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Intraspecific variability in life-history traits of a "freshwater shrimp", *Palaemonetes argentinus*

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Intraspecific variability in life-history traits was investigated comparing four geographically isolated populations of the shrimp *Palaemonetes argentinus* (Crustacea, Caridea, Palaemonidae) in the Province of Buenos Aires, Argentina. One population inhabits a creek (Vivoratá Creek, VC), which drains into the brackish coastal lagoon Mar Chiquita; three others live in inland lakes (Lakes Chascomús, LC; La Brava, LB; Los Padres, LP). Female size at the onset of sexual maturity, both realized and actual fecundity (i.e. number of eggs in an early stage of embryonic development and number of freshly hatched larvae per female, respectively), as well as the size of freshly hatched larvae were consistently largest at VC, intermediate at LC and LB, and lowest at LP. The opposite pattern was found in egg loss (estimated as difference between realized and actual fecundity), being lowest at VC, highest at LP, and intermediate in the other two populations. Initial embryonic dry weight (W) was higher at VC than in all other populations. However, the W of freshly hatched larvae was similarly high at VC, LC and LB, but significantly lower at LP. Intraspecific variation in life-history traits, in particular between shrimps from VC (lotic, slightly brackish; highly variable salinities) and those from inland lakes (lentic; low but stable ion concentrations) are discussed in relation to local variation in hydrological and other ecological conditions that may wield differential selection pressures in the life-history evolution of a species with a wide range of ecological and geographic distribution.

Keywords: palaemonid shrimp, life history, intraspecific variability, lotic water, shallow lakes.

Introduction

Intraspecific variation in life-history traits has been documented, even on small geographical scales, for conspecific populations of organisms living in environmentally variable habitats (e.g. Jonsson et al. 2001, Dhuyvetter et al. 2007). This may be a result of evolutionary forces and/or a more immediate plastic response to environmental factors (Begon et al. 2006).

Caridean shrimps belonging to the family Palaemonidae represent a particularly diverse and ecologically important crustacean group that can be found in marine, estuarine and freshwater habitats (Bauer 2004). There is general consensus that this taxon evolved in the sea, before it colonized brackish coastal or estuarine, and eventually, limnic environments (e.g. Jalihal et al. 1993, Liu et al. 2007). Interspecific variation in life-history traits associated with evolutionary freshwater invasions have frequently been studied in palaemonid shrimps (e.g. Jalihal et al. 1993, Odinetz Collard & Magalhães 1994). However, a few research studies have focused on the degree of intraspecific variability between or within populations (e.g. Alon & Stancyk 1982, Mashiko & Numachi 2000, and earlier studies cited therein).

The palaemonid shrimp *Palaemonetes argentinus* Nobili, 1901, occurs in limnic inland habitats such as lakes and streams, but also in brackish coastal lagoons, geographically ranging from central eastern Argentina to Uruguay and southern Brazil (Spivak 1997). It has an extended larval development (Menú-Marque 1973), which is typical of marine or brackish-water inhabiting species (Jalihal et al. 1993, Anger 2001). Its embryonic and larval development can be completed in a wide range of salinity conditions, so that all developmental stages may be considered as extremely euryhaline (Anger et al. 1994, Spivak 1997, Charmantier & Anger 1999, Ituarte et al. 2005). It has therefore been suggested that *P. argentinus* is in an early stage of evolutionary adaptation to life under freshwater conditions (Menú-Marque 1973, Anger 2001).

On one hand, aspects of the reproductive biology and ecology of this species have been studied in several popu-

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lations from Argentina and Brazil (e.g. Spivak 1997, Gonçalves & Fontura 1999, Félix & Petriella 2003, Dumont & D'Incao 2004, Oliveira Azevedo et al. 2004). On the other hand, simultaneous comparative investigations of life-history traits in different populations have so far not been available. In the present study, reproductive timing, realized and actual fecundity, brood loss during embryonic development, dry mass of eggs and larvae, larval size at hatching, and female size at the onset of maturity were compared among four separate populations of this shrimp species.

Material and methods

Study sites

Three inland lakes and one coastal creek were selected as study sites (Fig. 1; Table 1): Lakes Chascomús (LC), La Brava (LB) and Los Padres (LP) are shallow eutrophic "Pampa plain lakes" with fluctuating water renewal time and very low salinities (Quirós 2005). Vivoratá Creek (VC), by contrast, is located only 3 km from the Atlantic Ocean. It drains into the brackish coastal lagoon Mar Chiquita, where strong seasonal, daily and local variations of salinity occur, depending on tides, direction and force of winds, and rainfall (Anger et al. 1994, Spivak et al. 1994). Physical and chemical parameters on the study sites are summarized in Table 1.

Field collection and sample processing

Between September 2003 and March 2004 (except for January at LC, due to bad weather conditions), shrimp was collected in monthly intervals using a hand net (1 mm mesh size) and subsequently transported alive to laboratory, kept in water from sampling sites. Specimens were always caught along the banks (depth ca 1 m), especially near boulders and submerged vegetation. The hand net was dragged for different times until ca. 250 individuals were collected from each site at each sampling period. Among sampling sites, days of monthly collection varied by no more than one week. At VC, shrimp was collected during low tides because easier access. During each sampling, surface water temperature, salinity, conductivity, pH, and dissolved oxygen were measured with an U-10 Horiba water quality checker.

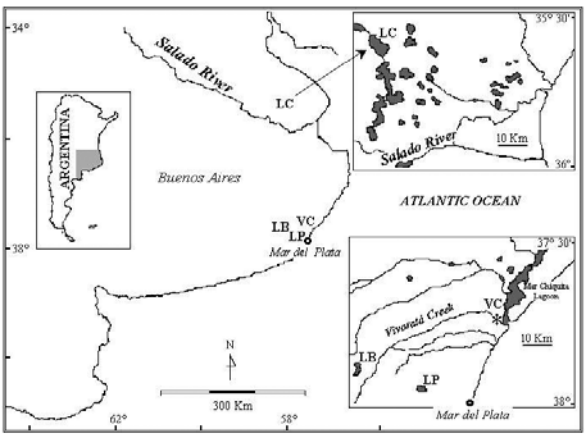

Fig. 1. Sampling sites in the Province of Buenos Aires, Argentina: Lakes Chascomús (LC), La Brava (LB), Los Padres (LP); Vivoratá creek (VC).

In the laboratory, ovigerous females were sorted in three groups according embryonic development stage. Based on microscopic observations (Ituarte et al. 2005), the following stages were defined: Stage I: ca 100 % of volume occupied by yolk, embryos showing little or no differentiation; Stage II: ca 50-60 % yolk, eyes visible as a reddish line, heartbeat visible but often irregular; Stage III: yolk largely depleted, eyes fully developed, heartbeat regular, differentiation of appendages in the final phase, ready to hatch. Percentage of females with embryos in each stage and percentage of ovigerous females per sample were recorded.

Table 1. Summary of physical and chemical information for sampling sites; u/d: unavailable data.

Site	Lake Chascomús (LC)	Lake La Brava (LB)	Lake Los Padres (LP)	Vivoratá Creek (VC)
Location	35° 36'S / 57°W	37° 51'S / 57° 58'W	37° 55'S / 57° 43'W	37° 44'S / 57° 27'W
Environment	lentic	lentic	lentic	lotic
Area (km^2)	28.7 [a]	4.3 [a]	2.0 [d]	-
Maximum depth (m)	1.9 [a]	4.8 [a]	2.4	Tide-dependent (~2 m)
Mean depth (m)	1.5 [a]	3.4 [a]	1.243	Tide-dependent
Salinity	hypo–oligohaline [b]	oligohaline [c]	hypo-oligohaline [c]	Tide-dependent
Total phosphorous (ug l^{-1})	100-500 [b]	u/d	100-400 [d]	0.35-2.24 [e]
Chlorophyll a (ug l^{-1})	92.9-219.9 [b]	u/d	20-90 [d]	1.15-60.4 [e]

[a]Quirós (2004), [b]Maizels et al. (2003), [c]Lenicov & Beresain (2001, 2002), [d]González Sagrario & Balseiro (2003), [e]Marcovecchio et al. (2005), from Mar Chiquita Lagoon

Shrimp was frozen at –20 °C, except for females with embryos in the final Stage III, which were used to obtain freshly hatched zoea I larvae. Those ovigerous females were observed 2-3 times per day, until larvae hatched. Within a few hours after hatching, the larvae were removed with a wide-bore pipette and counted. Both larvae and females were carefully dried on tissue paper and stored frozen for further processing.

Realized fecundity (N_e) was defined as number of Stage-I embryos per female, actual fecundity (N_z) as number of freshly hatched larvae per female. The N_e and N_z were estimated from ovigerous females collected during October and November, respectively. Dry weight (W) was determined on a H54 Mettler AR balance to the nearest 0.01 mg. Embryos and larvae were transferred to preweighed capsules of aluminum foil, dried at 90 °C to constant weight (at least 24 h). Larval and adult sizes were measured under a SZ40 Olympus stereo microscope as carapace length (CL), from the posterior orbital margin to the dorso-posterior border of the carapace. Larval size was measured in sub-samples of 10 larvae per brood, with $n = 9$ females (i.e. 90 larvae) from LC, and $n = 10$ females (100 larvae each) from all other populations. Shrimp sex was determined from the size and morphology of the endopod of the first pleopod and the presence of an appendix masculina. When none of these traits could clearly be observed, those individuals were classified as undifferentiated juveniles.

Ovigerous females and those with fully developed ovaries were considered as sexually mature.

Mean size at the onset of maturity (SOM) was calculated from a fitted logistic regression (Equation 1; modified from Oh & Hartnoll 2004):

Equation 1: $P = 1/(1 + \exp[-(a + b\,CL)])$

Where P is the proportion of mature females, CL is carapace length, and a and b are the logistic regression parameters estimated with the maximum likelihood method. Body size, at which 50 % of the females were mature (CL_{50}), was estimated for each population as negative ratio of the parameters a and b, considering $P = 0.5$ ($CL_{50} = -a/b$). Confidence intervals were calculated ($\alpha = 0.0125$), and mean SOM was compared among populations using a boostrap technique.

For each population, least-square regression models were fitted to describe the relationships between CL and egg production (both N_e and N_z). All variables were logarithmically transformed to satisfy the assumptions of normality and homogeneity of variances. Either N_e or N_z were compared among populations (tested with analysis of covariance, ANCOVA), using CL as the covariate. For all ANCOVAs, the equality of the slopes of regression lines was tested using a Parallelism test (Zar 1996). When the slopes were equal (homogeneous), ANCOVA was performed to test differences in mean Y adjusted for differences in X. When the regression lines were not parallel (heterogeneous slopes) the regression with a different slope was excluded from further statistical comparisons. The multiple comparison procedure (Student-Newman-Keuls, SNK) was used to test differences among individual Y-intercepts.

Difference between N_e and N_z was considered as a measure of brood loss. It was tested within each population using ANCOVA with CL as the covariate. Since individual slopes were not significantly different, a common slope was computed, and the recalculated Y-intercepts compared (Zar 1996). In each population, the brood loss was calculated as difference between the recalculated Y-intercepts (a) using Equation 2 (Oh & Hartnoll 1999), where a_z is the number of freshly hatching larvae and a_e the number of stage I embryos:

Equation 2: $100\,[1-\exp(a_z - a_e)]$

Differences in larval size within and among populations, were tested using separate one-way ANOVAs, because the data did not meet all assumptions for two-way ANOVA. Differences in dry weight of embryos or larvae among populations were tested using one-way ANOVA. *A posteriori* SNK tests were used when necessary.

Results

Environmental variables

Water temperature in October was below 18 °C in LB, LP and VC, but above 21 °C in LC (Fig. 2a). It increased later to a maximum in December (LC) or February (other sites). From March, it decreased at all sampling sites.

The lowest salinities were registered at LB and LP, intermediate values at LC, and the highest at VC (Fig. 2b). At LC and LP, salinity changed slightly between months, but not spatially (among local replicates). At LB, neither temporal nor spatial variation was observed, while both occurred at VC (Fig. 2b). Considering the whole study period, salinity was slightly but significantly different among sites (ANOVA, $F = 58.6$, $P < 0.0001$). The mean value was highest at VC (0.71 ± 0.13 ‰, mean ± SE), lowest at LB and LP (0.20 ± 0.00 and 0.23 ± 0.02 ‰, respectively), and intermediate at LC (0.44 ± 0.02 ‰). Likewise, average conductivity (in mS cm^{-1}) was lower at LB and LP (0.57 ± 0.02 and 0.65 ± 0.05, respectively) than at LC (1.03 ± 0.03), while the highest values occurred at VC (1.46 ± 0.25). Mean pH values ranged between 8.5–8.9, and those of dissolved oxygen between 1.33–2.74 mg L^{-1}. There were no consistent differences in pH or dissolved oxygen among sites or months.

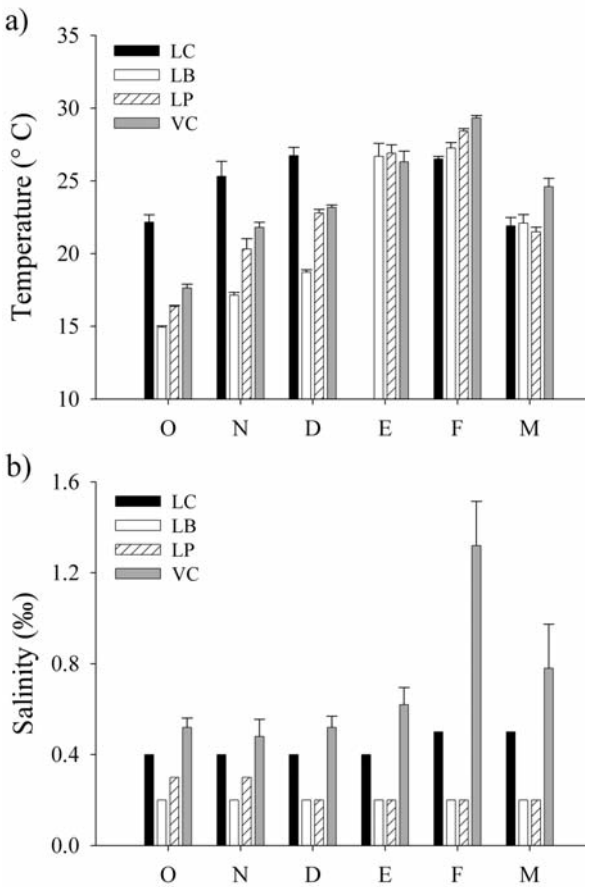

Fig. 2. Monthly mean (± 1 SD) of environmental variables measured at four sampling sites (see Fig. 1; Table 1) during the study period: (a) surface water temperature, (b) salinity.

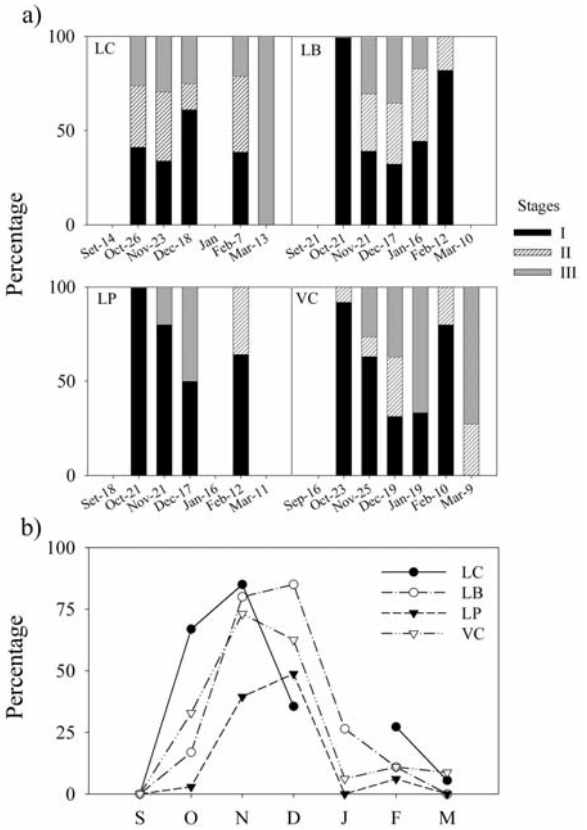

Fig. 3. Reproductive season at four sampling sites (see Fig. 1; Table 1): (a) percentage of ovigerous females with embryos in stage I (recently laid eggs), stage II (intermediate developmental stage), and stage III (near hatching); (b) ovigerous females (% of all females).

Reproductive season

Reproductive season differed among populations. In late October, almost all females at LB, LP and VC carried embryos in Stage I, while a high percentage of females at LC carried embryos in Stages II and III (Fig. 3a). This showed that spawning at LC population had started earlier. Spawning at LB and LP lasted only until February, but until March at VC and LC (Fig. 3b). Hence, the reproductive season lasted in total 5 months at LB and LP, 6 at VC, and 7 at LC. Peaks in the frequency of ovigerous females differed also among populations (Fig. 3b), indicating that the reproductive season started first at LC, subsequently at VC, and last at LB and LP. Maximum frequency of ovigerous females observed at LP was smaller (< 50 %) than in the other three populations (70-80 %).

Fecundity and brood loss

The number of freshly produced embryos (N_e, realized fecundity) as well as the number of freshly hatched larvae (N_z, actual fecundity) increased in all four populations linearly and positively with female CL (Table 2). The N_e differed significantly among populations. Slopes of N_e-CL regressions differed between LB and the other two freshwater population (Parallelism test, $F = 4.35$, $P = 0.017$), while that for VC was intermediate and not significantly different from any of the other populations (Table 2a). Regression line for LB crossed those for LC and LP. The crossing point between lines for LB and LC was at CL = 5.74 mm, N_e = 103, indicating that females from LB >5.74 mm carried on average more embryos than those from LC. The crossing point between lines for LB and LP was at CL = 5.32 mm, N_e = 77; in this case, females from LB >5.32 mm produced more eggs than those from LP. In summary, N_e changed at LB more strongly with female size than at the other two freshwater populations. Excluding LB, N_e differed among VC, LC and LP (ANCOVA, F = 3.25, P = 0.04). For equal female CL, the N_e values decreased in the order VC > LC > LP (Table 2a). In addition, N_e was higher at VC than at LB

Table 2. Comparison of fecundity in four populations of *Palaemonetes argentinus*: regression equations describing (a) realized fecundity (number of stage-I embryos, *Ne*), (b) actual fecundity (number of freshly hatched larvae, *Nz*) as functions of female body size (CL, mm; logarithmically transformed data). ANCOVA, with CL as covariable; where different lowercase letters indicate unequal slopes, it was not possible to compare the Y-intercepts (--); different capital letters indicate significant differences in the Y-intercepts in the order A > B > C (SNK test, P < 0.05).

	Population	Regression equation	*P*	r^2	*n*	ANCOVA	
						Slope	Y-intercept
a)	LC	$\text{Ln } N_e = 2.05 \cdot \text{Ln } CL + 1.05$	< 0.001	0.72	30	a	B
	LB	$\text{Ln } N_e = 3.84 \cdot \text{Ln } CL - 2.07$	< 0.001	0.71	20	b	--
	LP	$\text{Ln } N_e = 2.34 \cdot \text{Ln } CL + 0.43$	< 0.01	0.51	12	a	C
	VC	$\text{Ln } N_e = 2.88 \cdot \text{Ln } CL - 0.55$	< 0.001	0.72	22	a-b	A
b)	LC	$\text{Ln } N_z = 2.15 \cdot \text{Ln } CL + 0.49$	< 0.01	0.40	17	a	B
	LB	$\text{Ln } N_z = 3.38 \cdot \text{Ln } CL - 1.49$	< 0.001	0.65	18	a	B
	LP	$\text{Ln } N_z = 2.73 \cdot \text{Ln } CL - 0.85$	< 0.05	0.56	9	a	C
	VC	$\text{Ln } N_z = 3.34 \cdot \text{Ln } CL - 1.48$	< 0.001	0.79	18	a	A

Table 3. ANCOVA, comparing realized vs. actual fecundity within populations, with female size as covariable; (a) test for equality of slopes within each population (see regression equations in Table 2); *, significant differences between mean Y adjusted (P < 0.05; SNK test); (b) test for new mean Y adjusted (after recalculating a common slope for realized and actual fecundity in each population); all pair-wise tests were significant. SS: Sum of Squares; *d.f.*: degree of freedom; MS: Mean Square; *F*-ratio: statistic test; *P*: probability of error.

	Population	Source of variation	SS	*d.f.*	MS	*F*-ratio	*P*		SS	*d.f.*	MS	*F*-ratio	*P*
(a)	LC	Fecundity	0.00	1	0.00	0.03	0.87*	(b)	1.57	1	1.57	0.00	< 0.0001
		Error	1.17	43	0.03				0.00	44	0.00		
	LB	Fecundity	0.00	1	0.00	0.29	0.59*		0.26	1	0.26	0.00	< 0.0001
		Error	0.89	34	0.03				0.00	35	0.00		
	LP	Fecundity	0.00	1	0.00	0.11	0.74*		1.79	1	1.79	0.00	< 0.0001
		Error	0.54	17	0.03				0.00	18	0.00		
	VC	Fecundity	0.02	1	0.02	0.63	0.43		0.07	1	0.07	0.00	< 0.0001
		Error	1.12	36	0.03				0.00	37	0.00		

(ANCOVA, $F = 5.12$, $P = 0.029$). Similarly, the N_z differed among populations (Table 2b). All slopes were parallel, while the Y- intercepts differed significantly among populations (ANCOVA, $F = 13.7$, $P < 0.0001$). At equal CL, N_z values decreased in the order VC > LC = LB > LP (Table 2b).

In order to estimate brood loss, the regression lines for N_e and N_z, with CL as covariable, were tested for each population. In all four populations, the slopes of the two lines were equal, but the mean adjusted Y differed significantly, except for VC (Table 3a). This indicates in all three freshwater populations significant egg losses during embryonic development, but only an insignificant brood loss in VC population. After calculating a common slope, the new Y adjusted differed significantly between all four populations (Table 3b). The percentage of embryonic loss was highest at LP (47 %), intermediate at LC and LB (33 and 16 %, respectively), and lowest at VC (8 %).

Dry weight (W) of embryos and larvae

Dry weight of both early (stage I) embryos and freshly hatched larvae differed significantly among populations (ANOVA, embryonic W: $F = 9.64$, $P < 0.0001$; larval W: $F = 4.88$, $P < 0.01$), although with different patterns. Females from VC produced heavier eggs (0.085 mg W per embryo, $n = 22$, SE = 0.002) than those from any freshwater population (mean value of pooled data: 0.074 mg, $n = 61$, SE = 0.001). The average larval W at hatching was lowest at LP (0.048 mg W per zoea, $n = 11$, SE = 0.002), while consistently higher values were measured in the other three populations (mean value of pooled data: 0.057 mg, $n = 55$, SE = 0.001).

Size of larvae

Initial larval size (CL) at hatching varied within each population (i.e., among broods; Table 4a). In spite of this intra-populational variability, significant differences were

Table 4. ANOVA comparing larval size within and among populations of *P. argentinus*, (a) among broods in each population, (b) among populations (data transformed with 1/CL); populations: see Table 1. SS: Sum of Squares; *d.f.*: degree of freedom; MS: Mean Square; *F*-ratio: statistic test; *P*: probability of error.

	Population	Source of variation	SS	*d.f.*	MS	*F*-ratio	*P*
(a)	LC	Brood	0.059	8	0.005	2.74	< 0.05
		Error	0.175	81	0.002		
	LB	Brood	0.04	9	0.004	4.24	< 0.001
		Error	0.09	90	0.001		
	LP	Brood	0.05	9	0.005	4.99	< 0.0001
		Error	0.10	90	0.001		
	VC	Brood	0.057	9	0.006	3.61	< 0.001
		Error	0.157	90	0.002		
(b)		Population	0.274	3	0.091	30.44	< 0.0001
		Error	1.155	385	0.003		

Table 5. Size at maturity of female *Palaemonetes argentinus*, populations: see Table 1; CL: carapace length (mean value of size class), T: total number of females, M: number of mature females; PM: proportion of mature females; bold numbers show the size class at the onset of maturity (SOM, > 5% mature females).

	LC			LB			LP			VC		
CL (mm)	T	M	P	T	M	P	T	M	P	T	M	P
2.3	19	0	0	0	0	0	1	0	0	0	0	0
2.6	53	0	0	5	0	0	22	0	0	24	0	0
2.9	62	0	0	31	0	0	59	0	0	33	0	0
3.2	41	2	0.049	73	0	0	66	2	0.030	27	0	0
3.5	47	3	**0.064**	75	0	0	53	4	**0.075**	22	0	0
3.8	44	3	0.068	79	1	0.013	66	9	0.136	17	0	0
4.1	39	4	0.103	79	2	0.025	20	8	0.4	16	0	0
4.4	49	7	0.143	40	2	**0.05**	27	23	0.852	44	2	0.045
4.7	65	23	0.354	46	23	0.5	40	39	0.975	54	5	**0.093**
5	60	25	0.417	49	39	0.796	54	53	0.981	67	8	0.119
5.3	93	54	0.581	57	56	0.982	47	43	0.915	83	12	0.145
5.6	91	73	0.802	87	84	0.966	25	25	1	78	30	0.385
5.9	122	108	0.885	79	76	0.962	11	10	0.909	79	38	0.481
6.2	107	97	0.907	53	52	0.981	3	3	1	66	47	0.712
6.5	63	61	0.968	31	31	1	1	1	1	65	59	0.908
6.8	43	40	0.930	9	8	0.889	2	2	1	54	53	0.981
7.1	15	15	1	5	4	0.8				15	14	0.933
7.4	13	12	0.923	0	0	0				7	7	1
7.7	5	5	1	1	1	1				8	8	1
8	2	2	1							6	6	1
8.3	2	2	1							1	1	1
8.6										1	1	1
total	1,035	536		799	399		497	222		767	290	

also detected among populations (Table 4b). Mean larval size from VC, LC, LB and LP were 0.913 ± 0.005 mm (mean ± SE; n = 100), 0.893 ± 0.005 mm (n = 90), 0.891 ± 0.004 (n = 100) and 0.856 ± 0.004 (n = 100), respectively. Larvae from VC were significantly largest, those from LP smallest, and those from LC and LB had an intermediate size, which was similar at both sites.

Size at the onset of maturity (SOM) and mean size of mature females

Table 5 shows the number of females and the proportion of mature females in 0.3-mm size (CL) classes. Size class defining the SOM (> 5 % sexually mature females) differed slightly among populations, being 3.2 - 3.5 mm at LC and LP, 4.1 - 4.4 mm at LB, and 4.4 - 4.7 mm at VC (Table 5). The smallest ovigerous females had CL values of 4.6 (VC), 4.0 (LC), 4.4 (LB) and 3.7 mm (LP), respectively. Those females were collected near the end of the reproductive season (February 2004).

Relationship between CL and proportion of mature females (P) in each size class was calculated by fitting logistic functions (Fig. 4). The estimated size for 50 % sexual maturity differed significantly among populations (Fig. 5). The highest CL value was found in VC population, the smallest in LP, and intermediate values in LC and LB.

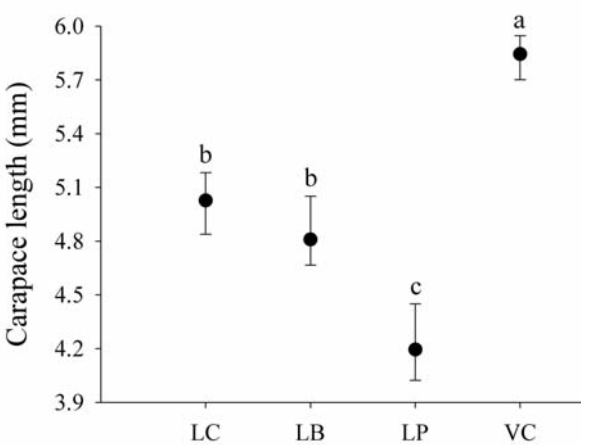

Fig. 5. Mean size at maturity of female *P. argentinus* from four populations (see Fig. 1; Table 1); error bars show confidence intervals (α = 0.0125), different letters indicate significant differences among populations.

Discussion

Several striking differences in life-history traits were observed among four populations of *P. argentinus*. The reproductive season, for instance, was longest at LC (7 months), while it lasted only 6 months at VC, and

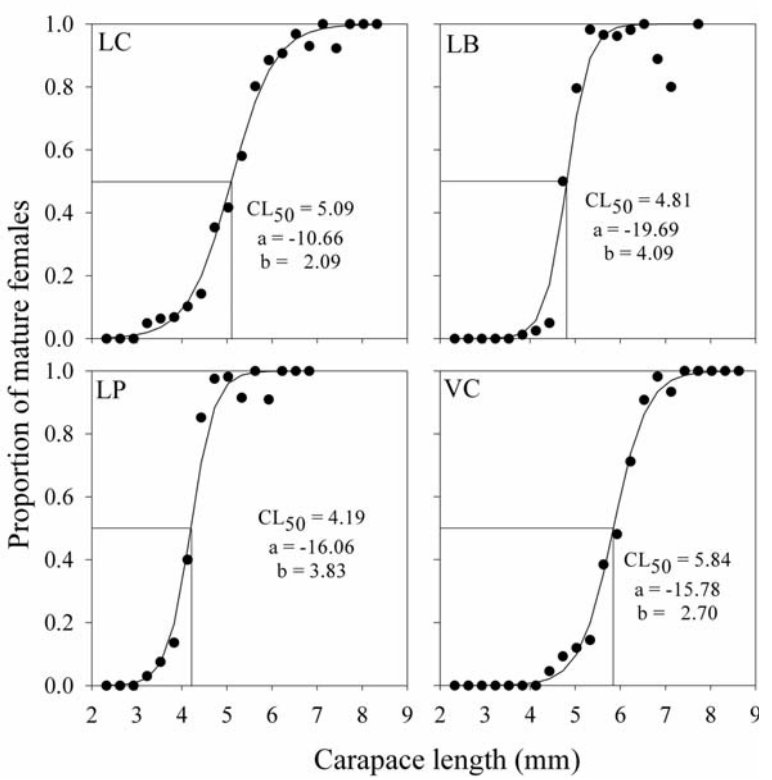

Fig. 4. Logistic functions fitting the proportion of mature females to carapace length, CL; CL_{50}: the size at which 50 % of the females were mature; a and b: fitted parameters. Populations: see Fig. 1; Table 1.

5 months at LB and LP. Higher water temperatures at the beginning of this study may explain the earlier beginning of reproductive activity in the LC population (Fig. 2a). The length of the reproductive season in the three southern populations was also correlated with water temperatures, which were on average higher at VC than at LB and LP.

Variability in the number of eggs per female was mostly explained by variation in female body size (in all four populations 51-72 %; Table 2a). However, when females with similar size are compared, the highest fecundity (both N_e and N_z) was found at VC population, while females living in freshwater produced on average fewer eggs and larvae. Also in a palaemonid shrimp from Japan, *Macrobrachium nipponense* de Haan, 1849, higher fecundity was observed in brackish-water populations compared to those living in freshwater (Mashiko 1983a, Mashiko 1990).

Moreover, in the three limnic populations of *P. argentinus* realized fecundity was highest in a lake, where salinity was slightly above the average (LC) and lowest in another one, where significantly lower ion concentrations occurred (LP). Thus, variability in the number of embryos among the three limnic populations may be associated with an increase in egg size due to hypo-osmotic conditions, rather than reflecting a higher female energy investment into egg production as in palaemonid shrimp from Japan (cf. Mashiko 1990).

In addition, females from the VC population produced heavier eggs, but the dry weight of the freshly hatched larvae was similar to that in limnic populations. This suggests a higher metabolic cost to complete embryogenesis in the VC population, and/or a difference in the biochemical composition of egg yolk between VC and other three populations. Both assumptions should be investigated in future experiments.

In *P. argentinus*, maximum fecundity and largest size at maturity were found in females from VC population. The same pattern was observed also in brackish-water populations of *Macrobrachium nipponense* compared to those from freshwater (Mashiko 1983a, b, Mashiko 1990). In *Palaemonetes pugio* Holthuis, 1949, by contrast, which is

ecologically similar to *P. argentinus*, these traits differed the opposite way: higher fecundity and larger size at maturity were observed in a population living in a less saline habitat (Alon & Stancyk 1982).

Salinity regime at VC is highly unpredictable, being strongly affected by the balance between rainfalls, river runoff, and tidal as well as wind-driven saltwater intrusions into the Mar Chiquita lagoon (Anger et al. 1994, Spivak et al. 1994). Salinities measured during this study in the Vivoratá creek were consistently low, being on average only slightly (but significantly) higher than in freshwater lakes (Fig. 2b). Such results may related with the fact that our measurements were only taken during sampling at low tide, when outflowing freshwater dominated. A typical brackish-water fauna, for instance reef-like aggregates of the tube-building polychaete *Ficopomatus enigmaticus* Fauvel, 1923 and an occurrence of grapsoid crabs (Spivak et al. 1994), indicate that the long-term habitat conditions at VC must actually be predominantly by higher, probably greatly fluctuating salt concentrations.

Besides with differential salinities, differences in fecundity, size at maturity and dry mass per embryo observed between *P. argentinus* populations at VC and those in three inland lakes, may be associated with the lotic nature of the Vivoratá creek; all other sites, by contrast, are lentic habitats (Table 1).

Hydrological characteristics seem to play an important role in the evolution of life-history traits of caridean shrimps in the Amazon region (Odinetz Collart & Magalhães 1994) as well as in southern Australia (Hancock & Bunn 1997, Richardson et al. 2004). One of the primary problems for life in lotic waters is that small organisms may be transported downstream towards estuaries or coastal waters, where salinities may become unfavourably high for most freshwater organisms. This should especially apply to physiologically sensitive planktonic larvae of decapod crustaceans (Anger 2001). Larvae of *P. argentinus* produced in VC may thus be removed from the parental habitats and eventually flushed into the adjacent Mar Chiquita lagoon, where brackish and sometimes fully marine conditions occur (Anger et al. 1994). Besides hyper-osmotic stress, the larvae presumably face here strong predation pressure by estuarine fish (Morgan 1995).

All this suggests that mortality of early developmental stages of *P. argentinus* may be much higher at VC than in limnic inland populations. For such a scenario, a stochastic model of effects of age-specific mortality predicts late maturity (see Alon & Stancyck 1982: 274). This is in agreement with our observations of larger size at maturity (which may also explain maximum fecundity) and lowest egg loss in VC population. In addition, larger (and presumably stronger) larvae produced at VC may better resist the advection to the adjacent Mar Chiquita lagoon. The same model predicts also an earlier reproduction (smaller size at maturity) when adult mortality is high. This may occur in the shallow inland lakes, where adult *P. argentinus* may be more conspicuous for visually directed predatory fish.

Intraspecific variation among three populations living in lentic waters may be related to differential morphologies and size of shallow Pampa plain lakes, which influence their functional dynamics and ecologies (Quirós 2004). Shrimp population inhabiting the smallest and shallowest lake (LP, Table 1) showed the smallest average size and weight of larvae, and smallest female size at the onset of maturity, the lowest percentage of ovigerous females (always < 50 %), the lowest fecundity, but highest brood loss. Altogether, the reproductive traits of this population suggest a particularly low level of fitness, probably reflecting live under generally unfavourable conditions.

Size and depth of a lake are key parameters for the trophic structure of its communities, which determines predation pressure and conditions for foraging, growth and overall fitness of its inhabitants (e.g. Werner & Anholt 1993). Pampa plain lakes show characteristic seasonal changes in their fish assemblages (Quirós et al. 2002, Berasain et al. 2005). This variation is particularly strong in shallow lakes with small surface areas (Quirós et al. 2002), affecting the intensity of predation and, through trophic cascade effects, the entire food web (Quirós 1998). Qualitative differences in the assemblages and dominant species of fish have been observed also in the three lakes studied here (Lenicov & Berasain 2001, 2002, Berasain et al. 2005). In *Palaemonetes pugio*, variations in size at maturity and body size were related to differences in the intensity of fish predation (Alon & Stancyk 1982). We therefore assume that predation pressure may be stronger on populations of *P. argentinus* living in particularly small lakes like LP.

In this study, we reported striking intraspecific variation in reproductive traits among geographically separated populations of *P. argentinus*. Differences in age-specific mortality may be a principal selection factor causing intraspecific variation (see Reznick et al. 1996). Some of the observed life history variations might have a genetic basis (e.g. Reznick 1982), while others may be related to phenotypic plasticity. Genetic differences, including those in the extent of phenotypic plasticity, or responsiveness to ecological factors, may reflect an incipient stage of speciation (cf. Mashiko & Numachi 2000, Dhuyvetter et al. 2007). Future comparative studies of intraspecific variation, conducted under both controlled laboratory and

natural field conditions (Reznick & Ghalambor 2005), may show if particular life history traits can be considered as adaptive in different scenarios of an ongoing evolutionary invasion of freshwater environments.

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