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Population Structure and Dynamics of *Lymnaea columella* (Say, 1817) (Gastropoda: Lymnaeidae) in Wetlands of Northeastern Argentina

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Lucila Prepelitchi, Silvia Pietrokovsky, Florencia Kleiman, Diana Rubel, Laura Issia, Ricardo Moriena, Oscar Racioppi, José Álvarez, and Cristina Wisnivesky-Colli (2011) Population structure and dynamics of *Lymnaea columella* (Say, 1817) (Gastropoda: Lymnaeidae) in wetlands of northeastern Argentina. *Zoological Studies* **50**(2): 164-176. We examined the abundance, the population structure and the dynamics of *Lymnaea columella*, an intermediate host of *Fasciola hepatica*, in the Ibera Macrosystem, Argentina, and their relationship with biotic and abiotic factors. A 6-month drought in the middle of the study provided an opportunity to analyze population recovery. Seasonal surveys were performed over a 3-year study period (2002-2005) in bañados and malezales, 2 typical wetlands of the Macrosystem. Snails of different taxa were collected in each environment and survey. *Lymnaea columella* (n = 7851) was found throughout the study period except during the drought. In humid periods, abundance differed seasonally ($p < 0.001$), being highest in winter, intermediate in autumn-spring, and lowest in the hot, dry summer (> 58.5%, 1.6%- 34.6%, and < 1.7% of the total collected, respectively). Sexually immature individuals (< 6.5 mm) appeared in autumn and peaked in spring (> 60%); adults (> 6.5 mm) dominated in winter (> 60%), and among these, intermediate-sized snails (6.6-13.1 mm) were the only ones found in summer and immediately after the drought. Intermediate-sized snails, which are resistant to environmental stress and capable of producing viable offspring when conditions become favorable, may allow rapid population recovery, which begins in autumn. Continuous reproductive activity was observed between autumn and spring. The bañado showed the highest abundance (410.9 snails/30 min; 62.8% of the total collected; $p < 0.001$) and probably serves as the aestivation site and as a source of *L. columella* in the area. *Biomphalaria* spp. and *L. columella* showed opposite patterns of seasonal abundances, which may explain the low and high abundances of the latter in winter and summer, respectively. This is the 1st report of *L. columella* in these wetland types. The successful establishment of this invasive lymnaeid suggests a broad distribution throughout the region. http://zoolstud.sinica.edu.tw/Journals/50.2/164.pdf

Key words: *Lymnaea columella*, Ecology, Abundance, Ibera, Argentina.

Snails of the family Lymnaeidae are distributed throughout the world and act as intermediate hosts of several digenetic trematodes (Prepelitchi and Ostrowski-de-Nuñez 2007,

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Żbikowska and Nowak 2009). Among these, *Fasciola hepatica* (Linnaeus, 1758) is of particular interest because it causes fasciolosis, a disease of veterinary and medical importance. Despite the numerous epidemiological studies on fasciolosis that have been carried out worldwide (Ollerenshaw 1971, Boray 1981, Amato et al. 1986), there is little information on the ecology of the intermediate host under natural conditions (Malone et al. 1984, Kleiman et al. 2007).

Populations of freshwater snails like lymnaeids are subjected to severe ecological constraints imposed by large temporal fluctuations in their environments (Gérard 2001). Their presence, abundance, and population structure and dynamics result from the interplay between the intrinsic properties of each species and the extrinsic properties of the local habitat, both biotic and abiotic. Predation and interspecific competition are recognized as the most important biotic structuring factors (Dillon 2000) while temperature and precipitation are considered major limiting abiotic factors (Ollerenshaw 1971, Torgerson and Claxton 1999). The relative influence of biotic and abiotic factors on freshwater snail populations may vary spatially and temporally. Lymnaeids undergo optimal development and reproduction at temperatures of 10-30°C and high soil moisture conditions (Torgerson and Claxton 1999). When environmental conditions become unfavorable, lymnaeids are capable of surviving by estivating during droughts and by hibernating during the coldest months (Boray 1981). Their survivorship after the estivation period depends on the tolerance to desiccation, which is influenced mainly by the drought duration, temperature and size of individuals (Harris and Charleston 1977a). They are known to estivate on or beneath the soil, in mud, on stems, trunks, fallen branches, and mats of dried aquatic vegetation, and within cracks in the mud (Jokinen 1978).

Lymnaeid populations show high growth and reproductive rates under favorable and constant environmental conditions. Under naturally fluctuating conditions, a boom-and-bust pattern of population dynamics is observed, with snails showing explosive growth and drastic declines in relation to alternating favorable and unfavorable periods (Malone et al. 1984). Depleted populations may rapidly recover because these snails are hermaphrodites capable of reproducing by both cross- and self-fertilization (Dillon 2000).

Lymnaeids inhabit a wide variety of habitats including transient pools, marshes, ponds, irrigation systems, margins of streams and rivers and mud along the shoreline (Malek 1985). Some species are more aquatic (e.g., *Lymnaea columella* (Say, 1817), (Harris and Charleston 1977b) while others are more amphibious or terrestrial (e.g., *L. viatrix* Orbigny, 1835, (Kleiman et al. 2007).

In Argentina, where fasciolosis is endemic, the family Lymnaeidae is mainly represented by 2 local species *Lymnaea diaphana* King, 1830 in Patagonia (Hubendick 1951) and *L. viatrix* in the south and center (Paraense 1982), and 2 non-native species *Galba truncatula* Müller, 1774 in northern Patagonia (Issia et al. 2008) and *L. columella* in the northeast (Paraense 1982). Among the non-natives, *G. truncatula* has a European origin (Jabbour-Zahab et al. 1997), while *L. columella* was first described in North America (Malek 1985).

In Argentina, only the ecology of *L. viatrix* has been studied in detail to date (Kleiman et al. 2007). However, a previous finding of a population of *L. columella* naturally infected with *F. hepatica* in northeastern Argentina (Prepelitchi et al. 2003) emphasizes the importance of studying the ecology and biology of this non-native species in the region.

The aim of the present work was to study some biological and ecological aspects of *L. columella* occurring in habitats typical of an important wetland system in northeastern Argentina. A particular emphasis was placed on describing its abundance, and population structure and dynamics and determining the influence of biotic and abiotic factors on the population. In addition, a drought in the middle of the study period offered the opportunity to analyze the recovery of this population.

The results presented herein, together with knowledge of the role of *L. columella* as an intermediate host of *F. hepatica* (unpubl. data) will contribute to a better understanding of the epidemiology of fasciolosis in the area in order to design effective control measures.

MATERIALS AND METHODS

Study area

The study was conducted in freshwater environments (27°33'S; 57°32'W) located in the north of Corrientes Province, Argentina (Fig. 1). The area is included within the ecoregion of the Ibera Macrosystem, one of the largest and most complex wetlands in South America (Neiff 2003). It is composed of a mosaic of herbaceous prairies, floating mats, and open water bodies and shows a variety of lentic wetlands, such as permanently waterlogged marshes (*estero*), temporary waterlogged marshes *(bañado*), and temporarily waterlogged grasslands (*malezal*). These environments were described by Neiff (2003) as follows: 1) the estero is a densely vegetated habitat dominated by paludal vegetation; 2) the bañado shows slight slopes and abundant paludal and aquatic vegetation, and the period with water is longer than the period without it; and 3) the malezal is formed by flat-topped columns supporting grass, surrounded by rills of variable width resulting from water erosion; it supports paludal and terrestrial vegetation and is waterlogged for about 6 months a year.

Phytogeographically, the study area belongs to the Eastern District of the Chaco Region (Cabrera and Willink 1973). The climate is humid, warm-temperate, with no dry season (Money 1990). Based on records of the last 10 yr, the mean annual temperature is 21.6°C, the lowest mean minimum temperature was recorded in winter (8.3°C in July), and the highest mean maximum temperature in summer (36.7°C in Jan.) (SMN 2009). Annual rainfall usually exceeds 1600 mm. The altitude ranges 20-100 m. Periods of very low rainfall or drought occur every 4-10 yr (Carnevali 1994).

Sampling methods

Snail surveys were conducted in a bañado and malezal (described above), which were chosen because (1) they are typical of the Iberá Macrosystem; (2) they were adjacent to one other, allowing the study of snail dispersal between them; and (3) they were distant from and more elevated than surrounding environments (10-45 km and 73 m, respectively; Fig 1), in order to study the dynamics of a population that did not receive a contribution of individuals from neighbouring wetlands. The bañado was nearly circular in shape, with a perimeter of 938 m; it was dominated by *Salvinia* spp. and *Pistia* spp. as aquatic floating vegetation, and *Pontederia lanceolata*

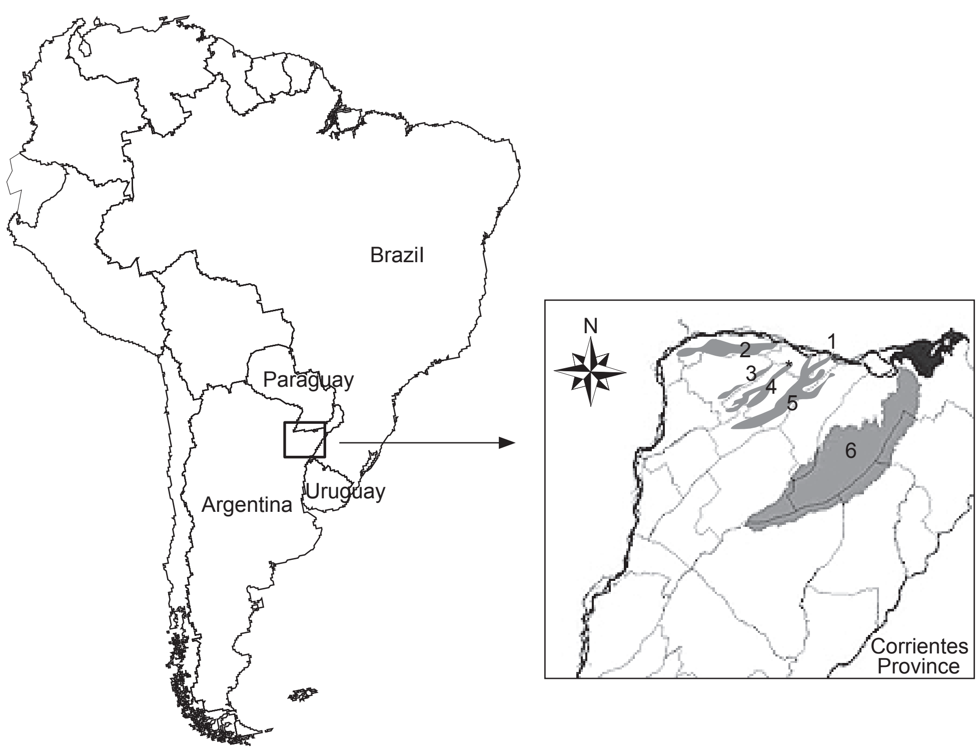

Fig. 1. Map of South America showing the location of Corrientes Province, Argentina. The study area is indicated by an asterisk. The surrounding wetlands are indicated by numbers (1, Paraná River; 2, Riachuelo marsh; 3, Maloyas marsh; 4, Santa Lucía marsh; 5, Batel marsh; 6, Iberá marsh).

and *Eleocharis* spp. as rooted vegetation, among others. The malezal, of about 24,300 m^2, was composed of columns dominated by the grass *Andropogon* spp. and numerous rills of variable width around them (Fig. 2A). Based on the width of the rills 2 potentially different snail habitats were recognized: wide and narrow rills (Fig. 2A). Wide rills were delimited on both sides by the columns and followed a sinuous longitudinal path of up to 270 m long; each wide rill measured 20-50 cm wide and up to 40 cm deep (Fig. 2B). Narrow rills were multiple small channels around the columns, constituting a dendritic net shaded by grass; each narrow rill measured 5-20 cm wide and up to 25 cm deep (Fig. 2C). The malezal was located higher and the bañado lower on the slope. All environments were filled only with rainwater and became interconnected in spring, after periods of heavy rainfall.

Sampling sites were selected using the following methodologies: in the bañado a transect was laid on the margin contiguous to the malezal (480 m; Fig. 2A). A systematic sampling method was used (Rabinovich 1980), with the 1st site being selected randomly and the rest being placed at intervals of about 60 m. In total, 8 sites were established in this wetland.

In the malezal, 4 wide rills and 8 columns were randomly chosen in an area of 50 × 90 m. The sampling sites in the wide rills were determined using a systematic sampling method, with a transect line located along these environments. The 1st site was randomly selected and the remaining ones were separated by 75 m. As a result, 4 sampling sites were established for each wide rill (Figs. 2A, B). In narrow rills, sampling sites were located around each selected column (Figs. 2A, C). The columns and sites remained the same during consecutive surveys.

Snail surveys were conducted seasonally between Nov. 2002 and 2005 in Mar. (summer), May (autumn), Sept. (winter) and Nov. (spring). In 2004, a prolonged period of low rainfall that took place between Apr. (autumn) and Aug. (middle of winter) caused the drying out of the studied environments. To analyze the drought's effect on the local snail population, an additional survey, hereafter referred to as "early spring", was performed in Oct. (spring) of that year. In total, 1 survey in 2002, 4 in 2003, 5 in 2004 (including the additional one) and 4 in 2005 were conducted.

For each survey and at each sampling site, gastropods of all groups were collected using the man-time collection method. Snails were collected by 1 person using a circular-framed hand net of 20 cm in diameter and 10 cm deep (with a mesh size 0.1 cm) for 30 min, and only lymnaeids were collected for another 90 min. When habitats were dry, snails were searched for on the surface and beneath the soil by digging ten 20-cm-deep holes over an area of about 560 cm^2; remnants of dry vegetation were also examined. Pulmonates and non-pulmonates were placed in separate containers with dechlorinated water and labeled by habitat and date.

All snails were taxonomically identified in the laboratory. About 10% of lymnaeids were processed following the method of Paraense (1984) for species identification, which is based on features of the shell and internal organs; individuals sharing common morphological features with those already identified were assigned to the same species. Non-lymnaeids were identified to family or genus level using descriptions or keys for freshwater snails from Argentina (Castellanos and Fernández 1976, Fernández 1981, Rumi 1991). The abundance of each taxon was expressed as the number of individuals found in 30 min.

The shell length of the lymnaeids collected during 120 min was measured from the apex to the anterior margin using a stereoscopic microscope equipped with an ocular micrometer. In particular for *Lymnaea columella*, individuals were divided according to their shell length into sexually immature and adult snails (> 6.5 mm, Appleton (1974)). Immatures were subdivided into newly-hatched (1-3.6 mm) and juveniles (3.7-6.5 mm) (Souza and Magalhães 2000) and adults into intermediate-sized (6.6-13.1 mm), large (13.2-19.7 mm), and very large (> 19.8 mm). The presence of newly-hatched snails indicated recruitment of new generations. These data were used to investigate the population structure and dynamics of *L. columella*.

Abiotic factors

Fot each survey and at each location, water temperature, pH and the height of the water column were measured. In addition, daily air temperatures were recorded every 90 min throughout the study period with a HOBO Data Logger to calculate the monthly mean air temperature; values were then grouped by season.

Daily rainfall values were obtained from the meteorological station at Corrientes Airport, Argentina (National Climatic Data Center), which is the nearest station to the study area (145 km

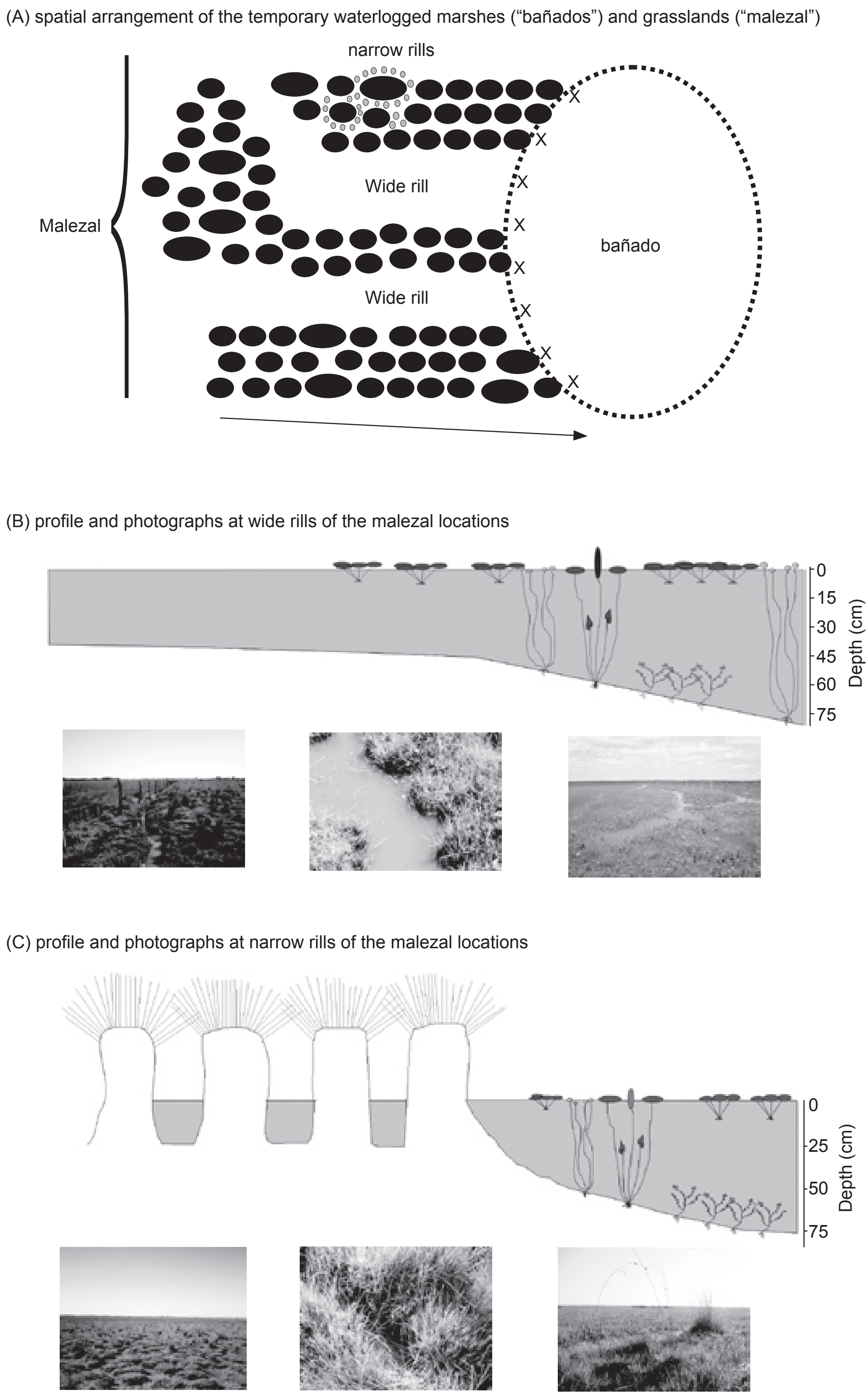

Fig. 2. Studied freshwater wetland types in northeastern Argentina. Black ovals and circles, columns of *Andropogon* spp.; small grey circles, narrow rills; arrow, slope direction; crosses, sampling sites along the bañado.

away). Data were used to estimate monthly and seasonal rainfall.

The monthly mean air temperature and monthly rainfall were also used to determine a water budget according to the method of (Thornthwaite and Mather 1957). In agreement with Malone et al. (1987), we considered that habitats suitable for snails were those having water in excess of that required to saturate the soil (i.e., surplus water).

Statistical analyses

Spearman's rank correlation coefficient (Daniel 1990) was used to test relationships between 1) lymnaeid abundances at each survey and monthly mean air temperature; 2) lymnaeid abundances at each survey and monthly rainfall; 3) lymnaeid abundances at each survey and water temperature, pH, and height of the water column; and 4) lymnaeid abundances and non-lymnaeid abundances at each survey. Monthly mean air temperature and monthly rainfall corresponded to the month before each survey was conducted.

A χ^2 goodness-of-fit test (Zar 1999) for more than 2 categories was used to examine for significant differences in lymnaeid abundances among periods; when significant differences were observed, differences between periods were compared by subdivision of the χ^2 test (Zar 1999). These same tests were used to compare snail abundances among seasons and among environments and to compare lymnaeid and non-lymnaeid abundances in each season.

In all cases, differences were considered significant at $p < 0.05$. All analyses were performed using the software STATISTICA, vers. 6.0 (StatSoft 2001).

RESULTS

In total, 7851 lymnaeid snails were collected, all of which were identified as *L. columella* based on the description of this species provided by Paraense (1983).

The water budget for the study period is shown in figure 3. Results are consistent with observations made in the field: there was no surplus water between Apr. and Aug. 2004, contrasting with the same period in 2002, 2003, and 2005 with 4, 2 and 2 months with surplus water, respectively. A recharge phase of soil moisture resulting from increased rainfall occurred between Sept. and Oct. 2004, with surplus water present from Nov. to the end of the study. On this basis, the study was divided into 4 consecutive periods, hereafter referred to as the "1st humid period" (H1), the "dry period", the "recharge period" and the "2nd humid period" (H2) (Fig. 3).

Surveys performed between spring 2002 and summer 2004 were included in H1, that in autumn 2004 in the dry period, those between winter and early spring 2004 in the recharge period, and those between spring 2004 and spring 2005 in H2 (Fig. 4).

As expected for a warm-temperate climate, the highest mean air temperature (25.7°C) was

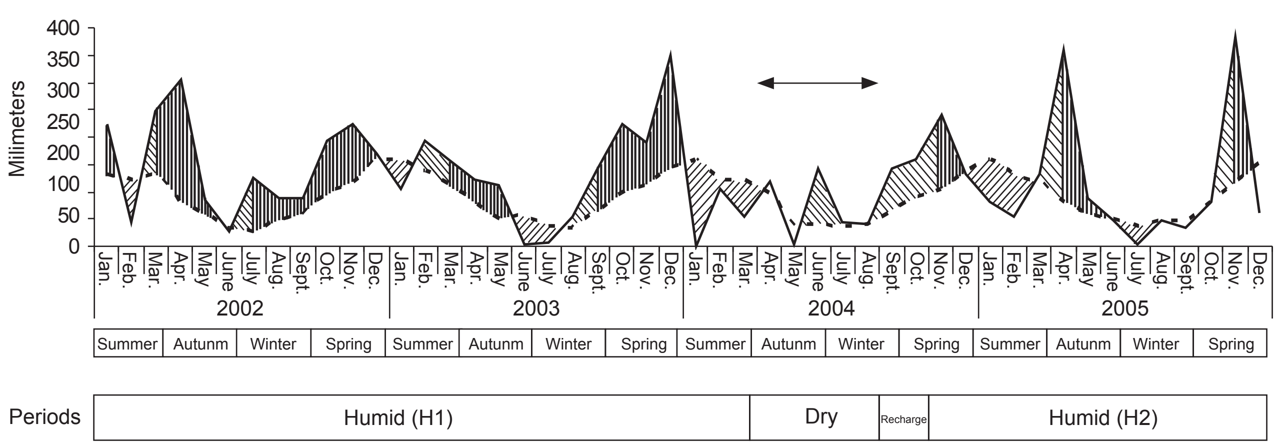

Fig. 3. Water budget for the period 2002-2005 in Corrientes Province, Argentina. Rainfall, solid line; potential evapotranspiration, dashed line; surplus water, vertical lines; soil moisture recharge, oblique lines ascending leftwards; soil moisture use, oblique lines ascending rightwards. The 2-headed arrow indicates the duration of the dry period; Humid H1 (1st period of excess water, from Jan. 2002 to Mar. 2004), Dry (period of scarce rainfall, from Apr. to Aug. 2004), Recharge (period of increased rainfall, from Sept. to Oct. 2004) and Humid H2 (2nd period of excess water, from Nov. 2004 to Dec. 2005).

recorded in summer, followed by spring (21.5°C), autumn (21°C) and winter (16.3°C). The mean seasonal rainfall amounts were 239.9 mm in autumn, 164.0 mm in spring, 117.3 mm in summer, and 52.1 mm in winter.

Environments

Lymnaea columella was found in all 3 environments studied, namely the bañado and the wide and narrow rills of the malezal. These temporarily waterlogged wetlands were completely dry during at least 1 season of the study period; the bañado dried out in autumn of the dry period while the malezal was also dry in summer 2003 of H1, in winter of the recharge period and in summer of H2.

In the bañado, water temperatures varied 14.3-36.4°C, pH 5.0-7.8 and the height of the water column 0.5-0 cm during the entire study period. In

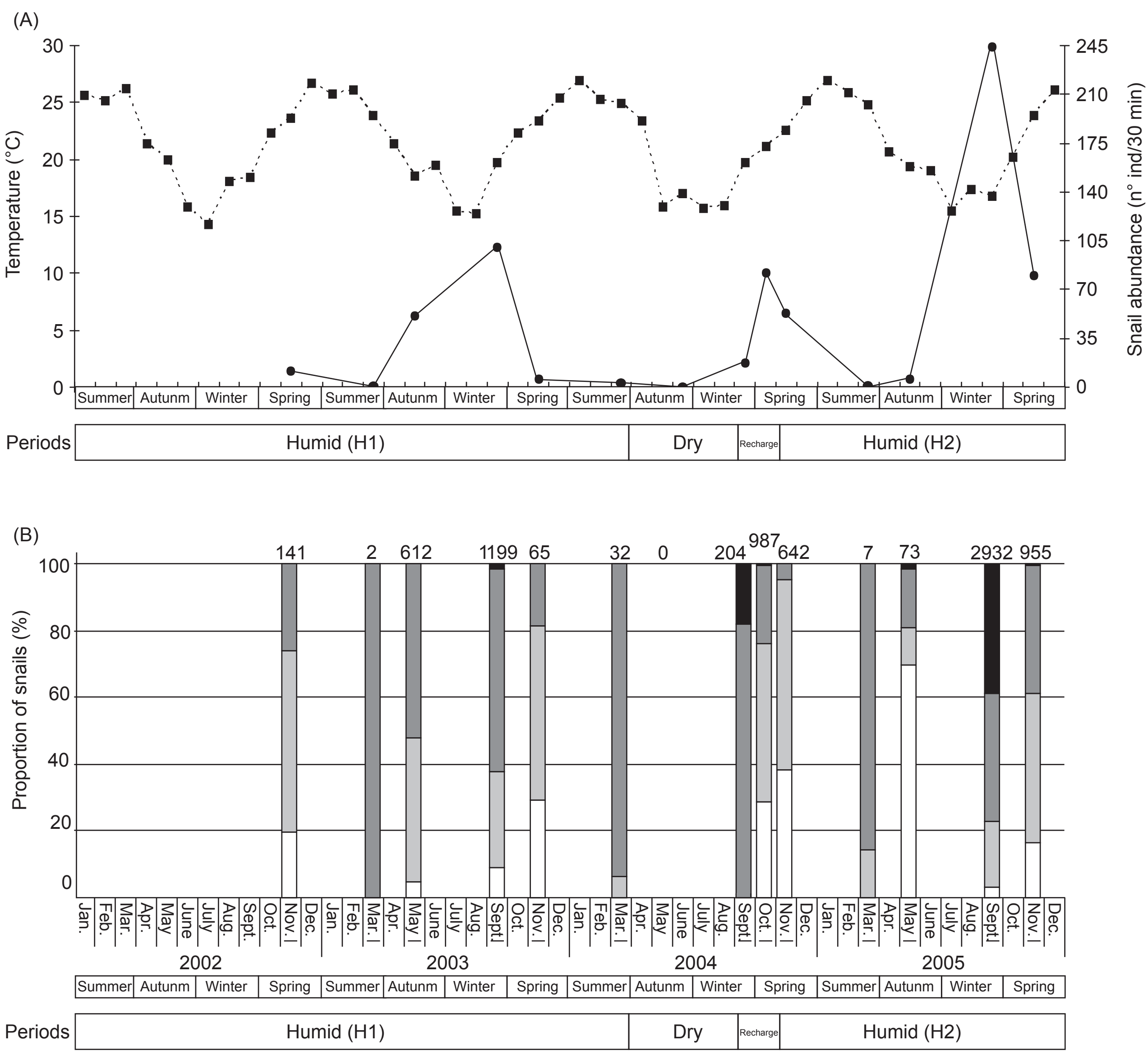

Fig. 4. Abundance and population structure of *Lymnaea columella* from northeastern Argentina. (A) abundance (solid line) and mean air temperature (dotted line); (B) proportion of snails in the different shell-length intervals (white, newly-hatched (1-3.6 mm); light grey, juveniles (3.7-6.5 mm); dark grey, intermediate-sized (6.6-13.1 mm); black, large (13.2-19.7 mm)); very large not shown. Numbers above the bars indicate the number of *L. columella* measured. Sampling dates are underlined. The sampling date Oct. 2004 is referred to in the text as "early spring". Dry, period of scarce rainfall; Recharge, period of increased rainfall; Humid H1 (1st period of excess water); Humid H2 (2nd period of excess water).

the wide rills of the malezal, water temperatures varied 17-29.1°C, pH 5.0-7.6 and the height of the water column 0.5-45 cm. In the narrow rills of the malezal, the water temperatures varied 18-28.5°C, pH 5.0-7.7 and the height of the water column 0.5-27 cm.

In spring the bañado and malezal become interconnected due to the increased precipitation (Fig. 3).

Abundances

Individuals of *L. columella* were found throughout the study, except in the survey of autumn 2004 (dry period), when all environments had dried out. Figure 4A shows the pattern of snail abundances during the study. In both humid periods, abundances were low in summer, increased in autumn, peaked in winter, and decreased in spring to reach values similar to those in autumn. In the recharge period, abundances increased with increasing rainfall: they slightly increased in winter and reached a maximum in early spring.

Abundances of *L. columella* significantly differed among periods (χ^2 = 5837.9, *d.f.* = 3, $p < 0.001$). The highest values were registered in H2 (384.1 snails/30 min; 58.7%), followed by H1 (170.9 snails/30 min; 26.1%) with the lowest in the recharge period (99.3 snails/30 min; 15.2%). All pairwise comparisons significantly differed ($p < 0.001$).

In both humid periods, abundances of *L. columella* at each survey were negatively correlated with monthly mean air temperature (H1: *rs* = -0.99, *n* = 6, $p < 0.001$; H2: *rs* = -0.90, *n* = 5, $p = 0.04$), while there was no correlation with monthly rainfall ($p > 0.05$ for both cases).

In both humid periods, abundances of *L. columella* individuals also significantly differed among seasons (H1: χ^2 = 153.8 and H2: χ^2 = 490.7, *d.f.* = 3, $p < 0.001$ in both cases). All pairwise comparisons significantly differed ($p < 0.001$; Table 1). In H1 and H2, the highest abundances were recorded in winter and the lowest in summer. In H1, the abundance in autumn was significantly higher than that in spring, while in H2 the abundance in spring was significantly higher than that in autumn (Table 1).

Abundances of *L. columella* also showed significant differences among environments in both humid periods (H1: χ^2 = 32.6 and H2: χ^2 = 92.8, *d.f.* = 2, $p < 0.001$ in both cases). In H1, abundances in the bañado and wide rills of the malezal did not significantly differ ($p = 0.19$; Table 1), while both abundances were significantly higher than that in narrow rills of the malezal ($p < 0.001$; Table 1). In H2, abundances in the bañado were significantly higher than that in wide rills of the malezal ($p < 0.001$), and both were significantly higher than that in narrow rills of the malezal ($p < 0.001$; Table 1).

For the 3 environments and in each survey, no correlations were found in either humid period between abundances of *L. columella* and water temperatures (*n* = 11, $p > 0.05$), abundances of *L. columella* and pH (*n* = 11, $p > 0.05$) or abundances of *L. columella* and the height of the water column (*n* = 11, $p > 0.05$).

In winter of the recharge period, *L. columella* individuals were only found in the bañado (17 *L. columella*/30 min), which was the only environment

Table 1. Abundance of *Lymnaea columella* in the Ibera Macrosystem

	Period		
	H1 *n* (%)	Recharge *n* (%)	H2 *n* (%)
Season			
Summer	2.8 (1.7)[a]	-	0.6 (0.2)[a]
Autumn	51.0 (29.8)[b]	-	6.1 (1.6)[b]
Winter	99.9 (58.5)[c]	17 (17.1)[a]	244.3 (63.6)[c]
Spring	17.2 (10.0)[d]	82.3 (82.9)[b]	133.1 (34.6)[d]
Environment			
Bañado	69.4 (40.6)[a]	98 (98.7)[a]	243.5 (63.4)[a]
Wide rills of the malezal	92.5 (54.1)[a]	1.3 (1.3)[b]	113.7 (29.6)[b]
Narrow rills of the malezal	9.0 (5.3)[b]	-	26.9 (7.0)[c]

H1, 1st humid period; H2, 2nd humid period. *n*, number of *L. columella collected* in 30 min. Values in the same column with different letters significantly differ ($p < 0.001$) in abundance between seasons or environments compared by the subdivision of the χ^2 goodness-of-fit test for more than 2 categories.

containing water. In early spring 2004, when all the habitats held water, the abundance reached a value of 82.3 *L. columella*/30 min, of which 80.9 and 1.4 snails were collected from the bañado and wide rills, respectively. No snails were found in narrow rills. In this period, the abundance in early spring was significantly higher than that in winter (χ^2 = 514.8, *d.f.* = 1, $p < 0.001$; Table 1), and that in the bañado was higher than that in wide rills of the malezal (χ^2 = 1127.9, *d.f.* = 1, $p < 0.001$; Table 1).

In the bañado and wide rills of the malezal, other snails of the gastropod community belonged to the genera *Biomphalaria*, *Physa*, and *Drepanotrema* and family Ampullariidae, while narrow rills of the malezal were only inhabited by *L. columella*. Although there was no correlation between *L. columella* abundances and those of gastropods ($p > 0.05$), a slight tendency was observed for an inverse relationship between *L. columella* and *Biomphalaria* spp. abundances (*rs* = -0.8, p = 0.2). Significant differences among gastropod abundances were found in each season (χ^2 = 172.5 in summer, χ^2 = 41.4 in autumn, χ^2 = 887.9 in winter, and, χ^2 = 68.3 in spring; *d.f.* = 4, $p < 0.0001$ in all cases). Table 2 shows the relative abundances of the members of the gastropod community in each season considering both humid periods together. In summer, only *Biomphalaria* spp. and *L. columella* were present, with the abundance of the former significantly higher than the latter. During other seasons all groups were present. In autumn, the most representative groups were *L. columella* and *Drepanotrema* spp., with abundances significantly higher than the others. In winter and spring, *L. columella* became the most frequent species (Table 2).

Table 2. Relative abundance (%) of members of the gastropod community in bañados and wide rills of the malezal, in the Ibera Macrosystem

	Humid period			
	Summer	Autumn	Winter	Spring
Gastropod				
Lymnaea columella	1.3[a]	38.5[a]	93.9[a]	42.0[a]
Biomphalaria spp.	98.7[b]	9.1[b]	0.8[b]	21.4[b]
Drepanotrema spp.	0	37.1[a]	0.8[b]	2.2[c]
Physa spp.	0	1.4[c]	3.1[b]	13.6[b]
Ampullariidae	0	13.9[b]	1.5[b]	20.8[b]

Values in the same column with different letters significantly differ ($p < 0.001$) in abundance between gastropods compared by the subdivision of the χ^2 goodness-of-fit test for more than 2 categories.

Individuals of *L. columella* were found actively moving about upside down at the water surface and resting or feeding all over floating and rooted plants or on the bottom. Snails were active at water temperature ranging 14.3-36.4°C, pH values of 5.5-7.8 and height of water column of 0.5-70 cm. When habitats became dried out, no snails or empty shells were found on or beneath the soil.

Population structure

The 7851 *Lymnaea columella* collected measured 1.1-25.3 mm long (mean 8.0 mm, standard deviation 4.2 mm).

The population structure of *L. columella* during the study period is shown in figure 4B. Despite seasonal differences in proportions of different shell length intervals, a clear pattern was detected. In summers of the humid periods, more than 86% of snails were intermediate-sized individuals (6.6-13.1 mm) and the few others, when present, were juveniles (3.7-6.5 mm). In autumn and spring snails corresponded to the same-length intervals (newly-hatched (1.1-3.6 mm), juvenile, and intermediate-sized snails), with immatures (< 6.5 mm) outnumbering mature ones in most cases (48%-95.3% immatures). In winter, the population attained maximum sizes, and a dominance of mature snails was observed (62.3%-77%) (Fig. 4B). Very large snails (> 19.8 mm) were only observed in winter 2005 (0.3%).

In the recharge period, almost all snails collected in winter 2004 immediately after the dry period were adults (> 6.5 mm); of these, 80.9% were intermediate-sized and 18.1% large individuals (13.2-19.7 mm). In early spring, the appearance of 29% of newly hatched individuals and 47.2% of juveniles indicated the recruitment of a new generation (Fig. 4B).

DISCUSSION

The occurrence of *L. columella* in the Ibera Macrosystem and in bañados and malezales is first reported in the present paper. In Argentina, it is found in lakes (Paraense 1986), rivers (Paraense 1986), ditches (Paraense 1986), irrigation channels (Rumi and Hamann 1990), and ponds (Castellanos et al. 1981), among other habitats. In addition, results indicate that *L. columella* is well established and capable of reproducing and developing in these typical environments of the Macrosystem, suggesting a broad distribution over this vast region of South America. These findings extend the knowledge of the diversity of habitats suitable for *L. columella* as well as of the biodiversity of these wetlands.

Lymnaea columella has a great capacity to establish itself in new habitats. The success of this species as an invader is partly due to its more-aquatic behavior (Harris and Charleston 1977b, Boray et al. 1984), tolerance to wide ranges of temperature (Harris and Charleston 1977c), pH, and salinity, and a relatively high intrinsic rate of natural increase (DeKock et al. 1989). In the studied population, individuals were active year-round in habitats with pH values of 5.5-7.8 and temperatures of 14.3-36.4°C. They were always found submerged in water, either on the bottom or attached to vegetation, regardless of the height of the water column (0.5-70 cm).

Due to its wide ecological plasticity, *L. columella* has almost spread around the world since it was first described in the US (Appleton 1974, Harris and Charleston 1977c, Paraense 1982, Boray et al. 1984, Malek 1985). Moreover, in certain countries, it has succeeded in becoming one of the most widely distributed freshwater snails (DeKock et al. 1989, Mitchell 1995). In Argentina, *L. columella* may be expanding its distribution. Given that it is an efficient intermediate host of *F. hepatica* (Boray et al. 1984, Coelho and Lima 2003), this situation could increase the risk of emergence of fasciolosis in new areas and/or the prevalence of the disease in endemic ones, as a result of the presence of greater numbers of susceptible hosts, as was observed in New Zealand, Australia and South Africa (Pullan and Whitten 1972, Brown 1980, Molloy and Anderson 2006).

In the study area, the bañado and wide rills of the malezal were the most suitable environments for *L. columella* compared to narrow rills. In the bañado, the abundance ranged 40.6%-98.7% of the collected *L. columella*, and it was the only environment with water and snails in summer and immediately before and after the dry period. Therefore, the bañado was probably the site for snail estivation and from where they emerged when environmental conditions became favorable, thus acting as a source of *L. columella* individuals in the study area. Although no snails were found on or beneath the soil during the dry period, self-burial rather than immigration seems to be a better explanation for their reappearance in the bañado considering the long distance between the study area and other freshwater bodies. The ability of *L. columella* to estivate and survive long periods of hot and dry conditions was reported under both natural and experimental conditions (Harris and Charleston 1977b, Amato et al. 1986).

In the malezal, the low number of snails in narrow rills (5.3%-7%) in relation to that of wide rills (29.6%-54.1%) could be explained by the combined effect of dense shade preventing algal growth and lack of aquatic plants as substrate.

High abundances of *L. columella* during humid periods compared to those in the recharge and dry periods may reflect the negative effect of the drought on the snail population. A similar response to a drought was observed for *L. columella* in Brazil (Amato et al. 1986) and for *L. bulimoides* in the US (Malone et al. 1984).

In humid periods, rainfall was unlikely the limiting factor because the absence of a correlation between lymnaeid abundances and rainfall suggests that the different environments contained the minimal amount of water needed for snail development.

In terms of the population dynamics during the humid periods, winter appeared to be the most favorable season for the studied *L. columella* population, as indicated by the highest abundance (68.5% of total snails collected) and the coexistence of individuals of all shell-length intervals. The largest specimens were found during winter, with the largest shell length ever reported for *L. columella* (25.3 mm) found in 2005. Until the present work, the largest specimens of this species collected from the field measured 20 mm (Mattos et al. 1997) and reared in the laboratory was 21.5 mm (Souza and Magalhães 2000). These results suggest that in this season, both air temperature and height of the water column are optimal for snail development and reproduction. Another factor that could explain the population boom of *L. columella* in winter would be the almost complete disappearance of *Biomphalaria* spp.

Eggs laid by the numerous adults present in winter (more than 62% of the population) were likely to hatch and develop in spring, accounting for the large proportion of immatures (> 60% of the population). In spring, the lower population abundance compared to winter could be related to: 1) the death of the large and very large snails found in winter due to, for example, senescence (Gutiérrez et al. 2001); or 2) the increase in the height of the water column and the consequent interconnection of the freshwater habitats after increased rainfall. With the latter option, a "dilution" effect may have caused the dispersal of snails to distant sites. A reduction in the snail population density due to increased rainfall was observed for *L. columella* in Brazil (Coelho and Lima 2003).

In summer, the absence of recruitment and only the presence of intermediate-sized snails combined with a significant decline in population abundance may reflect the negative impact of the unfavorable environmental conditions, such as a hot air temperature and lack or shortage of water. Additionally, the high abundance of *Biomphalaria* spp. may account for the low *L. columella* abundance in this season. This result, together with that obtained in winter, is in agreement with a study by Dillon (2000), who suggested that lymnaeids and planorbids such as *Biomphalaria* may compete for food since both are generalized feeders, and their diets broadly overlap. In summer, the population may undergo a greater investment in body growth in detriment to reproduction, as an adaptive strategy to overcome adverse environmental conditions.

In autumn, the appearance of immatures and the slight increase in population abundance compared to summer indicate the beginning of a population recovery. A similar pattern of higher and lower abundances in the coldest and hottest months, respectively, was reported for *L. columella* populations from other countries (Appleton 1974, Amato et al. 1986, Mattos et al. 1997).

In this study, during the humid periods the reproductive activity of *L. columella*, as inferred from the presence of newly hatched snails, was continuous between autumn and spring. In Brazil, Amato et al. (1986) reported 1 and Coelho and Lima (2003) 2 breeding seasons, respectively.

Intermediate-sized individuals appeared to be the most resistant to unfavourable environmental conditions, as indicated by their predominance both before (summer 2004) and after (winter 2004) the drought, as well as in the summer. Similar results were obtained by Malone et al. (1984), who found that medium-sized *L. bulimoides* predominated between snails estivating and emerging from estivation. A higher desiccation tolerance in adults was observed under laboratory conditions for a *L. columella* population in New Zealand (Harris and Charleston 1977a). The presence of adults capable of producing viable offspring as soon as conditions become favorable may allow a rapid population recovery. Indeed, in the recharge period, the studied *L. columella* population returned to levels of abundance similar to those observed before the dry period.

In this study, *L. columella* reappeared from estivation almost immediately after the drought, and the population had completely recovered after 1 month, based on similar abundances before and after the drought (99.9 snails in winter 2003 vs.82.3 snails in early spring 2004, respectively). In São Paulo, Brazil, Amato et al. (1986) found that *L. columella* reappeared 1 month after a drought that also lasted 6 months, with the population having recovered within 3 months. According to Gérard (2001), the time delay until snails reappear and the population recovers after a drought may depend on the time of the year. In this sense, the observed differences could have been related to the fact that the drought took place during the mild temperatures of spring in the present study and during the hot summer in São Paulo (Amato et al. 1986).

In the study area, the prevalence of fasciolosis in cattle is as high as 80% (Moriena et al. 2007). The results presented in this study suggest that *L. columella* may play an important role in the transmission of the parasite to cattle due to its: 1) almost-permanent presence and uninterrupted activity; 2) high abundance and aquatic behavior which may increase the probability of encounter with the parasite; and 3) its large body size, making it capable of harboring a large number of parasites.

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