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Rotifer dynamics in three shallow lakes from the Salado river watershed (Argentina): the potential modulating role of incident solar radiation†

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In turbid Pampean lakes, incident solar radiation is a major driver of plankton seasonal dynamics. Higher light availability in summer translates into higher primary production, and therefore more food for zooplankton grazers. However, experimental evidence suggests that food produced under the high irradiance conditions prevailing in summer are less suitable to sustain rotifer population growth than that produced under the lower irradiance conditions typical of winter. Here, we analysed time series datasets corresponding to three shallow lakes from the Salado river watershed. This analysis provided evidence for similar seasonal patterns of rotifer relative abundance over a large geographic area. In addition, we performed life table experiments to test the hypothesis that natural seston produced in winter could sustain higher population growth rates than seston produced in summer. We suggest that the natural seasonal changes in temperature and food generate successive time windows, which may be capitalized by the different grazer species, resulting in predictable phenology of grazer populations.

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Introduction

Light affects many ecological and physiological process of zooplankton. In fact, several morphological (small size, body transparency) and behavioural (surface avoidance, diel vertical migration) traits are customarily interpreted as adaptations to minimize exposure to damaging short-wave solar radiation¹ and/or mortality losses due to visual predation.² But the effects of light on zooplankton are not restricted to conditions entailing direct exposure. Incident solar radiation may also indirectly influence individual development and demographic parameters by affecting water temperature, as well as the amount and composition of food produced by photosynthetic algae and the plethora of microbial organisms (bacteria, heterotrophic flagellates and ciliates) that thrive upon them.^{3–5}

Most Pampean lakes are highly turbid environments,⁶ in which light exposure is limited to the few uppermost centimetres, thus limiting the direct influence of light on planktonic animals. The zooplankton of many Pampean lakes, as

well as other eutrophic lakes, is dominated by small-size and/or highly evasive species. Rotifers are the most representative group among zooplankton in floodplains lakes of Argentina (ref. 7 and references therein). The genera *Brachionus* and *Keratella* are particularly abundant.^{8–10} They tend to form assemblages dominated by a few species that persist over time, despite large variations in absolute abundance (ref. 7, 11 and references therein). Rotifer population dynamics and community composition are strongly modulated by environmental changes.^{12–15} Particularly, in Laguna Chascomús there is evidence that changes in temperature and food availability, control zooplankton dynamics.¹⁶

Pampean shallow lakes display strong seasonal variability in temperature, as well as in the concentration and composition of suspended particles. Primary production¹⁷ and total particle concentration¹⁸ are lower in winter, and gradually increase until they reach a maximum around summer solstice. In addition, many traits of the suspended material vary seasonally. For example, the mass-specific phosphorus content of seston in Laguna Chascomús has been reported to be lower in summer than in winter.¹⁸ Assuming an organic carbon content of 40%, the molar seston C:P ratio is estimated to range from 230 to 620. Thus, although not excessively high, these C:P ratios often exceed the threshold (C:P 250:1)¹⁹ above which the consumers becomes limited by food quality.²⁰ Moreover, many other features such as the mass-specific ash-content, the mass-specific chlorophyll *a* and accessory pigments concentrations, and several optical variables vary

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seasonally.²¹ Under natural conditions however, the unequivocal identification of light as a driver of the amount and composition of suspended particulates is precluded due its covariation with potentially confounding variables. To circumvent this limitation, we had conducted a mesocosm-scale study, wherein the amount of incident solar radiation was manipulated using different levels of shading.²² In that study, we successfully reproduced the natural trends in seston quantity and composition previously observed to occur in Laguna Chascomús seasonally. Interestingly, although the amount of particulate material increased with incident light, the abundance of rotifers declined. Therefore, we suspect that particles produced under high incident light conditions are of a lesser food value, on average, than those produced under lower incident light conditions.

In the natural environment, the food available to the rotifers is a complex mixture of particles, including many species of algae, detritus and heterotrophic bacteria.²³ Given that rotifers tend to feed selectively, the characterization of bulk seston properties (e.g., elemental composition, organic matter content) provide only rough estimates of the composition of the items that are actually ingested. Moreover, although *Brachionus* and *Keratella* have similar feeding modes²⁴ (they use ciliary currents to bring food particles into the mouth and can consume a broad range of particle sizes), they do differ in their food requirements.²⁵ For instance, algal foods that promote growth and reproduction in *Brachionus* (*Chlorella*, *Chlamydomonas*, *Euglena*, and other green algae) usually are poor foods for *Keratella*. Therefore, the suitability of a food mixture may differ between rotifer species. A valuable alternative is to use life table bioassays to estimate a suit of demographic parameters when the rotifers are offered different food mixtures.^{26,27} The suitability of different foods to sustain population growth is then inferred from some measure of demographic performance,²⁸ such as the net reproductive rate (R_0).

Based on time-series of rotifer abundance and environmental variables Diovisalvi and co-workers¹⁶ have shown that the population dynamics of rotifers in Laguna Chascomús has a strong seasonal component, which correlates with temperature and food availability (as estimated by chlorophyll concentration). In addition, a consistent seasonal pattern of rotifer relative abundance could be observed, in which *Keratella tropica* dominates in winter and is gradually replaced, initially by *Brachionus caudatus*, and subsequently by *B. havanaensis*. We suspect that these patterns may be the result of differences in demographic strategies and feeding selectivity. In fact, the genera *Brachionus* and *Keratella* are often described as members of an r/K consortium of species (sometimes referred to as opportunistic vs. gleaner strategists²⁹). The K -strategist (*Keratella*) is a generalist feeder³⁰ with a low threshold food concentration.²⁵ On the other hand, the r -strategist (*Brachionus*) has a higher threshold food concentration, but can attain, under favourable conditions, much higher growth rates.³¹ *Brachionus* and *Keratella* also differ in their demographic responses to temperature.³¹ So far however, such differences have not been assessed for indigenous Pampean populations.

Here, we first explore the generality of the seasonal pattern on rotifers abundance by analysing multi-year time-series data from two additional lakes (Carpincho and Gómez) occurring within the same watershed. Subsequently, we use life-table assays, performed with the three dominant species, to investigate if natural seston produced in winter could sustain higher net reproductive rates than seston produced in summer.

Results and discussion

Rotifer assemblage composition and seasonal succession

The three lakes included in this study are shallow, hypertrophic and highly turbid (see ESI†). *Brachionus* and *Keratella* were the dominant genera in the three lakes. Together they accounted for >90% of the total rotifer abundance (on average). The assembly of dominant species comprised *B. caudatus*, *B. plicatilis* and *K. tropica* in Laguna Carpincho and L. Gómez, and *B. caudatus*, *B. havanaensis* and *K. tropica* in L. Chascomús. Averaged over the whole study period, the genus *Keratella* accounted for ~20–46% of total rotifers abundance. *K. tropica* was, by far, the most abundant species of the genus, while *K. americana*, which only occurred in L. Chascomús, never represented more than 2% of total rotifers abundance. The genus *Brachionus* represented between 50 and 69% of total rotifer abundance. Less abundant (attendant) species of the genus *Brachionus* included *B. angularis*, *B. budapestinensis*, *B. calyciflorus*, *B. dimidiatus* and *B. pterodinoides*.

The population dynamics of the dominant rotifer genera, *Brachionus* and *Keratella*, are shown in Fig. 1 (L. Carpincho and L. Gómez) and Fig. 2 (L. Chascomús). The range of *Brachionus* absolute abundance spanned over more than three orders of magnitude (from nil to ~5000 ind L⁻¹) and displayed a distinct seasonal pattern, with maxima occurring in the warm season. The absolute abundance of *Keratella* fluctuated

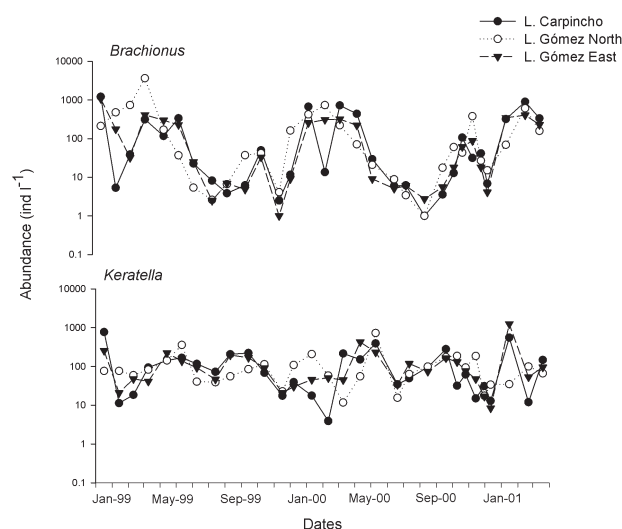


Fig. 1 Abundance of the genera *Brachionus* and *Keratella* in L. Carpincho and L. Gómez (Río Salado headwaters).

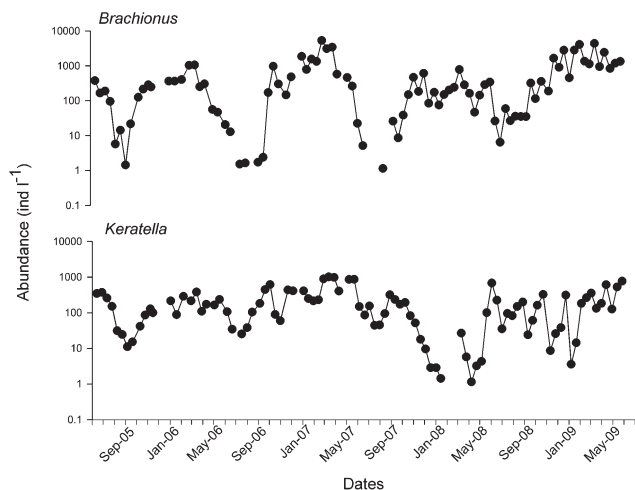


Fig. 2 Abundance of the genera *Brachionus* and *Keratella* in L. Chascomús (lower Salado river watershed).

within a slightly narrower range (from nil to ~ 1000 ind L^{-1}) and varied more or less haphazardly without displaying any clear seasonal trend.

The variations in absolute abundance described above translated into remarkable and repeatable seasonal patterns of relative abundance (Fig. 3 and 4), *i.e.*, the percentage of *Keratella* was higher during the winters, being gradually replaced by *Brachionus* species during spring and summer. To examine these cyclical trends, the time series of relative abundance of dominant *Brachionus* (*i.e.*, *B. caudatus* + *B. plicatilis* for

L. Carpincho and L. Gómez, and *B. caudatus* + *B. havanaensis* for L. Chascomús) were analysed. The autocorrelation functions (ACF) were statistically significant ($p < 0.0001$) for the three lakes. Despite differences in sampling frequency (monthly for L. Carpincho and L. Gómez, every other week for L. Chascomús), the highest autocorrelation (>0.80) occurred after a time lag of one sampling date in the three lakes. The ACF formed a waning wavy pattern of positive and negative values indicative of a cyclical behaviour. The examination of spectral density plots and the Fischer's periodicity indicated annual periodicity in all cases (Table 1).

The strength of the relationships between irradiance, water temperature, and *Brachionus* relative abundance time-series was estimated through cross-correlation analysis. Water temperature in L. Chascomús lagged behind solar irradiance by approximately one sampling date (cross-correlation lag 1 = 0.9). On the other hand, the relative abundance of *Brachionus* lagged behind water temperature by approximately one sampling date in the three lakes (cross-correlation lag 1 ranged from 0.81 to 0.89).

Summarizing, when expressed in terms of relative abundance, the rotifer assemblage exhibited remarkable seasonality. Within each lake, the three dominant species peaked every year at similar times. In general, the seasonal cycle is characterized by a dominance of *Keratella* species during winter followed by a gradual replacement by members of the genus *Brachionus*. The occurrence of these cycles suggests that external forcing variables related to incident irradiance (*i.e.*, temperature, food supply) are major drivers of the rotifer population dynamics in shallow Pampean lakes. These findings are in line with those reported by other authors for different rotifer assemblages.^{14,32–35}

Life table assays

Life table assays were performed to investigate the effects of different combinations of incubation temperature and food source on the demographic parameters of three dominant Brachionid rotifers, *B. caudatus*, *B. havanaensis* and *K. tropica* from L. Chascomús. In order to assess seasonal differences in the food value of natural lake seston, the experiments were performed once in summer and once in winter. The >2 μ m phytoplankton fractions in Laguna Chascomús are primarily dominated by small-cell colonies of cyanobacteria, which account for $\sim 80\%$ of total biovolume, and secondary by filamentous cyanobacteria, small chlorococcales and diatoms.³⁶ Known toxic cyanobacteria strains have not been reported; and sporadic assessments of cyanotoxins resulted consistently negative (O'Farrell comp. pers.). In both series of experiments, life tables were constructed by incubating the three species of rotifers at 9 °C and 20 °C.

The estimated values of the net reproductive rate (R_0) are shown in Fig. 5. *K. tropica* was the only species that displayed positive population growth (*i.e.*, $R_0 > 1$) under the four assayed treatments. However, compared to the other two species, *K. tropica* attained only modest maximum R_0 values and was the species least sensitive to changes in temperature and food.

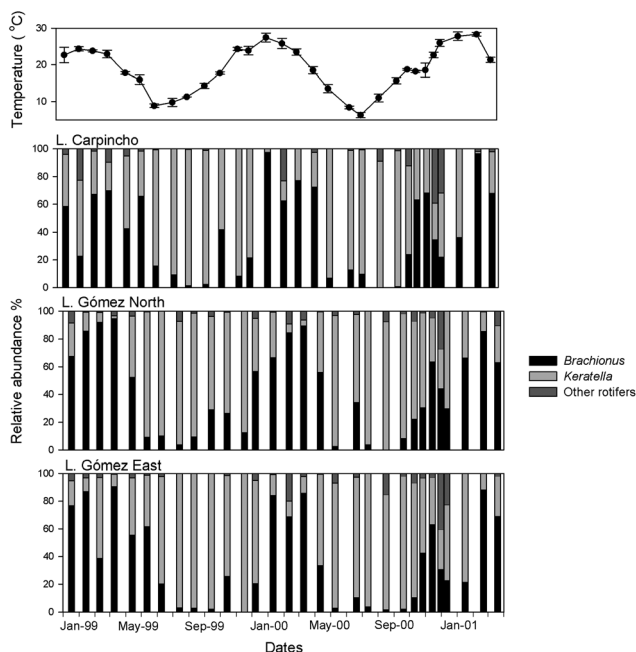


Fig. 3 Seasonal patterns of water temperature (upper panel) and relative abundance of the dominant genera of rotifers in L. Carpincho and L. Gómez (lower panels).

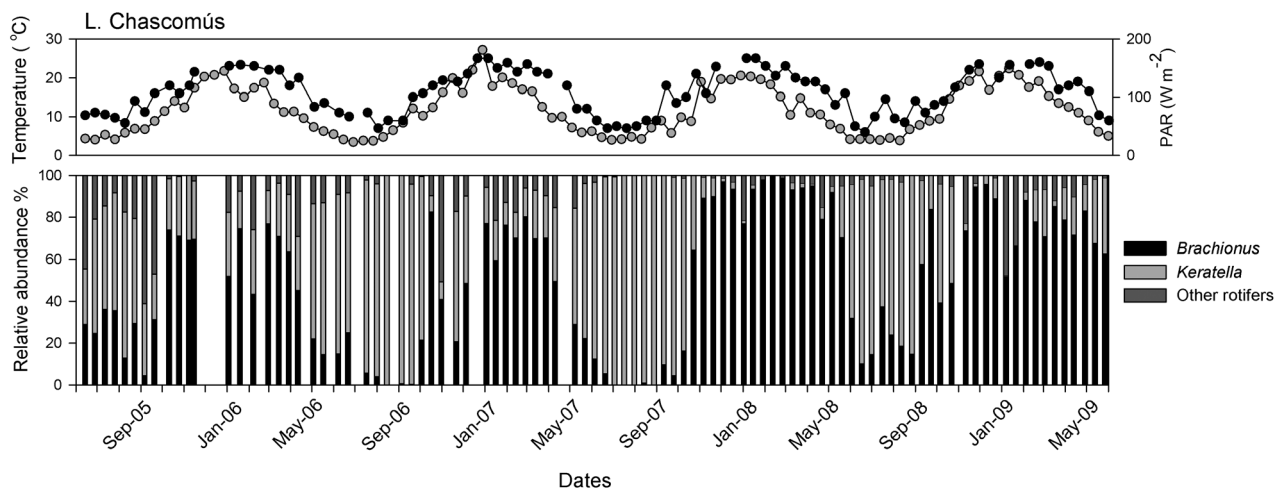


Fig. 4 Seasonal patterns of water temperature – black symbols – and PAR irradiance – gray symbols – (upper panel), and relative abundance of the dominant genera of rotifers in L. Chascomús (lower panel).

Table 1 White noise tests on time series of the relative abundance of the dominant *Brachionus* species for each lake. Fishers Kappa statistic tests normal distribution with variance of 1 (H_0) against periodic component in the series (H_1). Kappa is the ratio of the maximum value of the periodogram. H_0 is rejected if the probability (Prob) of observing a larger kappa is less than the significance level α

	Chascomús	Carpincho	Gómez east	Gómez north
Fisher's kappa	36.86	8.76	8.20	10.74
Prob > kappa	7.20×10^{-27}	3.97×10^{-5}	1.49×10^{-4}	8.24×10^{-8}

Only the treatment fed on seston produced on summer and incubated at 9 °C displayed significantly lower R_0 . There were no significant differences between the other three treatments, including the two “natural” sets of conditions, *i.e.*, rotifers incubated a 20 °C fed seston produced in summer (20S) and rotifers incubated a 9 °C fed seston produced in winter (9W). On the other extreme, *B. havanaensis* showed a radically different strategy. This species failed to produce progeny at the lowest temperature assayed (9 °C), which explains its absence in the lakes during wintertime. But at 20 °C, it attained high net reproductive rates. Such a strong dependence of reproduction on warm temperature has been previously reported by

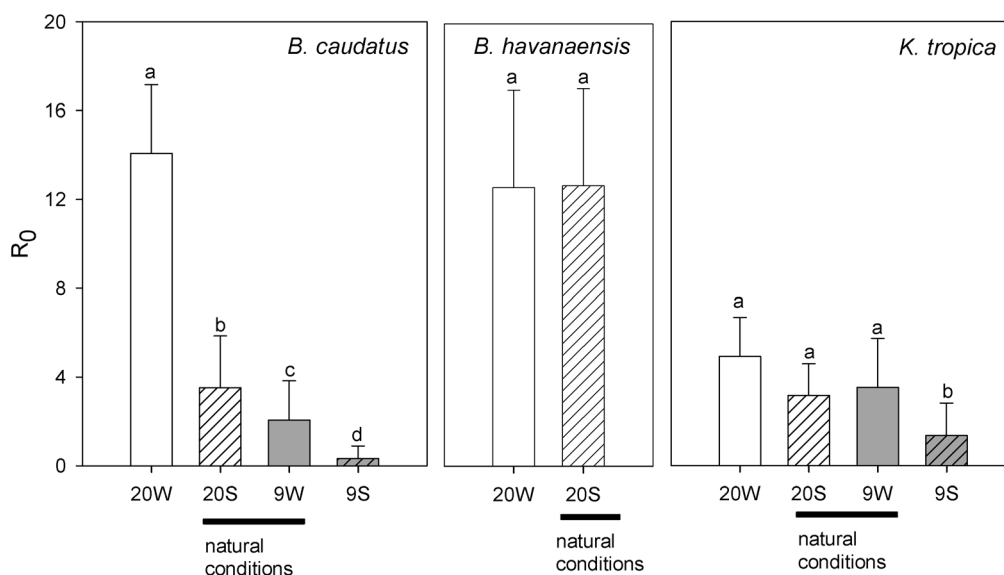


Fig. 5 Net reproductive rate (R_0) of the three assayed rotifer estimated from life table experiments. The animals were incubated at either 9 or 20 °C and offered seston produced in summer (S) or winter (W). The treatments 20S and 9W more closely resemble those experienced in the field, and are referred to as “natural conditions”.

Pavón-Meza and co-workers, who demonstrated that offspring production is hampered by low temperature.³⁷ Moreover, there were no significant differences between animals fed on seston produced in summer or winter, which is also in agreement with the study by Pavón-Meza *et al.* 2005 who reported a lack of interactive effects between temperature and the source of food for this species. Finally, the most plastic strategy was displayed by *B. caudatus*. This species could attain net reproductive rates comparable to those achieved by *B. havanaensis*, but only when fed seston produced in winter and incubated at the highest temperature (20 °C). *B. caudatus* showed significant differences between the four assayed treatments. The lowest values of R_0 were observed in the coldest treatment (9 °C) when fed on summer seston. The latter treatment resulted in $R_0 < 1$, indicating negative population growth. There were also significant differences between the two “natural” treatments, where R_0 was higher on summer (20S) than winter conditions (9W). These results suggest some sort trade-off mechanism for *B. caudatus*: as incident radiation increases seasonally, the deterioration in the value of seston as food appears to be somehow compensated by increases in water temperature; and reciprocally, when irradiance decreases, colder temperatures are compensated by improvements in the food conditions. Additional demographic estimates and their corresponding statistical analysis are listed on ESI.†

We believe that differences in rotifer performance were not due to the total amount of seston offered as food. First, because the experimental design was aimed at providing individual rotifers with enough food on a daily basis, so that the animals could feed *ad libitum*. The amount of autotrophic carbon in L. Chascomús water³⁸ exceeded by far (~80 fold) the critical threshold of food concentration for rotifers.³⁹ Furthermore, the results of the life table assays strongly suggest that the differences in rotifer performance are most likely due to differences in seston composition. Consider for instance, the fact that *B. caudatus* and *K. tropica* did better (*i.e.*, attained higher R_0) when offered winter seston (lower concentration of total suspended solids, TSS, and chlorophyll *a*, Chl *a*) than when fed summer seston (higher TSS and Chl *a* concentration). Thus, the life table assays strongly suggested that the bulk seston composition is less suitable to sustain the growth of *B. caudatus* and *K. tropica* in summer than in winter. On the other hand, we suspect that the lack of differences observed in *B. havanaensis* could be due to its higher feeding selectivity,⁴⁰ although this hypothesis remains to be tested.

Trade-offs between *r*-*K* demographic strategies are commonplace in rotifer communities.³⁰ The seasonal pattern of incident solar radiation is the major driver of the changes in water temperature and it also affects the amount of available food particles, as well as many of their properties,^{41,42} providing ever-changing conditions that affect the development of rotifer populations. The rotifers in turn, display a variety of demographic strategies, from relative unresponsiveness to environmental changes up to an explosive use of warm temperatures, regardless of food quality, or to a balance between temperature and food. The combination of these demographic

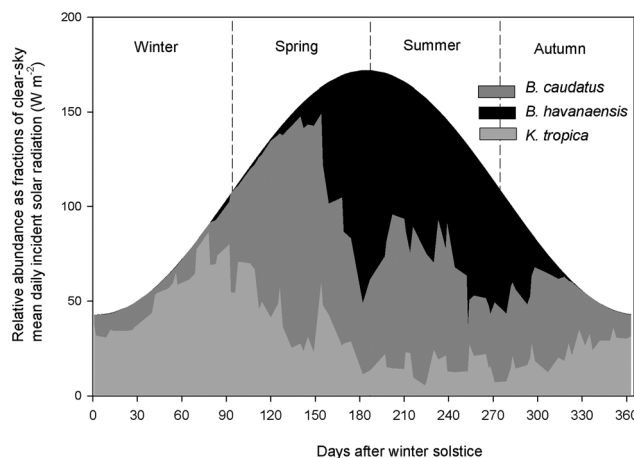


Fig. 6 A schematic representation of the seasonal cycle of rotifer in L. Chascomús. In this figure the relative abundances of the three dominant rotifer species are expressed as fractions of the estimated clear-sky mean daily incident solar radiation.

strategies results in a remarkable pattern of relative abundances in relation with the incident irradiance. Fig. 6 shows the changes in relative abundance of the three dominant species in Laguna Chascomús (expressed as fractions of incident solar irradiance) along the year. Schematically, species-dominance changes from *K. tropica* to *B. caudatus* to *B. havanaensis* from winter to summer and back to *K. tropica* by late fall. The pattern (Fig. 6) is not symmetrical, because the temperature lagged behind the incident irradiance, causing that the warmer temperatures favourable for the development of *B. havanaensis* are shift about a month to the right side of the figure (midsummer). On the other hand, *B. caudatus* is particularly successful during a time window in spring when the temperature is lower than those required by *B. havanaensis*, but the available food is presumably better than in summer.

Conclusion

Our study presented evidence on the generality of repeatable seasonal patterns in the planktonic rotifer assemblages of three shallow Pampean lakes. The life table experiments provide the mechanistic basis for understanding the replacement of rotifer species along the year. Although the major players of the rotifer staff share many morphological and physiological traits, they differ sufficiently in their ability to exploit different thermal and resource combinations, which ultimately are driven by the amount of incident solar radiation.

Experimental

Rotifer abundance time series

We assembled multi-year time series of rotifer abundance from three shallow Pampean lakes, located in the Salado river

watershed. Laguna Carpincho and L. Gómez are located in the Salado headwaters,⁴³ while L. Chascomús¹⁶ is part of a tributary system. The three shallow lakes studied have similar limnological characteristics (see ESI†). Carpincho and Gómez were sampled monthly from December 1998 to March 2001. Chascomús was sampled every other week from June 2005 to May 2009. Samples were collected from one (L. Carpincho, L. Chascomús) or two (L. Gómez) open-water sites. Zooplankton samples were collected by pouring 35 L of lake water taken from the upper 30 cm through a 45 µm mesh net (L. Chascomús) or by vertical net (69 µm mesh) tows from 0.4 m above the bottom to the surface (L. Carpincho and L. Gómez). Zooplankton samples were preserved in 4% formalin. Rotifers were counted under a compound microscope (Olympus CX31, Olympus Corporation; Shinjuku, TKY, Japan) on 1 mL Sedgwick-Rafter counting cell (Wildlife Supply Company; Yulee, FL, USA). The number of subsamples was adjusted in order to admit a maximum error of 20%, or count at least 300 individuals. Rotifers were identified following taxonomic literature.^{44–46}

Data from a total of ~200 samples are included in this study. The analysis of the time-series corresponding to Laguna Chascomús (95 samples) has been previously reported.¹⁶ The time series corresponding to L. Carpincho and L. Gómez were analysed in a comparable way. Briefly, for each sample we estimated the relative abundance of the dominant genus *Brachionus*. Whenever necessary, data from two consecutive dates were linearly interpolated in order to render the series equally spaced. The series were smoothed using a 3-date moving average. The Fischer's periodicity test was used to assess the seasonality of the series. Cross-correlation analysis was used for evaluating the time lagged between irradiance and temperature (L. Chascomús) and between *Brachionus* relative abundance and temperature (three lakes).

Incident solar radiation for Chascomús area was continuously recorded with an IL-1700 radiometer (International Light) equipped with a PAR (400–700 nm) sensor placed on the roof of the IIB-INTECH. Typical clear-sky mean daily PAR irradiance was empirically estimated by computing the conditional maxima, for each day of the year, using quantile regression.⁴⁷ Day of the year was converted to a sine value as:

$$\text{sine}(\text{day}) = \sin\left(2\pi\left(\frac{80.8 - \text{day}}{365.25}\right)\right)$$

Subsequently, we estimated the conditional maxima by using the linear equation for the 95th quantile of observed mean daily PAR irradiance vs. sine(day), using the quantreg package for R.⁴⁸ Complementary environmental variables, including common limnological parameters and abundance estimation of other plankton groups, were collected on each sampling date. For additional information see Rennella and Quirós (2006),⁴³ and Diovisalvi *et al.* (2015).¹⁶

Life table assay

Rotifers cultures were initiated at least two months before each assay. They were kept on EPA culture media (50% renewal every 4 days) and fed *Chlamydomonas reinhardtii* from stock cultures every other day (target density 6×10^4 cells per ml). Natural lake media (also referred to as seston) used in the assays was obtained by repeatedly (at least 3 times) filtering water from L. Chascomús through a 45 µm mesh, and subsequently allowing the water to rest for 24 h. This procedure efficiently removed planktonic animals and coarse inorganic particles, but retained most algae and other components of the microbial community, which form the natural diet of *Brachionid* rotifers.²⁵ Rotifers were transferred from EPA culture media to lake water 48 h prior to each experiment. After this acclimation period, batches of egg-carrying females were transferred to Petri dishes with fresh natural lake media. By the following day, new-born individuals were easily distinguishable from their mothers due to their slightly smaller size and thinner loricas. For each treatment between 15 and 27 new-borns of each species were placed individually into wells of multiwell plates filled with 250 µl of natural lake media. The plates were kept in the dark at the prescribed temperatures. The surviving individuals of parental generation (PG) were transferred daily to a new multiwell plate filled with fresh natural lake media. Newly produced eggs or newborns (F1) were recorded and removed. This procedure continued until the death of the last individual of PG.

Fertility life tables were constructed based on Birch (1948)⁴⁹ and Southwood (1978).⁵⁰ Rotifer performance under the different treatments was assessed by computing the net reproductive rate, R_0 :

$$R_0 = \sum l_x m_x$$

where l_x is the probability of surviving to age x and m_x is the number of progeny per female produced at age x . $R_0 > 1$ indicates positive population growth, while $R_0 < 1$ indicates population decrease.⁵¹ Additional life table parameters were estimated following Rabinovich (1980).⁵¹ Statistical significance of differences in population parameters was assessed using Jackknife technique.⁵² Jackknife pseudo-values were calculated using the software developed by La Rossa and Kahn (2003).⁵³ The results were analysed using one-way or two-way ANOVA, followed by Tukey's a posteriori test. Whenever the assumptions of the parametric statistical test were not met, the data were analysed using the non-parametric Kruskal-Wallis rank test.

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