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Biology of *Boeckella poopoensis* Marsh, 1906 (Copepoda, Calanoida) in natural conditions in temporary saline lakes of the central Argentina

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Abstract: *Boeckella poopoensis* Marsh, 1906 is the dominant copepod in saline lakes from northern Patagonia to southern Peru. It is a tolerant species, which has been registered at salinities between 20 and 90 g.L^{-1}, and is important because it integrates the diet of flamingos and fishes of commercial and sport interest. The aims of this study were to analyze the characteristics of populations of *B. poopoensis* in the central region of Argentina and to establish their relationships with environmental parameters. Monthly samples during 2007 were taken in four temporary lakes of La Pampa province. Environmental parameters and density, size, biomass, number and size of eggs were determined. The salinity ranged between 13.38 and 32.90 g.L^{-1}. In three lakes that had previously continuously contained water, *B. poopoensis* was registered throughout the whole study. In the fourth lake, which was filled in January, it was present only when salinity exceeded 15 g.L^{-1}. The population of the lake that was filled differed from that of the other lakes in terms of the density and biomass of adults and copepodites. The number of ovigerous females represented a higher percentage of the population during the colonization of the lake that had been dried and these produced the highest number of eggs. In the three lakes in which *B. poopoensis* was always recorded, its characteristics were more influenced by the availability of food than by temperature or salinity. It was found that the strategies of the species vary throughout the hydroperiod; at the beginning, thrives when the salinity rises and impedes the presence of less tolerant species. At this point, the production of relatively small eggs is high, allowing rapid colonization. When the lakes become relatively stable, *B. poopoensis* allocates more energy to reach larger sizes and although egg production is not so high, they are larger, allowing it to maintain stable populations.
Keywords: *Boeckella poopoensis, halophilic copepods, saline lakes, temporary lakes.*

VIGNATTI, A.M., CABRERA, G.C., ECHANIZ, S.A. **Biología de *Boeckella poopoensis* Marsh, 1906 (Copepoda, Calanoida) en condiciones naturales en lagos salinos temporarios del centro de Argentina.** Biota Neotropica. 16(2): e20150063. http://dx.doi.org/10.1590/1676-0611-BN-2015-0063

Resumen: *Boeckella poopoensis* Marsh, 1906 es el copépodo dominante en lagos salinos desde el norte de Patagonia hasta el sur del Perú. Es una especie halotolerante registrada con salinidades entre 20 y 90 g.L^{-1} y es importante dado que integra la dieta de flamencos y de peces de interés comercial o deportivo. El objetivo del estudio fue analizar características de poblaciones de *B. poopoensis* en la región central de Argentina y establecer sus relaciones con los parámetros ambientales. Durante 2007 se tomaron muestras mensuales en cuatro lagos temporarios de la provincia de La Pampa. Se determinaron parámetros ambientales y la densidad, espectro de tallas, biomasa, número y tamaño de los huevos. La salinidad varió entre 13,38 and 32,90 g.L^{-1}. En tres lagos que habían contenido agua en forma continua, *B. poopoensis* se registró durante todo el estudio. En el cuarto, que se llenó en enero, sólo estuvo presente cuando la salinidad superó 15 g.L^{-1}. La densidad y biomasa de los adultos y copepoditos de la población del lago que se llenó difirieron de las de los otros. El número de hembras ovígeras representó un mayor porcentaje del total de la población durante la colonización del lago que había estado seco y fueron las que produjeron el mayor número de huevos. En los tres lagos en los que *B. poopoensis* se registró siempre, sus características fueron influidas más por la disponibilidad de alimento que por la temperatura o salinidad. Este estudio mostró que las estrategias de la especie varían a lo largo del hidroperíodo; al principio, prospera cuando la salinidad aumenta e impide la presencia de especies menos tolerantes. En este momento, la producción de abundantes huevos relativamente pequeños permite una rápida colonización. Cuando los lagos alcanzan una relativa estabilidad, *B. poopoensis* destina más energía a alcanzar tamaños mayores y, aunque la producción de huevos no es tan elevada son más grandes, permitiéndole mantener poblaciones estables.
Palavras-chave: *Boeckella poopoensis, copépodos halófilos, lagos salinos, lagos temporarios.*

Introduction

In South America, shallow temporary lakes are abundant and are located mainly in tropical and subtropical latitudes of the Andes (Hurlbert et al. 1986, Williams et al. 1995, De los Ríos & Crespo 2004), in the center and northwest of the Pampa Plains (Quirós 1997) and in the Patagonian plateau (Soto et al. 1994, Campos et al. 1996).

The zooplankton structure of these lakes is regulated mainly by salinity (De los Ríos & Crespo 2004, De los Ríos 2005, Vignatti 2011) and therefore, they have low species richness (De los Ríos-Escalante 2010, Vignatti 2011). Lakes frequently contain calanoid centropagid copepods, which generally reach high densities (Soto & Zúñiga 1991, Modenutti et al. 1998a, b). Among these, *Boeckella poopoensis* Marsh, 1906, is one of the predominant halophilic species, which has been registered in lakes with salinities between 20 and 90 $g.L^{-1}$ (Hurlbert et al. 1984, 1986, Bayly 1993, Williams et al. 1995; Zúñiga et al. 1999; Acosta et al. 2003, De los Ríos & Crespo 2004, De los Ríos 2005, Locascio de Mitrovich et al. 2005). However, its tolerance range might be higher, since has also been found in a water body in the central region of Argentina, with a salinity close to 116 $g.L^{-1}$ (Echaniz 2010).

Boeckella poopoensis has a very wide geographical distribution, from the north of the Patagonian plateau, in Argentina and Chile, to the south of Peru (Menu-Marque et al. 2000). Since it is part of the diet of the flamingo *Phoenicopterus chilensis* Molina, 1782 (Locascio de Mitrovich et al. 2005, Battauz et al. 2013), De los Ríos-Escalante (2010) proposed that the migration of these birds might have contributed to the wide distribution of this copepod in the South American saline ecosystems.

Boeckella poopoensis has been found in both clear and turbid (organic and inorganic) environments, with a water transparency between 0.08 and 1.53 m and a chlorophyll-*a* concentration between 0.07 and 218.62 $mg.m^{-3}$ (Echaniz 2010, Echaniz & Vignatti 2010, Vignatti 2011).

Given that copepods provide a significant proportion of the total zooplankton biomass (Margalef 1983) and since *B. poopoensis* is a species that reaches a large size, its contribution to the biomass of zooplankton in South American shallow lakes is relevant (Locascio de Mitrovich et al. 2005, Echaniz et al. 2013). It is an ecologically important species, because besides being part of the diet of at least one species of flamingo (Locascio de Mitrovich et al. 2005), it is one of the food items of fishes with commercial and sport interest in the central region of Argentina, such as the silverside *Odontesthes bonariensis* (Cuvier & Valenciennes 1835) (Sagretti & Bistoni 2001, Escalante 2002, Grosman 2002).

Although some information is known concerning some aspects of the biology of *B. poopoensis* in natural conditions, including its important morphometric plasticity (De los Ríos-Escalante et al. 2011), information on *B. poopoensis* in general is scarce. Therefore, the objectives of this study were to analyze the population characteristics (density, biomass and size range), particularly of ovigerous females, including their size range, and the number and size of eggs, in four hypo-mesosaline (Hammer 1986) shallow lakes of the province of La Pampa (Argentina), and to establish relationships with the principal environmental parameters.

Material and Methods

Study area

Between January and December 2007, monthly samples were taken in four shallow lakes located in different regions of the province of La Pampa, Argentina (Figure 1): Chadilauquen (Cha) (64°19′W, 35°24′S), San José (SJ) (63°55′W, 36°21′S), Utracán (Ut) (64°36'W, 37°17'S) and El Carancho (EC) (65°03′W, 37° 27′S). In all cases, these are temporary ecosystems that are principally fed by rainfall and to a lesser extent by groundwater contributions. The lake basins are arheic and water loss occurs mainly by evaporation or infiltration (Vignatti 2011).

Although three lakes (Cha, SJ and Ut) had contained water for a relatively long time, EC was dry until January, when it was filled with torrential summer rains and could only be sampled from February onwards.

The lakes were surrounded by fields dedicated to cereal and oil cultivation and to extensive livestock cultivation. Among the avifauna, flamingos (*P. chilensis*) were present in all four lakes. Only Ut and EC were partially covered by the rhizomatous herbaceous macrophyta *Ruppia cirrhosa* (Petagna, Grande), which is characteristic of saline lakes (Vignatti 2011).

Field and laboratory work

Samples were taken at three sites, along the major axis of each lake. The pH (Corning® PS-15 peachimeter), transparency (22 cm diameter Secchi disk), dissolved oxygen concentration and water temperature (Lutron® DO 5510 oxymeter) were determined *in situ* and water samples for the physicochemical determinations were taken and kept in the dark and refrigerated until analysis. At each site, qualitative zooplankton samples were taken by vertical and horizontal tows with a net 22 cm in diameter and 0.04 mm mesh aperture and quantitative samples were taken with a Schindler-Patalas plankton trap of 10 L with a 0.04 mm mesh aperture. Samples were anesthetized with CO_2 and kept refrigerated to avoid loss of eggs and deformation of the specimens (José de Paggi & Paggi 1995). After making the measurements, all samples were fixed with 5% formalin.

The dissolved solid concentration (salinity) was determined by the gravimetric method with the drying at 104°C of 50 mL of previously filtered water. The concentration of chlorophyll-*a* was determined by extraction with 90% (v/v) aqueous acetone

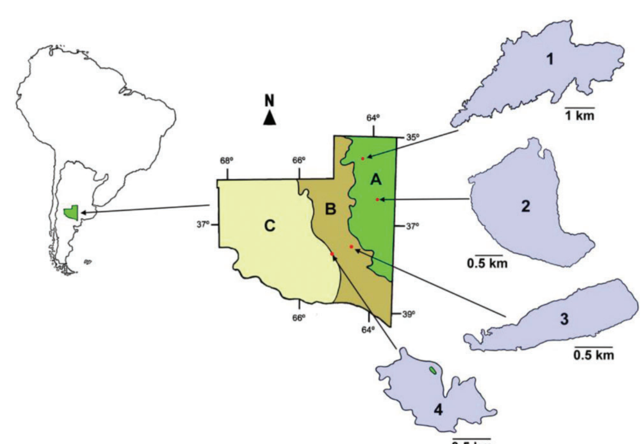

Figure 1. Location and maps of the four lakes studied. 1: Chadilauquen (Cha); 2: San José (SJ); 3: Utracán (Ut) and 4: El Carancho (EC). Phytogeographic regions of La Pampa province: Pampa Plains (A); Thorny Forest (B) and Monte (C).

Figura 1. Ubicación geográfica y croquis de los cuatro lagos estudiados. 1: Chadilauquen (Cha); 2: San José (SJ); 3: Utracán (Ut) y 4: El Carancho (EC). Regiones fitogeográficas de la provincia de La Pampa: Llanura Pampeana (A): Espinal (B) y del Monte (C).

and subsequent reading in a spectrophotometer (APHA 1992, Arar 1997), total Kjeldahl nitrogen (TKN) was analyzed by the Kjeldahl method and total phosphorus (TP) using the ascorbic acid method, previous digestion with potassium persulfate. The content of suspended solids was determined with Microclar FFG047WPH fiberglass filters, which were dried at 103–105°C to constant weight and later calcined at 550°C (EPA 1993).

The taxonomic determination of the species was performed following Menu-Marque & Locascio de Mitrovich (1998) and Bayly (1992a, b). The counts of adults and copepodites were made in 5 mL Bogorov chambers under a stereomicroscope (20X) and those of nauplii, in a Sedgewick-Rafter chamber. Aliquots were taken with a 5 mL Russell subsampler and 1 mL micropipettes, respectively. The number of aliquots was determined using the Cassie formula (Dowing & Rigler 1984). The species density was expressed as: i) nauplii, by integrating the sum of the different stages; ii) the sum of adults (including ovigerous females) and the different copepodites stages and, iii) the ovigerous females as a separate group.

Measurements of specimens and eggs were performed using a light microscope equipped with a 10X Leitz ocular micrometer. To determine the number of eggs, the ovigerous sacs were dissected and the eggs were directly counted under the microscope. Biomass was estimated by applying dry weight/body length regression equations (McCauley 1984, Dumont et al. 1975). The total biomass was calculated as the product of individual mean biomass and total density.

A parametric ANOVA test (F), Tukey pairwise comparations, nonparametric Kruskal-Wallis test (H) and Mann-Whitney pairwise comparations were applied to determine significant differences between the environmental and biological parameters. In order to examine relationships between environmental factors and the features of *B. poopoensis*, nonparametric correlation coefficients of Spearman (r_s) (Sokal & Rohlf 1995, Zar 1996, Pereyra et al. 2004) and Principal Components Analysis (PCA) (Pérez López 2004) were performed, which considered only adults and copepodites. We used Past (Hammer et al. 2001) and InfoStat (Di Rienzo et al. 2010) software.

Because no significant differences in physical, chemical and biological parameters of the three sites at each sampling were found, we used mean values.

Results

Limnological characterization of lakes

The salinity of lakes differed (H = 37.48; p = 0.00) and was higher in Cha, SJ and Ut, but was relatively stable, ranging from 7.0 to 8.6 $g.L^{-1}$ (Table 1). In EC, the mean salinity was lower, but its range of variation was close to 15 $g.L^{-1}$, and rose from a minimum of 5.7 $g.L^{-1}$ immediately after filling (February), to a maximum of 20.7 $g.L^{-1}$ (December). The water temperature of the four lakes did not differ and ranged from a minimum of 4.9°C in EC and SJ (June and July respectively), to a maximum of 25.1°C in Cha (January). The mean concentration of dissolved oxygen differed (H = 8.15; p = 0.04) and was slightly higher in Ut and EC (Table 1).

Water transparency varied (H = 16.89; p = 0.00), exceeding 1 m in Ut and EC and being less in Cha and SJ, and correlations between transparency and inorganic (r_s = -0.68; p = 0.00) or organic (r_s = -0.69; p = 0.00) suspended solid concentrations were found. The inorganic suspended solids were different (H = 20.11; p = 0.00), between four and nine times more abundant in the two lakes with a lower transparency (Table 1). The organic suspended solid concentrations were also different (H = 12.3; p = 0.01), and were much higher in SJ.

The nutrient concentration of the water was high and differed (TP: H = 7.87; p = 0.05 and TKN: H = 25.07; p = 0.00), and was slightly reduced in EC. The phytoplankton chlorophyll-*a* concentration differed (H = 13.59; p = 0.00), and was between three to four times higher in SJ than in the other lakes (Table 1).

Boeckella poopoensis: density, biomass and size range

In Cha, SJ and Ut, *B. poopoensis* was registered throughout the sampling period, whereas it was only was found in the last three months of study in EC.

The mean density and biomass of adults and copepodites were different (H = 8.59; p = 0.04 and H = 7.74; p = 0.05) and lower values of both parameters were recorded in the EC population. A higher mean annual density and biomass was reached by the population of SJ (Table 2). The maximum mean length of adults and copepodites was registered in SJ and the minimum in Cha (Table 2); however, the difference was not significant.

A correlation was observed between *B. poopoensis* adult and copepodite density and biomass and salinity (r_s = 0.64; p = 0.00 and r_s = 0.64; p = 0.00), chlorophyll-*a* concentration (r_s = 0.37; p = 0.01 and r_s = 0.35; p = 0.02), organic suspended solids (r_s = 0.53; p = 0.00 and r_s = 0.54; p = 0.00) and water transparency (r_s = -0.54; p = 0.00 and r_s = -0.54; p = 0.00). The adult and copepodite size did not correlate with any of the environmental parameters.

Table 1. Mean values and standard deviation of the environmental parameters determined in the studied lakes.
Tabla 1. Valores medios y desvíos estándar de los parámetros ambientales determinados en los lagos estudiados.

	Cha	SJ	Ut	EC
Salinity ($g.L^{-1}$)	26.16 (± 2.13)	30.82 (± 2.67)	32.90 (± 2.69)	13.38 (± 4.02)
Temperature (°C)	16.58 (± 7.05)	16.45 (± 7.10)	16.08 (± 7.17)	15.04 (± 7.32)
DO ($mg.L^{-1}$)	8.46 (± 1.1)	8.87 (± 1.8)	10.07 (± 2)	10.12 (± 1.3)
Transparency (m)	0.76 (± 0.26)	0.78 (± 0.41)	1.15 (± 0.29)	1.28 (± 0.36)
Inorg. susp. solids ($mg.L^{-1}$)	18.27 (± 24.23)	16.50 (± 15.28)	4.30 (± 3.77)	2.77 (± 2.48)
Org. susp. solids ($mg.L^{-1}$)	6.72 (± 4.95)	14.15 (± 10.05)	5.00 (± 1.89)	4.35 (± 3.45)
TP ($mg.L^{-1}$)	7.02 (± 3.55)	5.59 (± 1.29)	7.21 (± 3.75)	4.6 (± 1.9)
TKN ($mg.L^{-1}$)	15.94 (± 6.06)	18.58 (± 4.27)	13.03 (± 4.87)	7.79 (± 2.46)
Chl-*a* ($mg.m^{-3}$)	1.73 (± 1.25)	4.88 (± 4.52)	1.22 (± 0.92)	1.89 (± 3.7)

Table 2. Mean, minimum and maximum density, biomass and specimen size, and egg number of *Boeckella poopoensis* in the four studied lakes.
Tabla 2. Promedio, mínimos y máximos de densidad, biomasa y tamaños de los ejemplares y número de huevos de *Boeckella poopoensis* en los cuatro lagos estudiados.

		Cha	SJ	Ut	EC
Adults + copepodites density (ind.L^{-1})	**Mean**	**75.39**	**167.5**	**113.13**	**4.24**
	Min.–max.	2.1–182.3	30.3–460.3	16.0–251.7	0–26.3
Adults + copepodites biomass (µg.L^{-1})	**Mean**	**797.44**	**2240.56**	**1181.65**	**64.22**
	Min.–max.	15.9–1654.5	274.2–6757.7	208.0–2311.8	0–356.3
Adults + copepodites size (µm)	**Mean**	**1031.45**	**1174.2**	**1148.83**	**1052.9**
	Min.–max.	698.7–1297.2	931.8–1348.5	919.4–1376.7	635.3–1362.9
Ovigerous females size (µm)	**Mean**	1560.95	1802.12	1578.89	1910.00
	Min.–max.	1390.0–1677.5	1593.1–2010.0	1454.2–1642.5	1700.0–2130.0
Nauplii density (ind.L^{-1})	**Mean**	**49.87**	**162.86**	**216.58**	**81.94**
	Min.–max.	9.23–87.50	49.17–286.33	26.33–1013.33	35.00–153.00
Nauplii biomass (µg.L^{-1})	**Mean**	**42.13**	**136.46**	**194.68**	**63.45**
	Min.–max.	7.39–78.75	33.08–287.47	21.80–864.58	26.76–110.33
Nauplii size (µm)	**Mean**	**355.58**	**350.09**	**366.88**	**344.30**
	Min.–max.	202.0–514.8	200.2–529.1	214.2–557.4	171.6–500.5

The mean density and biomass of nauplii also differed (H = 17.99; p = 0.00 and H = 16.77; p = 0.00, respectively) and were both higher in Ut (Table 2). The nauplii size differed (H = 11.38; p = 0.01) and was slightly larger in Ut. Correlations were only observed between the density and biomass of nauplii and salinity (H = 0.65; p = 0.00 and H = 0.62; p = 0.00, respectively).

The density, biomass and size of adults and copepodites recorded during the annual cycle fluctuated differently between the lakes, although for three water bodies (Cha, SJ and Ut), lower densities and biomasses were registered during the autumn (April and May).

In Cha, two density and biomass peaks were recorded; the first occurred in summer (February) when the adults and copepodites reached a density of 182.3 ind.L^{-1} and a biomass of 1,637.3 µg.L^{-1}, although specimens of higher mean length (1,297 µm) were registered in November. The second peak occurred during the winter (June) and although the abundance was much lower (145 ind.L^{-1}), the biomass was as high as during the summer peak (1,654.4 µg.L^{-1}), due to the presence of larger animals that reached a mean of 1,218 µm (Figure 2A).

In SJ, the adults and copepodites reached a maximum density and biomass (460.3 ind.L^{-1} and 6,757.7 µg.L^{-1}) in early spring (September). Despite the high biomass, the maximum sizes were observed in November (1,348.5 µm). A second peak was observed in January (395.3 ind.L^{-1}), but the biomass was significantly lower than that in September, due to the presence of specimens with a smaller mean length (1,137.5 µm) (Figure 2B).

In Ut, density and biomass showed fluctuated greatly throughout the annual cycle. The highest density of 251.7 ind.L^{-1} was recorded in summer (February), but the highest biomass, 2,312 µg.L^{-1}, was observed in early spring (September), due to the presence of large specimens (Figure 2C).

Finally, in EC, where *B. poopoensis* was recorded from October, adults and copepodites reached a maximum density in November (26.3 ind.L^{-1}), but because the monthly mean size increased and reached a maximum in December (1,363 µm), the greatest biomass was calculated in this month (356.3 µg.L^{-1}) (Figure 2D).

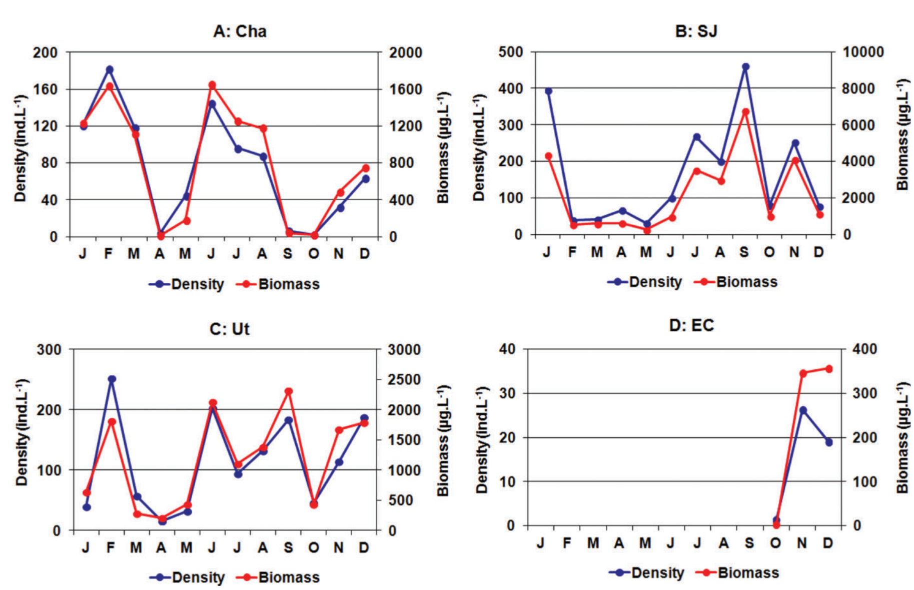

Figure 2. Monthly variation of the density and biomass of adults and copepodites of *B. poopoensis* in the four studied lakes.
Figura 2. Variación mensual de la densidad y la biomasa de los adultos y copepoditos de *B. poopoensis* en los cuatro lagos estudiados.

The fluctuations in nauplii density and biomass during the annual cycle also did not show a pattern that was common to all lakes, except for a slight decrease in spring in Cha, SJ and Ut (Figure 3). However, a strong summer peak of density and biomass was registered in Ut, which reached 1,013.33 ind.L^{-1}. The biomass of nauplii followed an identical pattern to that of the density and was not influenced by size variations. Because the body length was slightly higher during winter, a correlation was found between size and the water temperature (r_s = -0.58; p = 0.00).

Ovigerous females: proportions, size and fecundity

The mean number of ovigerous females in each population differed (H = 10.41; p = 0.02) and the density in SJ (8.56 ind. L^{-1}) was twice that in Cha (4.06 ind.L^{-1}) and 16 times higher than that in EC (0.5 ind.L^{-1}). However, the percentage of the total density in Ut, Cha and SJ was 1.90, 3.15 and 5.63%, respectively, and in EC was 14.01%, with a strong peak in October, when the ovigerous females represented 37.5% of the total density.

The ovigerous females recorded in Cha and Ut were similar in size but differed from those of EC and SJ (H = 20.2; p = 0.00) because the latter were larger, at about 1,800-1,900 µm (Table 2). Significant differences were also found in the mean number of eggs per female (H = 24.02; p = 0.00) and in this case, the females of EC produced a much higher number of eggs, more than 20 per female (Table 2). No significant correlations were found between environmental variables and the characteristics of ovigerous females.

Although the size of ovigerous females was not significantly correlated with the water temperature, the size spectrum of females with eggs throughout the annual cycle (Figure 4), showed some seasonality, because during the warmer months, specimens tended to be smaller, and larger individuals were recorded in winter especially in SJ and Ut (Figure 4). The size of individuals in Ut remained relatively more constant than in the other lakes, as it varied by only 188 µm, whereas in EC and SJ, the difference exceeded 410 µm (Table 2).

The mean egg number per female was higher in larger specimens (r_s = 0.71; p = 0.00) and differed between lakes (H = 26.97; p = 0.00). The minimum number was observed in Ut, where the specimens showed a mean of only 2.45 (± 1.53) eggs, compared with 21.67 (± 14.51) eggs in EC (Figure 5).

The highest mean number of eggs per female, 37.3, was recorded in October in EC, and this number decreased to 8.8 in December, at the end of the study (Figure 6). In SJ, a higher mean number of eggs per female was recorded during the winter months, with a maximum of nine in May, whereas the number in the other lakes never exceeded five (Figure 6).

The size of the eggs produced by females throughout the annual cycle in the four lakes ranged between 100 and 230 µm. Significant differences were found (F = 1,378; p = 0.00), since in EC smaller eggs were recorded in EC (mean: 112.92 ± 17.34 µm), whereas in the other lakes, the egg diameter exceeded 160 µm. Excluding EC, the mean egg size was not significantly different, since in the three lakes (Cha, SJ and Ut) smaller eggs were approximately 100–120 µm and larger eggs were 220–230 µm in size (Figure 7).

In order to compare the biology of *B. poopoensis* in a situation of relative stability against colonization at the beginning of a hydroperiod, a Principal Component Analysis (PCA) analysis was conducted for the three lakes in which the species was recorded throughout the year. The density, size and biomass of adults and copepodites were more influenced by component 1, which was particularly determined by chlorophyll-a and organic suspended solid concentrations (Figure 8), which implies the availability of food. In contrast, environmental conditions determined by salinity and especially by temperature (component 2) had a very limited influence on the density, biomass and the total size of adults and copepodites (Figure 8).

Discussion

Throughout the study, the halophilic (De los Ríos & Crespo 2004) and eurihaline character of *B. poopoensis* (Echaniz & Vignatti 2011, Echaniz et al. 2013) was evidenced, since it was recorded in a relatively wide range of salinities. The

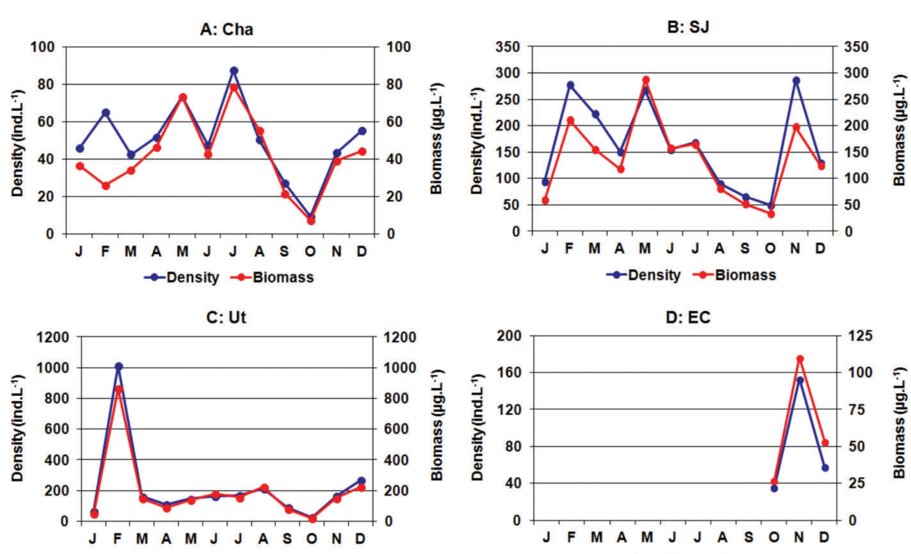

Figure 3. Monthly variation of the density and biomass of nauplii of *B. poopoensis* in the four studied lakes.
Figura 3. Variación mensual de la densidad y la biomasa de los nauplios de *B. poopoensis* en los cuatro lagos estudiados.

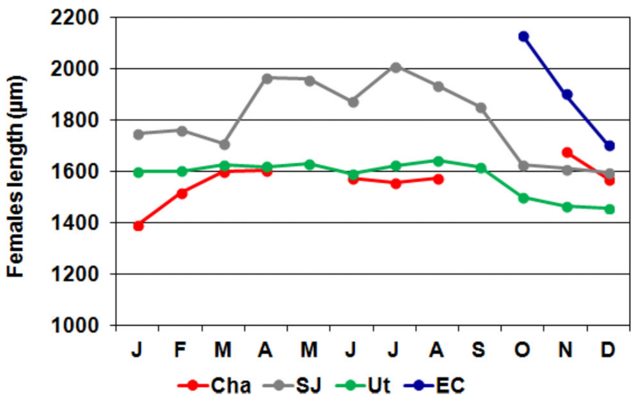

Figure 4. Monthly variation of the mean size of ovigerous females of *B. poopoensis* in the four studied lakes.
Figura 4. Variación mensual del tamaño medio de las hembras ovígeras de *B. poopoensis* en los cuatro lagos estudiados.

species was always present in three lakes (Cha, SJ and Ut), but was recorded only from October in EC. This might be because the salinity was relatively low until October, since the species appeared when the salinity exceeded 15 $g.L^{-1}$. It should be noted that the four studied shallow lakes are temporary and show wide variations in water level (Vignatti 2011, Echaniz et al. 2013), but during the study, salinity showed a relatively different behavior in the different lakes. Because Cha, SJ and Ut had contained water since 2001, the concentration of their dissolved solids was higher, so that they can be categorized as mesosaline lakes (Hammer 1986), and therefore, were relatively stable. The high salinity of the lakes probably prevented the establishment of other species that might compete and displace *B. poopoensis*, thus allowing it to thrive and maintain a stable population. However, in EC, the reverse situation was found; EC had remained completely dry since 2004 and in February

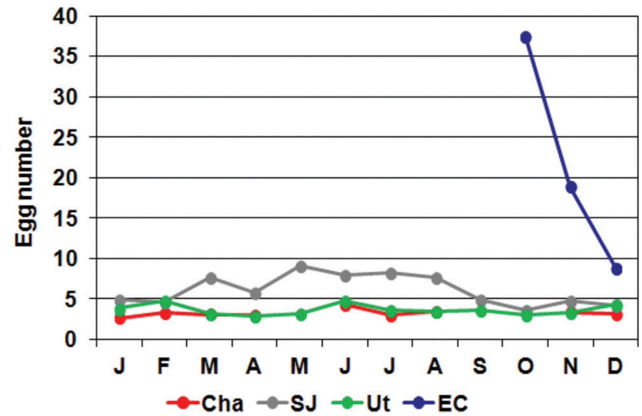

Figure 6. Variation in the number of eggs of *B. poopoensis* throughout the annual cycle in the four studied lakes.
Figura 6. Variación en el número de huevos de *B. poopoensis* a través del ciclo anual en los cuatro lagos estudiados.

2007, it reached a depth of 1.6 m, due to torrential summer rain typical for the region (Cano 1980). Although the lake then became hyposaline (Hammer 1986), the redissolution of salts from sediments caused a three-fold increase in the saline concentration, without large fluctuations in the depth, and thus, the salinity reached the mesosaline level in the last month of the study (Vignatti et al. 2012). Salinity is an abiotic factor that can determine the zooplankton assemblage of South American aquatic ecosystems (Hurlbert et al. 1986, Williams et al. 1995, De los Ríos & Crespo 2004, Vignatti 2011, Battauz et al. 2013), and therefore, one reason why *B. poopoensis* was recorded as present from October onwards, might be due to the recorded presence of *Boeckella gracilis* until the previous month, which is a much less salinity-tolerant species but a potential competitor of *B. poopoensis*. In these environments,

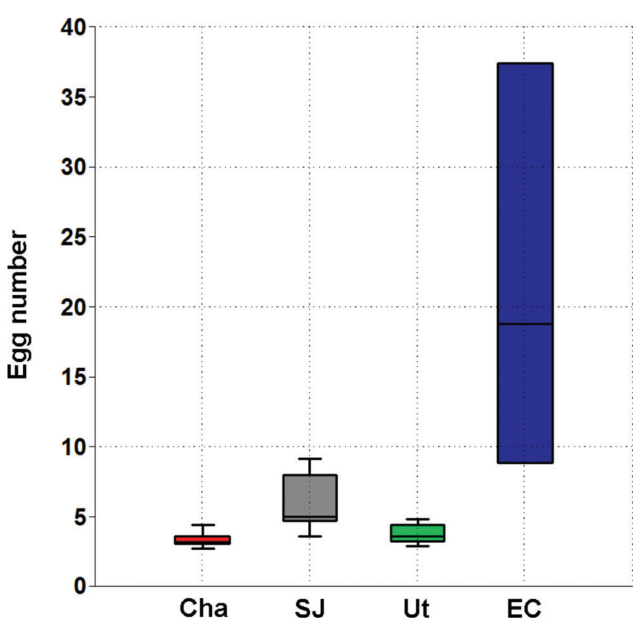

Figure 5. Mean egg number per ovigerous female of *B. poopoensis* in the four lakes studied.
Figura 5. Número medio de huevos por hembra ovígera de *B. poopoensis* en los cuatro lagos estudiados

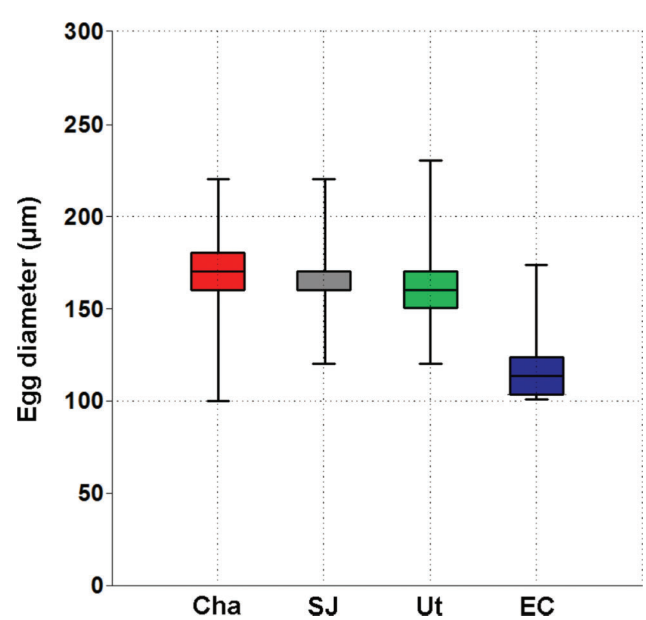

Figure 7. Comparison of the size of the eggs of *B. poopoensis* throughout the annual cycle in the four studied lakes.
Figura 7. Comparación del tamaño de los huevos de *B. poopoensis* a través del ciclo anual en los cuatro lagos estudiados.

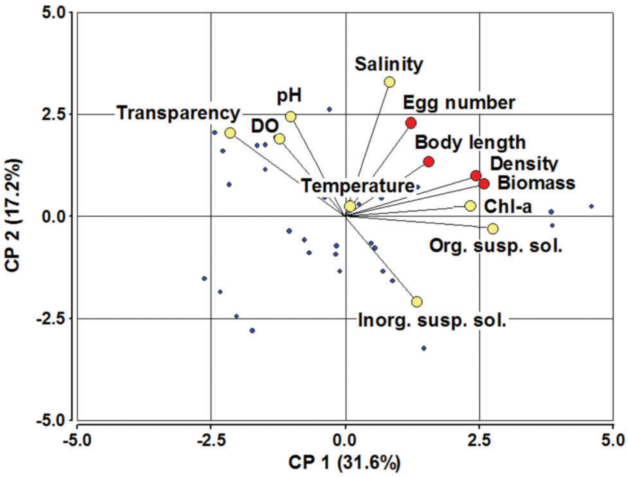

Figure 8. Biplot of the Principal Component Analysis, including only the three more stable lakes: Cha, SJ and Ut.Body length, density and biomass corresponds to that of adults and copepodites.

Figura 8. Resultados del Análisis de Componentes Principales que incluye sólo los tres lagos más estables: Cha, SJ and Ut. El largo del cuerpo, la densidad y la biomasa corresponden a los adultos y copepoditos.

which generate high physiological stress to organisms, species such as *B. poopoensis* might possess an adaptive advantage, since their ability to tolerate increased salinity allows them to find refuge against competition or predation by some fish (Herbst 2001, Santangelo et al. 2008), but not by flamingos (Battauz et al. 2013). Therefore, *B. poopoensis* could be considered a typical species for when temporary lakes have become relatively stable and not for the period of succession that occurs when a new hydroperiod begins. This conclusion is supported by the fact that *B. poopoensis* was observed at a low densities in EC, whereas its density in the remaining lakes was several times higher.

The analysis of the biology of *B. poopoensis* in a situation of relative hydrological stability found in the three lakes that had contained water for a long time, allowed the conclusion to be reached that the availability of food had a greater influence on the density, size and biomass of adults and copepodites than environmental conditions such as salinity or temperature. In the case of the size, this situation might be because the copepods have indirect development with many instars, which implies that they must allocate a significant amount of energy to reach maturity and reproduce. Since its growth in natural populations is mainly limited by the availability of food (Peterson & Hutchings 1995, Webber & Roff 1995, Havens et al. 2014), if the size is small, especially the ovigerous females, this might indicate a shortage of food resources and, on the contrary, a large size would be an indicator of better nutrition during development (Vignatti 2011). This could explain why larger ovigerous females were registered in SJ, the lake with greater availability of food, a situation similar to that reported by Lin et al. (2013).

Although the influence of water temperature on the size of epicontinental calanoid copepods continues to be discussed, it is thought to be very low, with the effect of predation being more important (Havens et al. 2014). In the three more stable lakes, water temperature had a very limited influence on the density, biomass and total size of adults and copepodites. The low influence of salinity might be because, given the halophyllic nature of *B. poopoensis*, the parameter fluctuations that occurred in the three stable lakes were not sufficient to produce significant changes in the biological parameters measured. Despite the small influence of temperature on *B. poopoensis*, the greatest egg production occurred in the three more stable lakes during the winter, which was reflected by a slight increase in the number of nauplii. This agrees with the results of numerous laboratory studies with marine calanoid that report that fertility increases with decreasing water temperature (Landry 1978, Johnson 1980, Jiménez-Melero et al. 2005) or with data for *Sinodiaptomus* (*Rhinediaptomus*) *indicus*, a freshwater calanoid, in which ovisac and egg production decreases significantly with increasing temperature (Dilshad Begum et al. 2012).

It is known that a higher concentration of food in the environment produces more rapid postembryonic development, a larger size at maturity (Ban 1994) and increased egg production per female (Durbin et al. 1983, Kimmerer & McKinnon 1987, Peterson et al. 1991, Tourangeau & Runge 1991, McKinnon & Ayukai 1996), so that a greater number of eggs might indicate that females devote more energy to their production (Vignatti 2011). Considering the three most stable lakes, larger ovigerous females and more eggs per female were recorded in SJ, which might relate to the relatively greater availability of food in this lake. However, the number of eggs per female in EC was four times higher in the period following when the species was first recorded, allowing the efficiency of *B. poopoensis* to colonize an environment where was not previously present, to be monitored.

Considering that *B. poopoensis* was recorded in the province of La Pampa in lakes with salinities over 40 gL^{-1}, the concentration of dissolved solids observed in the lakes in this study was not a limiting factor for the growth and reproduction of *B. poopoensis.* Furthermore, this study allowed the different strategies that are used by a species that faces two different environmental situations to be analyzed in the hypo-mesosaline range (Hammer 1986). This situation is very frequent in saline temporary lakes, depending on the hydroperiod in which an ecosystem is found. If a lake is created by filling a basin with lowly mineralized water, a succession involving the replacement of species with a low tolerance to salinity by more tolerant species occurs, which include *B. poopoensis* (Vignatti 2011). When a species newly appears, the production of relatively small size eggs from females is very high, which allows the ecosystem to be rapidly colonized. However, once lakes have become relatively stable, which typically involves high salinities due to the redissolution of solutes from sediments, and in the presence of adequate amounts of food, *B. poopoensis* expends more energy in attaining a larger size, and although egg production per female is not so high, they are relatively large and allow a stable population to be maintained.

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