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ORIGINAL ARTICLE

Reproductive pattern of the freshwater prawn *Pseudopalaemon bouvieri* (Crustacea, Palaemonidae) from hypo-osmotic shallow lakes of Corrientes (Argentina)

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ABSTRACT
Pseudopalaemon bouvieri undergoes complete abbreviated development. The reproductive cycle (proportion and size of the sexually mature population and juvenile recruitment), fecundity and egg size of this prawn were examined in three subtropical shallow lakes. The reproductive cycle was seasonal; gonadal maturation occurred during the winter, ovigerous females were abundant in the spring and breeding occurred at the end of spring. Females produced small numbers of eggs (9–55) of relatively large sizes (1.0–2.1 mm). The proportion of ovigerous females with respect to the total number of females, the fecundity and egg size differed among the lakes according to the trophic state of the environments. *Pseudopalaemon bouvieri* has a reproductive strategy similar to other Palaemonidae species that inhabit nutrient-poor inland waters.

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Gonadal development stages; egg size; wetlands

RESUMEN
Pseudopalaemon bouvieri tiene un desarrollo completamente abreviado. Fueron examinados el ciclo reproductivo (proporción y tamaño de la población sexualmente madura y el reclutamiento de los juveniles), la fecundidad y el tamaño de los huevos de este camarón en tres lagos subtropicales poco profundos. El ciclo reproductivo fue estacional; la maduración gonadal ocurrió durante el invierno, las hembras ovígeras fueron abundantes en primavera y las crías aparecieron a finales de la primavera. Las hembras producen un bajo número de huevos (9 - 55) de tamaño relativamente grande (1,0 - 2,1 mm). La proporción de hembras ovígeras con respecto al número total de hembras, fecundidad y el tamaño de los huevos difirieron entre los lagos, de acuerdo al estado trófico de los ambientes. *Pseudopalaemon bouvieri* tiene una estrategia reproductiva similar a otros Palaemonidae que habitan ambientes acuáticos continentales pobres en nutrientes.

Introduction

The evolutionary history of the species in the Palaemonidae is characterized by diverse reproductive patterns (Martínez-Mayén & Román-Contreras 2009; Almeida et al. 2011). Sollaud (1923) ascribed their evolution to a recent invasion from the sea by species of Palaemonidae and interpreted their abbreviated development as a common trend in adaptive radiation to freshwater environments such as occurs in other decapods (e.g. trichodactylid crabs, Aeglidae anomurans, and parastacid crayfish). This family has a wide geographical distribution and representative species occupy different habitats, such as freshwater, estuarine and marine environments (Holtuis 1952; Sastry 1983; Hartnoll 1985).

Studies on South American Palaemonidae species have focused on the genus *Macrobrachium*, presumably due to the commercial value (aquaculture, fishery) of its species, but information about other genera, including *Pseudopalaemon*, is scarce (Jayachandran 2001; Melo 2003). Environmental requirements and reproductive patterns vary among the *Macrobrachium* species as follows: *M. acanthurus* (Wiegmann 1836), *M. equidens* (Dana 1852) and *M. carcinus* (Linnaeus 1758) depend on brackish or seawater to complete their development and have high fecundity (Lara & Wehrtmann 2009; Maciel et al. 2011; Tamburus et al. 2012); *M. amazonicum* (Heller 1862) has breeding populations in both brackish and fresh water (Sampaio et al. 2007; Meireles et al. 2013); and *M. borellii* (Nobili 1896)

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and *M. iheringi* (Ortmann 1897) breed in fresh water and have low fecundity, between 55 and 110 eggs (Verdi 1996; Collins 2000; Fransozo et al. 2004).

Pseudopalaemon bouvieri Sollaud 1911 belongs to a group of species that complete their life cycles in freshwater environments and do not depend on estuarine water for successful development. As with *M. borellii* (Collins et al. 2007), this species has a completely abbreviated development without a free larval stage, so that juveniles with the general characteristics of adults hatch from the eggs (Boschi 1981; Jalihal et al. 1993).

The geographic distribution of *P. bouvieri* is restricted to the basins of the Uruguay and Paraná Rivers (Gomes-Corrêa 1977; Bond-Buckup & Buckup 1989; Verdi 2000). This species is adapted to living in oligohaline waters (Boschi 1981; Lopretto 1995) and lakes in northeastern Argentina, where it inhabits water bodies covered by submerged vegetation (Poi de Neiff 2003). *Pseudopalaemon bouvieri* is omnivorous, consuming a high proportion of algae and detritus (Carnevali et al. 2012), and in Uruguay it is the most common crustacean prey in the diet of *Caiman latirostris* (Borteiro et al. 2009). The species has ornamental value and is thus of great interest for aquaculture.

Aside from its habitat, the environmental conditions where this species lives and its population abundance (Verdi 2000; Carnevali et al. 2012), the reproductive biology of *P. bouvieri* is unknown. Information on this aspect of its biology would contribute to the understanding of the diversity of reproductive strategies of the Palaemonidae and add valuable information for aquaculture. The objective of this study was to compare the reproductive cycle (proportion and size of the sexually mature population and juvenile recruitment), fecundity and egg size of *P. bouvieri* in three shallow lakes (hereafter referred to as lakes) during a 13-month period. We hypothesized that *P. bouvieri* has low fecundity because it reproduces in oligohaline waters and that different reproduction patterns, fecundities, and egg sizes will be observed in these lakes due to the energetic costs of life in environments with low salinity and the different trophic or environmental quality conditions.

Materials and methods

Sampling area

The province of Corrientes is characterized by a subtropical climate with long, warm summers and short, generally mild winters (Bruniard 1999). The average annual temperature ranges from 13°C to 19.5°C. During summer, the absolute maximum temperature ranges from 42.5°C to 46.5°C, depending on the area. Although the absolute minimum of winter temperatures is as low as −5.5°C, the occurrence of frosts is rare (Carnevali 1994). In northeast Corrientes, there are more than 100 semi-rounded shallow lakes located on sandy hills (height < 2 m) that have low salinity and electrical conductivity ranging between 25 and 150 μS cm^{-1} (Poi & Galassi 2013).

Several lakes in the region have been impacted by land use in the surrounding areas, and this human activity causes a eutrophic state of the lakes due to illegal wastewater discharges from the neighboring areas (Poi & Galassi 2013). We selected three hypo-osmotic lakes near Corrientes city, Argentina, that are shallow (depth between 1.80 and 4.50 m) and fed by rains. One of them has eutrophic conditions (lake 1: 27°29′ S; 58° 45′ W), and the other two lakes correspond to typical natural wetlands of the region (lake 2: 27°29′ S; 58°45′ W, lake 3: 27°22′ S; 58°32′ W). Lake 1 has a surface area of 70 ha, and the dominant plant species *Egeria najas* Planch, *Eichhornia azurea* (Sw.) Kunth and *Oxycarium cubense* (Poepp. & Kunth) Lye cover approximately 85% of the lake. Thirty per cent of the area (26 ha) of lake 2 is covered by aquatic plants, mainly *E. najas*, *Chara* sp., and *Cabomba caroliniana* A. Gray (total area: 87 ha). At lake 3, *Oxycarium cubense* and *E. najas* cover 25% (5 ha) of the total area (22 ha).

Collection of Pseudopalaemon bouvieri

Monthly samples were taken from November 2005 to November 2006 during the daytime with a 35 cm-diameter hand net (962 cm^2) with 1 mm mesh size (Poi de Neiff & Carignan 1997; USEPA 2002). Six hand-net sweeps was defined as one sampling unit, and the number of individuals per sampling unit was expressed per lake and month. The abundance of *P. bouvieri* was also estimated in terms of individuals per m^2 in areas with plant cover (mean of $n = 6$ hand net actions) due to the dependence of their distribution on the presence of macrophytes. Each sample was collected from the dominant plant species and was placed in a single plastic bags for each hand-net action. In the laboratory, the plant fragments were washed to detach detritus and the prawns were sorted manually.

At each lake and on each sampling date, water temperature (surface) and electrical conductivity (a measure of water salinity) were recorded with the Checkmate 90 (Corning®) conductivity meter ($n = 13$ samples). Water depth and dissolved oxygen were recorded with the Oxy-meter Oxi-30 (WTW, Germany)®, pH was measured with a digital pH meter (330 WTW)® and transparency was measured with a Secchi disk. Values of insolation and rainfall were obtained from the meteorological station at the Fernando Piragine Niveyro Airport (Corrientes, Argentina) and were provided by the National Meteorological Service (SMN).

Assessing prawn size and reproductive conditions

The cephalothorax length (CL) of all individuals was measured from the tip of the rostrum to the end of the cephalothorax using a digital caliper (± 0.1 mm precision) under a stereoscopic microscope. Sex was identified by the presence (males) or absence (females) of the appendix masculina on the second pair of pleopods (Boschi 1981; Bauer 2004). Young individuals without distinct secondary sexual characteristics on their pleopods were considered to be juveniles (sex undetermined), with all of these individuals having a total length of equal or less than 20 mm.

The reproductive period was determined based on the temporal variation in the proportion of females with mature gonads (with oocytes in vitellogenesis I and II) and ovigerous females (carrying eggs under the abdomen between the pleopods) relative to the total number of adult females during the sampling period. Recruitment was assessed by the presence of individuals of undifferentiated sex in the sample. The degree of gonadal development in females was classified according to the color of the gonads observed through the transparent exoskeleton (colorless, light green or green) and the location of the gonads (base, middle or front of the dorsal cephalothorax), indicating three stages (e.g. immature gonads, incipient mature gonads, or mature gonads, respectively) (Tamburus et al. 2012).

Fecundity was estimated by the number of fertilized eggs and embryos adhered to the female pleopods (Lima et al. 2014). For the analysis of fecundity and egg size, egg masses were carefully removed from the pleopods using tweezers. The oval eggs were counted, and the major axis of each egg was measured with a digital caliper (± 0.1 mm) under a magnifying glass. The material was preserved in 10% formalin. Eggs were classified into the following two developmental stages: Group I: fertilized eggs with incipient embryos without eye pigmentation and Group II: advanced embryos in eggs with eye pigmentation, as proposed by Nazari et al. (2003).

Data analysis

We tested for differences in environmental factors (water temperature, electrical conductivity, dissolved oxygen, pH and transparency) among the lakes using the non-parametric random block Friedman test (T^2). The same analysis was used to test for differences among the lakes in terms of the number of prawns per sampling unit, the number of individuals per m^2, the proportion of females with mature gonads and of ovigerous females relative to the total number of females, and the proportion of juveniles relative to the total number of individuals sampled. The relationships between environmental factors (water temperature, electrical conductivity, dissolved oxygen, pH and transparency) and the number of ovigerous females and the number of eggs per female were tested using Spearman's correlation coefficient. For this analysis, we only included months in which ovigerous females were recorded. Analysis of covariance (ANCOVA) was used to evaluate the relationships between the number of eggs, cephalothorax length (CL), egg size and the CL of females among the three lakes. The Tukey post hoc test was used to compare means using Statistix 10.0 software. All other tests were performed with the InfoStat software (Di Rienzo et al. 2012). *P*-values equal to or less than 0.05 were considered to be significant.

Results

Environmental conditions

The three lakes were under similar climatic conditions due to their proximities to one another (distance maximum 22 km). The duration of sunshine hours ranged from 4.2 to 9.9 h per day (mean ± sd: 8.00 ± 1.14 h), and rainfall was 3.0 and 380.0 mm in June and November, respectively. The monthly average maximum and minimum air temperatures during the study period were 34.6°C in January and 9.5°C in August, respectively.

Water temperature was low during winter (minimum of 14°C) and high during summer (maximum of 31°C). Water temperature and electrical conductivity did not show significant differences among the three lakes throughout the year (Friedman test, Table 1). Dissolved oxygen was significantly lower in lake 1. Water transparency and pH were significantly different among the three lakes (Table 1).

Relative abundance of females in different reproductive stages

A total of 2971 *P. bouvieri* specimens were sampled, of which 282 were found in lake 1, 846 in lake 2 and 1843 in lake 3. Of this total, 703 were females (128 with mature gonads in different stages of development and

Table 1. Friedman test results for comparisons of physical and chemical variables among the three lakes, Corrientes province, Argentina. Different letters in the post hoc test indicate difference significantly.

	Lake 1		Lake 2		Lake 3		Friedman		
	Mean	SD	Mean	SD	Mean	SD	T^2	df	*p*-value
Water temperature (°C)	23.71	5.76	24.48	5.72	22.37	6.67	8.04	38	n. s.
Electrical conductivity (µS cm^{-1})	56.46	8.24	54.31	9.07	61.42	18.81	4.40	38	n. s.
Dissolved oxygen (mg l^{-1})	5.92^a	2.49	8.42^b	0.81	8.55^b	0.87	6.0	38	0.05
pH	7.05^a	0.38	7.32^{ab}	0.15	7.51^b	0.4	6.0	38	0.05
Water transparency (m)	0.87^a	0.28	1.33^b	0.47	1.2^{ab}	0.54	8.0	38	0.02

298 ovigerous females), 188 were males and 2080 were juveniles. The monthly numbers per sampling unit of *P. bouvieri* (Table 2) were significantly lower in lake 1 (Friedman: $T^2 = 10.53$, $p < 0.0005$) than in lakes 2 and 3. The density (number of prawns per m^2) did not differ significantly among the three lakes. The proportion of females with mature gonads or carrying embryos was high (> 83.3%) from July to October in lake 2 and from September to November in lake 3, whereas the proportion of these females was under 60% in lake 1 (Table 2).

In lake 1, females with mature gonads were sampled in June, August (highest proportions) and October. In lake 2, females with mature gonads were sampled in December, February and June to November, with the highest relative abundance in July and October. In lake 3, females with mature gonads were recorded in November, March, and June to October, with the highest relative abundance in July and August (Figure 1). We found ovigerous females from September to December, but their proportion was highest during November 2006 in lake 3 (Figure 1). The shortest reproductive period was recorded in lake 1. The proportion of females with mature gonads (Figure 1) was not significantly different among lakes (Friedman: $T^2 = 0.52$, $p < 0.6019$), but the proportion of ovigerous females differed significantly among the three lakes (Friedman: $T^2 = 3.71$, $p < 0.03$).

In lake 3, 5.5% of ovigerous females showed signs of additional gonadal development. In all lakes, juveniles were sampled from mid-winter (lake 2) to late spring (lakes 1 and 3) and reached a high proportion of the population during summer (Figure 1). No significant differences in the proportion of juveniles were found among the three lakes (Friedman: $T^2 = 0.371$, $p < 0.6953$).

Number and size of eggs in relation to ovigerous female length

In the three lakes, the number of eggs per female ranged from 9 to 55 and measured between 1.0 and 2.1 mm in diameter (Table 3). The cephalothorax length of ovigerous females (Table 3) ranged from 10 to 16 mm depending on the lake. The highest fecundity was recorded in lake 3 (Table 3). The eggs with incipient embryos (Group I) comprised between 62.5 and 88% of the total number of eggs in each lake. The egg diameters of this group were 1.5 ± 0.7, 2.1 ± 0.5 and 1.8 ± 0.2 in lakes 1, 2 and 3, respectively. The diameters of eggs with Group II embryos were 1.7 ± 0.2, 2.3 ± 0.6 and 1.6 ± 0.3 in lakes 1, 2 and 3, respectively.

Ovigerous females of large size were more frequent (55.5%) in lake 1 than in the other lakes (Figure 2). The comparison of the relationship between egg number

Table 2. Monthly number per unit effort and number of individuals per m^2 of *P. bouvieri* and proportion of females bearing mature gonads plus ovigerous females on the three lakes (L1, L2 and L3).

	Sampling units			Individuals per m^2			% mature + ovigerous females		
	L 1	L 2	L 3	L 1	L 2	L 3	L 1	L 2	L 3
November	10	108	32	13.8 ± 18.1	187 ± 443.1	39.8 ± 51.5	-	-	44.4
December	6	89	142	10.3 ± 25.4	154.2 ± 239.4	294.5 ± 217.2	-	40	28.5
January	12	14	165	20.8 ± 28.7	24.3 ± 26.8	325.7 ± 317.1	-	-	-
February	4	16	352	6.9 ± 10.7	29.5 ± 29	616.7 ± 399	-	16.6	-
March	3	110	83	5.2 ± 8.7	190.5 ± 186	279 ± 170.6	-	-	5.7
April	16	33	30	27.7 ± 28.4	57.2 ± 56.1	100.5 ± 107.7	-	-	-
May	1	42	24	1.7 ± 4.2	74.5 ± 71.2	79.6 ± 70.4	-	-	-
June	6	4	32	10.4 ± 16.1	6.8 ± 8.4	112.6 ± 55.6	25	25	10
July	-	10	28	-	17.3 ± 12.6	96.9 ± 87.8	-	83.3	50
August	17	31	39	29.4 ± 33.7	55.4 ± 51.6	162.8 ± 67.6	53.8	100	50
September	27	23	48	46.7 ± 42	39.9 ± 12.5	100.5 ± 52	60	100	94.5
October	148	201	133	256.4 ± 346.4	395 ± 311	249.5 ± 311	54.7	91	100
November	32	165	735	55.4 ± 42.4	294.5 ± 163.1	1361.7 ± 770.6	50	70.5	97

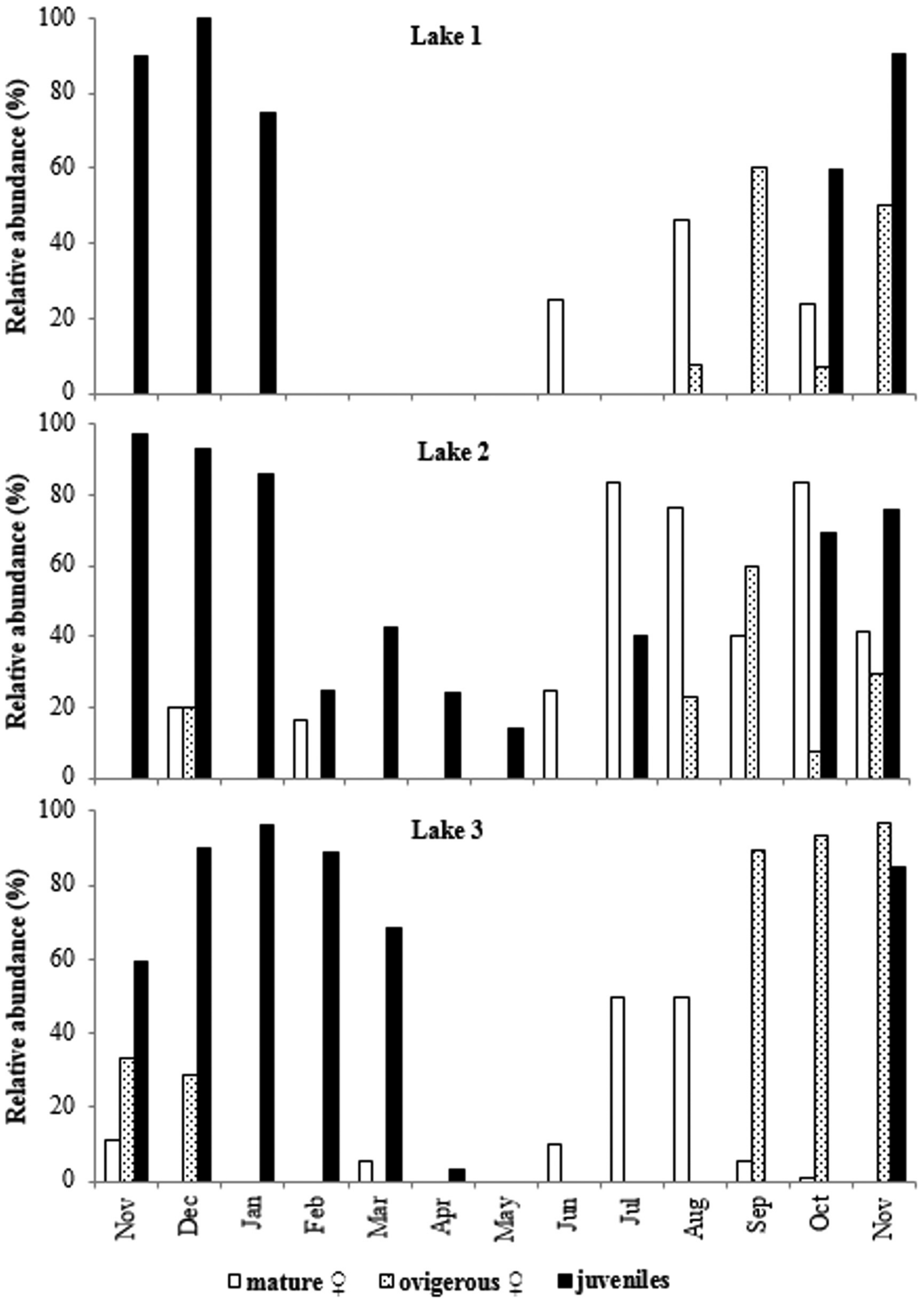

Figure 1. Proportion of females with mature gonads and of ovigerous females of the total number of adult females in that month, and proportion of juveniles (not sexed) of the total number of individuals of *P. bouvieri* collected per month in the three lakes, Corrientes, Argentina. The proportion of ovigerous females with respect to the total number of females differed significantly among the three lakes.

and cephalothorax length (mm) of the females in different lakes using ANCOVA showed that fecundity was higher in lake 3 than in the other two lakes ($F = 6.87$; $p = 0.0015$) (Figure 3). The tendency towards an increase in fecundity with increasing CL (Figure 3(A)) was statistically significant ($p < 0.05$) for lakes 2

Table 3. Comparison of mean (± standard deviation, range) cephalothorax length, fecundity and size of eggs of ovigerous females of *P. bouvieri* between three lakes (L 1, L 2 and L 3) in Corrientes, Argentina.

	L 1	L 2	L 3
	n = 31	*n* = 30	*n* = 78
CL (mm)	15 ± 1.0	13 ± 2.1	13.5 ± 1.7
	14–16	10–16	11.5–16
Number of eggs	29.8 ± 10.3	22.5 ± 4.2	33.3 ± 7.6
	9–46	18–31	10–55
Diameter of eggs (mm)	1.4 ± 0.4	1.8 ± 0.2	1.6 ± 0.1
	1.0–2.0	1.3–2.1	1.0–1.9

(y = 2.889x – 14.997; R^2 = 0.3702) and 3 (y = 4.7058x – 34.019; R^2 = 0.2273). The regression was not significant for CL and the number of eggs for lake 1 (y = 3.3118x – 19.977; R^2 = 0.0577) due to the wide range of egg number for each size class (Figure 3(A)). The ANCOVA analysis used to test the relationship between egg size and CL showed that the three lakes differed significantly (F = 17.37; p = 0.0001). The regression between CL and egg size was statistically significant ($p < 0.05$) for lake 3 (y = 0.0186x + 1.337; R^2 = 0.0103) but was not significant for lakes 1 and 2 (Figure 3(B)).

There was no significant relationship (Spearman test) between the number of eggs and the selected limnological environmental variables of pH, electrical conductivity, dissolved oxygen, water transparency and water temperature.

Discussion

In all three lakes, the reproductive cycle of *P. bouvieri* was seasonal; gonadal maturation occurred during the winter, ovigerous females were abundant in the spring and breeding occurred during the last months of spring. The high percentages of ovigerous females in the spring were most likely associated with an increase in available food, as they coincided with peaks in the abundance of algae and zooplankton (Poi & Galassi 2013). The development of food (e.g. prey) also coincided with an increase in the presence of juveniles. A seasonal pattern of reproduction in palaemonids is common (e.g. *M. gangeticum*, *M. idella*) (Jayachandran 2001), although other Palaemonidae (e.g. *M. amazonicum* and *M. acanthurus*) have a pattern of continuous reproduction (Sampaio et al. 2007; Tamburus et al. 2012).

The low content of dissolved oxygen and low water transparency, indicating eutrophic conditions in lake 1, could result in the low abundance of *P. bouvieri* prawns and the shortening of the reproductive cycle due to the energetic costs of maintaining the basal metabolism.

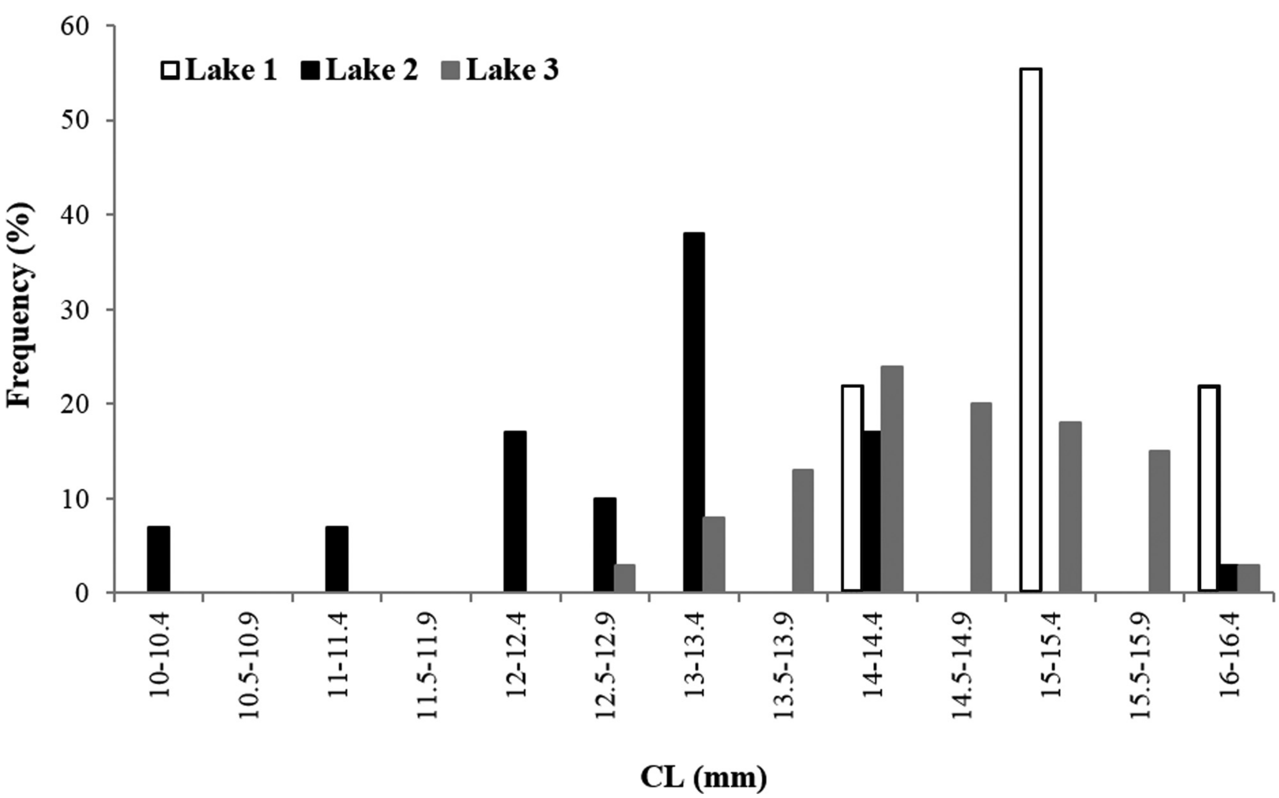

Figure 2. Histogram of frequency distribution of size classes of cephalothorax length (CL) from ovigerous females of *P. bouvieri* collected in three lakes, Corrientes, Argentina.

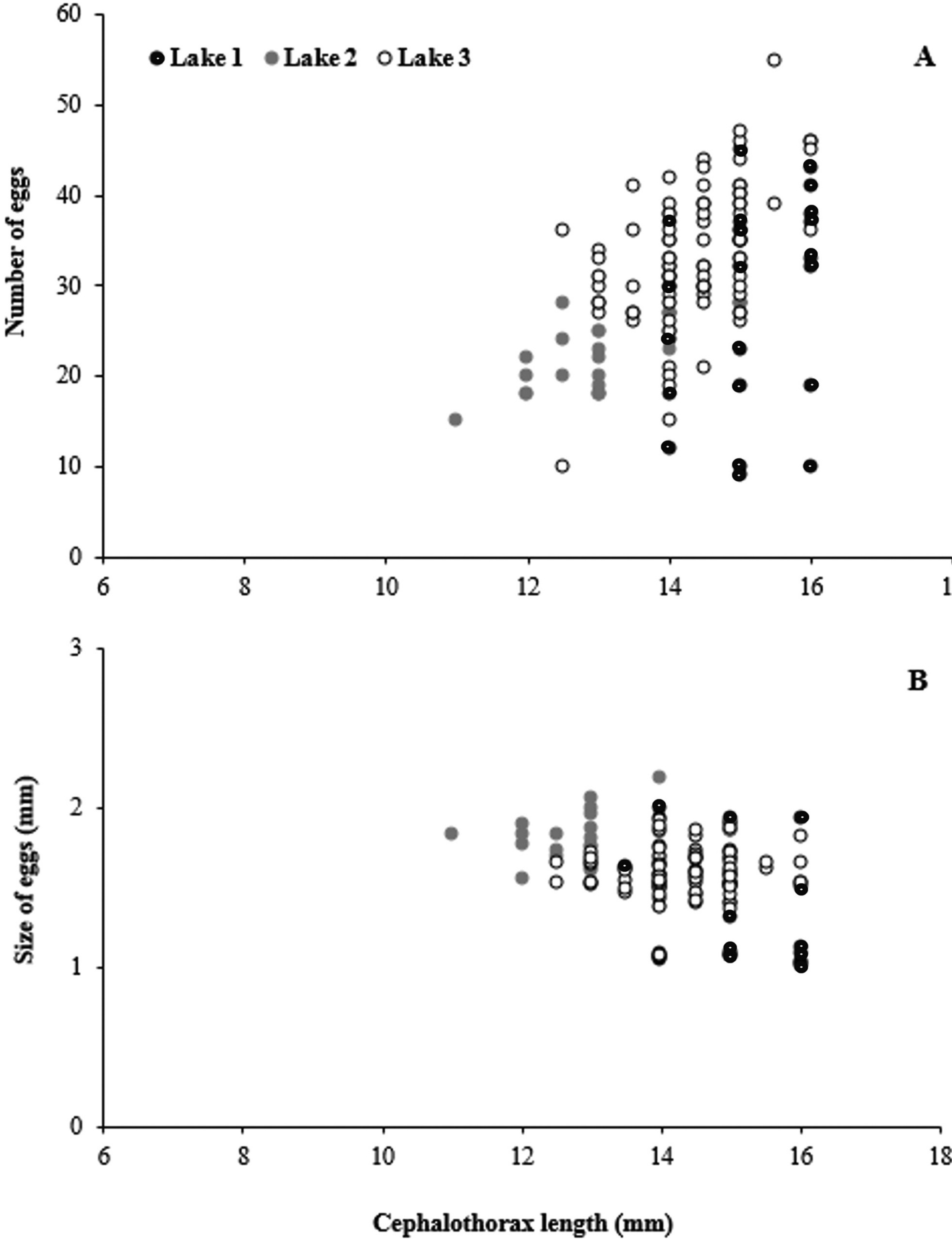

Figure 3. Plots of egg number (A) and egg size (B) against cephalothorax length (mm) of the females in the three lakes.

According to Zimmermann (1998), prawns show a physiological response to physical and chemical factors that are most important in their habitat, such as temperature, pH, dissolved oxygen, salinity and water level or seasonal rain. These factors promote or interfere with the temporal pattern of the reproductive season along with the distribution and frequency of the organisms over the entire year or in some months (Sipaúba-Tavares 1998). Moreover, other factors such as the presence of aquatic plants affect the seasonality of reproduction or the frequency and abundance of individuals due to the quality and quantity of refuge and food for prawns. The difference in these parameters is so low that two or more factors could act in a synergetic manner, e.g. the low number of eggs or fecundity caused by the hypo-osmotic environment in combination with the dissolved oxygen deficiency. These were stress factors for *P. bouvieri* in the lakes with a dense cover of aquatic plants, which also occurs in other aquatic invertebrates (Poi de Neiff & Carignan 1997), and determine the presence and abundance of the prawns. The ability of crustaceans to adapt to environmental salinity and its fluctuations is an important adaptive process (Charmantier & Anger 1999), which can be observed in the low number and large size of eggs, the absence of free larvae and the abbreviated larval development in the egg. Other factors that can occur but do not correspond with the aim of this work are an expanded molt cycle and a great increase in the size after each molt, caused by the intake of water to balance the difference in the osmotic potential between the low salt content of the environment and that of the cells of the prawns.

At all three sites, *P. bouvieri* did not breed throughout the year but began reproductive activity with gonadal maturation during the winter, and breeding occurred during the last months of spring. The temperature increase with longer days and a greater number of sunshine hours promoted a greater abundance of algae and zooplankton in these environments when the recently hatched juveniles of *P. bouvieri* need to feed. Similarly, Mossolin and Bueno (2002) found that *M. olfersii* has greater reproductive activity during warm months. The seasonal pattern of reproduction in several species of Palaemonidae has been linked to food availability in terms of its amount and quality (Odinetz-Collart & Magalhães 1994).

The marine ancestor evolutionary history and the adaptation to hypo-salinity environments occurred in all stages of the prawns. Moreover, *P. bouvieri* females produced a relatively small quantity of eggs that were very large to provide their larval stages developing within the egg with the protection of the chorion, as occurs in other decapods with abbreviated development (Negro et al. 2014). The mean number of eggs in our study was within the range observed in other Palaemonidae species, such as *M. shokitai* (Fujino & Baba 1973) (fewer than 60 eggs; Scaico 1992), *M. potiuna* (Müller 1880) (19–65 eggs; Nazari et al. 2003) and *M. borellii* (86–107 eggs; Collins 2000). These results in addition to the abbreviated development and the females carrying eggs until the hatching of juveniles indicate the adaptation of this species in response to oligohaline waters. In contrast, high fecundity was reported by Tamburus et al. (2012) and Meireles et al. (2013) in species that depend on brackish or seawater to complete their development, such as *M. carcinus*, *M. acanthurus* and *M. rosenbergii*, for which females can produce between 2299 and 100,000 eggs in each spawning. The fecundity of *M. amazonicum* varies widely and is much higher in seawater (2237 eggs) than in fresh water (lower than 60 eggs) (Da Silva et al. 2004; Meireles et al. 2013).

In contrast to the linear correlation between the size of ovigerous females and fecundity found in *Palaemonetes argentinus* (Azevedo et al. 2004), the fecundity of *P. bouvieri* does not depend on the size of females in the lakes studied. As demonstrated, the poor fit of the regression between CL and egg number was similar to that found for *M. amazonicum*, a palaemonid species with abbreviated larval development in hypo-osmotic environments (Odinetz-Collart & Enriconi 1993; Meireles et al. 2013). In relation to fecundity and size, *P. bouvieri* has larger eggs than *M. acanthurus* (Albertoni et al. 2002) and *M. amazonicum* (Hayd & Anger 2013), for which egg size varies from 0.5 to 0.6 mm and from 0.5 to 0.83 mm in diameter, respectively.

Pseudopalaemon bouvieri appears to have a reproductive strategy that has been observed in other Palaemonidae species inhabiting nutrient-poor inland waters, i.e. a freshwaterization process with few and large eggs and direct development (Magalhães & Walker 1988).

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