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The performance of ecological cage aquaculture of pejerrey Odontesthes bonariensis in Pampean lakes under two different hydrological scenarios

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Abstract

Ecological aquaculture promotes the development of sustainable farming systems, focusing on a wide range of ecosystem elements. The ecological aquaculture of the zooplanktivorous peierrey (Odontesthes bonariensis) in floating cages in Pampean shallow lakes (Argentina) needs to be carried out considering the hydrological and chemical variations as modulators of plankton community and consequently of the pejerrey yield. To assess its performance in lakes with contrasting hydrological regimes, an experiment was carried out in two water bodies: La Salada de Monasterio Lake (Mon), an endorheic environment, and San Lorenzo Lake (Lor), connected to several lakes and the Salado River. During the experiment, regional rainfall generated high hydrological variability in Lor Lake changing its status of unconnected lake to a run-of-the-river lake. High standard deviation in Chlorophyll-a values in Lor indicated the significant effects of hydrological instability on the plankton community. Microcrustaceans abundance and biomass were higher in Mon, and almost disappeared in Lor when it turns into run-of-the-river. The final fish growth and survival were significantly higher in Mon, endorsing the importance of zooplankton of high nutritional quality and hydrological, physical-chemical and biological stability. The results indicate that productive and stable environments with a sustained offer of natural food are better for the zooplanktivorous fish production. Connectivity with other water bodies and hydrological dependence on rainfall regimes have defining effects on phytoplankton, zooplankton and fish production, thus emerging as key factors to be considered for achieving better results in the ecological aquaculture implementation.

KEYWORDS

connectivity, fish production, floating cages, hydrological influence, natural food availability

1 | INTRODUCTION

Freshwater cage aquaculture has been implemented in the production of many fish species worldwide (Beveridge, 2004), and in many cases, it can be carried out extensively (without artificial food). Extensive cage culture is highly dependent on the characteristics of

the environment, mainly light, temperature and primary production (Beveridge, 2004; Le Cren & Lowe-McConnell, 1980; OECD, 1982), and it allows achieving low-cost results in productive environments rearing fish species that feed on the lower levels of the food chain (Little & Muir, 1987). Its close relationship with the environment makes this type of rearing systems suitable to be carried out

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following the guidelines of the ecological aquaculture paradigm. This new model promotes the development of aquatic farming systems that preserve and enhance the forms and functions of the natural and social environments in which they are situated (Costa-Pierce, 2002). Thus, it takes advantage not only of what the environment gives but also of the work and knowledge of local stakeholders, contributing to environmental sustainability, rehabilitation and enhancement (Hambrey et al., 2008). However, to successfully apply this aquaculture system, it is important to obtain detailed ecological information, carrying out research that focuses on a wider range of ecosystem elements, be they hydrological, chemical or biological.

One of the largest wetland areas of South America is the Pampean region of Argentina. According to data reported by INTA (Instituto Nacional de Tecnología Agropecuaria), this region has about 13,800 shallow lakes with a surface area greater than 10 ha, a number that increases up to 146,000 if also small lakes and temporary ponds are considered (Geraldi et al., 2011). These shallow lakes (known as 'Pampean lakes') are commonly eutrophic freshwater environments characterized by high limnological variability, strongly influenced by the hydrologic dynamics driven by regional rainfalls and water table regimes (Claps et al., 2004; Colautti et al., 2015; Diovisalvi, Bohn, et al., 2015; Izaguirre et al., 2015; Quirós et al., 2002; Rosso & Quirós, 2009; Torremorell et al., 2007). Such variability is reflected by fluctuations in physical and chemical features and primary production (Lagomarsino et al., 2011; Pérez et al., 2011; Torremorell et al., 2009) and is also strongly dependent on their basin configuration. Some Pampean lakes are endorheic, whereas others form chained water bodies systems linked by streams, which promote water, nutrients and organisms flow and interchange (Toresani et al., 1994). The hydrological regime within these systems of lakes determines the degree of lake water exchange by surface flow, according to the hydroperiod conditions. Thus, some Pampean shallow lakes can behave as backwater or run-of-the-river lakes, in relation to the Salado River, and can even turn into river-flushed lakes. Such hydrological behaviour can produce relevant physicochemical and planktonic community changes when compared to endorheic shallow lakes (Gabellone et al., 2001; Renella & Quirós, 2006; Rosso & Quirós, 2009; Solari et al., 2002). In addition, most of them are subjected to a progressive eutrophication process due to a combination of human activities in their catchment (Quirós et al., 2006; Quirós & Drago, 1999; Diovisalvi et al., 2010). Such situation determines that most of these environments have high phytoplankton biomass (Izaguirre et al., 2015). Regarding the zooplankton, the structure and abundance of the community are regulated not only by hydrology, water quality and food availability (Benítez & Claps, 2000; González Sagrario et al., 2009; Solari et al., 2002) but also by fish planktivory (Diovisalvi, Salcedo Echeverry et al., 2015).

Among the fish assemblages inhabiting these lakes, the pejerrey *Odontesthes bonariensis* (Valenciennes, 1835) is the main fishing resource (Baigún & Anderson, 1994; Baigún et al., 2009; Colautti et al., 2010). This freshwater zooplanktivorous fish (Garcia de Souza et al., 2017) is considered a first quality food in every country of southern South America (Reartes, 1995; Somoza et al., 2008). It

has been intensively produced since the early twentieth century (Somoza et al., 2008), but its production cycle was completed only in recent years using tanks (Berasain et al., 2015; Velasco et al., 2008). Although mass production of eggs and larvae can be achieved, one of the main constraints is the acquisition of large numbers of juveniles for stocking or grow-out. In this context, extensive cage culture is an alternative tool to overcome some of the current constraints in pejerrey aquaculture, and it has been successfully applied for juvenile production (Colautti et al., 2009, 2010; Garcia de Souza et al., 2015, 2017; Solimano et al., 2015). Considering the success achieved following this simple aquaculture system, the ecological aquaculture of pejerrey in floating cages represents an opportunity to take advantage of productive environments such as the Pampean shallow lakes. This possibility is enhanced by the local knowledge and the social networks built around this emblematic fish resource for more than a century.

Therefore, a better understanding of the relationships between hydrology, abiotic factors and different components of the food web in these lakes is crucial to produce food without significantly affecting the environment, and to carry out better management measures for natural resources. In this sense, Gabellone et al. (2001) found that in a backwater lake associated with a lowland river, changes in the hydrological connection generate changes in dissolved phosphorus forms and the composition of the plankton. Rosso and Quirós (2009) suggested that abundance of O. bonariensis in run-of-theriver Pampean lakes may have been favoured during conditions of null or very low flow through increasing salinity and food availability. Lentic conditions could positively affect the pejerrey production because according to Rennella and Quirós (2006) macrozooplankton biomass in these lakes is negatively affected by high flow conditions. Similar observations were made by Colautti et al. (2003) when Lobos Lake turned its status from lentic to run-of-the-river and the condition of the pejerrey experienced a significant decrease.

New information about *O. bonariensis* floating cage culture and the variables that can influence its performance would not only be important to enhance and develop more accurate management guidelines for the ecological aquaculture, but also to make decisions regarding its sport and commercial fishing. Our hypothesis is that the hydrological and chemical variations of the lakes modulate the development of plankton and consequently the pejerrey production in floating cages. Thus, the objective of this study is to evaluate simultaneously the chemical parameters, plankton structure and performance of *O. bonariensis* reared in floating cages in two Pampean lakes with contrasting hydrological regimes.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in two Pampean lakes belonging to the Salado River basin, La Salada de Monasterio (Mon) (35° 47′ S, 57° 52′ W) and San Lorenzo (Lor) (36° 04'S, 58°01'W) (Figure 1). Mon

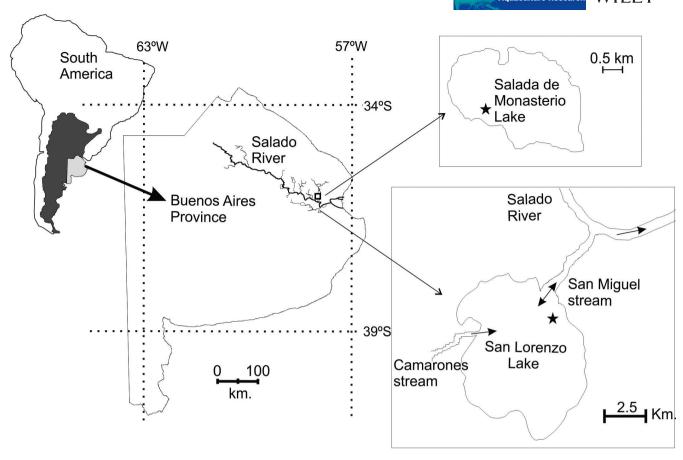


FIGURE 1 Geographical position of La Salada de Monasterio and San Lorenzo lakes in Argentina and their hydrological connections. Stars indicate the locations of floating cages used in the experiment and square the location of the meteorological station of INTECH (Instituto Tecnológico de Chascomús). Arrows in San Lorenzo Lake indicate the direction of water circulation

is an endorheic, kidney-shaped shallow lake with an area of approximately 600 ha, and reduced catchment surface. While its mean depth is 1.3 m, according to our previous studies maximum depth can vary between 0.9 m (autumn of 2009) and 2.6 m (spring of 2016). It has an abundant coverage of rooted emergent vegetation, Schoenoplectus californicus (C.A. Mey.) Soják, distributed in patches. Lor is the last of several chained Pampean lakes linked by the Camarones stream which flow to the Salado River through the San Miguel stream (Colautti et al., 1998). It is semicircular in shape, with an area of approximately 1700 ha and an extensive catchment about 1400 km². Its maximum depth can vary from less than 1 m up to 4 m related to the hydro-meteorological conditions of the region. Its surface water exchange depends on the hydrometric level, null below 1.5 m of depth (lentic) and progressively higher as depth increases (run-of-the-river). The hydrological regime is closely linked to the rainfall of the region and of the upper Salado river basin because the occasional floods reverse the direction of water circulation (Colautti et al., 1998), determining that it can behave also as backwater lake.

Land use of the surrounding area of both lakes is of moderate agricultural activity and extensive cattle rearing. The climate is warm-temperate, characterized by seasonality, with an important variability in rainfall regime, which is also affected by interannual phenomena like the ENSO (Diovisalvi, Bohn, et al., 2015; Elisio et al., 2018).

2.2 | Experimental design, sampling and measurements

Two floating cages of 12 m³ were set in each lake as experimental units. The cages were designed, constructed and installed according to Colautti et al. (2010). They were installed leaving more than 100 m between them to guarantee the independence of replicates. Each experimental unit was stocked with 76-day-old pejerrey reared in the same environment from larvae. The stocking density was 50 ind/m³ (600 juveniles of pejerrey per cage). The experiment was conducted from 29 December 2016 to 20 April 2017 (112 days). Environmental and fish samplings were made approximately every three weeks.

Lake water temperature, conductivity and pH were measured using a multi-parameter sensor (Hanna HI 98130; Smithfield); depth and transparency were measured with a graduated bar and a Secchi disc respectively. Hourly values for rainfall were provided by the meteorological station of INTECH (Instituto Tecnológico de Chascomús). Subsurface water samples for total phosphorous

(200 ml), dissolved nutrient analysis (200 ml) and chlorophyll-a analysis (1 L) were collected; the last two were promptly filtered through glass fibre filters (Whatman GF/C, 1.2 μ m pore) and transported refrigerated to the laboratory for further analysis. Soluble reactive phosphorus (P-PO₄³⁻), nitrite (N-NO₂), nitrate (N-NO₃) and ammonia nitrogen (N-NH₄⁺) were determined according to Mackereth et al. (1978). Total phosphorous was determined according to Clesceri et al. (1998). Chlorophyll-a was determined spectrophotometrically according to Clesceri et al., 1998, and its final concentration (μ g/L) calculated according to Lorenzen (1967).

Triplicate samples of phytoplankton and zooplankton were collected in diurnal time, three metres upwind the experimental units. Phytoplankton sampling was carried out collecting 125 ml of subsuperficial water, and zooplankton was sampled filtering 40 L of water through a plankton net of 50- μ m mesh size. Samples were fixed with 4% formalin.

Phytoplankton was counted with an optical microscope (Olympus BX51) at 200X, using a Sedgwick–Rafter chamber (APHA, 1995). Algal density was expressed in cells/mL, taking into account the main taxonomical groups present: chlorophytes, diatoms, cyanobacteria, euglenophytes and cryptomonas (due to low densities, euglenophytes and cryptomonas were grouped by the name 'others' for statistical purposes).

The zooplankton samples were analysed qualitatively and quantitatively in Sedgwick-Rafter (APHA, 1995) and Bogorov (Gannon, 1971) counting chambers. Zooplankton was identified to genus or species level and counted to estimate abundance per litre (ind/L). At least 20 individuals of each species per sample were measured to obtain an estimate of their size (length). According to length, the zooplankton components were grouped in three size classes: I, up to 0.3 mm (rotifers and nauplii larvae of copepods); II, 0.3-0.7 mm (small copepods and cladocerans); and III, more than 0.7 mm (large copepods and cladocerans), being qualitatively significant categories for O. bonariensis feeding habits (Garcia de Souza et al., 2017). Dry weights (µg/L) of the zooplankton components were estimated for each sampling date and for each lake, and also for total zooplankton. In the case of the rotifers, these were estimated from volume measurements using geometric approximations (McCauley, 1984; Ruttner-Kolisko, 1977). For the microcrustaceans, estimates were made from length-weight regressions available for similar species (Bottrell et al., 1976; Dumont et al., 1975; Lawrence et al., 1987).

The fish were sampled starting one week after they were stocked in the cages. In each sampling date, 15 individuals per cage were anaesthetized (10 ml of benzocaine solution [1 g: 100 ml alcohol] in 1000 ml of water) and were measured in length in situ (total and standard length in cm). Another five fish were slaughtered by overdose of benzocaine to avoid food regurgitation and were carried to the laboratory where they were measured and weighed (total weight in g). At the end of the trials, all fish in each cage were counted.

Care during handling of fish for this study complied with the Buenos Aires Province (Argentina) Wildlife and Fisheries Authority guidelines and policies (Law 11477) which also authorized the experimentation with pejerrey in floating cages by official permission: DI-2010-99-GDEBA-DAPAYCPMAGP. Moreover, ethical international standards were complied with following McGrath and Lilley (2015) and Bayne and Turner (2019).

2.3 | Statistical analysis

Differences in physical–chemical parameters among lakes were tested with MANOVA analysis. The relationships that could explain the differences between the lakes were determined by Spearman correlations among the physical–chemical parameters, plankton abundance and biomass. Partial eta squared (η^2) was retained as a measure of the effect size, following the guide values suggested by Cohen (1988) to distinguish between a strong effect $(\eta^2 > 0.8)$, a moderate effect $(0.8 < \eta^2 > 0.25)$ and a small effect $(\eta^2 < 0.25)$. Depth, transparency, conductivity, pH and rainfall values were transformed (observed/mean) to standardize, and then plotted as function of time to show the magnitude of changes and their relationships along the experiment.

ANOVA tests were carried out to search for differences between lakes in terms of phytoplankton biomass (chlorophyll a) and total lake zooplankton biomass.

Differences of phytoplankton and zooplankton structures among lakes were tested though one-way ANOSIM (Clarke & Warwick, 2001). Similarity percentages (SIMPER, with Bray–Curtis measure of similarity) were used to identify the groups that account for the observed dissimilarity between samples. For these analyses, the abundance of different groups of phytoplankton was transformed to relative abundance, and the zooplankton data to $\log(x+1)$ in order to reduce the contribution of highly abundant species and moderate the extreme values.

Fish length and weight were compared by repeated measures two-way analysis of variance (RM ANOVA) (Quinn & Keough, 2002; Ruohonen, 1998; Sokal & Rohlf, 1995). This analysis tested the effects of the time, of the lake and of the interaction between those two factors over the period of pejerrey growth. These comparisons were made firstly among the cages of the same lake and then between lakes. When there was no difference between cages, the entire pool of sampled lengths for each date was used to search for differences between lakes. After the RM ANOVA, Bonferroni post hoc tests were carried out to evaluate the differences in growth at each sampling date.

The specific growth rates (SGR) (Hopkins, 1992; Weatherley & Gill, 1987) of reared fish were calculated using the measurements obtained for TL (SGRL) and W (SGRW), following Garcia de Souza et al. (2015) and then compared with ANOVA; the mean survival rate percentage (S %), using the O'Connell and Raymond formula (1970), and mean final biomass per cage (B) were calculated. Finally, specific growth rates obtained in each lake were compared with plankton abundance and biomass values using correlations in search of their significance as influential variables. The significance level used in all performed statistical tests was $p \le 0.05$.

TABLE 1 Physical and chemical parameters: mean values and standard deviations obtained during the experiment

Parameter	La Salada de Monasterio (Mon)	San Lorenzo (Lor)	MANOVA	Partial \mathfrak{y}^2
Depth (m)	2.2 ± 0.1	1.6 ± 0.5	p = 0.005	0.481
Transparency (Secchi m)	0.25 ± 0.6	0.34 ± 0.12		
Temperature (°C)	24.3 ± 3.9	22.3 ± 7.5		
рН	9.2 ± 0.1	8.6 ± 0.2	p = 0.0001	0.713
Conductivity (µS/cm)	1506 ± 31.5	6976 ± 3761	p = 0.002	0.533
N-NH ₄ (μg/L)	6.8 ± 3.5	4 ± 1.6		
$N-NO_2$ (µg/L)	8.2 ± 6.7	4 ± 4.7		
N-NO ₃ (μg/L)	76.6 ± 38.4	30.5 ± 18.4	p = 0.014	0.374
P-PO ₄ (μg/L)	13.8 ± 15	16.8 ± 13.8		
PT (μg/L)	150.6 ± 52.8	135.3 ± 35.3		

3 | RESULTS

3.1 | Physical-chemical, meteorological and hydrological parameters

The main differences between lakes were observed in depth, nitrate concentration (N-NO₃), pH and conductivity (Table 1). During the study period, Lor Lake was shallower and with significantly higher conductivity than Mon Lake, while the latter showed higher concentrations of nutrients, particularly nitrates, and higher values of pH. The values of partial η 2 showed that all the significant parameters have a moderate effect. MANOVA general result using every parameter shown in the table indicated that the lakes were significantly different (p = 0.029).

Accumulated rainfall during the previous week of each sampling date ranged from 0 mm to 82 mm and was considered equal for both lakes because they are within the same area of influence. However, as a forcing factor, its effects on the hydrological conditions of both lakes and their limnological parameters were evidently different. For instance, hydrometric level in Mon Lake varied between 2.18 m and 2.44 m during the experiment, being the minimum value registered in February and the maximum in April, whereas in Lor Lake, it showed higher variability, with values between 1.2 m and 2.53 m, with the minimum and maximum also in February and April, respectively, and it correlated significantly with transparency (r = 0.982p = 0.017). Moreover, the magnitude of the changes in transparency and conductivity observed in Lor between March 9th and 16th, when it changed its condition to a run-of-the-river lake (Figure 2), denotes the link between the instability (hydrological and physicalchemical) of this lake with regional rainfall.

3.2 | Phytoplankton density, biomass and composition

Maximum total phytoplankton abundances were similar in both lakes, reaching 43,000 cells/ml in Mon and 43,600 cells/ml in Lor. However, related to minimum counts, while Mon had 11,000 cells/

ml, Lor only had 6100 cells/mL. The chlorophyll-a concentrations found in Mon varied between 15 and 48 μ g/L, while those of Lor varied between 22 and 61 μ g/L (Figure 3). No statistical differences were found in total phytoplankton counts or in chlorophyll-a concentrations between the two lakes.

Phytoplankton composition in Mon Lake was dominated by Chlorophyta in almost all the samples, reaching its maximum abundance in January (41,200 cells/mL), and being surpassed by Cyanobacteria only in the first sampling of March. Diatoms, on the other hand, had its maximum abundance in December, with 3300 cells/mL (Figure 3). Lor Lake was dominated by Cyanobacteria (mostly *Anabaenopsis* sp.), with a maximum abundance of 25,900 cells/ml, except for the sample of March, where the Chlorophyta were more abundant with 8600 cells/ml. In general, both groups exhibited the same temporal dynamics. Diatoms instead had low abundances during the whole experiment in this lake, with maximum density in December of 600 cells/ml (Figure 3). Euglenophyta and Cryptophyta were not abundant during the experiment, reaching a maximum density of 300 cells/ml in January in Lor Lake (not shown in the figure).

The ANOSIM carried out with the relative abundances of the different phytoplankton groups showed significant differences between lakes (Global R = 0.397, p < 0.05), while the SIMPER analysis showed that the main contributor to the dissimilarity between lakes (average dissimilarity = 36.2%) was the Cyanobacteria group, dominant in Lor Lake (46.2%).

3.3 | Zooplankton density, biomass and composition

Total zooplankton abundance varied from 270 to 1500 ind/L in Mon, while in Lor, the minimum was 150 ind/L and the maximum 950 ind/L. Rotifera was the dominant group in both lakes at every sampling date. Total zooplankton biomass found in Mon varied from 20 to 340 $\mu g/L$, and that of Lor, between 19 and 245 $\mu g/L$ (Figure 4). Statistical differences in biomass of cladocerans were found between lakes (ANOVA, F=5.53, p<0.05) being higher in Mon.

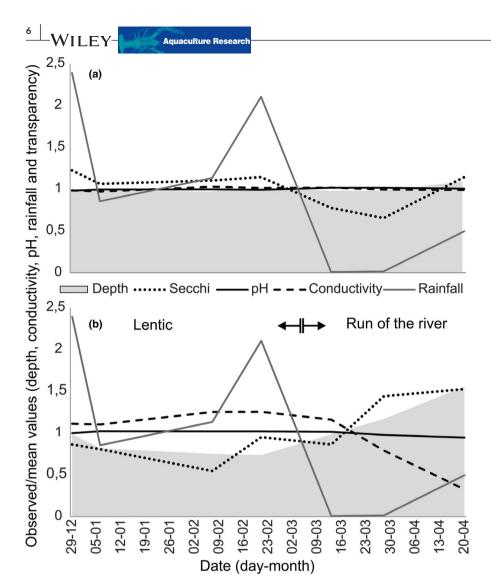


FIGURE 2 Depth, transparency, conductivity, pH and rainfall transformed (observed/mean) values in Salada de Monasterio (a) and San Lorenzo (b) lakes during the experiment

The abundance of zooplankton species was different between lakes (ANOSIM, $R=0.559\ p<0.05$), with the rotifers *Brachionus plicatilis* (Müller, 1786) and *Keratella americana* Carlinas discriminant species identified by SIMPER (average dissimilarity = 59%). *Brachionus plicatilis* had higher abundances in Lor Lake, while *K. americana* was more abundant in Mon Lake. Nauplii larvae of copepods (size class I) showed higher abundance in Mon at every sampling date, except for the first one, and it never surpassed 271 ind/L. Juvenile and adult microcrustaceans (size classes II and III) were best represented in Mon mainly due to their abundance at the beginning of the experiment (190 ind/L of copepods and 190 ind/L of cladocerans); in the case of Lor, they were not abundant and almost disappeared in the middle of the experiment (copepods and cladocerans never surpassed the 20 ind/L in the last four sampling dates).

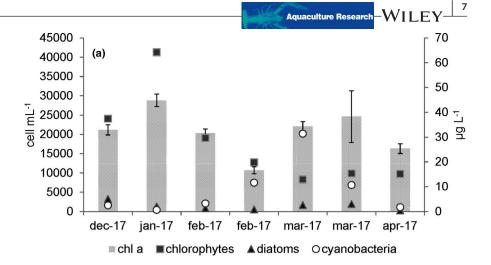
3.4 | Pejerrey growth, survival and production

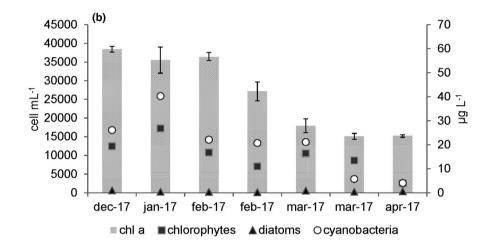
The pejerrey growth in length and weight was not different among cages in both lakes (Mon lake: RM ANOVA, p = 0.33, F = 1.05 and p = 0.69, F = 0.17, for length and weight respectively; Lor lake: RM ANOVA, p = 0.51, F = 0.57 and p = 0.36, F = 0.95, for length and

weight respectively). Meanwhile, growth in terms of length and weight was different between lakes (RM ANOVA, p < 0.05, F = 5.05and F = 35.02 respectively). The interaction between time and lake was significant (RM ANOVA, p < 0.05, F = 9.43 and F = 13.62, for length and weight respectively), and the Bonferroni test indicated that the significant differences between lakes, in terms of length and weight, were at 150 and 188 days old (March 13th and April 20th respectively), being the final growth value higher in Mon (Tables 2 and 3). These differences were also observed for specific growth rates (SGR), in length and weight, at 150 (ANOVA, p < 0.05, F = 11.73) and 188 (ANOVA, p < 0.05, F = 94.95) days old. The SGRL and SGRW declined progressively in both lakes, with the exception of one sampling date in Mon, where both increased. This moment of significantly higher growth was between 116- and 150-day-old fish, corresponding to the period between February 7th and March 13th.

Statistical differences between lakes were also observed in the fish mean survival, their mean final weight and the final biomass (Table 4). This table also shows the mean values of chlorophyll-a concentration and zooplankton biomass for the entire period, with a positive correlation (r = 0.93 and 0.84 in Mon and Lor respectively). Chlorophyll-a mean values were not statistically different, but the

FIGURE 3 Chlorophyll-a concentration (chl a, in bars) ± standard deviation, and phytoplankton mean groups densities in Salada de Monasterio (a) and San Lorenzo (b) lakes, in the different sampling dates





high standard deviation in Lor, together with the variations in the physicochemical parameters shown in Figure 2, turned out to be indicators of its hydrological instability and of the significant influence on fish growth and production. Fish growth rates in weight and length showed positive correlation with zooplankton biomass (r = 0.80 and 0.92 in Mon and Lor, respectively, for SGRW and R = 0.77 and 0.95 in Mon and Lor, respectively, for SGRL).

4 | DISCUSSION

Ecological aquaculture development requires comprehensive attention to ecosystem elements (Costa-Pierce & Page, 2012). This study reports the first evaluation of the relationships between hydrology, physicochemical parameters, phytoplankton and zooplankton structure, and its effects on the fish growth in floating cages in Pampean lakes.

The main physicochemical differences found between the two studied lakes, those related to depth, conductivity, nitrates concentration (N-NO₃) and pH, are linked to their differences in terms of hydrological dynamics and the structure and area of catchment. As stated above, Mon is an isolated environment, while Lor is connected to the Salado River. During the present study, Lor Lake was

receiving water from the Camarones stream and at a certain moment it turned into a run-of-the-river lake delivering water to the Salado River, which was evidenced by the increment of depth, and the consequent decrease in conductivity. This was the result of regional precipitations, as could be confirmed analysing their accumulation during the previous week of each sampling date.

The hydrological instability of Lor had significant effects on the plankton community. The degree of connection with other water bodies influences the phytoplankton structure, in terms of abundance and biomass, taking as an indicator of the latter the chlorophyll-a concentration. Although the chlorophyll-a mean concentration showed no significant differences between the lakes, the standard deviation values demonstrate that it was much more stable in Mon than in Lor, in which it declined throughout the study period. Besides, chlorophyll-a showed a significant negative correlation with depth, which increased after the rains of February, reaching its maximum value in April. This indicates that concerning primary production, an environment with greater stability such as Mon Lake is better for extensive aquaculture. This statement becomes more evident when comparing this type of environment with others that, despite being able to record very high productivity values, they can also be very unstable. Furthermore, several studies showed that the high hydrological variability of some Pampean shallow lakes influences phytoplankton

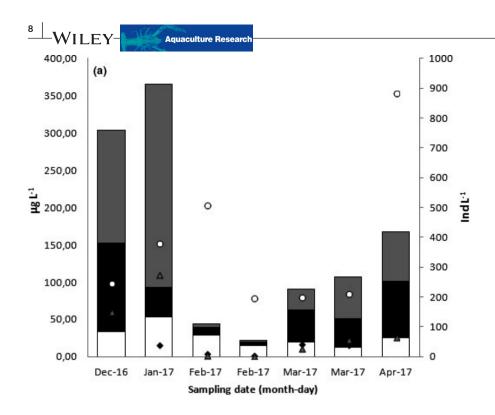
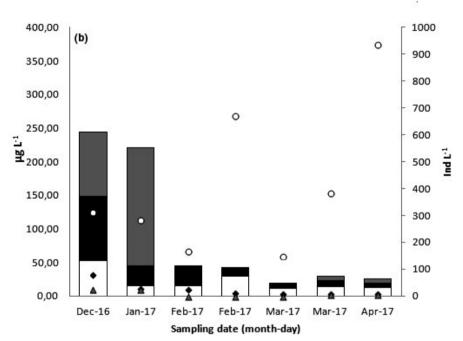


FIGURE 4 Zooplankton biomass (μ g/L, in bars) and abundance (ind/L, in markers), discriminated by size classes, in Salada de Monasterio Lake (a) and San Lorenzo Lake (b) in the different sampling dates: I, up to 0.3 mm (rotifers and nauplii larvae of copepods); II, 0.3–0.7 mm (small copepods and cladocerans); III, more than 0.7 mm (large copepods and cladocerans)



□ I Biomass ■ II Biomass □ III Biomass O I Abundance ◆ II Abundance ▲ III Abundance

Sampling date (month/day/year)	Age of fish (days of life)	Mean length (mm)	Mean weight (g)	SGRL (mm/day)	SGRW (g/day)
12/29/2016	76	57.33 ± 0.05	1.96 ± 0.15		
1/6/2017	84	71.91 ± 5.86	2.82 ± 0.78	0.028	0.062
2/7/2017	116	80.70 ± 20.56	4.14 ± 2.28	0.004	0.012
3/13/2017	150	100.64 ± 6.15*	6.76 ± 1.11*	0.006*	0.014*
4/20/2017	188	113.31 ± 5.96*	8.47 ± 1.19*	0.003*	0.006*

Significant differences with San Lorenzo Lake are indicated with asterisks.

TABLE 2 Growth and specific growth rates (SGR) by sampling date, in length (mean and deviation in mm) and weight (mean and deviation in g), of pejerrey reared in La Salada de Monasterio Lake

TABLE 3 Growth and specific growth rates (SGR) by sampling date, in length (mean and deviation in mm) and weight (mean and deviation in g), of pejerrey reared in San Lorenzo Lake

Sampling date (month/day/year)	Age of fish (days of life)	Mean length (mm)	Mean weight (g)	SGRL (mm/day)	SGRW (g/day)
12/29/2016	76	57.33 ± 0.05	1.96 ± 0.15		
1/6/2017	84	72.20 ± 2.82	2.62 ± 0.28	0.028	0.062
2/7/2017	116	89.10 ± 5.82	3.60 ± 0.64	0.007	0.010
3/13/2017	150	91.30 ± 7.86*	4.11 ± 1.11*	0.001*	0.004*
4/20/2017	188	91.73 ± 5.50*	4.14 ± 1.05*	0.0001*	0.0002*

Significant differences with La Salada de Monasterio Lake are indicated with asterisks.

TABLE 4 Mean survival (%), mean final weight (g), final production (kg/ha), mean chlorophyll-a concentration (μ g/L) and mean zooplankton biomass (μ g/L) for each lake

	La Salada	San Lorenzo
Mean Survival (%)	98ª	70 ^b
Mean final fish weight (g)	8.5ª	4.1 ^b
Final Production (kg/ha)	4180 ^a	1195 ^b
Chlorophyll-a (μg/L)	31.9 ± 9^{a}	41.3 ± 16.2^{a}
Zooplankton biomass (μg/L)	142.9 ± 20^{a}	89.2 ± 21.6 ^b

Significant differences (p < 0.05) between lakes are indicated in superscript letters.

growth and favours the establishment of cyanobacteria (O'Farrell et al., 2015). The Cyanobacteria group has a wide range of ecological traits that make them more adaptable to changing conditions of light intensity (antenna pigments), nutrient concentration (especially nitrogen by heterocytes), buoyancy (gas vacuoles), ability to store phosphorous and survival during long adverse periods by akinetes (Izaguirre et al., 2012; Litchman et al., 2010). In this study, the relative abundances of the phytoplankton groups showed significant differences especially due to the Cyanobacteria group, dominant in Lor Lake (46.2%), while in Mon Lake, the dominant phytoplankton group was Chlorophyta. This is important since some algal groups such as Chlorophytes, together with some diatoms, are known to be a more suitable food source for zooplankton. The nutritional quality of algae for zooplankton is determined by many aspects, including the suitable size range, digestible cell wall, non-toxicity and adequate chemical composition (Ahlgren et al., 1990). In this context, the Cyanobacteria group has been historically considered as a poor food resource for zooplankton (e.g. De Bernardi & Giussani, 1990; Gołdyn & Kowalczewska-Madura, 2008), mostly in their big colonies or filamentous forms, as the ones present in Lor Lake (Anabaenopsis sp.), what eventually affected the performance of the fish in this lake.

Regarding the zooplankton, the results achieved here and in our previous studies endorse the importance of the nutritional quality of this community in the feeding habits of zooplanktivorous fish (Andersen & Hessen, 1991; Hessen et al., 2006; Hessen et al., 2006; Morris & Mischke, 1999), which takes a particular value when these fish are intended to be produced through extensive aquaculture methods. The best parameters of the fish cage culture regarding growth and survival were obtained in the lake with more and better

zooplankton in terms of their nutritional quality. It should be mentioned that due to the nature of the experimental design, when using the individual measures to test the differences in fish growth between lakes during the sampling period (RM ANOVA), pseudo-replication was committed (Hurlbert, 1984), and this should be taken into account when interpreting the results obtained. In any case, our results reinforce the idea that the greatest pejerrey growth is achieved with the highest zooplankton availability, mainly of the largest individuals, such as zooplankton size class III represented by copepods and cladocerans of more than 0.7 mm in mean length. Microcrustaceans were best represented in Mon mainly due to their abundance at the beginning of the experiment; in the case of Lor, they were not abundant and almost disappeared in the middle of the experiment (Figure 4). Furthermore, and according to Welker and Walz (1999), it can be concluded that in flushed lakes, plankton growth depends on residence time. In these unstable environments, rotifers are the dominant group mainly because of their low generation time (3 days) as compared to crustaceans (longer generation times 8-14 days) (Sarma et al., 2005; Snell & King, 1977). In this sense, several authors observed an inverse relationship between discharge and primary productivity in rapidly flushed lakes, as well as in lochs and ponds, where phytoplankton and zooplankton only increased in periods of greater residence times (Brook & Woodward, 1956; Dickman, 1969; O'Connell & Andrews, 1987). In our study, during the last sampling dates, Lor Lake became a run-of-the-river lake. The factors determining its plankton dynamics can be analysed following Reynolds and Descy (1996), who evaluated the relationship between rotifers and crustaceans regarding residence time. Furthermore, taking into account that in unstable environments the intra-community regulation recedes into the background with respect to physical factors (Walz, 1993), it can be said that in Lor the zooplankton dynamics are determined more physically than biologically. The opposite situation was observed in Mon, where the zooplankton dynamics followed the seasonal fluctuations as described in Garcia de Souza et al. (2017). Thus, our results suggest that in Lor the influence of hydrological functioning was more important than the seasonality effects on the structure of the zooplankton. The zooplankton biomass in Lor lake after its transformation into run-of-the-river lake did not surpass the 100 µg/L; therefore, in relation to the fish food needs, the best zooplankton in terms of nutritional quality was less available when it was more necessary, because larger fish require bigger amounts of energy. The fish survival and biomass obtained in this highly unstable environment were significantly lower than in Mon. The hydrological,

physical-chemical and biological stability of Mon during the experiment allowed for better fish production, indicating that although the ecological aquaculture of pejerrey depends on quality and quantity of zooplankton (Garcia de Souza et al., 2017), a sustained offer of food is necessary to reach better fish yield.

5 | CONCLUSIONS

Our results suggest that productive and stable environments in terms of hydrological conditions are better for the implementation of ecological cage aquaculture systems because it has important and defining effects on phytoplankton, zooplankton and fish production. Connectivity with other water bodies, and hydrological dependence on rainfall regimes, emerge as key factors to be considered for achieving better results taking advantage of natural food of higher quality.

The hydrological conditions of the studied lakes are common for a large number of water bodies; thus, the results are relevant to the applicability of the method elsewhere. Therefore, these concepts should be added to the guidelines for managing and improving this kind of aquaculture systems, together with the choice of site, the optimal stocking density and the best season for rearing fish (Costa-Pierce, 2015; Garcia de Souza et al., 2015, 2017). Finally, this paper supports the idea that focusing on a wider range of ecological elements can help advance the development of ecological aquaculture on a productive scale, as noted in Costa-Pierce (2002, 2010, 2015) and FAO (2011).

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