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ARGENTINE PAMPEAN SHALLOW LAKES

Fish assemblage of a Pampean shallow lake, a story of instability

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Abstract Pampean lakes are characterised by the alternation of flood and drought periods, but little is known about its effects on fish assemblage in an extended temporal scale. This study analyses the temporal variability of the fish assemblage in Chascomús Lake, and discusses the role of temperature and precipitation as potential drivers of fish composition shifts. Data acquisition was based on experimental fishing performed from 1999 to 2013 and from historical fishing records. Two alternative fish assemblage configurations were identified by cluster analysis. *Odontesthes bonariensis*, *Parapimelodus valenciennis* and *Cyphocharax voga* were the dominant species, which accounted for 70–80% of the relative abundance. The species *O. bonariensis* showed temporal fluctuations in its representativeness, changing from dominant to almost absent, whereas *C. voga* and *P. valenciennis* changed their abundance following a similar pattern along time. When historical data were considered, *Platanichthys platana* appeared as the fourth most relevant species. Precipitation, critical temperatures and fish mortalities were identified as the main drivers of species abundance shifts. This study highlights the importance of long-term assessments to understand the influence of climatic factors and the need to maintain or restore natural ecological processes as the basis to support dynamic sustainable fisheries in Pampean shallow lakes.

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Introduction

Pampean lakes are located in the central part of Argentina in a plain territory of about 300,000 km^2. These freshwater waterbodies are shallow and commonly eutrophic environments (Quirós & Drago, 1999), characterised by a high limnological variability (Quirós et al., 2002a, b; Allende et al., 2009; Izaguirre et al., 2012). Such variability is strongly influenced by their hydrologic dynamics (Quirós et al., 2002a; Torremorell et al., 2007) driven not only by regional rainfalls but also by water table regimes, which maintain and expand lake areas (Bohn et al., 2011), whereas low precipitation periods along with evaporation and infiltration promote their drying. However, in the Pampean region, these processes have been artificially altered during the last century, due to the development of man-made channels and weirs installed at lake outlets, associated with water management goals. Environmental conditions in Pampean lakes have also been linked to agricultural development and climatic events (Quirós et al., 2002a, 2006; Echaniz & Vignatti, 2013). For example, Conzonno & Claverie (1990) stated that high precipitation levels promote noticeable changes in water chemistry. In fact, it was postulated that extreme rainfall events may increase the phosphorus loading of lakes by runoff from surrounding lands (Mooij et al., 2005), creating eutrophication problems for shallow lakes, demonstrating how water level fluctuations modify lake ecological characteristics (Hofmann et al., 2008; Leira & Cantonati, 2008). Indeed, shallow lakes are a paradigmatic example of highly variable waterbodies where biological communities respond to hydrology, regional climate and land use, which influence primary and secondary production (Kosten et al., 2009).

Although cyclical alternation of wet and dry periods has been documented as a common feature in the Pampean region (Sierra et al., 1994), no long-term data (more than 10 years) have been obtained to assess the influence of these factors on fish assemblages. As species are affected by changes in lake environmental conditions, the temporal analysis of fish assemblage structure can be considered a reliable indicator of natural and anthropogenic impacts. Significant changes in Pampean fish assemblages have been observed during the last decade (Colautti et al., 2003; Berasain et al., 2005), which have also been associated with natural and anthropogenic variables (Rosso & Quirós, 2009). These authors demonstrated that conductivity, water residence and land use were involved in temporal and spatial patterns of fish abundance and distribution in four Pampean lakes during four consecutive summers. Clearly, such an environmental-based approach emerged as relevant, considering that the fish assemblages of the Pampean lakes are composed of several species found in the southern distribution of the Brazilian subregion, inhabiting an extended and fluctuating ecotone which limits with the Austral subregion (Ringuelet, 1975; Baigún et al., 2002; López et al., 2002; Rosso & Quirós, 2010). Additionally, as a complementary source of changes for fish composition, Menni (2004) suggested that species movements among the waterbodies of the Pampean region occur during flood periods, when the connectivity increases and thus facilitates the ingression of several migratory species from the inner part of the Río de la Plata estuary. Moreover, fish mortalities have occasionally been observed in these lakes and rivers (Freyre, 1967; Gómez, 1996; Colautti et al., 1998), and although these events appear to be recurrent, its effect over the fish assemblage have never been analysed.

Chascomús Lake is the most limnologically studied Pampean lake, and was considered a typical water body of the region (López et al., 2008). This lake, as other lakes located in the area, shows pronounced hydrological variability as a common feature characterised by alternations of the wet and dry periods (García-Rodríguez et al., 2009; Scarpati & Capriolo, 2011) that affects lakes connectivity (Quirós et al., 2002a). The valuable fishing resources of this lake have promoted several studies on fish population density (Freyre et al., 1967; Alaimo & Freyre, 1969), species composition (Berasain & Remes Lenicov, 2004; Berasain & Argemi, 2006, 2008), richness and diversity (Barla, 1991), biological characteristics of species (Ringuelet, 1942; Destefanis & Freyre, 1972; Ringuelet et al., 1980), seasonal fish assemblage variations (Berasain et al., 2005) and the structure and functioning of the lake (Diovisalvi et al., 2010). However, understanding of the mechanisms involved in the dynamics of changes in fish assemblage over time, encompassing multiannual drought and flood cycles in the region, deserves further research. As fish assemblage reflects the influence of natural gradients, climate fluctuations and anthropogenic disturbance (Herwig et al., 2010), the study of its changes on a long-term basis, their timings and links with environmental variables become critical not only to increase ecological knowledge, but could also provide insights into the management of the fisheries that have high socio-economic relevance for the Pampean region (Baigún & Anderson, 1994; Balboni et al., 2011). Therefore, the aim of this study was to analyse the temporal variability of fish assemblage in Chascomús Lake between 1999 and 2013, to compare these results with historical records and discuss the role of precipitation cycles, critical temperatures occurrence and fish mortality events, as the potential main drivers for fish composition shifts.

Materials and methods

Study area

Chascomús Lake belongs to the Salado River basin, which is the main Pampean course running along a wide flat valley, forming and connecting marginal lakes before entering the Río de la Plata estuary. The lake is connected through chained lakes to the Salado River (Fig. 1). The lake area is about 3,000 ha with a mean depth of 1.53 m under normal hydrological conditions (Dangavs et al., 1996). Nevertheless, this water body is characterised by the periodic alternating drought (0.70 m) and flood periods (3.3 m) (Diovisalvi et al., 2010). According to its salinity, it was classified as oligohaline (<5 g/L of total dissolved solids), sodic and chlorine bicarbonate type (Ringuelet et al., 1967a). The lake is polymictic and exhibits eutrophic conditions, in agreement with other Pampean lakes (Quirós et al., 2002b). Based on phosphorous contents, it can be classified as hypereutrophic (Conzonno & Claverie, 1990) as it also has a high primary production rate (Torremorell et al., 2007). The surrounding area, as the whole Pampa plain, is characterised by agricultural and cattle ranching profile, meaning that the landscape is heavily modified (Viglizzo et al., 2011).

The Pampean climate exhibits humid subtropical conditions with a mean annual precipitation ranging from 400 to 1,080 mm, depending on a west-east rainfall gradient, and the mean annual air temperatures ranging between 11.5 and 16.9°C (Hijmans et al., 2004). Its climatic profile corresponds to the Cfb type according to Köppen–Geiger climate classification (Kottek et al., 2006).

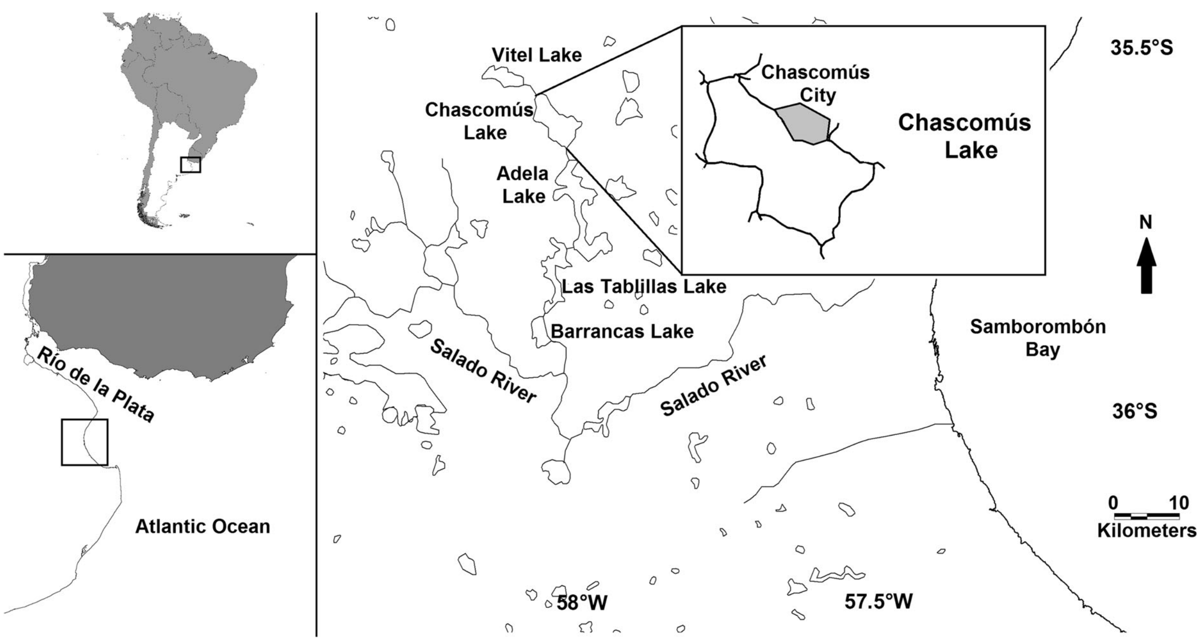

Fig. 1 Chascomús Lake geographical location and related shallow lakes

Samplings and data analysis

Experimental fishing was applied from 1999 to 2013. Samplings were performed seasonally between 1999 and 2004 (except 2003) and bimonthly between 2005 and 2013 (except 2009). In both sampling periods, trap nets (Colautti, 1998) were used in two lake sites during one night. All of the fish captured were identified and counted. The identification was done to the species level following Ringuelet et al. (1967b) and specific names, when required, were updated by means of recent taxonomic papers. The captures were standardised to a fishing effort of 12 h (CPUEn).

To avoid seasonal effects within years, annual averages of species relative abundance were estimated, and the obtained matrix was normalised. Fish assemblage among years was assessed by hierarchical agglomerative cluster, and group-average linkage method was used based on the Bray–Curtis (dis)similarity index. To determine whether or not significant differences in assemblage structure had occurred among the fish groups identified by cluster analysis, an ANOSIM test (non-parametric analysis, permutation-based one-way ANOSIM) was applied considering the fish assemblage groups obtained as factors. The fish species most responsible for the multivariate pattern were identified by means of a similarity-percentages analysis (SIMPER). Species that contributed greatly to the dissimilarity between the groups were selected as those accounting for the assemblage differences ("discriminating species"). These multivariate techniques were performed using the PRIMER 6 statistics package (Clarke & Warwick, 2001).

The results from experimental fishing were compared with historical data available in Alaimo & Freyre (1969) and Freyre et al. (2003), compiled in Berasain et al. (2005), where data from samplings performed in 1995 were also available. As these data were acquired by means of a beach seine net, which has low selectivity, like traps (Colautti, 1998), they were considered appropriate for detecting temporal changes in the relative abundance of species.

Depth and conductivity records at each sampling date were provided by the Laboratory of Aquatic Ecology and Photobiology (INTECH). Daily values of precipitation (1957–2013) and air temperature (1995–2013) were obtained from local Instituto Nacional de Tecnología Agropecuaria (INTA) station, with rainfall values considered proxies of lake hydrological regime. Maximum month mean temperature, minimum month mean temperature, average maximum mean temperature of the year's hottest month and average minimum mean temperature of the year's coldest month were calculated. Historical flood and drought periods were obtained from Diovisalvi et al. (2010). Fish mortality events registered by the authors since 1995 were linked to the environmental variables mentioned above.

Results

According to the experimental fishing, fish assemblage included a total of 19 species belonging to 18 genera and 11 families, although the greatest diversity belonged to the order Siluriformes (7 species) and Characiformes (6 species) (Table 1).

The cluster analysis for the entire data set containing the yearly fish assemblage composition produced two different groups at 65% level of similarity reflecting the existence of temporal changes in fish assemblage (Global $R = 0.72$, $P < 0.01$; ANOSIM) (Fig. 2). Group 1 encompassed 1999, 2000, 2001, 2008, 2010, 2011, 2012 and 2013 and presented an average similarity of 77.71% (Table 2). These years shared a high abundance of *Parapimelodus valenciennis*, *Odontesthes bonariensis* and *Cyphocharax voga* (Fig. 3). These three species explained more than 90% of intra-group similarity (Table 2). Group 2 included 2002, 2004, 2005, 2006 and 2007 years and showed a similarity of 79.02% (Fig. 2; Table 2). It was characterised by a dominance of *P. valenciennis* and *C. voga*, explaining 90% of the intra-group similarity, and by an almost absence of *O. bonariensis* (Fig. 3; Table 2). In Table 2, the average dissimilarities between groups are presented, highlighting that the difference between groups was primarily caused by variation in the relative abundance of the dominant species (*O. bonariensis*, *P. valenciennis* and *C. voga*) and to a lesser extent by four other species.

A large difference between historical records and the results obtained from experimental sampling was found when the relative abundance of the dominant fish species was compared. Values of relative abundance of *P. valenciennis* ranged from less than 5% in 1966 to almost 80% in 2007 and a similar trend of change was observed for *C. voga*, but reaching lower abundance values. Conversely, *O. bonariensis* exhibited an opposite trend characterised by minimum

Table 1 List of species comprising the Chascomús fish assemblage during the sampling period

Family	Species
Clupeidae	*Platanichthys platana* (Regan, 1917)
Curimatidae	*Cyphocharax voga* (Hensel, 1870)
Characidae	*Astyanax eigenmanniorum* (Cope, 1984)
	Astyanax fasciatus (Cuvier, 1819)
	Bryconamericus iheringii (Boulenger, 1887)
	Hyphessobrycon anisitsi (Eigenmann, 1907)
	Oligosarcus jenynsii (Günther, 1864)
	Cheirodon interruptus (Jenyns, 1842)
Erythrinidae	*Hoplias malabaricus* (Bloch, 1974)
Callichthydae	*Callichthys callichthys* (Linnaeus, 1758)
	Corydoras paleatus (Jenyns, 1842)
Loricariidae	*Loricariichthys anus* (Valenciennes, 1846)
	Hypostomus commersoni (Valenciennes, 1836)
Pimelodidae	*Parapimelodus valenciennis* (Lütken, 1874)
Heptapteridae	*Pimelodella laticeps* (Eigenmann, 1917)
	Rhamdia quelen (Quoy & Gaimard, 1824)
Atherinopsidae	*Odontesthes bonariensis* (Valenciennes, 1835)
Anablepidae	*Jenynsia multidentata* (Jenyns, 1842)
Cyprinidae	*Cyprinus carpio* (Linnaeus, 1758)

values of abundance between 2002 and 2007. In turn, *Platanichthys platana* was dominant (60%) in 1966 and 1984, but drastically diminishing its relative abundance from 1999 until the present (Fig. 3). The year 1995 was characterised by an almost equal dominance of *P. platana* and *P. valenciennis* and a low percentage representation of *O. bonariensis* and *C. voga*. For this year, the relative abundance of the species could be considered as intermediate between 1966 and 1984 data and that obtained during experimental fishing.

The annual rainfall regime for the last six decades was highly variable and, according to Diovisalvi et al. (2010), includes seven flooding and seven drought events (Fig. 4). Drought periods were in agreement with years of low rainfall, as occurred between the 60s and 70s, whereas flood events appeared mainly during years of high precipitation, from 1980 to 2003. After 2003, a weak precipitation regime was noted, again promoting drought episodes. During the sampling period, the most frequent conductivity was around 1.73 mS cm^{-1} varying from 0.5 to 4 mS cm^{-1} during drought and flood periods, respectively.

From 1995 to the present, three fish mortalities occurred as punctual events (Fig. 5). They were

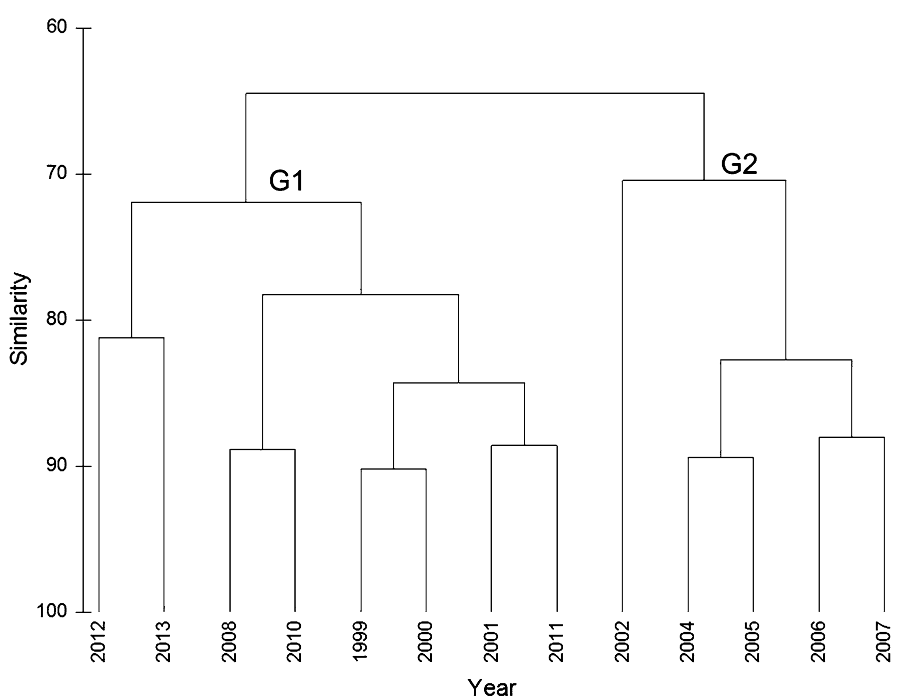

Fig. 2 Cluster analysis showing the temporal pattern of the Chascomús Lake fish assemblages during the experimental sampling period. *G1* group 1, *G2* group 2

Table 2 Average dissimilarities between groups highlighting those species most responsible for inter-group discriminations

Groups 1 and 2 Species	Avg. Diss. Group 1 Av. Abund.	35.51 Group 2 Av. Abund.	Avg. Diss.	Diss./SD	Contrib. %	Cum. %
O. bonariensis	24.82	0.80	12.01	4.11	33.83	33.83
P. valenciennis	44.68	61.88	8.63	1.48	24.32	58.15
C. voga	16.96	19.47	5.22	1.47	14.71	72.86
H. commersoni	1.67	4.95	1.94	1.38	5.47	78.33
C. interruptus	2.84	2.28	1.45	1.27	4.08	82.41
Astyanax sp.	1.15	3.47	1.34	1.72	3.77	86.18
P. laticeps	1.77	1.88	1.14	1.00	3.22	89.39
P. platana	2.13	1.82	1.09	1.22	3.08	92.47

Avg. Diss. average dissimilarities, *Av. Abund.* average abundance, *Contrib. %* percentage contribution, *Cum. %* accumulative percentage contribution

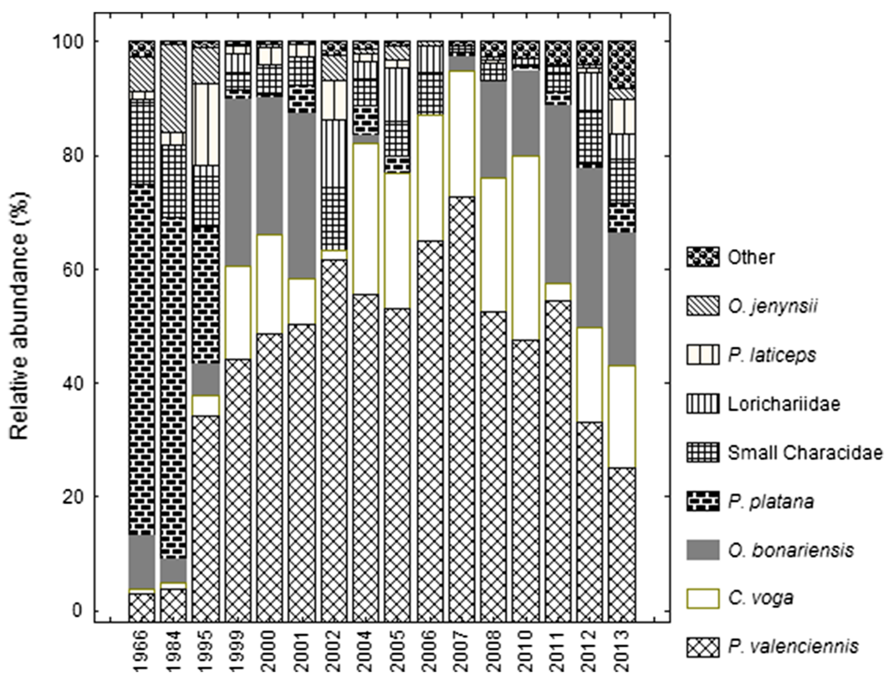

Fig. 3 Relative abundance for the fish assemblage of Chascomús Lake. Note that *Loricariichthys anus* and *Hypostomus commersonii* were considered together as family Loricariidae as well as *Astyanax eigenmanniorum*, *Astyanax fasciatus*, *Bryconamericus iheringii*, *Hyphessobrycon anisitsi* and *Cheirodon interruptus* were pooled in the small Characidae category due to the uncertain taxonomic identification in the historical data

detected only in drought situations, twice when the values corresponding to minimum month mean temperature fell below the mean temperature of the year's coldest month for more than 1 month in the same year, and once when the maximum month mean temperature remained close to the average of maximum mean temperature of the year's hottest month for several months. The affected species mainly corresponded to Neotropical orders Siluriformes and Characiformes. The mortality event of 1996 dominated by *Hoplias malabaricus* and *Cyprinus carpio* can be associated to high temperatures, while that occurring during the same year but linked to low temperatures showed that *P. valenciennis* was the main species killed (77%) followed by *Hypostomus commersoni* (11%), *H. malabaricus* (4%) and others (8%). In turn, in 2007, the most affected species were *P. valenciennis* (75%), *H. commersoni* (17%), *Loricarichthys anus* (6%) and *C. voga* (2%), with this event being related to extremely low temperatures. These two winter fish

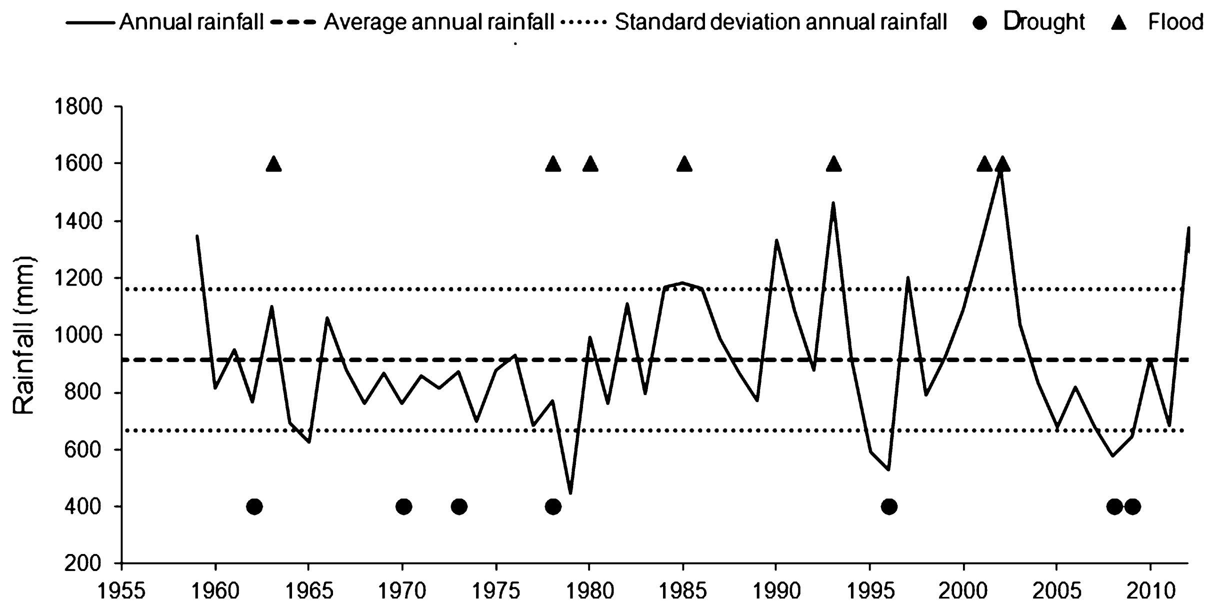

Fig. 4 Annual rainfall in the last six decades in Chascomús area. Flood and drought events were considered according to Diovisalvi et al. (2010)

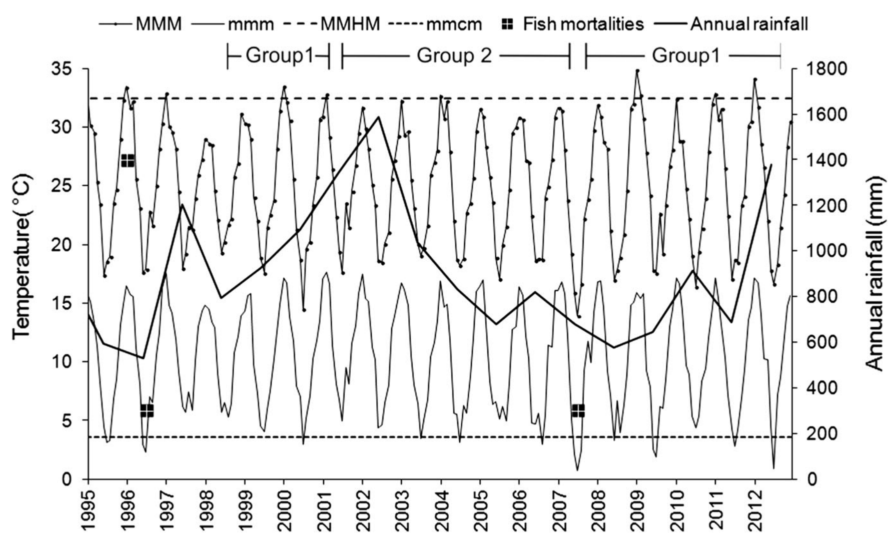

Fig. 5 Air temperature, fish mortalities and annual rainfall between 1995 and 2012 in Chascomús area. *MMM* maximum month mean temperature, *mmm* minimum month mean temperature, *MMHM* average of maximum mean temperature of the year's hottest month, *mmcm* average of minimum mean temperature of the year's coldest month. G1 and G2 are the years belonging to the groups detected by cluster analysis

mortality events affected almost the same species as those documented by Freyre (1967), also during a winter kill.

It is important to note that group 1, identified by cluster analysis, included those years that followed fish mortality events in 1996 and 2007, whereas group 2 contained the years between the 2002 flood period and the 2007 winter fish kill event (Figs. 2, 5).

Discussion

The current study provides, for the first time, analysis of the fish assemblage shifts in Chascomús Lake by describing how such changes could correspond to climate variables that have influenced the Pampean region during the last fifteen years.

According to our results, zooplanktivorous species such as *O. bonariensis* and *P. valenciennis*

(Quirós et al., 2002a; Freyre et al., 2009; Garcia de Souza et al., 2013) and to a lesser extent the detritivorous–planktivorous *C. voga* (González Sagrario & Ferrero, 2013), accounted for more than 70% of the differences between fish assemblage groups (Fig. 2). This study identified *O. bonariensis* as the discriminant species that explains the major differences between the fish composition groups over time. This species almost disappeared when flooding reached its peak in 2002, and remained practically absent until 2007, when an exceptionally cold and dry winter generated fish mortality that affected other species. After 2007, *O. bonariensis* progressively increased its relative abundance, reaching values of around 25%, as shown by the group 1 composition (Figs. 2, 3, 5; Table 2). In upper Salado River lakes, Rosso & Quirós (2009) stated that *O. bonariensis* abundance suffered a strong depletion at the peak of the flood period, suggesting that this species moves inside the basin following a conductivity gradient (7.8 mS cm^{-1}) according to its brackish water affinity. In Chascomús Lake, the conductivity variation was narrower (3.5 mS cm^{-1}) than that recorded by the referred authors; nevertheless, *O. bonariensis* showed the same population response to flood, becoming scarce in the flooded water body. This is an indicator that species life history traits include a behaviour pattern triggered by intense flooding events, which could be envisioned as an ecological mechanism to disperse among connected lakes in the Pampean region, recolonising them after long dry periods. Such phenomena of spread and colonisation of new environments, as pioneer species, are common for other atherinids (Bamber & Henderson, 1988).

Conversely, the abundance of *P. valenciennis* and *C. voga* increased after the flooding event, becoming the main components of the fish assemblage and corresponding to the group 2 identified by cluster analysis (Figs. 2, 3, 5; Table 2). This is in agreement with Rosso & Quirós (2009), who observed that in wetter summers, with low salinity and short water residence time, the abundance of *C. voga* is favoured. The referred authors carried out their study in open lakes of the upper Salado River basin, and although the present study was performed in a semi-closed lake of the lower basin, the response of dominant species was similar. Thus, changes in Pampean fish assemblage inhabiting such type of lakes appear to be linked to other climatic variables besides conductivity and water residence time.

Temperature is another factor that can critically affect Pampean fish assemblages, as most of them have a brasilic origin, with the Salado River watershed being considered the southernmost distribution limit (López et al., 2002). Low temperature has been identified as the most important factor determining the southern boundary of neotropical fish distribution in Argentinean freshwater ecosystems (Gómez, 1996; Menni, 2004; López et al., 2008; Cussac et al., 2009), although some species (*Corydoras paleatus*, *Jenynsia multidentata*, *Astyanax eigenmaniorum*, *Oligosarcus jenynsii* and *Cheirodon interruptus*) have shown better acclimation to colder conditions (Baigún et al., 2002). The observed selective mortality events during 1996 and 2007, which mainly affected two of the dominant species (*P. valenciennis* and *C. voga*), can therefore be explained by unfavourable thermal conditions associated with droughts. In turn, Balboni et al. (2011) showed that the demographic structure and abundance of *H. malabaricus*, the top predator fish of the Pampean region, appears to be regulated by extreme cold temperatures. These situations do not represent unusual events, since were previously reported in Chascomús Lake by Freyre (1967), and in other Pampean lakes by Gómez (1996) and Colautti et al. (1998). However, the influence of temperature could be buffered or potentiated by hydrological conditions, explaining why mortality events do not occur during normal or high water level periods. In fact, as shown in the results, temperature presented acute short-term effects only when the minimum or maximum values remain below the minimum monthly mean temperature or above the maximum monthly mean temperature for more than one month (Fig. 5). Hence, temporal matching of unfavourable thermal conditions and low water level promotes changes in fish assemblage toward a configuration like the group 1 identified by the cluster analysis (Figs. 2, 3; Table 2).

Rosso & Quirós (2010), based on a four consecutive summer sampling programme, demonstrated that water residence time, total phosphorus, NO_3:NH_4 ratio and water conductivity determined fish abundance and distribution in several lakes of the upper Salado River basin. However, on a longer-term basis, our results indicate that flood and drought cycles coupled to extreme temperatures appear to be the main driving factors in structuring fish assemblages in Chascomús Lake. This is clearly displayed by the alternation of different assemblage structures along time, which appear to be closely related to extreme hydrology events and fish mortalities. It is remarkable that these punctual or short-term episodes have long-lasting effects over the fish assemblage, which remain until a new extreme event occurs. However, the human alteration of natural flood regimes through Pampean lakes, mainly for agricultural purposes, could produce changes in the frequency and intensity of fish mortality events, suddenly affecting the structure of fish assemblages.

A noticeable feature that emerged from this study when the results were compared with historical data was the dominance of *P. platana*, a zooplanktivorous species (Destefanis & Freyre, 1972), before 1995 (Fig. 3). The high dominance of *P. platana* in 1966 and 1984 can be associated with the high fishing pressure exerted on *O. bonariensis* populations in Pampean lakes during the XX century (Baigún & Delfino, 2003). In the last decades, the growing abundance of *P. valenciennis* could also explain the low representativeness of *P. platana*, since these species compete for the same food resources. In addition, according to Quirós et al. (2006), the agricultural and urban development during the last century have impacted not only on the natural hydrological regime on the Pampa plain, but also on its nutrient loads. This kind of impact, which operates on a different temporal scale, has also modified the Chascomús Lake fish assemblage composition, favouring the increment of *P. valenciennis* and *C. voga* abundance (Berasain et al., 2005) (Fig. 3). The affinity of both species to anthropogenically impacted environments was also observed by Rosso & Quirós (2009). Therefore, the abundance increments of these two species in Pampean lakes could be considered a reliable indicator of anthropogenic impacts, as observed for other freshwater fish species (Ibarra et al., 2003; Egertson & Downing, 2004).

The findings of the present study demonstrate the need to maintain reliable and long-term fish assemblage studies along with limnological data acquisition, in order to detect major shifts in fish composition in different time scales. Although our results and conclusions were mostly developed on a descriptive basis, pointing out the potential influence of climate factors, they are still valid for drawing attention to how climatic events can be related to the existence of different fish assemblage composition patterns, changing on an inter-annual scale. Certainly, long-term data would be required to validate the findings in a sounder statistical way, also considering that climate factors can exert delayed effects and be auto-correlated. Freyre et al. (2003) noted that short-term fish assemblage characterisation could have low predictability when applied to Pampean lakes management. Climatic variables seem to be of extreme relevance for modelling fish assemblages at an inter-annual scale, suggesting that fish composition as a whole, and particularly the abundance of the recreational target fish species *O. bonariensis* and *H. malabaricus*, are at least partially regulated by density-independent effects triggered by hydrological cycles and temperatures. As fish assemblage changes in Chascomús and other Pampean lakes are environmentally driven, traditional management practices, considered from an annual focus (http://www.maa.gba.gov.ar/pesca/), have a very low impact. This is a challenge for managers to apply new and more dynamic criteria based on climatic phenomena, and their ecological implications over a longer scale than was considered until the present. Such a feature could have strong relevance in view of the incoming climate change (IPCC, 2007), which predicts an increase in temperature of 1.5–3°C in the region, but no major changes in precipitation (Barros et al., 2006).

In conclusion, a better understanding of how Pampean lake fish assemblages respond to climate and man-made impacts should be achieved, as changes could have significant socio-economic consequences at the regional level. This highlights the need to develop an ecosystemic perspective to maintain or restore natural ecological processes that affect the Pampean shallow lakes and to support long-term data acquisition for a better comprehension of their structure and functioning patterns.

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