

Influences of ENSO and PDO phenomena on the local climate variability can drive extreme temperature and depth conditions in a Pampean shallow lake affecting fish communities

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Abstract The aim of this study was to characterize occurrence of extreme temperature and depth conditions affecting fish community in a shallow lake as result of local climate variability, in turn influenced by the ENSO and PDO phenomena. Extreme depth and water temperature events (modeled from local weather conditions) were characterized from 1966 to 2012 to estimate changes in *Chascomús* lake fish communities. The ENSO and PDO influences on the occurrence probability of these ecosystem changes were investigated. Four significant changes in *Chascomús* Lake fish assemblage were identified during period assessed, as response to extreme temperature and depth events. Extreme high depth conditions would have changed fish community during 1987 and 2002, leading to a configuration characterized by the absence of the most emblematic fish species in *Chascomús* Lake, the pejerrey (*Odontesthes*

bonariensis). On the other hand, extreme low water temperatures would have promoted a fish community characterized by the dominance of this last species during 1966–1986, 1997–2001 and 2008–2013 periods. Furthermore, extreme shortening in pejerrey spawning season was significantly related with decrease of its relative abundance. The occurrence probability of the extreme physical conditions modifying *Chascomús* Lake fish communities was significantly explained by ENSO (by depth influences) and by PDO (by water temperature influences). Thus, this study showed strong correlations between the ENSO and PDO influences and the occurrence probability of the extreme physical conditions changing fish community in *Chascomús* Lake.

Keywords Climate variability · ENSO-PDO · Shallow lakes · Extreme temperature and depth · Fish assemblage · Pejerrey reproduction

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Introduction

Shallow lakes represent the most frequent type of lentic water body along the global landscape (Downing et al. 2006). These aquatic ecosystems are of a high value not only for biodiversity conservation, but also by supporting several valuable activities such as sport and commercial fishing. These activities give to the fish community a relevant role for the economical importance of these environments.

Because of their low depth and relatively small size, prevailing changes in local weather shape tightly the

water temperature and depth patterns in shallow lakes (Mooij et al. 2005, 2008; Bohn et al. 2011, 2016; Elisio et al. 2015; Tao et al. 2015; Nsubuga et al. 2017). In turn, modifications in these parameters can produce significant changes in the structure of fish and other biological communities (Greten and Adrian 2001, 2002; Scheffer et al. 2001; Ficke et al. 2007; Colautti et al. 2015).

In the Pampas region of Argentina, shallow lakes are the most spread continental water bodies (Diovisalvi et al. 2015; Bohn et al. 2016). These lakes generate important economical resources for many localities in the region, mainly associated with recreational fisheries (Baigún and Anderson 1994; Baigún and Delfino 2003). Several species such as *tararira* (*Hoplias malabaricus*), *bagre sapo* (*Rhamdia quelen*), and common carp (*Cyprinus carpio*) are recognized as important game fishes in these lakes, but the main attractive fish for anglers is the pejerrey (*Odontesthes bonariensis*, Baigún and Delfino 2003).

The structure of fish community in Pampean shallow lakes, with pejerrey as a key species, present important inter-annual changes associated with the weather-driven physical variations of these water bodies (Menni 2004; Berasain et al. 2005, 2015; Rosso and Quirós 2009; Colautti et al. 2015). Specifically, the occurrence of extreme temperatures (affecting fish mortality) and flooding conditions (affecting conductivity, connectivity, and fish migration) have been recognized as the main events determining the fish assemblage in these ecosystems (Menni 2004; González Naya et al. 2011; Colautti et al. 2015). Furthermore, modifications in fish reproductive outputs as consequence of changes in temperature patterns (Van der Kraak and Pankhurst 1997; Zieba et al. 2010; Zucchetta et al. 2012), would also contribute to shape these communities. Particularly for pejerrey, not only the length of spawning season, but also the sex ratio of progeny can change annually depending on the water temperature regimens (Strüßmann et al. 2010; Miranda et al. 2013; Elisio et al. 2015).

Air temperature and rainfall have been demonstrated as the most important climatic variables driving the inter-annual changes of temperature and depth patterns in Pampean shallow lakes (Fernández Cirelli and Miretzky 2004; Bohn et al. 2011, 2016; Diovisalvi et al. 2015; Elisio et al. 2015). Thus, extreme regimens of these weather variables can modulate the occurrence of the extreme physicochemical events in these lakes. In this sense, it is well known that ENSO (El Niño

Southern Oscillation) and PDO (Pacific Decadal Oscillation) are the two leading phenomena of atmosphere-ocean coupled variability in the Pacific Ocean (Gershunov and Barnett 1998) affecting climate in several parts of the world. In particular, the warm and cold phases of ENSO are well known as “El Niño” and “La Niña” respectively. Both ENSO and PDO are responsible of large part of the year-to-year variability of air temperature and rainfall anomalies in many regions of South America (Grimm et al. 2000; Mantua and Hare 2002; Andreoli and Kayano 2005; Kayano and Andreoli 2007; Da Silva et al. 2011; Grimm 2011), including the Pampas region of Argentina (Barros et al. 2004, 2008). Particularly in this last region, significant negative (positive) rainfall anomalies have been associated to “La Niña” (“El Niño”) events (Grimm et al. 2000; Barros et al. 2004, 2008; Grimm 2011), and these anomalies appear to be enhanced (weakened) when PDO is in the same (opposite) phase than ENSO (Barros et al. 2004; Andreoli and Kayano 2005; Kayano and Andreoli 2007; Da Silva et al. 2011). In addition, although much less documented, ENSO influences air temperature anomalies in the region, and probabilities of cold (warm) events are enhanced during “La Niña” (“El Niño”) episodes (Rusticucci and Vargas 2002). In accordance with the above climatic patterns, a recent study demonstrated that ENSO modulates, through its influences on rainfall regimens, the morphology of Pampean shallow lakes, being associated the increasing (decreasing) of lake areas, to “El Niño” (“La Niña”) events (Bohn et al. 2016). Thus, the consideration of the ENSO and PDO phenomena appears to be important to understand the occurrence of the extreme temperature and depth events in Pampean shallow lakes leading to the changes in fish community.

Chascomús Lake (35°36', 58°02'W, mean depth 1.53 m, surface 3000 ha; Dangavs 1976) is the most studied Pampean shallow lake (Diovisalvi et al. 2010). This water body is connected to other six shallow lakes which in turn drain to the Salado River (Diovisalvi et al. 2010). Connectivity of these lakes can change significantly as response to the hydrological state associated with the rainfall regimen (Quirós et al. 2002). The structure of fish community in *Chascomús* Lake presents significant inter-annual changes. Particularly, two alternative fish assemblage configurations were identified by Colautti et al. (2015) in *Chascomús* Lake between 1999 and 2013, characterized by the dominance or almost absence of pejerrey. This shift would be

caused by the mortality and migration events driven by the occurrence of extreme temperatures and flooding conditions (González Naya et al. 2011; Colautti et al. 2015). Also, changes in pejerrey abundance could occur as consequence of reproductive disruption provoked by the inter-annual changes in temperature (Elisio et al. 2015) and salinity patterns (Berasain et al. 2015). The understanding and prediction of these extreme conditions affecting fish community in this and other Pampean lakes is a very important point to consider for the economical development programs of many counties in this region. A recent study has modeled the water temperature and depth conditions in *Chascomús* Lake from 1966 to 2012, using as predictor variables local air temperature and rainfalls (Elisio et al. 2015). The modeled data evidenced the occurrence of significant inter-annual oscillations in both depth and water temperature, and as consequence in the length of pejerrey spawning season (Elisio et al. 2015). In this sense, the aim of this study was to assess the information obtained by Colautti et al. (2015) and Elisio et al. (2015) on a global climate variability scenario, analyzing how influences of ENSO and PDO can drive the environmental events that modify fish community in a Pampean shallow lake.

Materials and methods

Historical extreme anomalies in water temperature, depth and length of pejerrey spawning season in *Chascomús* Lake

Data of daily maximum and minimum water temperature, monthly maximum depth and yearly date of the end of pejerrey spawning season in *Chascomús* Lake (as the Julian day at which occurred at least eight previous consecutive days in which maximum daily water temperatures surpassed 21 °C) from 1966 to 2012 were taken from the models performed by Elisio et al. (2015). Anomalies for the different variables were based on the mean values obtained over the whole 1966–2012 period. Anomalies in the date of end of pejerrey spawning season were considered as anomalies in the length (days) of this reproductive event.

Extreme anomalies for each variable were considered in accordance with the criterion previously established by Rusticucci and Vargas (2001). Positive anomalies for depth and daily maximum water temperature were

considered extremes when values were higher than the 75% percentile value of the yearly maximum anomaly values distribution of each variable, while negative anomalies for depth and daily minimum water temperature were considered extremes when anomalies were lesser than the 25% percentile value of the yearly minimum anomaly values distribution of each variable. The proportion of days with positive and negative extreme temperatures associated with extreme low depth conditions was calculated. Similarly, the 75% and 25% percentile values of the anomalies distribution of the yearly length of pejerrey spawning season were considered to characterize the occurrence of extreme conditions in this variable.

The critical temporal window for the occurrence of extreme positive and negative anomalies in *Chascomús* Lake temperature was delimited as the months in which days associated with each anomaly condition were registered. Persistence of extreme positive and negative anomalies was calculated as the number of days in which each water temperature extreme anomaly was registered during each year (considered from November to October in order to encompass the critical period for the occurrence of both positive and negative extreme anomalies). The frequency of occurrence of each extreme lake temperature condition was calculated as the number of years elapsed between consecutive years in which the same extreme temperature event was registered.

An extreme depth event was considered as a continuous period in which an extreme anomaly of the same sign was registered. The persistence of extreme depths was calculated as the number of months encompassed during each event. The frequency of occurrence of each extreme depth anomaly was calculated as the number of months (divided by 12 and expressed in years) elapsed between the different consecutive events of the same extreme anomaly.

Extreme positive and negative anomalies in the estimated length of pejerrey spawning season in *Chascomús* Lake was assessed based on the intensity of each extreme anomaly (number of days of shortening or prolongation) and the frequency of occurrence as the number of years elapsed between consecutive years with the same extreme anomaly.

The minimum, maximum, 25% and 75% percentile distribution of persistence (only for temperature and depth) and frequency of occurrence was calculated for each extreme event of each variable.

Assessing of Chascomús Lake fish assemblage and pejerrey relative abundance in response to extreme temperature and depth events

Based on the study performed by Colautti et al. (2015), two different groups of fish assemblage configuration were considered according to the relative abundance of pejerrey fish. Group 1 was characterized by the presence of pejerrey as dominant species, while Group 2 was characterized by the absence or very low abundance of this species. When fish assemblage was represented by the Group 1 configuration, pejerrey relative abundance was compared between consecutive years considering two qualitative categories: lower or higher was assigned when pejerrey relative abundance registered in a given year decreased or increased compared to that registered in the preceding year, respectively.

Changes in *Chascomús* Lake fish assemblage were estimated from 1966 to 2013 in response to the occurrence of extreme events in depth (associated with high accumulated rainfall and flooding conditions) and water temperature, based on the following criterion previously established by Colautti et al. (2015). The occurrence of an extreme low water temperature event during a given year was considered to cause mortality in most fish species less pejerrey, leading to fish assemblage to a Group 1 configuration in the next year, while the occurrence of extreme high depth events was associated with re-colonization of most species and a change to a Group 2 configuration. When fish assemblage was expected to be in a Group 1 configuration, changes in pejerrey relative abundance were estimated as follow. If the estimated length of pejerrey spawning season was extremely short during a given year, a decrease of its relative abundance was predicted during the next year (qualitative category estimated: lower), while the opposite response or a stability condition was predicted if the estimated length of pejerrey spawning season in the previous year was normal or extremely long (qualitative category estimated: higher or equal).

The estimated responses of *Chascomús* Lake fish assemblage and changes in the relative pejerrey abundance were compared with the data previously reported by Colautti et al. (2015). Considering those results, data of fish assemblage were taken from Fig. 2 and qualitative change in pejerrey relative abundance were taken from Fig. 3, following the next criterion: higher or equal was categorized when percentage value of pejerrey

relative abundance during one year was higher or equal than the value observed during the preceding year, while lower was categorized when percentage value of pejerrey relative abundance during one year was lower than the value observed during the preceding year. Data taken from the Colautti et al. (2015) results arise from analysis of annual averages species relative abundance calculated from caught of seasonally or bimonthly experimental fishing carried out in two different lake sites by using trap nets during one night. The proportion of coincidence between observed and estimated data was calculated.

ENSO and PDO

The monthly values of the Niño-3.4 Index from January 1966 to December 2012 were downloaded from the National Oceanic and Atmospheric Administration (NOAA, http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_change.shtml). This index is based on the sea surface temperature (SST) anomalies spatially averaged on the El Niño 3.4 region (5° S–5° N, 90–150° W). The SST anomalies are calculated based on multiple centered 30-year base periods, recalculated each 5 year, to filter the influences of long-term trends associated with the “global warming” (see references in the website above). The ENSO index was then monthly defined as the average of the Niño-3.4 Index values during five consecutive months.

The monthly values of the PDO index from January 1966 to December 2012 were downloaded from the database available in the *Joint Institute for the Study of the Atmosphere and Oceans* (JISAO) website (<http://research.jisao.washington.edu/pdo>). This index represents the time series of the leading pattern of monthly SST variability computed in the North Pacific Ocean, poleward of 20°N, obtained from an Empirical Orthogonal Function (EOF) analysis (e.g. Mantua and Hare 2002). SST long-term trends, as defined by the monthly SST anomaly global average, were previously removed to avoid “global warming” influences.

Influence of ENSO and PDO on the occurrence of extreme environmental events associated with changes in the fish community in Chascomús Lake

Water temperature and mainly depth conditions are a delayed result of local changes in air temperature and

rainfalls, which in turn, are influenced by the conditions of the ENSO and PDO. Thus, different temporal lags were considered to describe the largest influence of the climatic conditions on the occurrence of extreme events in the variables considered. In this sense, both ENSO and PDO monthly indexes were assessed from 1 to 32 previous months. For the case of extreme low water temperatures, PDO and ENSO indexes were correlated with the monthly accumulated degrees of extreme anomalies considering only from June to August (the critical temporal window for the occurrence of these events, see Table 1). For the case of extreme depths, the PDO and ENSO indexes were correlated with the monthly value of the extreme depth anomalies. Due to the occurrence of high temperature events causing the shortening or prolongation of pejerrey spawning season in *Chascomús* Lake were registered between November and December (Elsio et al. 2015), the extreme events for this variable were correlated with the different conditions of ENSO and PDO calculated from December. When no extreme event was registered in a given month (for temperature and depth) or year (for length of pejerrey spawning season), a value of 0 was assigned. The Pearson correlation coefficient (r) was calculated for each correlation assessed and its statistical significance was evaluated by the Student's t -test. The temporal lag of PDO and/or ENSO condition showing significant correlation and highest r for each case were selected and considered for the posterior analysis.

Generalized Linear Models (GLMs) were developed to analyze the occurrence probability of an extreme low temperature or a high depth event during a given month (for the case of temperature, considering only from June to August) depending on the PDO and/or ENSO condition variable selected in the previous analysis. Also, a GLM was developed to assess the occurrence

probability of an extreme shortening in pejerrey spawning season. A binomial distribution for response variable and a logit-link function were used to develop the models. The adjustment of GLM parameters was evaluated using the Student's t -test. When both ENSO and PDO indexes showed significant correlations with the same variable in the above analysis, two different GLMs were assessed (one with the previously selected ENSO predictive variable and other one with the selected PDO predictive variable) and the model with the highest R^2 was chosen.

Results were considered statistically significant at $P < 0.05$. Statistical analyses were performed using GraphPad Prism, ver. 5.0 (GraphPad Software, San Diego, CA, USA), and R, ver. 3.1.0 (R Foundation for Statistical Computing, Vienna, Austria) software.

Results

Occurrence of extreme water temperature and depth events in Chascomús Lake

Extreme anomalies in *Chascomús* lake maximum depth (>2.97 m for extreme positive anomalies and <1.41 m for extreme negative anomalies) were observed in 116 of the 564 months assessed over 1966–2012 period. Most months with extreme depths (80 months) had positive extreme anomalies, while only 36 months had the opposite extreme depth condition. All positive extreme anomalies in depth were observed between 1986 and 2003, with an occurrence frequency lower than 5 years. The 75% of these extreme events lasted between 1 and 21.5 months. In contrast, the negative extreme anomalies in depth were spread over the whole assessed period (1966–2012) with an occurrence frequency between 0.3 and 8.3 years, and had in general a lower persistence, lasting most of times (75%) between 1 and 5.75 months (Fig. 1 and Table 1).

For the case of *Chascomús* Lake temperature, extreme anomalies (>29 °C for extreme positive anomalies and <4.9 °C for extreme negative anomalies) were observed in a total of 155 days (approximately 10% of total days encompassed in the 1966–2012 period). Extreme high-water temperatures were observed during 76 days that occurred in spring-summer (between November and March). Conversely, extreme low temperatures, were observed during winter in 79 days (between June and August). The occurrence frequency of extreme positive

Table 1 Occurrence of extreme depth anomalies in *Chascomús* lake from 1996 to 2012

| Extreme depth anomalies | Minimum - 25% percentile - 75% percentile - Maximum | |
|-------------------------|---|------------------------------|
| | Persistence per event (months) | Occurrence frequency (years) |
| Positive | 1–2 | 0.2–0.3 |
| | 21.5–34 | 5 – at least 20.3 |
| Negative | 1–1.25 | 0.3–1.8 |
| | 5.75–14 | 8.3–18.8 |

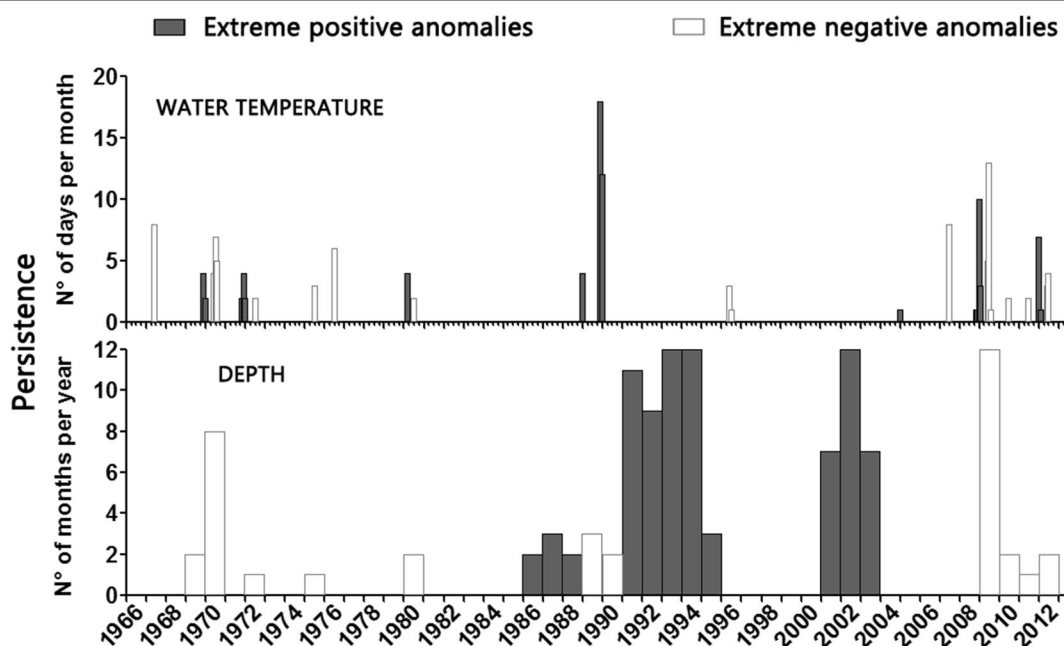


Fig. 1 Occurrence and persistence of extreme anomalies in *Chascomús* Lake water temperature and depth between January from 1966 and December from 2012

anomalies in temperature varied between 1 and 15 years (with a mean frequency between 2 and 9 years), and the persistence during each event varied between 1 and 30 days, lasting the half of times between 4 and 13 days. It must be noted that most of these extreme events (80.3% of days) occurred associated with low extreme depth conditions. The occurrence frequency and persistence of extreme negative anomalies in temperature were like the observed for the case of positive ones, being between 1 and 16 years and between 2 and 19 days, respectively. However, only 39.2% of days in which occurred these last extreme temperatures were associated with extreme negative anomalies in depth (Fig. 1 and

Table 2). No extreme water temperature anomalies were observed associated with high extreme depth conditions (Fig. 1).

Estimated extreme anomalies in the length of pejerrey spawning season in *Chascomús* Lake as response to the changes in the November–December temperature regimens

The estimated extreme anomalies in the length of pejerrey spawning season in *Chascomús* Lake involved more than 22 days of differences between opposite extreme events. The occurrence frequency for both extreme anomalies was similar, with an equal 25% percentile value of 1 year, and a 50% and 75% percentile value that differed by only 1 year between opposite events (2 and 7 years for positive anomalies, and 3 and 6 years for negative anomalies, respectively). The more marked difference between both extreme anomalies was observed in the maximum frequency value, which was 10 years for positive anomalies and 18 years for negative anomalies (Fig. 2). Only 3 of the 11 years in which extreme shortening of pejerrey spawning season was estimated were associated with extreme negative depth anomalies in *Chascomús* Lake during November and/or December.

Table 2 Occurrence of extreme water temperature anomalies in *Chascomús* lake from 1966 to 2012

| Extreme temperature anomalies | Seasonal window of occurrence | Minimum - 25% percentile – 75% percentile – Maximum | |
|-------------------------------|-------------------------------|---|------------------------------|
| | | Persistence per seasonal window (days) | Occurrence frequency (years) |
| Positive | November to March | 1–4 13.25–30 | 1–2 9–15 |
| Negative | June to August | 2–2 8–19 | 1–1 4–16 |

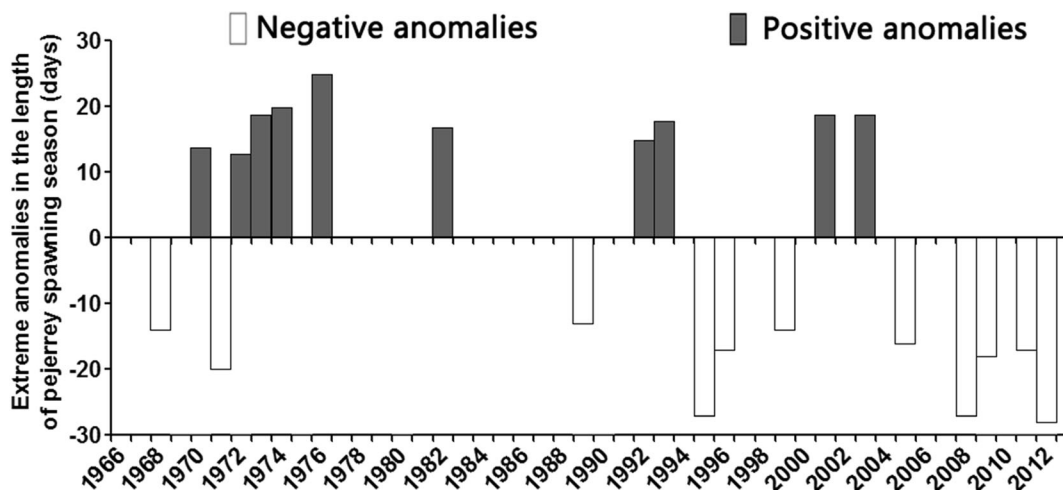


Fig. 2 Occurrence and intensity of extreme anomalies in the estimated length of pejerrey spawning season in *Chascomús* Lake between January from 1966 and December from 2012

Estimated changes in *Chascomús* Lake fish assemblage and pejerrey relative abundance in response to extreme conditions in temperature and depth

Four significant episodes of changes in *Chascomús* Lake fish assemblage were predicted between 1966 and 2013 as response to the occurrence of extreme temperature or depth conditions. Estimations showed that a fish assemblage with pejerrey as representative species (Group 1, according to Colautti et al. 2015) persisted between 1966 and 1986, a long period in which occurred several days with very low water temperatures coinciding with normal or low depth conditions. After some months with extremely high depth conditions between 1986 and 1988, the Group 1 of fish assemblage changed to a configuration characterized by absence or very low abundance of pejerrey (Group 2, according to Colautti et al. 2015). This last fish assemblage persisted for at least 10 years characterized in general by long flooding periods. The occurrence of 4 days with extremely low water temperatures during the winter of 1996 made that fish assemblage returned to the Group 1 configuration during 1997, lasting until 2001 when a new episode of extremely high depth occurred. This last environmental event made that fish assemblage changed again to the Group 2 configuration during 2002 and lasting until 2007 when extreme and persistent cold-water temperature episodes occurred returning the fish assemblage to a Group 1 condition. This fish assemblage lasted at least until 2013 (Fig. 3). Based on the above estimations, the Group 1 fish assemblage was the dominant situation (almost 67% of the total period assessed) lasting 32 years distributed in three

different periods of an average duration of at least 10 years. In contrast, the Group 2 configuration of fish community lasted only 16 years (the half time compared to the Group 1), distributed in two different periods of 10 and 8 years of duration. It must be noted that the estimated changes of fish assemblage presented a 100% of coincidence with the data taken from Colautti et al. (2015) study (Fig. 3).

During the periods in which persisted the Group 1 fish assemblage, annual changes in pejerrey relative abundance estimated as response to the occurrence of extreme anomalies in the length of its spawning season presented a 100% of correspondence with the annual changes observed in *Chascomús* Lake [data taken from Colautti et al. 2015 study]. In accordance with changes in reproductive season, the relative abundance of pejerrey in *Chascomús* Lake presented short periods of no more than 2 years of increasing followed by decreasing. However, it was also observed a 14 years period between 1973 and 1986, in which estimations performed indicated a situation of stability or even an increase in pejerrey relative abundance (Fig. 3).

Influences of ENSO and PDO on the occurrence of extreme temperature and depth conditions modifying fish assemblage and pejerrey relative abundance in *Chascomús* Lake

The occurrence and intensity of monthly extreme temperature and depth events in *Chascomús* Lake showed a significant relationship with the previous condition of ENSO and/or PDO indexes. Both ENSO and PDO

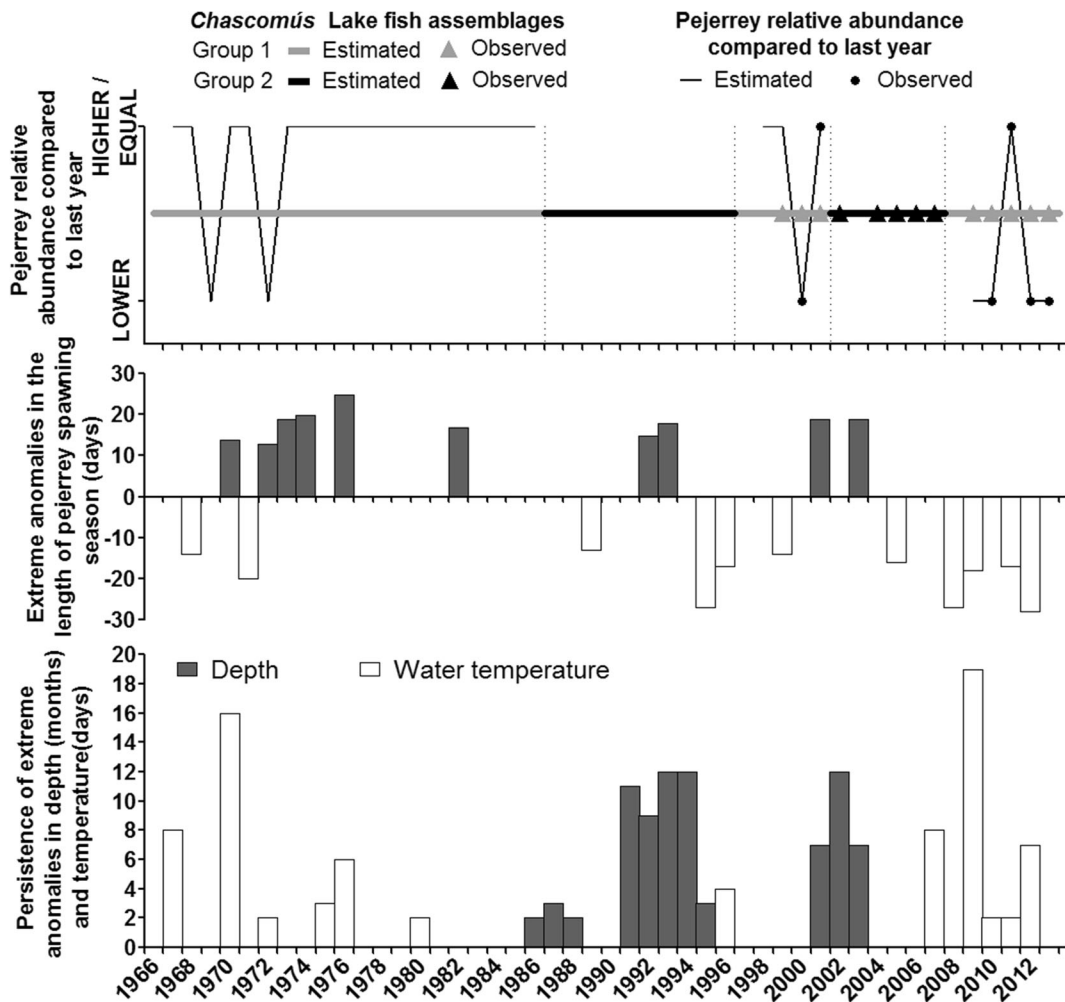


Fig. 3 Changes in fish assemblage and pejerrey relative abundance in *Chascomús* Lake between 1966 and 2013 (upper plot). Observed data were taken from Colautti et al. (2015), while estimated data correspond to the response predicted in the present

indexes showed a significant influence on the occurrence and intensity of extreme depths in *Chascomús* Lake (Fig. 4a). Monthly values of ENSO and PDO indexes averaged over 21 and 17 previous months, respectively, showed the maximum explanation level of occurrence and intensity of extreme depth anomalies. However, compared to PDO (data not shown), ENSO explained better the occurrence probability of extreme positive anomalies in depth, which would lead to a fish assemblage of Group 2. The occurrence probability of an extreme positive anomaly in *Chascomús* Lake depth increased significantly with the rise of the ENSO index averaged during 21 previous months (Fig. 4b).

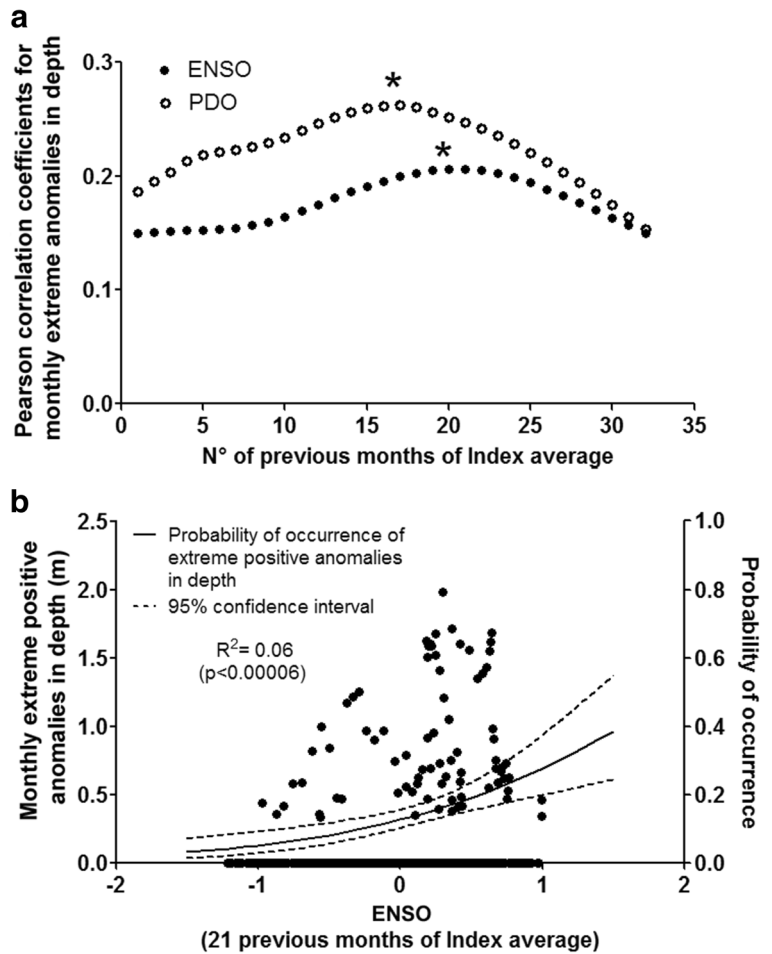
Extreme low temperatures in *Chascomús* Lake, leading to a fish assemblage of Group 1, were significantly

study according to the occurrence of extreme anomalies in the length of pejerrey spawning season (middle plot), extreme negative anomalies in water temperature, and extreme positive anomalies in depth (lower plot)

associated with the PDO and not with the ENSO conditions. The PDO index averaged over the 22 previous months was the best predictor variable to explain the monthly accumulated extreme negative anomalies in water temperature (Fig. 5a). A significant increase in the occurrence probability of an extreme low water temperature event was observed when the PDO index averaged over 22 previous months became more negative (Fig. 5b).

On the other hand, the extreme anomalies in the length of pejerrey spawning season in *Chascomús* Lake as response to the November and December temperature regimens were significantly related with the PDO, and not with ENSO phenomenon (Fig. 6a). Particularly, the occurrence probability of an extreme shortening in

Fig. 4 Influence of ENSO and PDO on monthly extreme positive anomalies in *Chascomús* Lake depth. Changes in R^2 for the correlations performed between monthly extreme positive anomalies in depth and the different number of previous months of ENSO and PDO index average (a). Asterisk = significant statistically correlations for all analysis performed ($p < 0.05$). Probability of occurrence and monthly extreme positive anomalies in *Chascomús* lake depth as a function of the 21 previous months of ONI average (b). Black line indicates the average values of probabilities for the predictor-variable range evaluated (GLM). The dashed lines indicate 95% confidence intervals



pejerrey spawning season, which would affect negatively its relative abundance, was significantly predicted by the average of PDO index during the last 5 months considered from December. A significant increase in the occurrence probability of an extreme shortening in pejerrey spawning season was observed when PDO condition became more negative (Fig. 6b).

Discussion

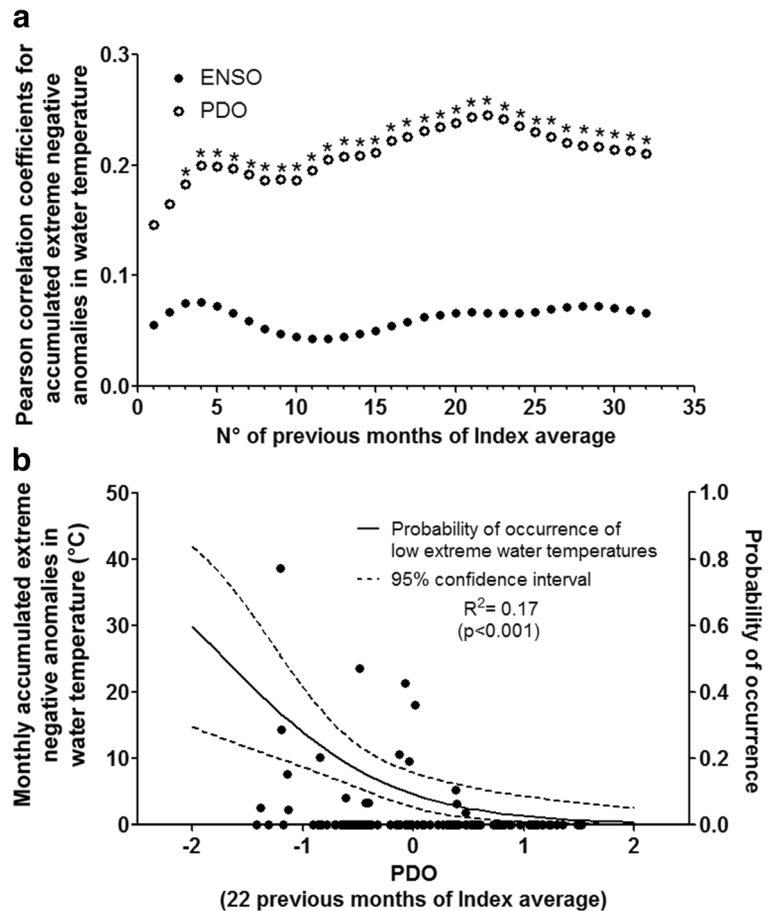
The present study showed strong correlations between the activity of two global climatic phenomena (ENSO and PDO) and the local occurrence of extreme depth and temperature conditions in a Pampean shallow lake that can affect the structure of fish community.

Extreme anomalies in *Chascomús* lake water temperature were observed only during specific months along the year. Extreme high temperatures ($>29\text{ }^\circ\text{C}$) occurred

between November and March (warm season), meanwhile extreme low ones ($<4.9\text{ }^\circ\text{C}$) occurred only between June and August (cold season). This seasonal difference in the occurrence pattern of the high and low extreme temperatures in *Chascomús* Lake is the result of the marked air temperature seasonality typical of temperate climate in South America (Eidt 1969). In contrast, extreme depths resulting of high accumulated rainfalls occurred along the year. It must be noted that rainfalls not only conditioned the occurrence of extreme depths in *Chascomús* Lake, but also influenced the occurrence of extreme water temperatures through the modification of the thermal inertia of lake, according to the model performed by Elisio et al. (2015). Particularly, it is important to highlight that high depths in *Chascomús* Lake appeared to be effective to avoid the occurrence of extreme water temperature conditions.

From the extreme anomalies in the lake physical conditions, the present study focused only on the

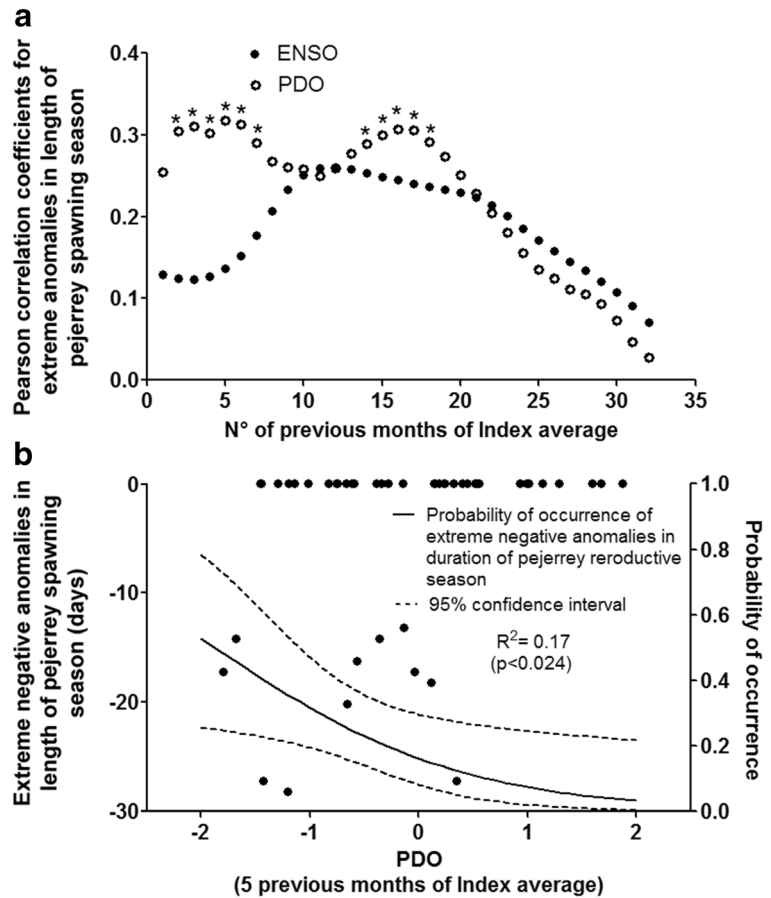
Fig. 5 Influence of ENSO and PDO on monthly accumulated extreme negative anomalies in *Chascomús* lake water temperature. Changes in r for the correlations performed between monthly accumulated extreme negative anomalies in water temperature and the different number of previous months of ENSO and PDO index average (a). Asterisk = significant statistically correlations ($p < 0.05$). Probability of occurrence and monthly accumulated extreme negative anomalies in *Chascomús* Lake water temperature as a function of the 22 previous months of PDO average (b). Black line indicates the average values of probabilities for the predictor-variable range evaluated (GLM). The dashed lines indicate 95% confidence intervals



occurrence of extreme low temperatures during winter (causing differential fish mortalities), early spring high temperature conditions (modifying length of pejerrey spawning season) and high depths (promoting fish migration and recolonization) as the main environmental events structuring fish community in *Chascomús* Lake. These environmental events have also been considered important drivers of fish community changes in other studies discussing the potential impacts of climate change on different aquatic ecosystems (Ficke et al. 2007; Brander 2010; Jeppesen et al. 2010; González Naya et al. 2011). Present estimations showed that a Group 1 fish assemblage persisted between 1966 and 1986, period characterized by the occurrence of several extreme low water temperature events tolerated by the pejerrey (Gómez et al. 2007) and causing mortality of most fish species typical of warmer regions, such as *Parapimelodus valenciennis*, *Cyphocharax voga*, *Hypostomus commersoni*, *H. malabaricus* and *C. carpio* (González Naya et al. 2011). In this sense, it is important to mention

that *Chascomús* lake is localized on the southern margin of the *subtropical Potamic Axis* ichthyological ecoregion, and the southward distribution of fish species inhabiting this ecoregion appeared to be limited by low temperatures (Cussac et al. 2009). On the other hand, extreme high depth conditions occurred during 1986 could have promoted migration and recolonization of most species in the lake (mainly *P. valenciennis* and *C. voga*), displacing the dominance of pejerrey, and leading to the fish assemblage to a Group 2 configuration. The frequent high depth conditions between 1987 and 1995 avoided the occurrence of extreme low temperatures, favoring thus the persistence and dominance of *P. valenciennis* and *C. voga*. Also, high depth events probably promoted emigration of pejerrey to areas of higher salinity conditions into the *Salado* River watershed (Rosso and Quirós 2009). It must be noted that the increase of rainfall leading to the high depth events produces a dilution of the lake and a significant decrease of salinity, which would be unfavorable for pejerrey (Tsuzuki et al. 2000;

Fig. 6 Influence of ENSO and PDO on extreme anomalies in the estimated duration of pejerrey spawning season in *Chascomús* lake. Changes in r for the correlations performed between the extreme anomalies in the estimated length of pejerrey spawning season and the different number of previous months of ENSO and PDO index average (a). Asterisk = significant statistically correlations ($p < 0.05$). Probability of occurrence and extreme negative anomalies in the estimated length of pejerrey spawning season in *Chascomús* Lake as a function of the 5 previous months of PDO average (b). Black line indicates the average values of probabilities for the predictor-variable range evaluated (GLM). The dashed lines indicate 95% confidence intervals



Rosso and Quirós 2009; Kopprío et al. 2010; Berasain et al. 2015). The persistence of this last fish assemblage (Group 2 configuration) would have lasted until the occurrence of a new low extreme water temperature event during 1996, favoring again the pejerrey increase and dominance, and returning fish community to a Group 1 assemblage in 1997. From this last year to 2013, two more events of fish community changes were estimated for *Chascomús* Lake. The first change (from the Group 1 to the Group 2) would have occurred during 2002 driven by the flooding observed in 2001, meanwhile the last change (returning fish community to the Group 1 configuration) would have occurred in 2008 driven by the selective fish mortality occurred during 2007 as consequence of the extreme low temperature events observed.

It must be remarked that gather wild evidences supporting the ecological changes predicted as response to environmental variability represents a very important challenge for the reliability of predictions made in this kind of studies. In this sense, all fish mortality events and fish assemblage changes registered in *Chascomús*

Lake (Gómez 2014; Colautti et al. 2015) were properly reflected by the changes estimated in the present study by using the occurrence of extreme temperature and depth conditions as predictive variables. However, although only temperature and depth were considered as the main drivers of *Chascomús* Lake fish assemblage changes, other factors such as dissolved oxygen, pH, conductivity, ionic composition and toxicity of pollutants should be considered to fully understand the dynamic of fish communities (Ficke et al. 2007; Gómez et al. 2007; Jeppesen et al. 2010; Gómez 2014).

While fish community in *Chascomús* Lake was represented by the Group 1 configuration, data presented by Colautti et al. (2015) showed evident yearly changes in pejerrey relative abundance. Noteworthy, these inter-annual changes in pejerrey relative abundance were explained by the occurrence of extreme anomalies in the length of pejerrey spawning season as response to the early occurrence of high water temperature conditions during spring. Interestingly, this last result supports in part the inferences made in other studies in relation to

the expected influences that climate change has on pejerrey reproduction in the wild (Soria et al. 2008; Strüssmann et al. 2010; Elisio et al. 2012, 2015; Miranda et al. 2013). Thus, it appears that the dynamics of pejerrey population in *Chascomús* Lake under absence of flooding conditions will depend not only on the other fish species populations and the inter-specific interactions, but also largely on the inter-annual changes of its reproductive performance as response to the extreme shortening of its spawning season. It is worth noting that fish reproductive changes in response to temperature variations is one of the most addressed aspect of the climate change influences on aquatic ecosystems (Pörtner et al. 2001; Nöges and Järvet 2005; Ballón et al. 2008; Mooij et al. 2008; Pankhurst and Munday 2011; Miranda et al. 2013).

Even though the influences of ENSO and PDO on local climate have been approached in several works, implications of these influences on the physical conditions of Pampean shallow lakes and consequent changes on its biological communities have been scarcely evaluated. In this sense, this study showed how influences of both global climate phenomena are related with the occurrence of extreme physical events in *Chascomús* Lake modifying significantly its fish community. Results showed that the probability of occurrence of an extreme positive anomaly in *Chascomús* Lake depth, leading to the fish community to a Group 2 configuration (absence of pejerrey) increased significantly when ENSO (and in a lesser extent PDO index) was mostly in its positive phase during at least 21 months. This period of delay in the ENSO influences is consistent with the fact that *Chascomús* Lake depth is the result of 20 months-accumulated rainfall (Elisio et al. 2015). Moreover, this result is in agreement with the well known positive rainfall anomalies observed in the geographical region encompassing *Chascomús* County under the influences of the extreme warm phase of ENSO (associated with “El Niño”) and also PDO (Grimm et al. 2000; Barros et al. 2004, 2008; Andreoli and Kayano 2005; Kayano and Andreoli 2007; Da Silva et al. 2011; Grimm 2011).

On the other hand, PDO and not ENSO was related with the occurrence of extreme low water temperatures in *Chascomús* Lake. The occurrence probability of this extreme thermal anomaly, increased significantly when PDO index was mostly in its negative phase during at least 22 months. Because of part of the extreme low temperatures were associated with extreme low depths or even avoided by extreme high depths, the influences

that PDO has on this variable would be generated in part by the negative anomalies of local accumulated rainfalls (decreasing *Chascomús* lake depth) under the influences of the negative PDO phase (Barros et al. 2004; Andreoli and Kayano 2005; Kayano and Andreoli 2007; Da Silva et al. 2011). However, it appears that the influences that PDO has on the occurrence of extreme low water temperatures in *Chascomús* Lake would be driven mostly by the influences that this phenomenon has on the local air temperatures during winter. In this sense, it was demonstrated that previous conditions of PDO index correlate positively with the anomaly values of monthly air temperatures in *Chascomús* County between June and August (Elisio personal comments). Moreover, PDO showed a significant influence on the occurrence probability of an extreme shortening in the pejerrey spawning season in *Chascomús* Lake, associated also with a decrease in its relative abundance during the next year. This influence would be associated mainly with the effects that PDO has on the local air temperature patterns during November and December period, and would be scarcely related with the low depth conditions driven by scarce rainfall. In fact, only 3 of the 11 years in which extreme shortening in pejerrey spawning were observed, were associated with extreme low depths. The mechanisms by which PDO leads to cause anomalies in air temperature patterns are beyond of the scope of the present study. Nonetheless, it appears that these mechanisms are not completely elucidated and should be addressed in future studies.

In conclusion, the present study suggested through strong correlations between climatic phenomena and ecological variables, that the ENSO and PDO influences can affect significantly the occurrence probability of extreme depth and temperature events in a shallow lake driving changes in the structure of its fish community, probably induced by selective mortality, migrations, and reproductive performance variations.

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