difference in environmental conditions between the present study sites could yield differences in growth between the cohorts from the two sites. Our results demonstrated that the growth rates of the most representative cohorts from the Coronda River varied from 0.047 to 0.065 mm/day (i.e., 17–24 mm/year). By contrast, the growth rates of the most representative cohorts from the Santiago River were 0.026 to 0.035 mm/day (i.e., 10–12 mm/year). According to our prediction, mussels from the more polluted Santiago River grew more slowly than those from the less polluted Coronda.

We are aware that our study does not infer that polluted waters account directly for the differences we found in larval density, settlement, shell allometry, and growth in the two populations of mussels we sampled. In order to understand completely the causality of the differences we observed in the present study, experimental manipulations – both *in situ* and *in vitro* – of the multitude of factors that could conceivably affect the populations of *L. fortunei* would be needed. Such recourse would be both logistically difficult and highly time consuming. We believe, however, that this study has provided useful information on the potential effects pollution might have upon key bioecological aspects related to the life cycle of *L. fortunei*. Our results might therefore assist in the implementation of management protocols to prevent and/or diminish the ecologic and economic impact of nonnative species upon an ecosystem where that invader becomes established.

The invasive freshwater *L. fortunei* exhibits tolerance to a wide range of environmental conditions and can survive in many polluted water bodies with low pH, low oxygen, and low calcium concentrations where other invasive species (e.g., *D. polymorpha*) cannot (Karatayev et al., 2007). Our results, however, allow us to strongly suggest that the environmental conditions of heavily polluted environments might have a negative effect on larval density, the density in settlement plates, allometry, and the mussels' growth rates. Comparative studies are essential in the field of invasion ecology, because populations of nonindigenous species and their impacts are not homogeneous in either space or time (Boltovskoy et al., 2009a). An elucidation of the temporal and spatial population patterns of this bivalve will improve our understanding of its ecology, invasion dynamics, and impacts (Boltovskoy et al., 2009a). The evidence found in this work supports the idea that *L. fortunei* can inhabit heavily polluted environments that would be unsuitable for other invasive species, but nevertheless with a significant decrease in its biological potential.

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