ARGENTINE PAMPEAN SHALLOW LAKES

Seasonal patterns and responses to an extreme climate event of rotifers community in a shallow eutrophic Pampean lake

Nadia Diovisalvi · Gladys E. Salcedo Echeverry · Leonardo Lagomarsino · Horacio E. Zagarese

Abstract Shallow lakes of temperate areas experience seasonal and inter-annual variability in weather conditions, impacting on their biological communities. Here, we studied the temporal fluctuation of the zooplankton community in a highly eutrophic shallow lake, Laguna Chascomús. Rotifers and the cyclopoid copepod *Acanthocyclops robustus* dominated the community. The most important rotifers were *Brachionus caudatus*, *B. havanaensis,* and *Keratella tropica*. The abundance of the two *Brachionus* species reached maximum values in late summer/early autumn. In contrast, *K. tropica* and *A. robustus* did not display seasonal patterns. A prolonged period of low water temperature resulted in a massive fish winterkill event (in 2007), which seemingly allowed the development of unusually dense populations of cladocerans. We used vector autoregressive models to analyze the rotifer time series. The model accounted for 76% of the variance in rotifer abundance and provided evidence of their dependence on temperature and chlorophyll *a*. In addition, the impact of the fish winterkill on rotifer abundance could be assessed through intervention analysis. The evidence collected here suggests that the zooplankton community structure is controlled by fish planktivory, while rotifers population dynamics are mostly driven by temperature and available food. Both processes seem highly responsive to forcing weather variables.

Keywords Zooplankton community · Rotifers · Seasonal dynamics · Fish winterkill · Shallow turbid lake

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Introduction

Temperate shallow lakes experience strong annual variability in weather conditions (Lewis, 1983). These recurring changes in environmental conditions are transmitted through networks of interacting organisms, which shape the structure and dynamics of communities (Winder & Schindler, 2004; Kratina et al., 2012; Shurin et al., 2012). The resulting seasonal patterns may nevertheless be affected, or even disrupted, by inter-annual variability in critical variables, such as water level (Coops et al., 2003) and temperature (Winder et al., 2009). Moreover, shallow lakes may occasionally experience extreme climatic events,

defined as an episode or occurrence in which statistically rare or unusual climatic conditions alter ecosystem structure and/or functions well outside the bounds of what is considered typical or normal variability (Reichstein et al., 2013).

Pampean lakes are typically shallow and eutrophic aquatic systems, which display remarkable seasonal patterns in temperature, suspended solids, optical properties (Torremorell et al., 2007; Pérez et al., 2011), phosphorus concentration (Lagomarsino et al., 2011), and primary production (Torremorell et al., 2009). These lakes also display substantial inter-annual variability in weather and hydrological variables (Rennella & Quirós, 2006). Laguna Chascomús is a large Pampean shallow lake that has been intensively studied (Torremorell et al., 2009) and is presently one of the research site of the PAMPA[2] network (Diovisalvi et al., this volume). The zooplankton assemblage of this lake is numerically dominated by small-sized rotifers (Diovisalvi et al., 2010). Due to their high population growth rates and short generation times, small organisms like rotifers are highly sensitive to changes in environmental conditions (Herzig, 1987), which makes them excellent model organisms for investigating community responses to climate variability.

Many studies on rotifer responses to environmental variability have addressed effects at the level of species (Herzig, 1987; López et al., 2007) particularly focusing on phenology (Winder & Schindler, 2004; Hampton, 2005; Dupuis & Hann, 2009). However, responses by individual species to environmental variability are connected through interactions with others at the same or adjacent trophic levels (Walther, 2010). Overall, the abundance of rotifers is thought to be mostly driven by factors such as temperature (Berzins & Pejler, 1989; Andrew & Andrew, 2005), food availability (González & Frost, 1992), and interactions with competing filter-feeding cladocerans and predatory copepods (Stemberger & Evans, 1984; Yoshida et al., 2000). However, there is a great deal of variability in the reported patterns, ranging from marked seasonality, associated with food availability (Gulati et al., 1992; Beaver & Havens, 1996), to a complete lack of it (Castro et al., 2005). Here, we investigate the temporal patterns of zooplankton abundance in response to environmental variability in Laguna Chascomús during a period of 4 years.

Our aim was to assess the dependence of rotifer populations on environmental factors.

Method

Study site

Laguna Chascomús (35°36′S 58°W) is a large (surface = 30.1 km^2) shallow lake (mean depth ~1.9 m), located in Pampa region of Argentina. It belongs to the Salado river watershed, an 801 km^2 floodplain, characterized by a very gentle slope and poorly developed drainage. Chascomús is a polymictic, eutrophic, and alkaline lake (Conzonno & Claverie, 1990; Torremorell et al., 2007). The biotic community is dominated by the autotrophic fraction, mainly represented by the nanoplankton (Diovisalvi et al., 2010). The rich and diverse community includes hundreds of autotrophic and heterotrophic microbial species, zooplankton grazers, and 19 fish species (Berasain et al., 2005; Torremorell et al., 2009; Fermani et al., 2013).

Sampling

Laguna Chascomús was sampled every other week, from June 2005 to May 2009. Samples were collected at three sample sites evenly distributed along the lake's largest axis. Routine measurements of lake depth, water temperature, pH (Orion pH-meter; ATI Orion, VWR Scientific; Boston, MA, USA), conductivity (Hach conductimeter; Hach Company; Loveland, CO, USA), dissolved oxygen concentration (YSI 5000 meter; YSI Incorporated, Dayton, OH, USA), and Secchi disk readings were measured in situ. Profiles of the photosynthetic active radiation (PAR; 400–750 nm) were recorded with an IL1700 radiometer (International Light, Inc.; Peabody, MA, USA). Subsurface water samples were collected and immediately transported to the laboratory for chemical analysis. Suspended particulate matter (also referred to as seston), ash-free dry weight (AFDW), total phosphorus, and particulate phosphorus were determined the following APHA (1992). Chlorophyll *a* concentration (Chl *a*) was assessed after extraction with methanol (Lopretto & Tell, 1995). The lake has a high degree of homogeneity and temporal coherence, showing minimal differences in the above variables between sampling sites (Torremorell et al., 2007).

Zooplankton samples were collected from the westernmost sampling site (35°34′880S, 58°02′184W) by pouring 35L of lake water taken from the upper 30 cm through a 45-µm mesh net and preserved in 4% formalin. Rotifers and copepod nauplii 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). Other zooplankton species (i.e., the remaining crustaceans) were counted under a dissecting microscope Olympus SZ (Olympus Corporation; Shinjuku, TKY, Japan) with a 5-mL Bogorov counting chamber (Gannon, 1971). 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 Ruttner-Kolisko (1974), Pontin (1978) and Koste (1978), and crustaceans, according to Pennak (1989), Reid (1985), and José de Paggi (1994).

Data analysis

For the assessment of the inter-annual environmental variability, we split the four-year time series into growth cycles (GC). These GC were defined on an astronomical basis, i.e., each GC started on the winter solstice (June 21) and ended on the winter solstice of the following year, as follows: first GC: June 2005–June 2006, second GC: June 2006–June 2007, third GC: June 2007–June 2008, and fourth GC: June 2008–May 2009.

For data processing, we first conducted an exploratory analysis using graphical tools and conventional stepwise multiple regression. These procedures are not appropriate for the formal analysis of time series datasets but are helpful to identify independent variables that are likely to affect rotifer dynamics. As independent variables, we considered lake depth, water temperature, pH, conductance, alkalinity, dissolved oxygen, nephelometric turbidity, seston, Secchi disk depth, phosphorus concentration (total, dissolved and orthophosphate), nitrogen concentration (total and dissolved and organic nitrogen, nitrite, nitrate, ammonium), and Chl a. This exploratory analysis suggested that water temperature and Chl a concentration were the two most relevant variables affecting rotifer dynamics. Afterward, we fitted the first-order vector autoregressive model denoted as VAR (1). This particular model belongs to the family of multivariate AR models, which from

observational time series data describe the stochastic dynamics of m interacting variables (e.g., species, environmental, biological) (Hampton et al., 2013). The VAR (1) gives a system of m linear equations, each one with the corresponding measure of the goodness-of-fit (R^2). The assumptions of residual's normality and homoscedasticity were assessed through Kolmogorov–Smirnov and Spearman rank tests, respectively. Autocorrelation was assessed using a Durbin-Watson test.

Time series are frequently affected by some unusual external factors, and the impacts generated are some abrupt changes in mean or variance of the time series. The technique to evaluate these impacts is called intervention analysis (IA). Mantua (2004) studied different approaches for detecting regime shifts in marine ecosystems. One of these methods follows the approach of Solow & Beet (2005) based on the use of VAR (1) model as a formal statistical approach to detecting regime shifts in a collection of ecological time series. IA has been used in ecology to examine the effects of perturbation where the cause is known (Jassby & Powell, 1990), such as after the manipulation (Carpenter et al., 1989) or human alteration (Gerten & Adrian, 2001). Here, we assess the impact of unusual fish winterkill (third GC) on rotifer abundance time series through IA.

Finally, to assess the presence of periodic components, we performed a Fisher's periodicity test (Fisher, 1929) to the rotifer time series, prior, and subsequent obtained to the IA, as well as for the Chl a and temperature. Similarly, the contribution of dominant *Brachionus* species (*B. caudatus* and *B. havanaensis*) to total rotifer abundance was analyzed using this test. We inferred that the time series contains a periodic component and a seasonal behavior if the calculated statistic T resulted greater than the critical value $g_\alpha = 0.1273$, corresponding to an overall significance level of 5% (i.e., $\alpha = 0.05$).

Results

Physical and chemical characteristics of lake water

Mean values and ranges for most physicochemical variables recorded for the study period in Laguna Chascomús were comparable to previously reported data (Torremorell et al., 2007) and well within the range reported for continuous warm-polymictic

Table 1 Main physical, chemical, and biological parameters for Chascomús Lake

Parameters	Mean (SD)	Range: min–max
Temperature (°C)	16.2 (5.6)	6.0–25.0
PAR mean (W m^{-2})	75.3 (46.6)	3.8–170.4
Depth (m)	1.9 (0.3)	1.1–2.4
Secchi disk (cm)	10.2 (3.1)	5.0–18.3
pH	8.9 (0.2)	8.0–9.4
Conductivity (mS cm^{-1})	2.1 (0.5)	1.4–3.7
DO (mg l^{-1})	9.3 (1.8)	5.1–14.6
Chl a (μg l^{-1})	328.5 (173.4)	50.6–856.3
Seston (mg DW l^{-1})	227.3 (113.7)	66.3–61.4
AFDW (mg l^{-1})	78.6 (29.6)	37.7–196.8
TP (μM)	21.5 (7.1)	8.5–41.7
Ppart (μM)	18.1 (6.6)	7.7–37.6

Data are means, standard deviation (SD), and range (minimum–maximum) values

PAR Mean mean daily incident PAR irradiance, *DO* dissolved oxygen, *Chl a* chlorophyll a, *AFDW* ash-free dry weight, *TP* total phosphorous, *Ppart* particulate phosphorous

(Lewis, 1983), hypertrophic, shallow lakes (Table 1). Water temperature ranged from 6 to 25°C, exhibiting a repeated and expected seasonal pattern. However, in the winter of 2007, we observed a subtle difference in thermal conditions of the lake. During this period, water temperature remained low (<7°C) for a longer time (>1 month) than in any other studied winter (Fig. 1a). This period of low water temperature was coincident with a massive fish kill event (see "Discussion").

Several other variables also displayed marked seasonal trends (e.g., water transparency, total phosphorus and seston concentrations; data partially shown in Lagomarsino et al., 2011), which were consistent with the previous reports for this lake (Torremorell et al., 2007). Despite considerable inter-annual variability, the Chl a concentration reached the highest values by the end of summer, while lowest values occurred in winter. An exception to this trend was observed during the third GC, in which Chl a level was dropped by mid-summer, remaining low ($\sim$150 mg l^{-1}) for the rest of this GC (Fig. 1b).

Zooplankton composition

The zooplankton community of Laguna Chascomús was typically dominated by rotifers and cycloid copepods (Table 2). Cyclopoid copepods were nearly an order of magnitude more abundant than calanoids. The mean annual abundance of the cyclopoid *Acanthocyclops robustus* exceeded 200 ind l^{-1} (considering all instars), while that of *Notodiaptomus incompositus*, the only calanoid copepod species, was only one tenth to one fifth as abundant.

Cyclopoid abundance was highest (>300 ind l^{-1}) either in summer (second GC), spring (third GC), or autumn (fourth GC). Calanoid copepod abundance was highest ($\sim$100 ind l^{-1}) immediately prior to summer in the third GC and at the beginning of spring in the fourth GC. For both cyclopoids and calanoids, the abundance patterns of adults, copepodites, and nauplii were similar (Fig. 2a, b). All cladocerans recorded, including *Bosmina huaronensis*, *Moina micrura,* and an unidentified chydorid, were small-bodied species. Their abundances were generally below 10 ind l^{-1}. However, exceptionally higher abundances were recorded during the spring and summer following the fish winterkill. During this brief period, *Bosmina huaronensis* and *Moina micrura* achieved abundances of 493 and 240 ind l^{-1}, respectively. We observed a much lower increase of *B. huaronensis* during the spring of the fourth GC (Fig. 2c).

A total of 23 species of rotifers were identified during the four-year study. From this pool of species, *Brachionus caudatus*, *B. havanaensis,* and *Keratella tropica* were the most abundant, with annual mean abundances for each GC typically exceeding 100 ind l^{-1} (Table 2). Within each GC, these three species alternated their dominance in a rather predictable way (see below). In contrast, the set of species occasionally contributing more than 10% to the total rotifers abundance (attendant species) varied between GC. These attendant species included *B. plicatilis* (fourth GC), *Hexartha intermedia* (second GC), *K. americana* (first and second GC), *Polyarthra dolichoptera* (second and fourth GC), *Pompholyx sulcata* (first GC), *Trichocerca ruttneri* (second GC), and unidentified belloids (second and fourth GC). During the third GC, only the three dominant species contributed more than 10% to total rotifer abundance.

The two dominant *Brachionus* species (*B. caudatus* and *B. havanaensis*) exhibited marked seasonality (Fig. 3). Both species developed large populations during warm seasons but were present at very low densities during winter. In fact, *B. havanaensis* was
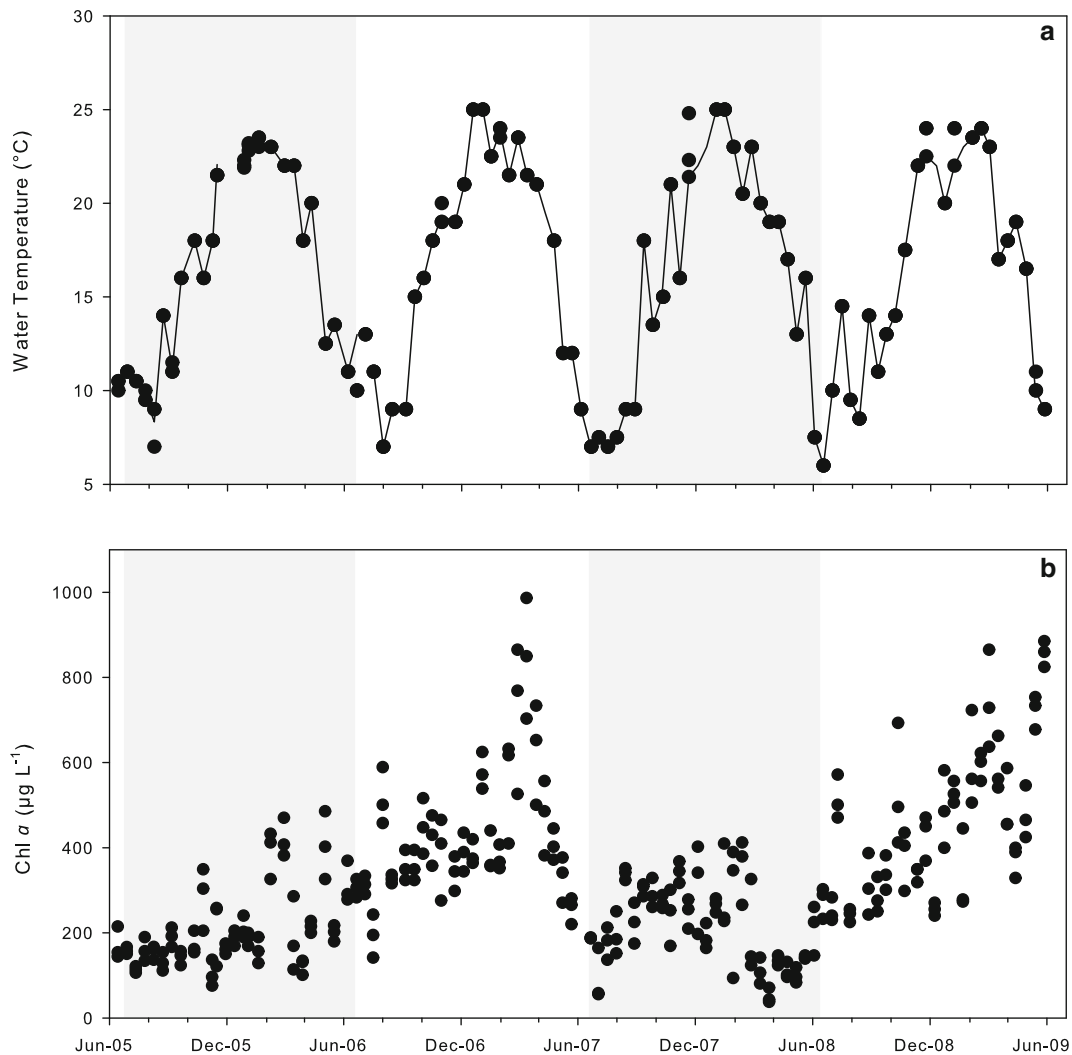
Fig. 1 Temporal change of **a** water temperature (mean data) and **b** Chl *a* concentration (for each sampled site) in Laguna Chascomús. *Shaded* and *non-shaded areas* defined the GC. Gaps between observations indicate lack of data for a particular sampling date

often undetectable for winters. In contrast, the density of the third dominant species, *K. tropica*, was comparatively less variable and its seasonality less evident. The only occasion when *K. tropica* was undetectable occurred during summer and early autumn of the third GC (Fig. 3). The relative contribution of the two dominant *Brachionus* species to total rotifer abundance was greater during the warm seasons and lower during the cold months (Fig. 4).

Total rotifer abundance also fluctuated seasonally in a rather repeatable way. Within each GC, the highest abundance occurred in late summer. This trend was particularly evident during the second and fourth

GC, when total abundance exceeded 3000 ind l^{-1}. Despite the comparatively lower mean abundances for the first GC, a similar pattern could be recognized. The only exception was observed for the third GC, when the rotifer assemblage failed to develop the typical late summer peak (Fig. 2d).

The VAR (1) model fitted for the rotifer abundances gives the next equation system:

$$\ln R_t = 1.12 + 0.0018\text{Chl } a_{t-1} + 0.045T_{t-1} \\ + 0.60 \ln R_{t-1} + e_{1,t}$$
$$\text{Chl } a_t = 42 + 0.89\text{Chl } a_{t-1} + e_{2,t}$$
$$T_t = 1.67 + 0.90T_{t-1} + e_{3,t}$$

,

Table 2 Zooplankton abundance mean and range (minimum–maximum) for each GC

Abundance (ind l^{-1})	First	Second	Third	Fourth
Rotifers	497 (32–1,491)	1,432 (27–6,614)	275 (44–1,061)	1,491 (44–5,103)
Dominant species				
B. caudatus	150 (1–520)	238 (0–1,386)	104 (0–441)	506 (6–1,895)
B. havanaensis	103 (0–851)	637 (0–4,643)	58 (0–528)	480 (0–3,223)
K. tropica	115 (10–223)	337 (25–867)	93 (0–676)	194 (4–762)
Attendant species				
B. plicatilis	–	6 (0–114)	7 (0–32)	148 (0–733)
B. calyciflorus	3 (0–37)	3 (0–56)	3 (0–55)	7 (0–126)
Filinia longiseta	1 (0–15)	1 (0–29)	3 (0–37)	8 (0–60)
Hexarthra intermedia	8 (0–94)	29 (0–181)	– (0–8)	–
K. americana	45 (1–194)	42 (0–210)	2 (0–27)	–
Polyarthra dolichoptera	7 (0–77)	43 (0–257)	2 (0–21)	89 (0–1,123)
Pompholyx sulcata	57 (0–573)	6 (0–116)	2 (0–21)	0 (0–6)
Trichocerca pusilla	6 (0–40)	24 (0–171)	–	31 (0–289)
Bdeloideos		53 (0–328)	– (0–5)	22 (0–169)
Copepods	305 (94–602)	589 (81–2,671)	432 (79–1,449)	401 (120–1,577)
Acanthocyclops robustus				
Nauplii	214 (54–446)	415 (50–2,214)	259 (48–1,066)	270 (40–1,238)
Adults and Copepodites	61 (21–109)	127 (24–399)	93 (14–505)	80 (8–318)
Notodiaptomus incompositus				
Nauplii	25 (3–72)	40 (0–113)	55 (2–306)	35 (5–181)
Adults and Copepodites	4 (0–17)	7 (1–22)	25 (0–165)	16 (2–143)
Cladocerans	5 (0–69)	7 (0–26)	123 (0–611)	20 (0–67)
Bosmina huaronensis	– (0–2)	4 (0–22)	72 (0–493)	13 (0–62)
Moina micrura	– (0–1)	– (0–1)	31 (0–240)	1 (0–6)
Chydoridae unidentified	1 (0–3)	2 (0–7)	2 (0–27)	5 (0–41)

No individual (–). Miscellaneous rotifers species include *Brachionus urceolaris*, *B. bidentata*, *B. quadridentatus*, *B. budapestinensis*, *B. leidigii* (=*B. rotundus*), *B. angularis*, *Lecane* sp., *Lepadella ovalis*, *Monostylla bulla*, *M. subulata*, and *Euchlanis* sp.

where ln R is the natural logarithm of the rotifer abundance, Chl a is the chlorophyll a concentration, T is the water temperature, and e_i represent the residual terms for each model (sub index 1 for ln R_t, 2 for Chl a_t and 3 for T_t). The sub index t refers to values recorded on the current sampling date, and $t - 1$ to values recorded on the previous sampling date.

The VAR model accounted for 76% of the variance (i.e., $r^2 = 0.76$) in the ln transformed rotifer abundance and 72 and 81% of that of Chl a concentration and temperature, respectively. The original data and the adjusted VAR model are plotted in Fig. 5a. The IA performed on the rotifer time series after the winterkill (third GC) showed that the expected rotifer abundance would be have been higher than those that were actually observed for that period (Fig. 5b).

As expected, annual periodicity was supported for temperature ($T = 0.89$), though it was rejected for Chl a. The Fisher's periodicities test failed to detect annual periodicity when it was run on raw rotifer abundance, but provided evidence of annual periodicity when conducted using the intervened time series data set ($T = 0.60$). Finally, annual periodicity was also confirmed when the test was applied to the contribution of two dominant *Brachionus* species to total rotifer abundance ($T = 0.63$).

Discussion

The available evidence indicates that the zooplankton structure of Laguna Chascomús is strongly influenced
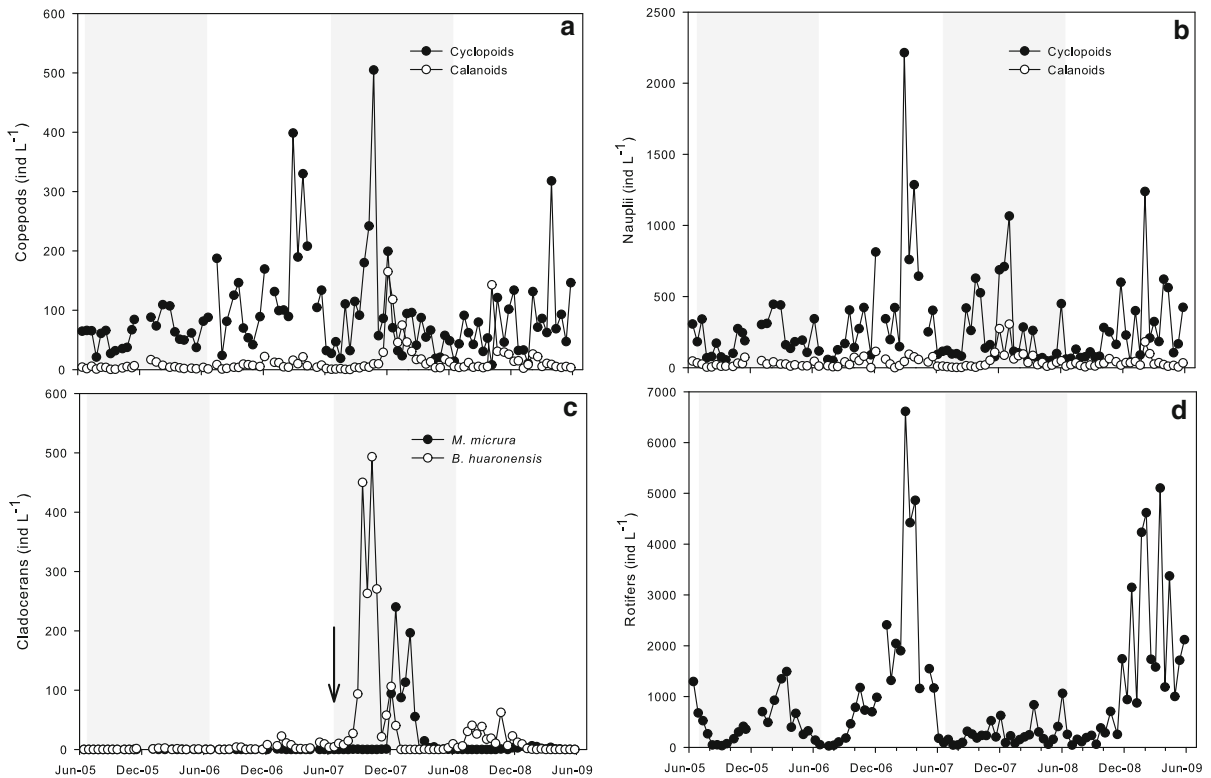
Fig. 2 Temporal change of zooplankton abundance: **a** copepods (copepodites and adults), **b** copepods nauplii, **c** cladocerans, and **d** rotifers. *Arrow* shows the approximate date of massive fish kill, and gaps indicate no data for sampling date

by intense fish planktivory, as inferred by the cladocerans outbreak observed during the period of exceptionally low fish predation pressure. However, even within the rather stringent constraints imposed by fish planktivory (Hrbácek & Hrbáckóvá-Esslová, 1960; Brooks & Dodson, 1965; Iglesias et al., 2011), the zooplankton community exhibited a great deal of inter-annual and seasonal variability. In addition to the striking increase in the abundance of cladocerans recorded for the third GC, the mean and maximum annual abundances of rotifers were several folds higher during the second and fourth GC than during the first and third GC. However, despite large inter-annual differences in total abundance, the species composition of the rotifer assemblage remained fairly stable. In fact, only three species dominated the rotifer community in every GC, namely *B. caudatus*, *B. havanaensis*, and *K. tropica*. The dominance of rotifers and cyclopoid copepods (cyclopoids outnumbered calanoids by about 10 to 1, while the abundance of cladocerans was almost always negligibly) is

characteristic of eutrophic environments that are subjected to strong predation pressure by omnivore-planktivore fish (Iglesias et al., 2011).

The massive winterkill that occurred on 2007 was attributed to the extended period of low water temperatures based on two pieces of evidence. First, winterkill events occurred simultaneously in several water bodies on a geographical scale of roughly 460,000 km^{-2} (Liotta et al., 2007). Second, in Laguna Chascomús, all affected fish were the cold-sensitive species, specifically *Cyphocharax voga* (Günter), *Parapimelodus valenciennesi* (Kröyer), and *Hypostomus commersoni* (Valenciennes) (Gómez, 1996), while there was no noticeable effect on cold-tolerant species, such as the silverside *Odontesthes bonariensis* (Valenciennes) (Gómez et al., 2007). Interestingly, Laguna Chascomús is near the southernmost (i.e., coldest) distribution limit of the affected species (Ringuelet, 1975; Cussac et al., 2009). The combination of changes in certain weather variables, *per se* considered not extreme, may affect the function of

Fig. 3 Abundance
fluctuations for the
dominant rotifer species:
a *B. caudatus*, **b** *B.
havanaensis*, and **c** *K.
tropica*. The water
temperature is shown in
gray line
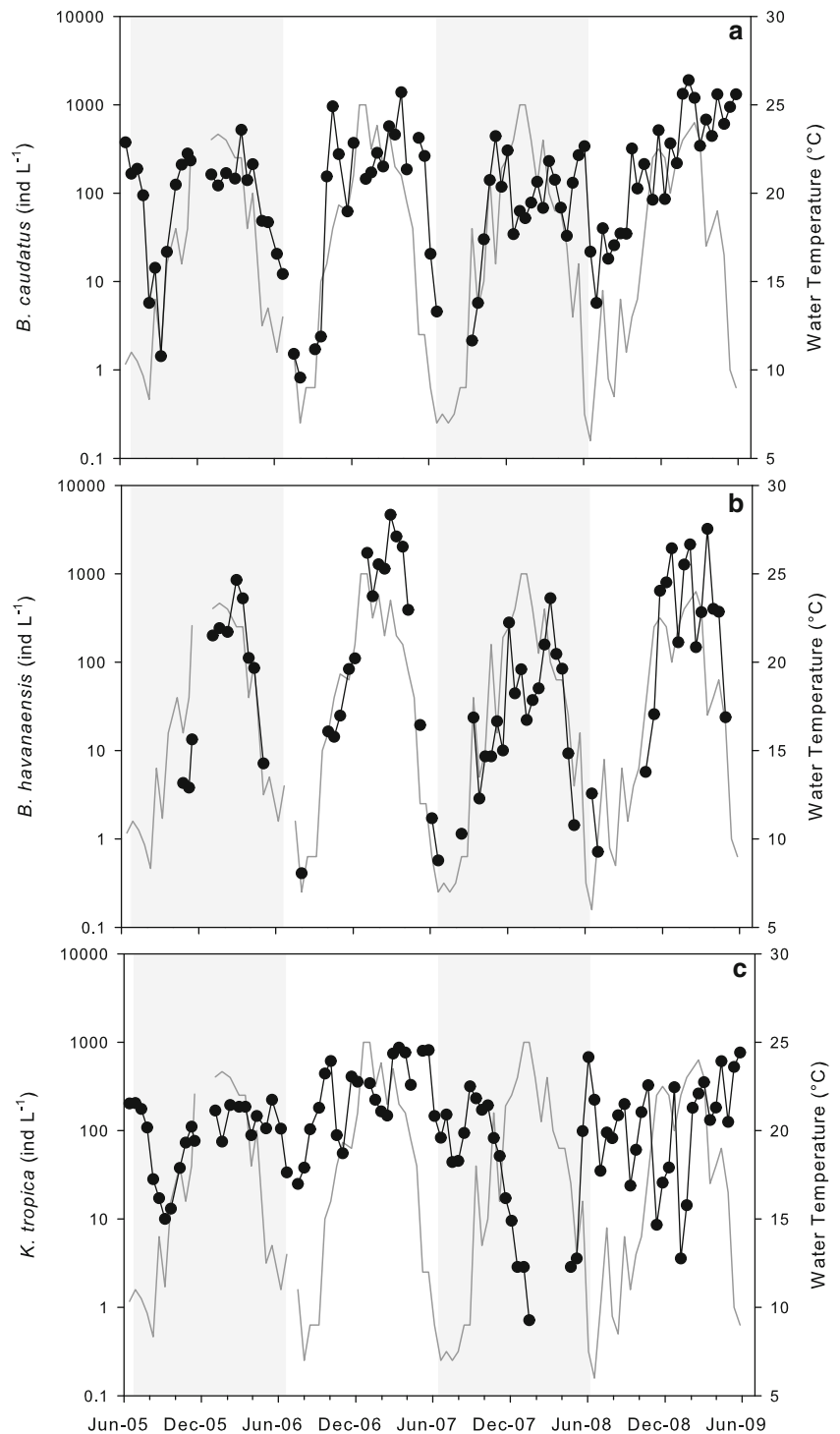
ecosystems when they occur simultaneously (Reich-stein et al., 2013). Here, the extended period of low water temperature happened along with the decrease of lake depth (i.e., reduced thermal inertia), due to

extensive drought season, could have driven the fish winterkill. Regardless of its cause, the massive fish kill may have relaxed planktivory, thereby allowing the development of unusually high populations of small-

Fig. 4 *Brachionus* contribution to total rotifers abundance. The water temperature is shown in *gray line*. Gaps between observations indicate lack of data for a particular sampling date
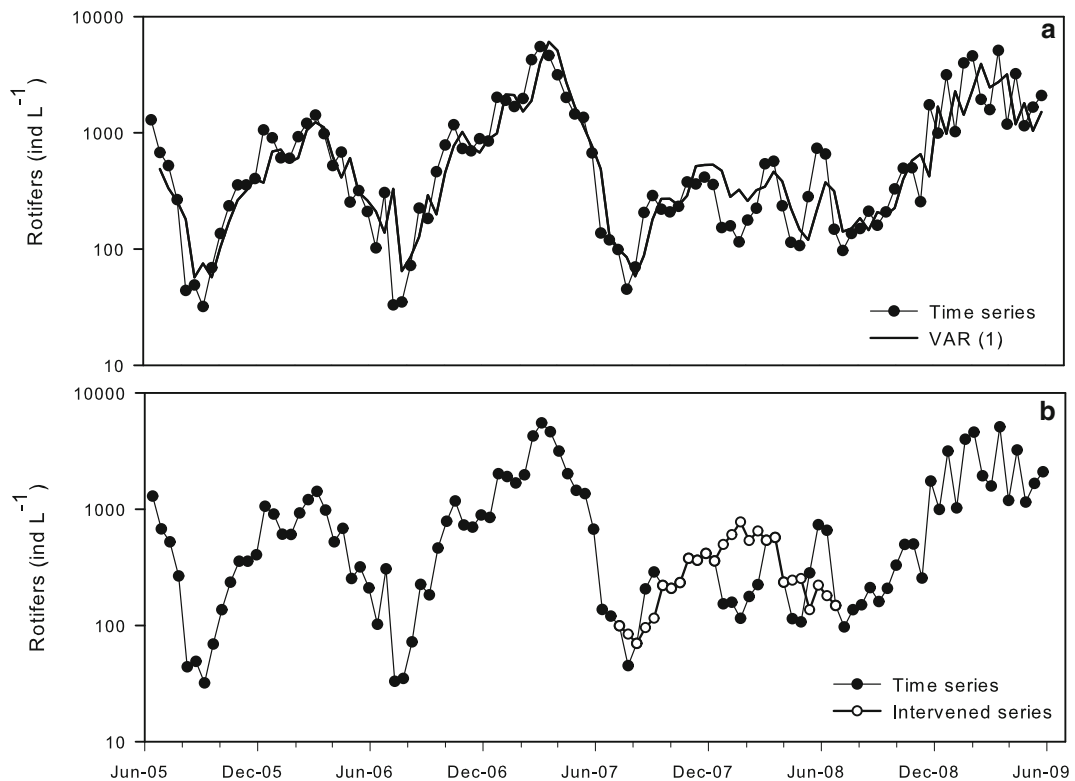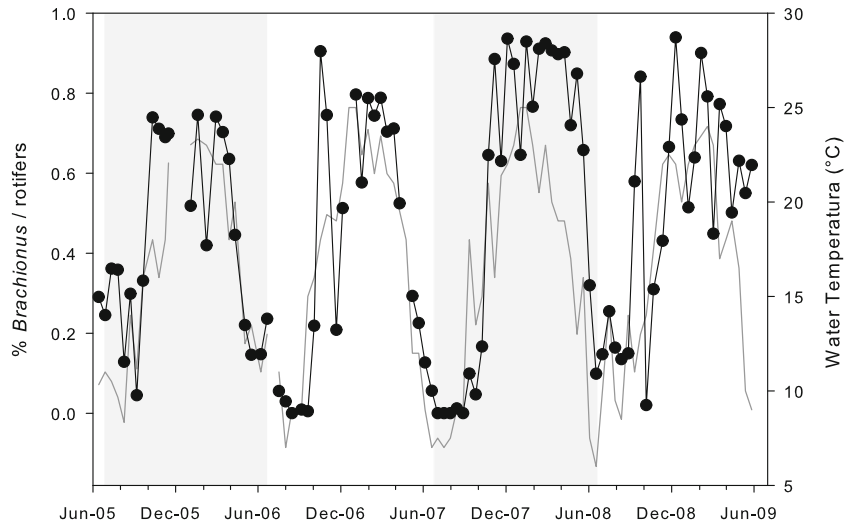

Fig. 5 Model adjusted to rotifer abundance temporal series: **a** VAR, **b** IA for third GC. Rotifer abundance data are presented with points connected by *line*

bodied cladocerans. Essentially, the same pattern was observed in a mesocosm study performed with water from Laguna Chascomús, in which fish were experimentally excluded (Llames et al., 2009).

The VAR developed for rotifer time series accounted for a large amount of the variance (76%) in rotifer abundance. The model provided correlational evidence of the dependence of rotifer abundance on temperature

and Chl *a*, while the complementary IA provided a means to estimate the impact of fish mortality and the subsequent increase in cladoceran abundance on the rotifer community. Temperature directly affects the growth rates of rotifers (Edmondson, 1965; Pavón-Meza et al., 2005) and other zooplankton. An increase in temperature results in a decrease in development times; therefore, the life span is sharply shortened (Walz, 1995), and reproduction is restricted to a narrower age interval (Snell & King, 1977). The population parameters of rotifers change in relation to temperature and so its effects could be viewed through their dynamics in the natural environment. Furthermore, rotifers are capable of very fast population growth due to their short generation times and large reproductive potential. Under appropriate environmental conditions (e.g., temperature), the availability of suitable food items stimulates high fecundity rates (Dumont, 1977; Lynch, 1979; Ooms-Wilms et al., 1999). It comes as no surprise that increased food availability—measured variously as seston, Chl *a*, or direct phytoplankton counts—be a precondition for the development of large rotifer populations (Dumont, 1977; Gulati, 1990). In the shallow eutrophic Lake Okeechobee, for example, Beaver & Havens (1996) observed that rotifer population density was positively related to increased levels of Chl *a*. Nevertheless, we acknowledge that a direct relationship between rotifer abundance and Chl *a* is not always observed. Some authors suggest that the ability of rotifers to feed on detritus and bacteria makes them less dependent on phytoplankton than planktonic crustaceans (Ruttner-Kolisko, 1974; Conde-Porcuna et al., 2002). However, there is no conflict between these seemingly opposite views. In a study of optical properties in Laguna Chascomús, Pérez et al. (2011) found that the major process controlling light availability was not phytoplankton self-shading, but the depletion of radiant energy was caused by absorption and scattering due to non-algal particulates (the so-called background light attenuation). On the other hand, the dynamics of these non-algal particulates was driven, to a large extent, by the amount of incident light. Therefore, we suspect that the non-algal particulate matter corresponds to heterotrophic components that develop at expense of phytoplankton primary production. We suggest that temperature has multiple effects on the rotifer community of Laguna Chascomús: (i) it sets habitability limits for warm stenotherm species, such as *B. havanaensis* (Ruttner-Kolisko, 1974), (ii) it has a

positive effect on population growth rates by decreasing generation time, and (iii) due to its strong correlation with incident solar radiation, temperature (along with Chl *a*) provides an indirect measure of environmental productivity and food availability (Torremorell et al., 2009).

Some interesting seasonal patterns emerged from the analysis of the rotifer time series. The abundance of the two dominant *Brachionus* species, *B. caudatus* and *B. havanaensis*, peaked through summer and early autumn, and remained lower during winters. As result, the joint relative contribution of these two species to total rotifer abundance also varied seasonally, even during the third GC, when rotifer populations failed to develop the usual late summer-early autumn peak. The abundance of rotifers as a whole also tended to increase during late summer and early autumn. This trend is consistent with patterns reported for other eutrophic lakes (Whitman et al., 2004; Castro et al., 2005). During the third GC, however, the rotifer assemblage failed to develop the usual late summer-early autumn peak. The IA confirmed the impact of the winterkill event on rotifers abundances, presumably mediated by the development of dense cladoceran populations. Moreover, the Fisher's test confirmed the annual periodicity of the intervened rotifer time series. Rotifers are known to be negatively affected by large numbers of cladocerans (Walz, 1995; Pollard et al., 1998). Two possible mechanisms have been proposed to account for the depressive effect of cladocerans on rotifers: mechanical interference (MacIsaac & Gilbert, 1991; Fradkin, 1995) and competition for limiting resources (Fussmann, 1996; Conde-Porcuna, 2000). Mechanical interference appears to be restricted to large-bodied cladocerans, such as *Daphnia* (MacIsaac & Gilbert, 1991). Therefore, it seems unlikely that small-size species, such as *B. huaronensis* and *M. micrura*, could have directly affected the performance of rotifers. On the other hand, cladocerans and rotifers feed on a similar size and type of particles (Walz, 1995), but being more efficient feeders, cladocerans have an advantage over rotifers (Gilbert, 1985). We, therefore, suspect that the failure of rotifers to increase their abundance during the third GC was caused by the depletion of food availability (as measured by Chl *a*) due to the presence of the unusually abundant cladoceran populations developed as a consequence of decreased fish planktivory.

To summarize, we suggest that the plankton community of Laguna Chascomús is strongly driven

by intense and persistent fish planktivory. Under these circumstances, only highly evasive (cyclopoids) or small and fast growing (rotifer) groups have chances of developing large populations. These conditions may be temporarily affected by external climatic events. But, at least in the case examined here, the community reverted to pre-fish mortality conditions by the following year. The rotifer community species composition was rather stable, but the population dynamics of the dominant rotifer species seems strongly influenced by environmental productivity (as measured by temperature and Chl a). Put in another way, the collected evidence suggests that zooplankton community structure is controlled by top-down processes, while rotifers' population dynamics are driven by bottom-up forces, and both are highly responsive to external climate variables.

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