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### Dynamics of ostracod populations from shallow lakes of Patagonia: life history insights

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## Dynamics of ostracod populations from shallow lakes of Patagonia: life history insights

Corina Coviaga<sup>a</sup>, Gabriela Cusminsky<sup>a</sup>, Nora Baccalá<sup>b</sup> and A. Patricia Pérez<sup>c\*</sup>

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Wetlands are one of the most valuable natural resources, providing a number of ecosystem services and socio-economic values. Small ponds sustain a rich aquatic biodiversity and because of their short hydrological regimen and small size are excellent environments for population studies of microcrustaceans such as ostracods. This study describes the population dynamics of the Ostracoda fauna in three temporary shallow lakes during one hydroperiod in Argentine Patagonia. Three cosmopolitan species were determined: *Cypris pubera*, *Tonnacypris lutaria* and *Eucypris virens*. Among them, *T. lutaria* is here reported for the first time from the Neotropical region. Multivariate ordination techniques were used to examine the relationships among environmental variables and ostracod density on each sampling site. High values of conductivity, absorption at 320 nm (as a measure of dissolved organic matter), dissolved oxygen concentration, temperature and chlorophyll *a* concentration correlated positively with ostracod density. All the populations studied reproduced parthenogenetically, and the life cycles of *E. virens* and *C. pubera* were followed in detail by weekly sampling of their populations. The former displayed continuous reproduction, whereas the latter showed a multi-voltine strategy. The life history of *C. pubera* was affected by the seasonality of the habitat. The development rate correlated positively with water temperature; conductivity and temperature had a positive effect on adult size in *C. pubera*, while conductivity had a negative effect on adult size in *E. virens*. In this study, we present the first data set on the development and life history of ostracods in Patagonian freshwater environments. However, several questions remain and encourage us to further investigate the relative importance of ostracods in food webs, as well as the importance of inter-specific interactions between ostracods and other taxa.

**Keywords:** microcrustacean; wetlands; development; life cycle

### Introduction

Ostracods are one of the most diverse crustacean groups that can be found in all types of water bodies (Horne et al. 2002). Species distribution and abundance have been correlated with different environmental factors, such as altitude and habitat type (Malmqvist et al. 1997), oxygen content (Dole-Olivier et al. 2000; Liberto et al. 2012), temperature (Horne 1983) and ionic composition (Baltanás et al. 1990). Given that

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ostracods have clear environmental preferences, each environment has specific species associations (Laprida and Ballent 2008). Particularly, in Argentine Patagonia, ostracod assemblages have been related to three different environments: ephemeral ponds, springs and streams, and permanent ponds and lakes. These types of aquatic environments are distinguished mainly by their ionic concentration and composition (Schwalb et al. 2002; Cusminsky et al. 2011; Ramón Mercau et al. 2012).

The environmental features, mainly temperature and conductivity, influence not only the species associations, but also the population dynamics of aquatic environments. Water temperature is a key factor for survival, growth and reproduction of ostracods, although the direction and intensity of the effects depend on the species (Mesquita-Joanes et al. 2012 and references cited therein). In general, at higher temperatures, the development rate and calcification increase and the lifespan and size decrease (Martens 1985; Mezquita et al. 1999; Majoran et al. 2000; Aguilar-Alberola and Mesquita-Joanes 2014). In addition, salinity modulates the hatching phenology, survival and larval moulting. As conductivity decreases, the appearance of adult stages is delayed and the mean size of adults decreases (Rossi et al. 2013). Moreover, each moult is critical because it is immediately followed by rapid calcification of the shell and if conductivity is too low, it has a negative effect on ostracod survival and growth (Mezquita et al. 1999).

In this study, three natural ponds close to each other were chosen to study the dynamics of ostracod populations under different natural environments, i.e. temporary versus permanent, vegetated versus non-vegetated and sandy versus muddy bottom. Weekly sampling allowed the life cycle of the main species to be characterized, the role of biotic and abiotic factors in the life cycle and structure of the populations to be evaluated, and relationships between ostracod density and environmental variables during one hydroperiod to be established.

## Materials and methods

### *Study area*

Sampling was carried out in three close temporary fishless ponds: Refugio de Jesús, herein after referred as Refugio, Ñireco and Teleférico. All sites are situated near to San Carlos de Bariloche city, in Nahuel Huapi National Park (Argentine Patagonia). The area belongs to the Sub-Antarctic biogeographical zone. The climate is dry and cold, the austral winter corresponds to the rainy season and the summer is the dry season. The sampled lakes are located along a west–east transect of 15 km resulting in a gradient of precipitation from 1200 mm to 800 mm (Mermoz et al. 2009). Refugio pond [41° 07' 11" S, 71° 13' 10" W, 829 m above sea level (a.s.l.)] comprises an area of 1.5 ha and has two different zones: a large shallow area of 1.35 ha with 0.40 m depth and a small deeper zone, with an area of 0.15 ha and a maximum depth of 0.7 m (Perren 2008). Samples were extracted from the deepest zone, where both the submerged vegetation and the zooplankton community were abundant. The pond is rainwater fed, the muddy bottom is partially covered by grass and the surface is moderately covered by floating vegetation. Ñireco pond (41° 10' 54" S, 71° 19' 01" W, 906 m a.s.l.) is located next to the carriageway of National route 40; the water input comes from a swamp located upstream. This pond covers an area of 0.3 ha, reaching a maximum depth of 0.8 m. Ñireco has a fine sandy substrate without vegetation.

Teleférico (41° 07' 40" S, 71° 22' 05" W, 816 m a.s.l.) is a 0.7 ha semi permanent pond located within a swampy area with muddy bottom, and its maximum depth is about 1.5 m. Vegetation, both surrounding and submerged, is abundant.

### **Field work**

Sampling began shortly after the winter rainy period and finished when the ostracod populations disappeared or the ponds dried up. Weekly sampling was carried out around midday from August 2009 to January 2010. Zooplankton was collected with a hand net (D frame, 200 µm mesh aperture) along the water–sediment interface, in a 1 to 6 m long transect depending on the environment (Schaffer et al. 1994). In the field, samples were fixed with ethanol 50%, and once in the laboratory ostracods were transferred into 70% ethanol solution for permanent storage. The abundance of the ostracod fauna was expressed in volume units rather than in surface units to achieve a better representation of the density fluctuations due to the fact that ostracod species were nektobenthic. Maximum depth, temperature (T, °C), pH (Hanna Instruments 8424), conductivity (C, µS/cm, ORION 115) and dissolved oxygen concentration (DO, mg/L, Hanna Instruments 9142) were measured *in situ*. Water samples were collected in 5 L containers and returned immediately to the laboratory to analyse the concentration of chlorophyll *a*, main ions, seston and nutrients.

Precipitation and air temperature data were obtained from nearby weather stations (National Weather Service, San Carlos de Bariloche Airport for Refugio, and Photobiology Laboratory, INIBIOMA UNComahue for Teleférico and Ñireco).

### **Laboratory work**

Spectrophotometric chlorophyll *a* concentration was quantified in ethanolic extracts following Nusch (1980) (UV-Vis HP 8453). Water absorbance coefficients were estimated from spectrophotometric measurements of filtered (pre-muffled filters, GF/F) water samples, in the spectral range of 250–750 nm at intervals of 1 nm. Absorption at 320 nm ( $a_{320}$ ) and attenuation coefficient of visible light ( $K_{dPAR}$ ) were determined following Morris et al. (1995) and Kirk (2003), respectively. Seston concentration was quantified following Wetzel and Likens (2000). Cation concentrations (Ca, Mg, K and Na) were measured using atomic absorption spectrometry (Perkin Elmer Analyst 100). Total phosphorus (TP) concentration was analysed by spectrophotometry after following the molybdate–ascorbic acid extraction method (APHA 1989). Total nitrogen (TN) concentration was measured by oxidizing with persulphate and determining nitrate with second-derivative spectroscopy (Bachmann and Canfield 1996).

### **Ostracod identification**

Ostracods were determined to species level following Van Morkhoven (1963), Martens (1990), Cusminsky and Whatley (1996), Meisch (2000), Cusminsky et al. (2005) and Van der Meeren et al. (2009). The individuals were sorted, counted and measured under a stereomicroscope or a standard light microscope. Developmental instars were established according to carapace size and to chaetotaxic modifications. Instars A-5, A-6 and A-7 were grouped based on appendage development, i.e.

absence of thoracopods (Ferguson 1944). The mesh size (200  $\mu\text{m}$ ) allows individuals at instar A-8 to escape. Therefore, only data for older instars were used for population structure analysis.

### **Data analysis**

Total ostracod density, frequency of developmental instars along sampling time and variations of physical, chemical and biological parameters were determined for each site. Nine variables were selected to construct a correlation matrix. Ionic and nutrient concentrations were left out because they were measured monthly. The gradient length in environmental data was measured by a detrended correspondence analysis. This analysis revealed a gradient length of 0.4, showing that the data set has a mainly linear response and suggesting that a linear-based principal component analysis (PCA) is more appropriate (Hill and Gauch 1980; Ter Braak and Prentice 1988). Therefore a standardized PCA was applied to characterize the environment at each site and to compare it with ostracod abundance. For this analysis, the nine physico-chemical variables were used in a correlation matrix. Canocowin 4.5 and Système Portable pour L'Analyse des Données (S.P.A.D.) software were used to process the data.

The mean ontogenetic stage index (MOS-index) was calculated for the major species, with the aim of describing differences in the advance of ontogenetic development (Majoran et al. 2000). The index was calculated as follows:

$$\text{MOS} = 1 \cdot N_A + 2 \cdot N_{A-1} + 3 \cdot N_{A-2} + \dots / N_{\text{total}}$$

Where  $N$  represents the abundance of the ostracods in each instar and  $N_{\text{total}}$  is the total number of individuals. Therefore, higher index values indicate a younger population, while values close to 1 reflect adult dominance.

Life cycle duration was estimated from sequential abundance peaks of different instars (Ikeda and Imamura 1992).

## **Results**

### ***Environmental characteristics of the three ponds studied***

The main features of the three ponds are summarized in Table 1. The ponds showed major differences in maximum depth, dissolved oxygen concentration, water conductivity and water light absorption ( $a_{320}$  and  $K_{d\text{PAR}}$ ). Regarding depth, Teleférico remained constant around 0.7 m, Ñireco had an irregular water level, and Refugio began filling in early August (austral winter and rainy season) and dried completely in January. The concentration of dissolved oxygen was significantly higher in Teleférico ( $p < 0.001$ ), whereas conductivity was significantly higher in Refugio ( $p < 0.001$ ) and tended to increase along the hydroperiod. The light absorption at 320 nm, a measure of the concentration of dissolved organic matter, gradually attenuated from Refugio to Teleférico and Ñireco, corresponding with the highest to lowest dissolved organic matter concentration, respectively. Based on chlorophyll  $a$  concentration, Teleférico qualifies as meso-eutrophic, whereas Refugio and Ñireco qualify as oligotrophic ponds. However, chlorophyll  $a$  concentration was highly variable in all of them.

Table 1. Mean values and standard deviations of the environmental variables measured along the hydroperiod in the three shallow lakes.

Variables	Refugio	Nireco	Teleférico
Air temperature (°C)	7.6 ± 3.6 ( <i>n</i> = 126) (1.4–14.5)	7.6 ± 3.6 ( <i>n</i> = 100) (1.4–14.5)	7.8 ± 3.3 ( <i>n</i> = 107) (1.9–13.2)
Water temperature (°C)	13.2 ± 4.6 ( <i>n</i> = 18) (5.6–20.6)	10.4 ± 4.8 ( <i>n</i> = 12) (2.3–20.3)	12.3 ± 3.5 ( <i>n</i> = 15) (8.6–19.6)
Maximum depth (m)	0.8 ± 0.1 ( <i>n</i> = 19) (0–1)	0.6 ± 0.2 ( <i>n</i> = 13) (0–1)	0.7 ± 0.0 ( <i>n</i> = 15) (0.63–0.73)
Dissolved oxygen concentration (mg/L)	8.4 ± 1.9 ( <i>n</i> = 18) (4.7–12.3)	9.5 ± 0.8 ( <i>n</i> = 12) (8.4–10.8)	11.9 ± 2.0 ( <i>n</i> = 15) (8.6–15.4)
Conductivity (µS/cm)	377.9 ± 59.8 ( <i>n</i> = 18) (280–506)	78.7 ± 9.6 ( <i>n</i> = 12) (53.5–91.1)	200.4 ± 18.2 ( <i>n</i> = 15) (152.3–222)
Ca <sup>2+</sup> (mg/L)	32.3 ± 8.2 ( <i>n</i> = 5) (19.9–38.6)	7.0 ± 1.4 ( <i>n</i> = 4) (5.2–8.5)	19.6 ± 3.6 ( <i>n</i> = 4) (16.4–24.3)
Mg <sup>2+</sup> (mg/L)	6.4 ± 0.9 ( <i>n</i> = 5) (5.3–7.7)	2.17 ± 0.6 ( <i>n</i> = 4) (1.4–2.8)	5.7 ± 2.2 ( <i>n</i> = 4) (2.7–7.7)
K <sup>+</sup> (mg/L)	14.0 ± 6.5 ( <i>n</i> = 5) (4.0–20.5)	0.5 ± 0.2 ( <i>n</i> = 4) (0.3–0.6)	0.6 ± 0.2 ( <i>n</i> = 4) (0.4–1.6)
Na <sup>+</sup> (mg/L)	3.9 ± 1.0 ( <i>n</i> = 5) (2.4–4.9)	2.6 ± 0.7 ( <i>n</i> = 4) (1.7–3.5)	5.2 ± 1.2 ( <i>n</i> = 4) (3.5–5.9)
pH	7.8 ± 0.3 ( <i>n</i> = 18) (7.3–8.3)	7.8 ± 0.3 ( <i>n</i> = 11) (7.4–8.6)	7.6 ± 0.5 ( <i>n</i> = 14) (7.05–8.9)
Seston (mg/L)	4.6 ± 3.8 ( <i>n</i> = 18) (1.5–17.5)	4.6 ± 4.8 ( <i>n</i> = 12) (1.6–18.5)	9.8 ± 9.2 ( <i>n</i> = 15) (2.1–49.2)

(Continued)

Table 1. (Continued).

Variables	Refugio	Nireco	Teleférico
Chlorophyll <i>a</i> ( $\mu\text{g/L}$ )	$1.0 \pm 0.9$ ( $n = 18$ ) (0.1–3.8)	$0.3 \pm 0.4$ ( $n = 12$ ) (0–1.5)	$3.8 \pm 3.1$ ( $n = 15$ ) (0.7–12.7)
Total Phosphorus ( $\mu\text{g/L}$ )	$121.4 \pm 66.7$ ( $n = 5$ ) (82.9–240.3)	$38.0 \pm 12.8$ ( $n = 4$ ) (24.3–54.5)	$86.7 \pm 59.0$ ( $n = 4$ ) (34.3–155.8)
Total Nitrogen ( $\text{mg/L}$ )	$2.5 \pm 0.9$ ( $n = 5$ ) (1.6– 4)	$0.3 \pm 0.1$ ( $n = 4$ ) (0.3– 0.4)	$5.3 \pm 1.1$ ( $n = 4$ ) (4.2– 6.4)
$Kd_{\text{PAR}}$ (1/m)	$7.7 \pm 2.1$ ( $n = 16$ ) (4.7–11.6)	$1.2 \pm 1.1$ ( $n = 12$ ) (0.2–3.9)	$8.0 \pm 3.0$ ( $n = 15$ ) (4.5–14.7)
$a_{320}$ (1/m)	$37.7 \pm 16.5$ ( $n = 17$ ) (0.9–64.2)	$4.6 \pm 2.1$ ( $n = 12$ ) (1.6–9.6)	$17.7 \pm 5.3$ ( $n = 15$ ) (11.6–30.3)

Maximum and minimum values are between brackets.

Abbreviations:  $a_{320}$ , absorbance coefficient at 320 nm;  $Kd_{\text{PAR}}$ , attenuation coefficient of visible light.



The main environmental gradients between sites were identified by PCA (Figure 1). Refugio samples were on the positive side of axis 1, corresponding with higher values of conductivity and light attenuation. Additionally, these samples showed a temporal ordering with respect to the first component, with highest values at the end of the hydroperiod (see R15 to R19 in Figure 1), due to a clear concentration effect of dissolved solutes and organic matter. Teleférico was on the negative side of axes 1 and 2, associated with high values of dissolved oxygen, seston and chlorophyll *a* concentration, whereas Ñireco samples were distributed along the negative side of axis 1 and positive part of axis 2, characterized by low values of conductivity, temperature and light attenuation.

In addition to the environmental features, the three ponds displayed different zooplankton assemblages. The accompanying zooplankton in Refugio was diverse and dominated by large crustaceans, mainly calanoid copepods, cladocerans, one species of brine shrimp and one clam shrimp. In Teleférico, the fauna was dominated by copepods and cladocerans. In spring, we also observed tadpoles and several species of aquatic insects. In Ñireco, the zooplankton community was scarce and besides ostracods, only cyclopid copepods, one aquatic beetle and a few tadpoles were observed (a complete taxonomic list is available in the Supplementary Material).

### Ostracod assemblages

Three ostracod species belonging to the family Cyprididae were identified. The sub-family Cypridinae was represented by *Cypris pubera* Müller, 1776 (Figure 2A–D), and

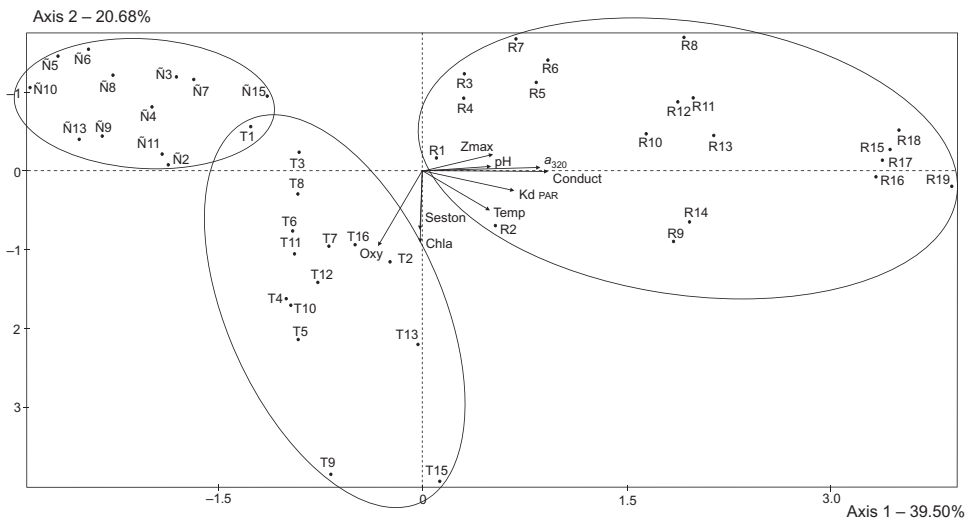


Figure 1. Samples scores and first factorial plane of principal components analysis for the three sampling sites. Abbreviations: Oxy, dissolved oxygen concentration; chl *a*, chlorophyll *a*; Seston, seston concentration; Temp, temperature; pH;  $a_{320}$ , absorbance coefficient at 320 nm;  $Kd_{PAR}$ , attenuation coefficient of visible light; Conduct, water conductivity;  $Z_{max}$ , maximum depth. Site identification: R, Refugio de Jesús; Ñ, Ñireco, and T, Teleférico. Numbers correspond with the sampling weeks.

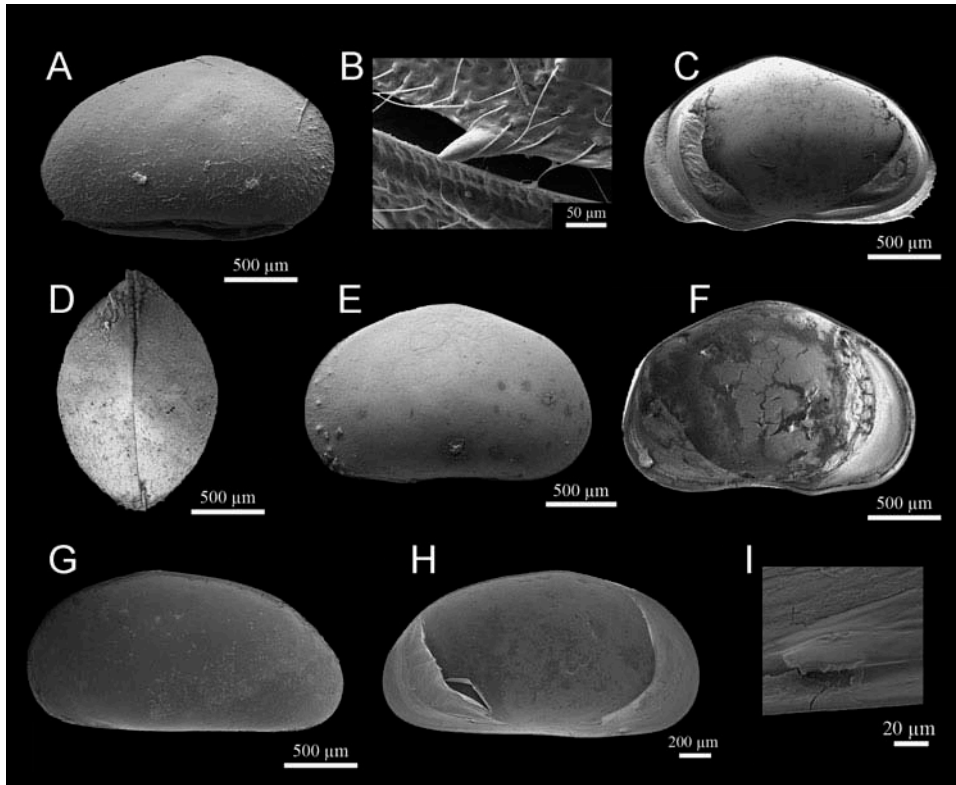


Figure 2. (A–D) *Cypris pubera*. (A) right valve in external view; (B) spine detail; (C) right valve in internal view; (D) carapace in dorsal view. (E, F) *Eucypris virens*. (E) left valve in external view; (F) left valve in internal view. (G–I) *Tonnacypris lutaria*. (G) left valve in external view; (H) left valve in internal view; (I) peg detail.

the subfamily Eucypridinae by *Eucypris virens* (Jurine, 1820; Figure 2E,F) and *Tonnacypris lutaria* (Koch, 1838. Figure 2G–I). All sites can be considered as mono-specific, because Refugio showed a clear dominance of *C. pubera* (95%) during the period sampled, coexisting with *E. virens* during the whole hydroperiod and with *T. lutaria* in the initial samples. *Eucypris virens* was the only species recorded in Teleférico and the dominant species in Ñireco (98%), coexisting with *T. lutaria* in winter. Only female individuals were recorded for all species in the three ponds. In Teleférico, around 70% of gravid *E. virens* were sampled throughout the hydroperiod. In Refugio, gravid females of *C. pubera* were found in mid-September and in the last samples, representing 66% of total females.

Total ostracod density in Refugio and Teleférico was significantly higher ( $p < 0.001$ ; Figure 3A) than in Ñireco. The abundance of *E. virens* in Teleférico increased during the hydroperiod, reaching a maximum in mid-spring, and then decreased towards summer. The *C. pubera* population from Refugio showed two peaks of abundance, in mid-spring and at the end of spring. The population reached its maximum density at the end of spring and then decreased. The population density of *E. virens* from Ñireco was low and variable, and then decreased markedly from November (Figure 3B).

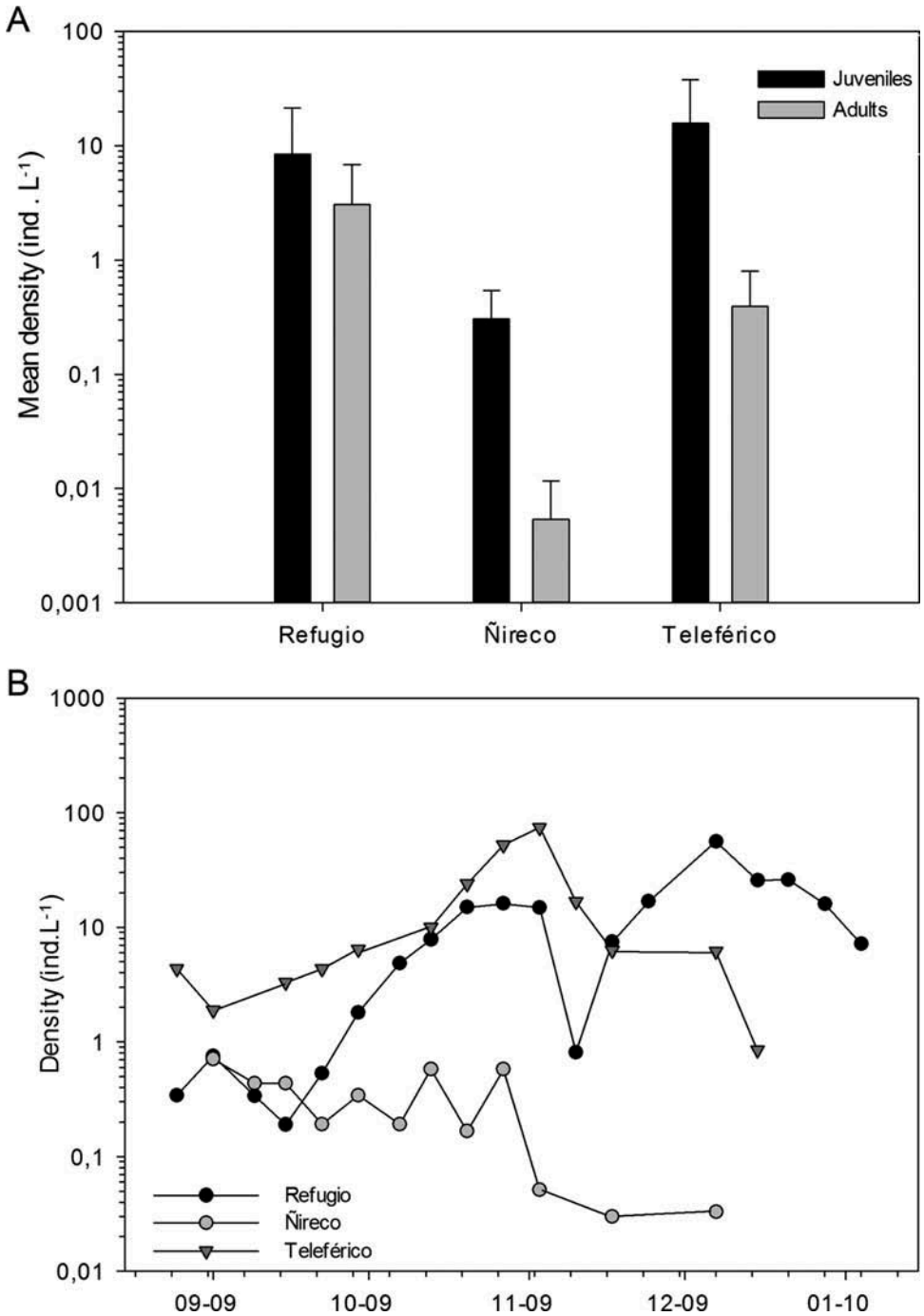


Figure 3. (A) Mean and standard deviation of ostracod abundance in each pond; (B) Ostracod temporal pattern density in the three sampling ponds. Note the low abundance in Ñireco.

**Valve size**

The mean carapace length for each developmental instar of *E. virens* and *C. pubera*, in each pond is shown in Table 2. Adult females of *E. virens* from the Teleférico population were larger than from the Ñireco population ( $p < 0.001$ ). The same pattern was detected for juvenile instars.

Seasonal size effects were detected for *C. pubera* and *E. virens*. The mean length of adult *C. pubera* varied significantly between seasons, being smaller in winter and larger in summer (Figure 4A; ANOVA for length:  $DF = 2$ ,  $F = 120.4$ ,  $p < 0.001$ ). Water conductivity and temperature were positively correlated with adult size (linear regression for conductivity and length:  $DF = 143$ ,  $F = 33.73$ ,  $p < 0.001$  and  $R^2 = 0.19$ , linear regression for temperature and length:  $DF = 143$ ,  $F = 21.89$ ,  $p < 0.001$  and  $R^2 = 0.13$ ). The opposite pattern was observed for *E. virens* in both ponds (Figure 4B and C), larger individuals were sampled in winter in comparison with spring (Mann–Whitney *U*-test for length of Teleférico adult females  $U$  statistic = 275.5,  $p = 0.052$ , *t*-test for length of Ñireco adult females  $DF = 71$ ,  $t = 6.27$ ,  $p < 0.001$ ). The Ñireco population showed a negative relationship between conductivity and adult size (linear regression for conductivity and length:  $DF = 68$ ,  $F = 11.37$ ,  $p = 0.001$  and  $R^2 = 0.13$ ).

**Life cycle of *Cypris pubera* and *Eucypris virens***

The information summarized in Figures 5 and 6 allows the life cycle of the dominant species *C. pubera* and *E. virens* to be described.

In Refugio, the first cohort of *C. pubera* hatched in early August, shortly after the beginning of the rainy season, from resistant eggs deposited in the sediment. Evidence for this hatching event is the presence of adults and oldest instars in the initial samples at the end of August. Shortly after, early juvenile instars were dominant at the

Table 2. Mean of carapace length (mm) for *Cypris pubera* and *Eucypris virens* in each pond.

Instars	<i>C. pubera</i> – Refugio	<i>E. virens</i> – Ñireco	<i>E. virens</i> – Teleférico
A-7	0.32 ± 0.04 ( $n = 8$ ) (0.22–0.35)		0.33 ± 0.03 ( $n = 14$ ) (0.27–0.35)
A-6	0.38 ± 0.01 ( $n = 18$ ) (0.34–0.40)	0.39 ± 0 ( $n = 2$ ) (0.39–0.39)	0.38 ± 0.02 ( $n = 23$ ) (0.36–0.41)
A-5	0.45 ± 0.03 ( $n = 84$ ) (0.40–0.50)	0.47 ± 0.04 ( $n = 7$ ) (0.41–0.50)	0.50 ± 0.04 ( $n = 47$ ) (0.43–0.57)
A-4	0.60 ± 0.04 ( $n = 87$ ) (0.52–0.72)	0.57 ± 0.03 ( $n = 11$ ) (0.52–0.61)	0.63 ± 0.02 ( $n = 50$ ) (0.59–0.69)
A-3	0.78 ± 0.04 ( $n = 63$ ) (0.73–0.89)	0.74 ± 0.03 ( $n = 32$ ) (0.68–0.82)	0.84 ± 0.04 ( $n = 57$ ) (0.75–0.93)
A-2	1.09 ± 0.05 ( $n = 127$ ) (0.93–1.23)	1.00 ± 0.06 ( $n = 38$ ) (0.93–1.18)	1.16 ± 0.05 ( $n = 44$ ) (1.05–1.25)
A-1	1.57 ± 0.08 ( $n = 167$ ) (1.34–1.80)	1.34 ± 0.08 ( $n = 61$ ) (1.23–1.50)	1.58 ± 0.06 ( $n = 50$ ) (1.43–1.69)
A	2.19 ± 0.08 ( $n = 144$ ) (2.02–2.36)	1.78 ± 0.1 ( $n = 74$ ) (1.55–2.05)	2.09 ± 0.07 ( $n = 67$ ) (1.91–2.23)

Maximum and minimum values are between brackets.

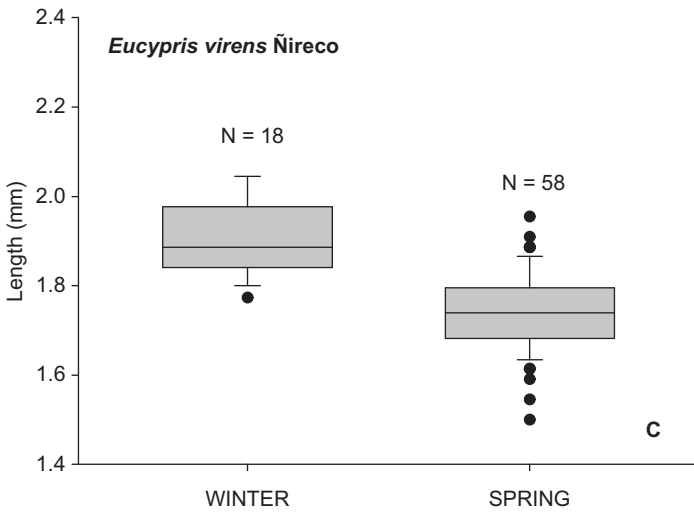
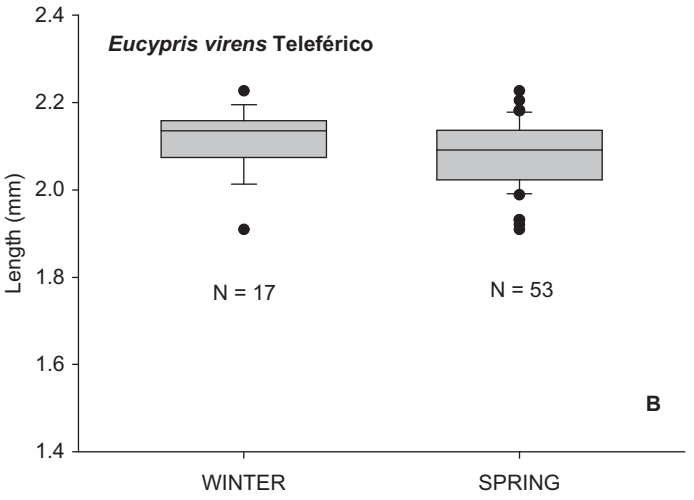
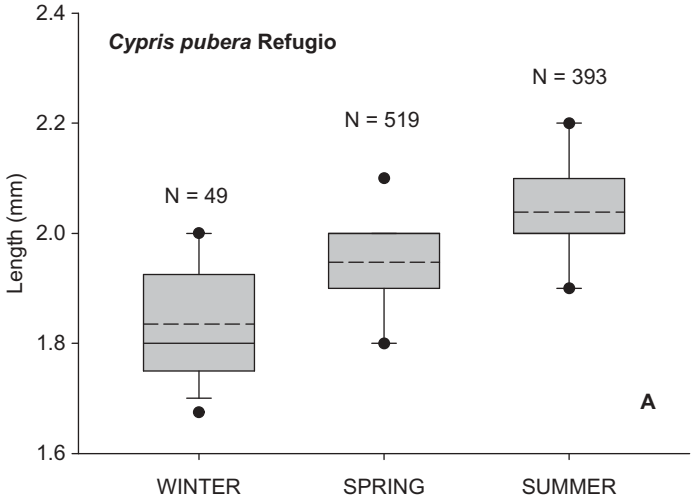
beginning of the austral spring (22 September), growing until recruitment of the second adult generation on 10 November. One week later, a third cohort of juveniles started the last generation cycle, attaining adulthood by the end of December. At the end of the hydroperiod, only adults of *C. pubera* were found. The development time of *C. pubera* depended on the season: the spring cycle (from mid-September to mid-November) lasted around 8 weeks, and the summer cycle (from late November to early January) lasted about 5 weeks (Figure 5A). The faster development was related to summer temperatures that were significantly higher than in the previous 2 months ( $t$ -test: DF = 13;  $t = -3.599$ ,  $p = 0.003$ ). Indeed, the MOS index of *C. pubera* showed a cyclic pattern with two peaks in September and December. Higher numbers indicate the predominance of younger instars and suggest that the population had two hatching events during the sampling period (Figure 5B).

*Eucypris virens* was the dominant species in Ñireco and the only species in Teleférico. In general, both populations showed co-dominance of all instars and low adult abundance. In particular, Figure 6 shows a predominance of two younger instars of *E. virens* in Teleférico, suggesting two hatching events in September and December. However, it is not possible to differentiate clearly between the cohorts because hatching was continuous. Regarding the Ñireco population, the MOS index showed that the younger instars dominated during the first weeks of the sampling period, but we were not able to distinguish between the different cohorts (Figure 7).

## Discussion

### *Ostracod assemblages*

During this study, we found three cosmopolitan species of ostracods: *E. virens*, *C. pubera* and *T. lutaria*. *Eucypris virens* has been reported in lacustrine surface sediments in Buenos Aires province (Fontana and Ballent 2005), as well in recent Holocene sediments from a shallow lake in Patagonia (Cusminsky and Whatley 1996). In our study we reported for the first time extant individuals of this species in the Patagonian region. *Cypris pubera* might have been recently introduced into Patagonia, as no fossils of this species have yet been found in the region. Nevertheless, it has already been mentioned for Lake Los Juncos in the extant fauna (Gilbert 2012; Ramón Mercau et al. 2012). Our study is the first record of *T. lutaria* in the Neotropical region (Martens and Savatnalinton 2011). There is no fossil record for this species in Patagonia therefore we might hypothesize a recent colonization. Unfortunately, lack of sampling in potential intermediate habitats impairs our ability to hypothesize about the colonization tracks of these species in Patagonia. We are currently carrying out several ostracod surveys across a west–east transect in north Patagonia. Our preliminary results show a broader distribution of these species, mainly inhabiting sites with low conductivity, pH and  $\text{Na}^+$  and  $\text{Mg}^{2+}$  concentrations (Coviaga et al. 2013). Therefore, we suggest that the three species could be more widespread than previously thought. However, more complete data are needed concerning their distribution and dispersion mode in the Neotropical region. Also, genetic data are crucial for differentiating histories and geographical pathways of colonizations from anthropogenic introductions (Koenders et al. 2012).



The biodiversity was low and is probably a common feature in temporary ponds in the southern region of South America. This is in agreement with other authors, who reported only one species for three out of four north Patagonian samples (Ramón Mercau et al. 2012) and four species over eight sampling stations in Martín García island, Buenos Aires (Liberto et al. 2012).

*Tonnacypris lutaria* was sampled only in Refugio and Ñireco at the beginning of the rainy season, when both ponds were characterized by low values of conductivity, temperature and chlorophyll *a* concentration, and high dissolved oxygen concentration. These observations agree with previous reports that considered *T. lutaria* as an early form that prefers freshwater and low temperature (Mezquita et al. 1999; Meisch 2000; Altınsaçlı 2001; Yılmaz and Külköylüoğlu 2006; Van der Meeren et al. 2009). The dominance of *E. virens* during the hydroperiod in diluted waters like Ñireco confirmed that this cosmopolitan species is very tolerant to low ionic concentration and fluctuating and unpredictable environments (Pieri et al. 2006; Martins et al. 2009).

The results show that abundance of ostracods in general was positively related to conductivity, light attenuation ( $a_{320}$  as a measure of dissolved organic matter), dissolved oxygen concentration, temperature and chlorophyll *a* concentration. These results agree with previous studies suggesting that these environmental factors favour the presence of ostracods (Palacios-Fest et al. 1994; Park et al. 2003; Ramón Mercau et al. 2012). Furthermore, the substrate of Refugio and Teleférico is muddy and covered by abundant submerged vegetation that provides protection and increases the surface for ostracod oviposition (Aguilar-Alberola and Mesquita-Joanes 2011). Moreover, the presence of submerged vegetation is coupled with well oxygenated waters, which improves the development of ostracod populations (Rossetti et al. 2004; Liberto et al. 2012), as shown in Teleférico, which displayed the maximum abundance of *E. virens* correlated with dissolved oxygen concentration. In Teleférico and Refugio, the abundance of small cladocerans and rotifers could have been an additional source of food. The authors' personal observations confirmed that at least *C. pubera* was predatory on *Daphnia* sp., and Gilbert (2012) reported the predatory behaviour of *C. pubera* on the rotifer *Keratella tropica*. Carnivory has also been reported for *E. virens* (Meisch 2000) and other ostracods from temporary pools, such as *Heterocypris incongruens* (Ganning 1971). However, this hypothesis needs further confirmation with predation experiments.

### Valve size

The environmental features of host waters affect the size and shape of valves (e.g. Alcorlo et al. 1999). However, size variability in natural populations remains insufficiently known. Our results showed that *E. virens* from Ñireco were smaller than those from Teleférico, and were associated with low values of conductivity, ionic and total nitrogenous concentrations. Nevertheless, the evidence is not conclusive. Martins et al. (2009) verified that *E. virens* adults from the site with the highest salinity and

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Figure 4. Box-plot of length for the adults from the different seasons. (A) *Cypris pubera*; (B) *Eucypris virens* from Ñireco; (C) *Eucypris virens* from Teleférico.

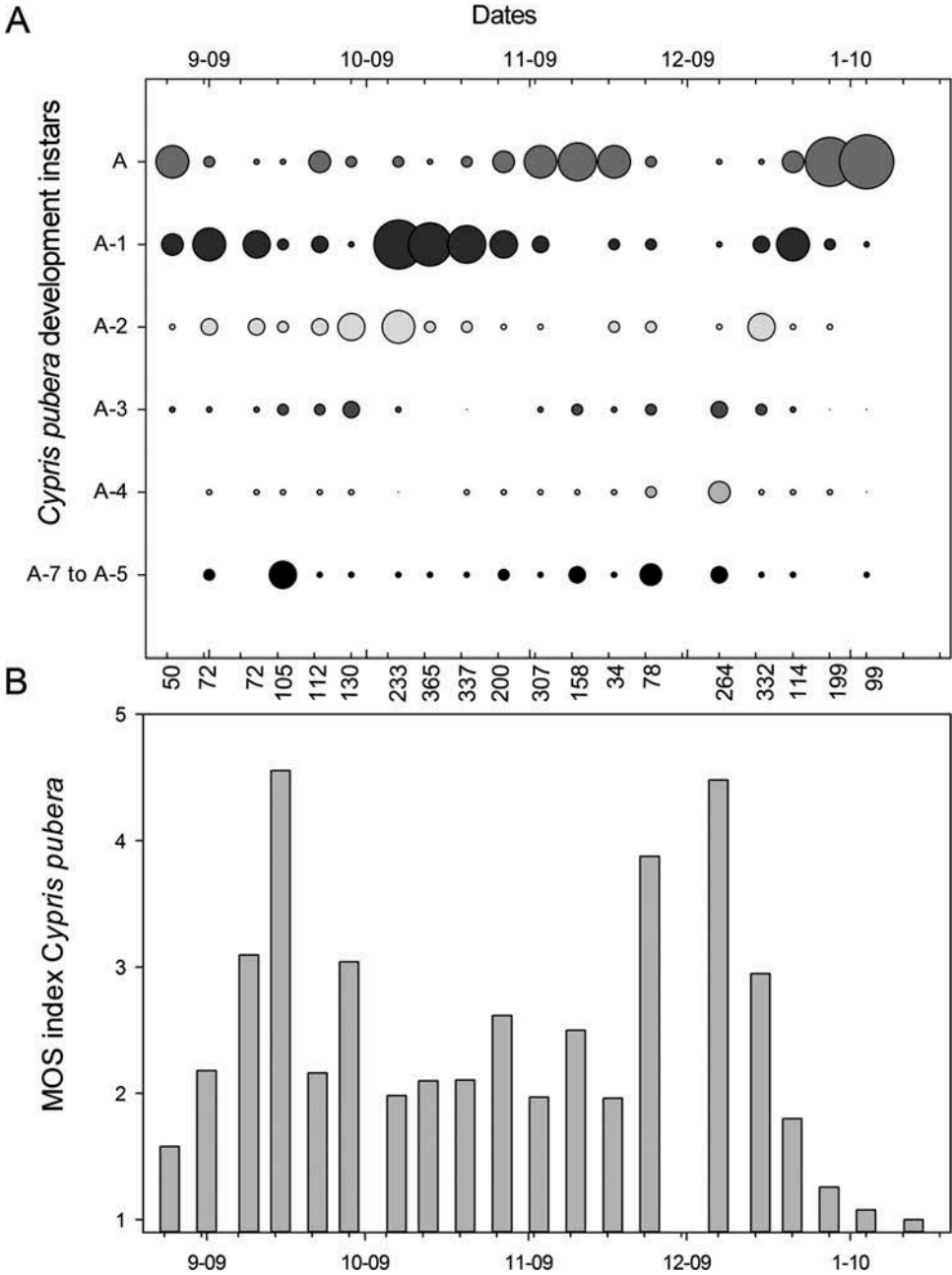


Figure 5. *Cypris pubera* at site Refugio. (A) Temporal changes in relative density of development instars A-7 through to Adults, bubble size represents the relative abundance of each life stage. The total number of individuals counted per sample is indicated at the bottom of the graph. (B) Mean ontogenetic stage index (MOS).

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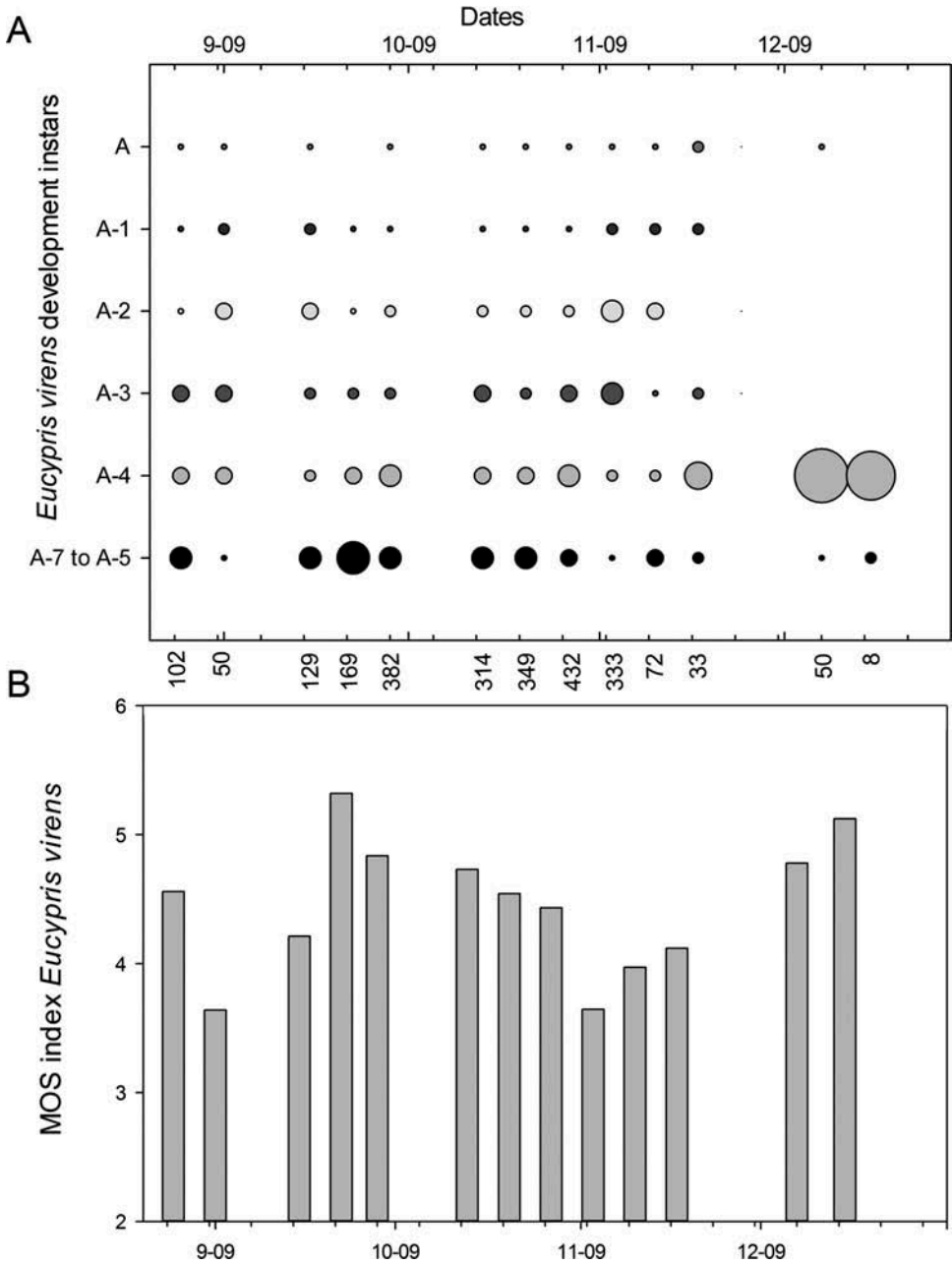


Figure 6. *Eucypris virens* from Teleférico. (A) Temporal changes in relative density of development instars A-7 to Adults, bubble size represents the relative abundance of each life stage. The total number of individuals counted per sample is indicated at the bottom of the graph. (B) Mean ontogenetic stage index (MOS).

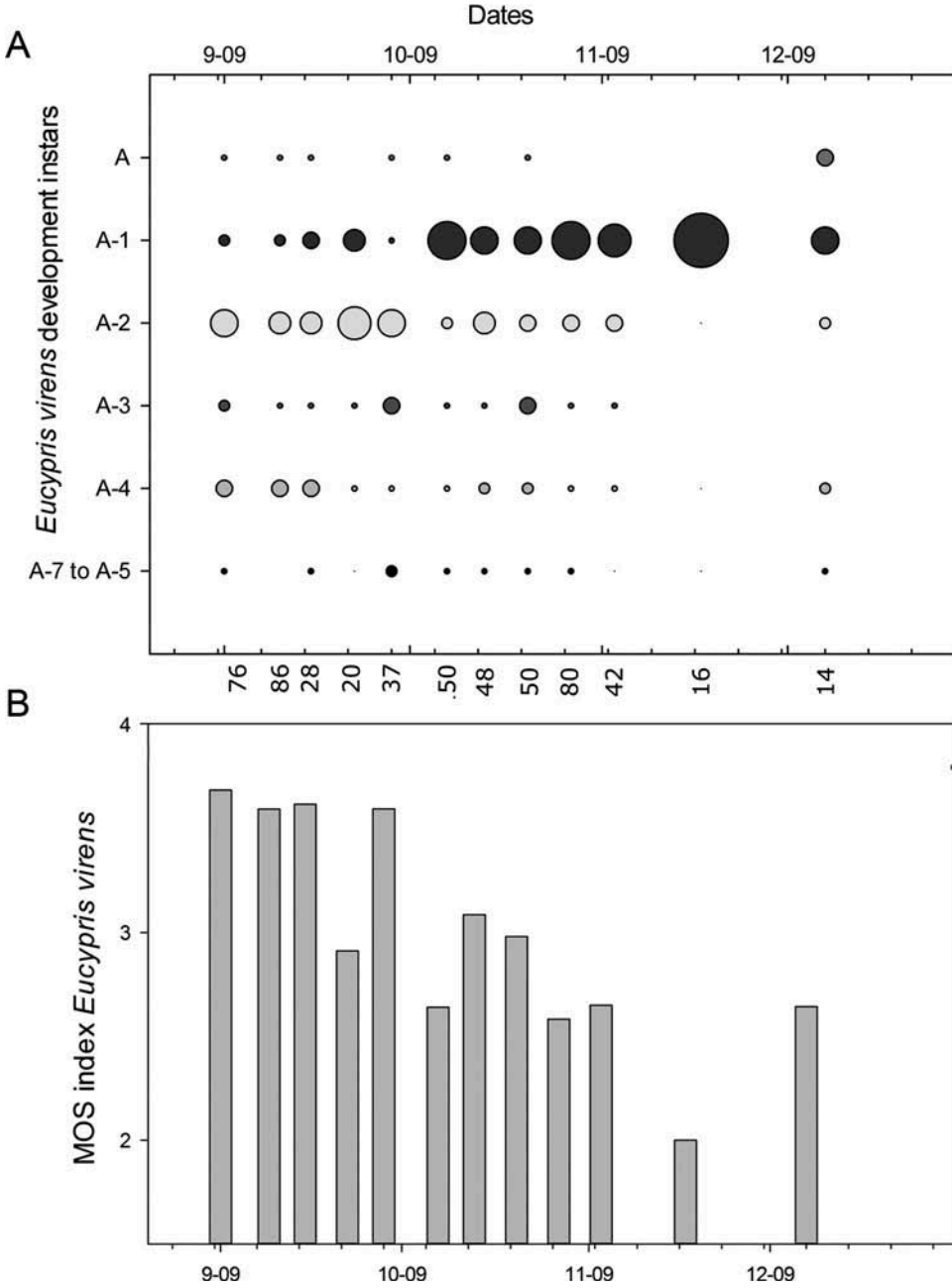


Figure 7. *Eucypris virens* from Ñireco (A) Temporal changes in relative density of development instars A-7 to Adults, bubble size represents the relative abundance of each life stage. The total number of individuals counted per sample is indicated at the bottom of the graph. (B) Mean ontogenetic stage index (MOS).

ionic concentrations were smaller than those from other sites. In addition, Aguilar-Alberola and Mesquita-Joanes (2008) suggested that the higher amount of food resources might explain the larger size of *Heterocypris bosniaca* Petkowski, Scharf and Keyser, 2000.

Moreover, we observed two different seasonality–size effects in both species. *Cypris pubera* were smaller in winter and larger in summer, while *E. virens* were larger in winter than in spring. Many factors are responsible for ostracod adult size in natural populations and changes between seasons are more pronounced in temporary than in permanent ponds. Our results suggest that the adult size of *C. pubera* has a positive relationship with conductivity. This conductivity–size effect has also been reported in *Limnocythere inopinata* (Baird, 1843) (Yin et al. 1999) as well as in *Cyprideis torosa* (Jones, 1850) (Van Harten 1996). Nevertheless, *E. virens* from Ñireco has a negative response to water conductivity, the same pattern that was reported for a Spanish population of *E. virens* (Martins et al. 2009). On the other hand, in our study, *C. pubera* attained the largest size in summer. Even though the association between low temperature and larger body size is a common feature in ectotherms (Angilletta et al. 2004), ostracods do not show a clear pattern response to temperature (Aguilar-Alberola and Mesquita-Joanes 2014). For example, experiments with *Heterocypris barbara* (Gauthier and Brehm, 1928) have shown that low temperatures lead to larger individuals most of the time, but, when conductivity and photoperiod combine adequately with high temperature, then the largest individuals can be found (Alcorlo et al. 1999). We cannot determine which factors are influencing the size differences observed in our study. Besides temperature and conductivity, many other factors are influencing the seasonality of the environment including food availability, predation pressure, vegetation cover, hydroperiod duration, among others. Furthermore, genotypic differences, phenotypic plasticity and hatching phenology are no less relevant to final body size attained. However, our results suggest that temperature, conductivity and specific genetic responses appear to be important in determining adult size.

Further studies are needed to understand the mechanisms responsible for size patterns, and how they are influenced by environmental parameters.

### ***Reproduction strategies and life cycle***

The exclusive presence of adult females indicates that all the populations studied reproduce parthenogenetically. This is particularly common in organisms from temporary ponds, including *E. virens*, *T. lutaria* and *C. pubera* (Meisch 2000; Little 2005; Martins et al. 2009; Van der Meeren et al. 2009). According to Schwalb and co-workers, parthenogenesis seems to be the dominant strategy in species inhabiting small lagoons with low conductivity in Patagonia (Schwalb et al. 2002). Additionally, the three ponds sampled during this study are located in the Andean Patagonian region, which was under glacial influence in the Upper Pleistocene (Markgraf 1998). We suggest that this type of reproduction is the most effective strategy in post-glacial colonization, as was proposed by Van der Meeren et al. (2009) and Horne et al. (1998). Therefore we expect that one would be likely to find mostly parthenogenetic populations in the area. However, patterns of geographical parthenogenesis of ostracods in Patagonia are still not well understood.

*Eucypris virens* and *C. pubera* populations had different life histories. In Teleférico, *E. virens* displayed continuous reproduction, as demonstrated by the dominance of ovigerous females and the presence of younger instars throughout the sampling period. In Refugio, *C. pubera* showed synchronous reproduction, with three generations within a hydroperiod. This multivoltine strategy may be related to appropriate environmental conditions, such as temperature, conductivity, dissolved oxygen concentration and food supplies. *Heterocypris salina* (Brady 1868), another Cyprididae inhabitant of shallow ponds, is able to produce two or three generations per year depending on water temperature (Ganning 1971). Additionally, several studies have shown that other crustaceans, like copepods, can alternate between univoltine and multivoltine strategies according to relevant environmental variables, such as temperature, food availability, photoperiod and hydroperiod (Rossi et al. 2013).

It is known that water temperature and conductivity are important factors controlling the development rate of aquatic crustaceans (Roca and Wansard 1997; Aguilar-Alberola and Mesquita-Joanes 2011; Rossi et al. 2013). In fact, the estimated development time of *C. pubera* was clearly dependent on these parameters, being shorter towards the summer, when temperature and conductivity increased. The Refugio population showed relatively discrete cohorts moving through ontogeny with different speeds at different temperatures, whereas in Teleférico such discrete cohorts were not obvious. This may be because diapause or hibernation may cause cohorts to accumulate at some ontogenetic stage, and constancy in the environment may interfere with the normal breakdown of diapause, leading to more continuous population structures.

Although Teleférico maintained its water level throughout the season, *E. virens* was not recorded after mid-December. *Eucypris virens* belongs to Type I phenology, which includes species that appear within a week of pond filling and continue to be present until the ponds dry, with multiple generations (Ripley and Simovich 2009). Different hypotheses could explain this disappearance. First, the absence of *E. virens* coincided with the appearance of aquatic predators such as giant water bugs, backswimmers and water beetles (Jara and Perotti 2010). These organisms need more time to develop and therefore their trophic effects on ostracods and other micro-invertebrates are seen in later successional stages (Palacios-Fest et al. 1994; Martins et al. 2009). The increase in temperature together with the decrease in dissolved oxygen concentration could be other abiotic factors affecting *E. virens* populations. However, the percentage of oxygen saturation in Teleférico was around 125% in December. Future experimental studies are needed to evaluate the aforementioned hypotheses.

In spite of the many ecological studies carried out in aquatic environments of Patagonia, there are still many unresolved issues in this little-explored region. The information provided in this study shows that shallow, vegetated ponds support diverse ostracod populations and point out the importance of small and newly emerged ponds and their possible role as “stepping stones” connecting larger lakes. To our knowledge, this is the first study to provide data about the development and life history of ostracods in Patagonian freshwater environments. However, biological factors that influence the population dynamics and development of ostracods in these small ponds are also still not well understood.

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## Supplemental material

Supplemental material for this article can be accessed online: <http://dx.doi.org/10.1080/00222933.2014.981310>

## Geolocation information

Refugio de Jesús (point): 41° 07' 11" S, 71° 13' 10" W; (point): 41° 10' 54" S, 71° 19' 01" W; (point): 41° 07' 40" S, 71° 22' 05" W.

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