

Research Article

Seasonal and reproductive migrations in the Creole perch *Percichthys trucha* (Actinopterygii: Percichthyidae) promote both intra-lake and inter-lake habitat connectivity

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Abstract: In this research work, biology of Creole perch, *Percichthys trucha*, the largest top predator in the North Patagonia's freshwater communities, in a deep oligotrophic lake in the region, focusing on (i) the differential use of littoral depth strata by age, (ii) age at maturity and spawning season and (iii) occurrence of reproductive migrations to vegetated shorelines has been described. Individuals from 12 locations within the lake were sampled and found that *P. trucha* makes differential use of the littoral zone through the year and through its life stages. From hatching and through their first year, juveniles prefer shallow vegetated littoral strata; 50% of the individuals have reached maturity at 1-year-old, and all are reproductive by 3-year-old. Overall, our results show that the reproductive behavior of *P. trucha* improves habitat connectivity between different zones of the lake and between the lake and other lakes connected to it by tributary streams.

Keywords: Patagonia, Reproductive behavior, Spawning season, Habitat connectivity.

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Introduction

Adequate conservation status assessments require knowing species habitat requirements, and how such habitats are used through a species' life stages – i.e. how different habitat patches are connected by reproductive and non-reproductive migration patterns (Zampatti et al. 2018). Patch connectivity is believed to be crucial to design effective conservation and management policies (Crooks & Sanjayan 2006), yet this life history trait is still uncharacterized for many species.

In freshwater lakes, connections between littoral and pelagic habitats vary according to lake size and type, and depending on the daily and seasonal

movement patterns of fish species inhabiting these habitats (Schindler & Scheuerell 2002; Crooks & Sanjayan 2006; Dolson et al. 2009). Seasonal migration patterns associated to reproduction have been characterized in several species of Percidae and Percichthyidae, (e.g. *Perca flavescens*, *Perca fluviatilis* or *Macquaria australasica*) (Muncy 1962; Wang & eckmann 1994; Appleford et al. 1998; Broadhurst et al. 2012; Sullivan & Stepien 2014; Wesolek 2014). These species prefer habitats with underwater vegetation, but will also spawn on open sand, gravel or rubble (Mecozzi 2008; Čech et al. 2009). Despite their disjoint geographical and taxonomic distribution, all these species share similar

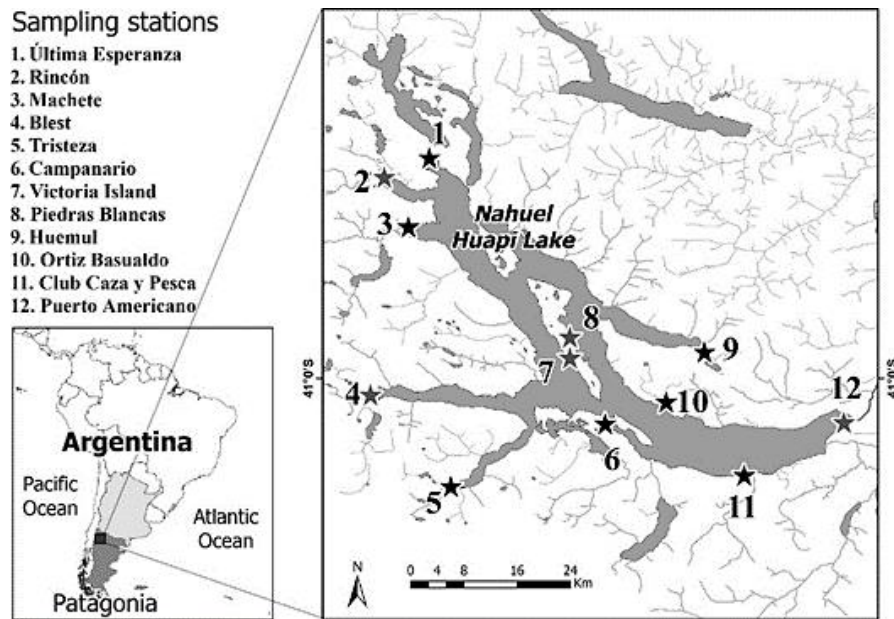


Fig.1. Distribution of sampling stations within Nahuel Huapi Lake. Stations marked by lighter gray stars were only sampled during winter and summer seasons.

spawning preferences and migration patterns, suggesting habitat similarity is a strong driver of the natural history of a species (Cadwallar & Rogan 1977; Mecozzi 2008).

The South American Creole perch *Percichthys trucha* (Valenciennes, 1833) is endemic to southern South America, inhabiting the rivers and lakes of Patagonia from 38°S to 55° S (Arratia 1982, 2003). It is a key member of fish communities in the Patagonian freshwater bodies: being the largest native fish species within its range (reaching up to 430 mm in length), its presence modulates the composition of fish communities in the region, and it was the sole top predator until the introduction of salmonid species (Macchi et al. 2007; Lopez Cazorla & Sidorkewicj 2008; Amalfi 2009; Fernández et al. 2018). Published data shows *P. trucha* has considerable ability to undergo trophic and reproductive migrations throughout its life stages (Milano 1996; Buria et al. 2007; Rechencq et al. 2014), and that it prefers shallow vegetated habitats for spawning (Schenone 2016) and warm, thermally fluctuating refuges for larvae and juveniles (Aigo et al. 2008). However, characterization of habitat use by each life stage of *P. trucha* is still lacking, hampering

assessments of the role of this species in habitat patch connectivity.

In this work, we describe the biology of *P. trucha* inhabiting a deep oligotrophic lake in North Patagonia, focusing on i) the differential use of littoral depth strata by age, ii) age at maturity and spawning season and iii) occurrence of reproductive migrations to vegetated shorelines.

Materials and Methods

Study Area: We chose as our study system the Creole perch population of Nahuel Huapi lake (North boundary: 40°41'S, 71°43'W, South boundary: 41°09'S, 71°42'W, East boundary: 41°02'S, 71°09'W and West boundary: 41°01'S, 71°50'W; Fig. 1). This oligotrophic lake is the largest in north Patagonia, with a 557 km² area and maximum depth of 464 m (Cordini 1950; Quirós 1988). Its basin is composed by seven reaches with a lakeshore that adds up to 357 km long and lakeshore that receives numerous affluent streams. The lake is drained by the Limay River towards the Atlantic Ocean. Its main channel is oriented from west to east along the Andean rain shadow, so that while its western reaches are subject to temperate rainforest regimes of

up to 3000 mm/year of rain, its eastern end is subject to semiarid conditions with less than 500 mm/year of rain (Modenutti et al. 1998; Paruelo et al. 1998). This precipitation gradient is reflected in a steep shoreline vegetation gradient that goes from dense a *Notophagus* rainforest in the west to a shrubby steppe in the east.

The shoreline can be classified in four main categories: rock cliffs (32%), rocky beaches (50%), sandy or pebbly beaches (17%), and rush beds (1%). Western shores are dominated by cliffs, with few intercalated narrow beaches, while eastern shores have shallow littoral areas with wider beaches composed by a mix of rocks, pebbles, coarse sand and fine sand. Due to high transparency of the water, the littoral zone extends down to 50 m in depth (Balseiro et al. 2007). Rooted aquatic vegetation is present in small patches, and is dominated by *Myriophyllum* sp., *Juncus* sp., *Scirpus californicus*, *Isoetes savatieri* and *Equisetum bogotensis* (Thomasson 1959). There are five native species (*Olivaichthys viedmensis*, *Galaxias maculatus*, *Galaxias platei*, *Odontesthes hatcheri* and *Percichthys trucha*) and three introduced species (*Oncorhynchus mykiss*, *Salmo trutta* and *Salvelinus fontinalis*), all inhabiting the littoral zones of the lake in a patchy distribution.

Sampling: Fish were sampled at 12 stations distributed through the lake during winter and summer (Fig. 1, Table 1). Additional sampling was made during spring and fall was made at Brazo Última esperanza, Brazo Machete, Brazo Tristeza, Brazo Campanario, Brazo Huemul, Brazo Ortiz Basualdo and Club de Caza y Pesca. Fish smaller than 10 cm long were caught using seine nets and fyke traps on shallow littoral areas. Fish larger than 10 cm were caught using gill nets deployed following a depth-stratified array as in Vigliano et al. (1999). Relative abundance was calculated as captures per unit effort (CPUE), standardizing the number of fishes caught by either seining distance (for seine nets), deployment time (for fyke traps), or net mesh area and deployment time (for gill nets). Each

Table 1. Sampling stations and dominant coastal habitat. See Figure 1 for locations.

ID	Station	Ddominant coastal habitat
1	Última Esperanza	rush bed and rocky/pebbly beach
2	Rincon	rush bed
3	Machete	rush bed
4	Blest	rush bed and rocky/pebbly beach
5	Tristeza	rock cliff
6	Campanario	rush bed and sandy beach
7	Victoria Island	rush bed
8	Piedras Blancas	rush bed
9	Huemul	rocky/pebbly beach
10	Ortiz Basualdo	rush bed
11	Club Caza y Pesca	rocky/pebbly beach
12	Puerto Americano	rocky/pebbly beach

individual caught was measured and weighted, and scales were sampled over the lateral line of a subset of individuals. Scales were mounted on slides and annulation patterns were used to estimate age as in Guerrero (1991). Fish gonads were dissected to determine sex and gonadal stage.

Data processing and parameter estimation: A chi square test was used to test for deviation from 1:1 sex ratio. Gonadal maturity stage for females and males was determined macroscopically using a 6-stage maturity key. These stages included: immature (I), developing (II), pre-spawning (III), spawning (IV; V) and resting (VI). The spawning period was estimated based on the changes in the gonads in the different seasons of the year sampled. A gonadosomatic index (GSI) was calculated as $GSI = (\text{gonad weight} / \text{total weight}) \times 100$ and the values of 10.5 onwards along with size of first maturity were taken as a spawning (TL50), as done elsewhere (Milano 1996; Cerna & Oyarzun 1998; Leal et al. 2011). Length at first sexual maturity was used for the determination of size at first maturity (TL50), using the logit model $P = 1 / (1 + e^{-(\beta_0 + \beta_1 L_{450\%})})$, where P is the fraction of mature fish, $L_{450\%}$ is the size at first sexual maturity (defined as the size at which half of the population is mature) and β_0 y β_1 are estimated parameters (Milano 1996). Spearman rank statistics were used to test for

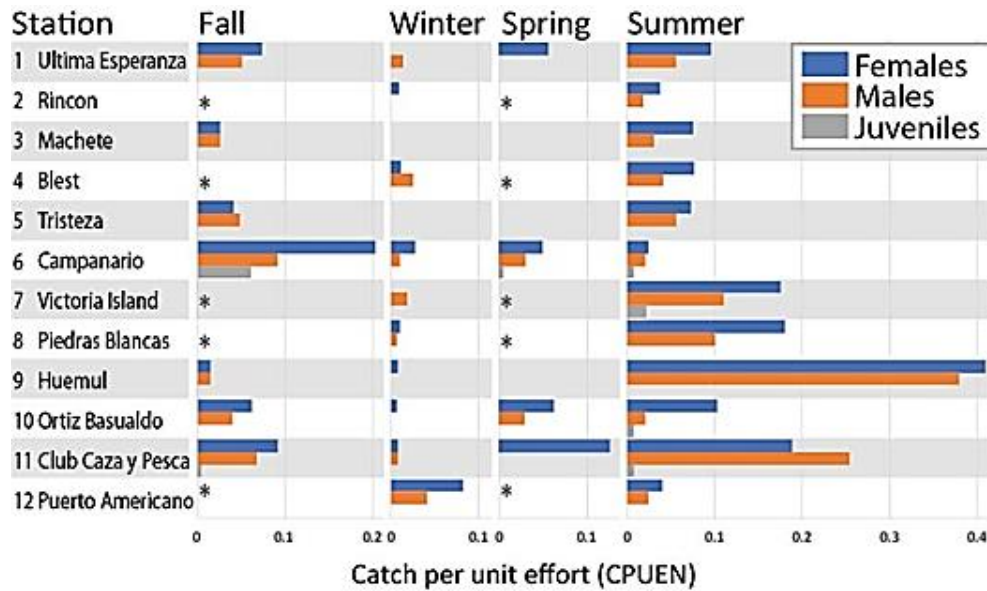


Fig.2. Seasonal distribution of creole perch catches per unit effort (CPUEN) at each station, by sex.

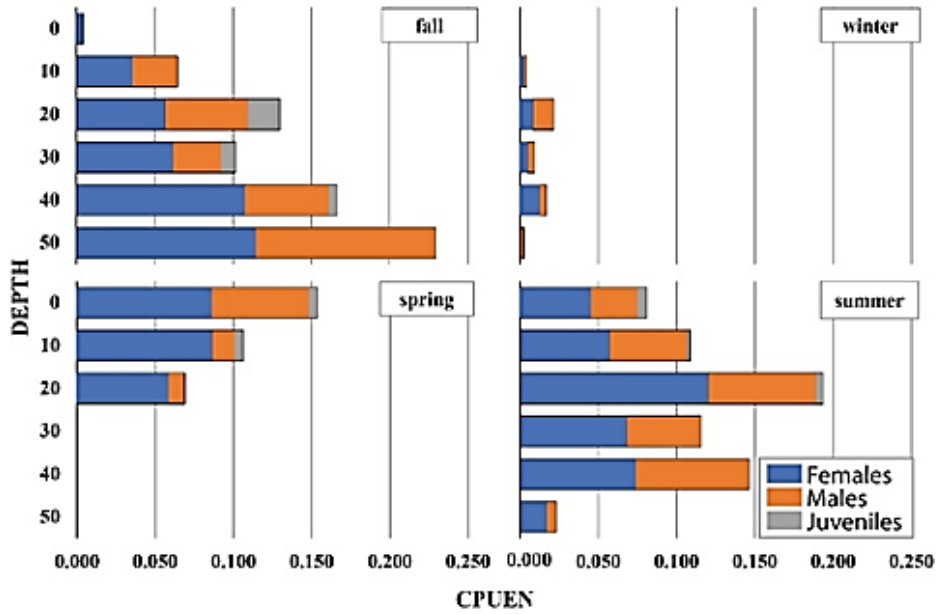


Fig.3. Depth distribution of Creole perch through the year. Catch per unit effort (CPUEN) in the different depth strata of the littoral zone by season.

correlations between demographic (overall relative abundance, mature male and female, and virgin juvenile abundances) and environmental (depth, temperature and season) variables.

Results

A total of 489 Creole perches were caught during the sampling period. 57 % were female, 39% were male and 4% were virgin juveniles. Four juveniles

individuals were captured with fyke traps or seine nets; the rest was caught on gill nets. Sex ratio was not significantly different from 1:1 (Chi-Square = 21.5 df = 470 $P=1$).

Seasonal age distribution:Adults were caught at all sampling stations and seasons but winter (and fall when available) catches were fewer than summer (and spring when available) captures (Fig. 2). Juveniles were found at two stations during the fall

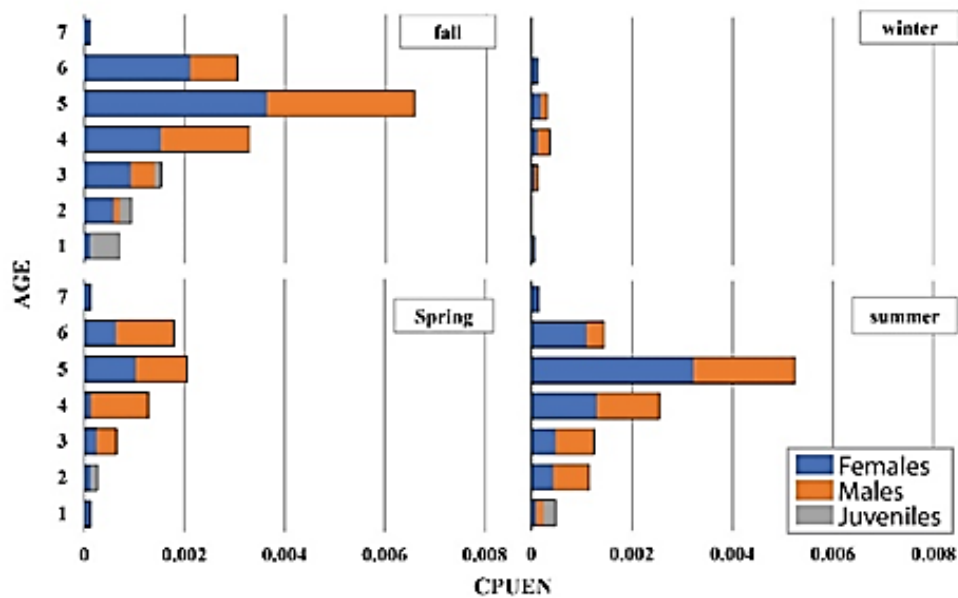


Fig.4. Age distribution of catch per unit effort (CPUEN) of Creole perch by sex throughout the year.

Table 2. Catch per unit effort (CPUEN) and percentage of total catch, by age and sex.

Age	Females		Males		Youngs		% total catch
	CPUEN	% fish caught	CPUEN	% fish caught	CPUEN	% fish caught	
1	0.619	1	1.031	3	2.268	73	4
2	3.093	5	3.505	9	0.619	20	7
3	5.155	9	4.742	12	0.206	7	10
4	11.340	20	9.897	25	0.000	0	21
5	24.536	43	16.082	41	0.000	0	41
6	11.753	20	4.124	10	0.000	0	16
7	1.031	2	0.000	0	0.000	0	1

(Brazo Campanario and Club de Caza y Pesca), no stations during winter, just a single station during spring (Brazo Camapanario) and four stations during the summer (Victoria Island, Brazo Campanario, Ortiz Basualdo and Club de Caza y Pesca).

Seasonal depth distribution: Catches of Creole perch showed seasonal variation in their depth distribution (Fig. 3). Fall catches were higher at the deeper strata (40 and 50m deep). In contrast, spring catches were higher at the shallower strata (from 0 down to 30m deep). Interestingly, most fishes were caught in the summer at 20 m depths.

Age distribution: Age ranged from 1 to 7 years (Table 2), with 5-year-olds being the most abundant (39%). Among females, 5-year-olds were most frequent (41%), followed by 6-year-olds (20%). Among males, 5-year-olds were most frequent (40%),

followed by 4-year-olds (25 %). Among virgin juveniles, 73% were 1-year-old, 20 % were 2-year-old and only 7% were 3-year-old.

Only 3 to 6-year-old females and 3 to 5-year-old males were found in spring, while during the summer all ages were found except for 7-year-old males (Fig. 4). One- and two-year-old juveniles were not found in winter catches and were most abundant in the fall (Table 2). One-year-old individuals were found only at shallow depths (0 to 30m), while older individuals were found at all depths (Fig. 5).

Size distribution and age at first maturity: The overall size distribution ranged from 63.5 to 515mm TL. Females ranged from 138 to 515mm (mean=397±73), males ranged from 130 to 476mm (mean = 368±83) and juveniles ranged between 63.5 and 250mm (mean=158mm ±51).

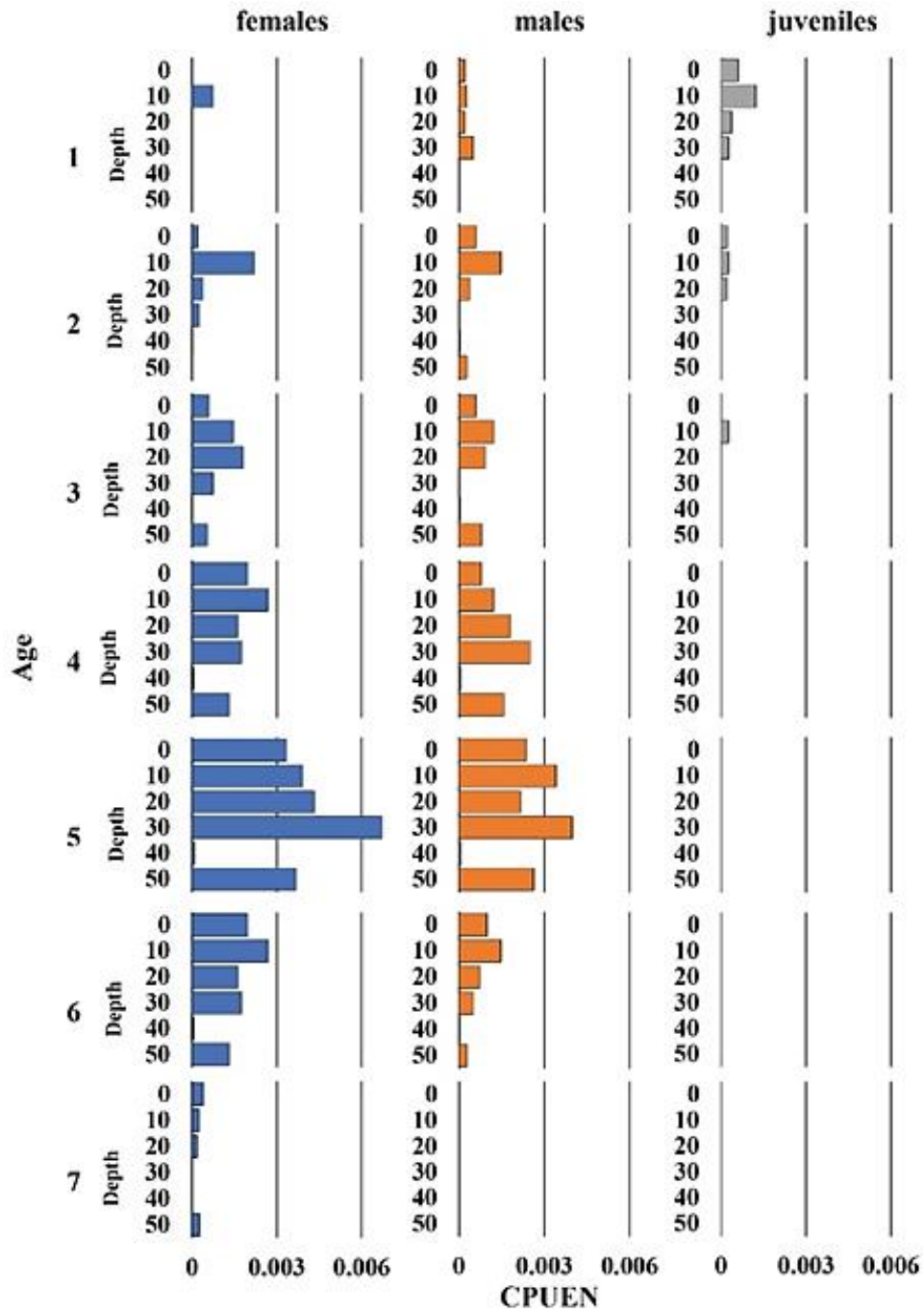


Fig.5. Depth distribution of catch per unit effort (CPUEN) of Creole perch by age and sex.

The mean length of half of the sexually mature individuals was 177mm for females and 159 mm for males. The logit model was fit as $p=1/(1+e^{-(6.9+0.04*Lst)})$ for females and $p=1/(1+e^{-(5.26+0.03*Lst)})$ for males. Thus, age at first maturity was estimated to be 1 year-old for both females and males. At 325 mm and 3 year-old age, 100% of the

individuals had reached maturity (Fig. 6).

Gonadal maturation: Caught Creole perches showed the full range of gonadal stages (I to VI, Table 3). Virgin juveniles (stage I) were found through the year, though abundance varied seasonally – with most found in the summer (50%), and fewer during fall (31%), winter (4%) and spring (15%). Most

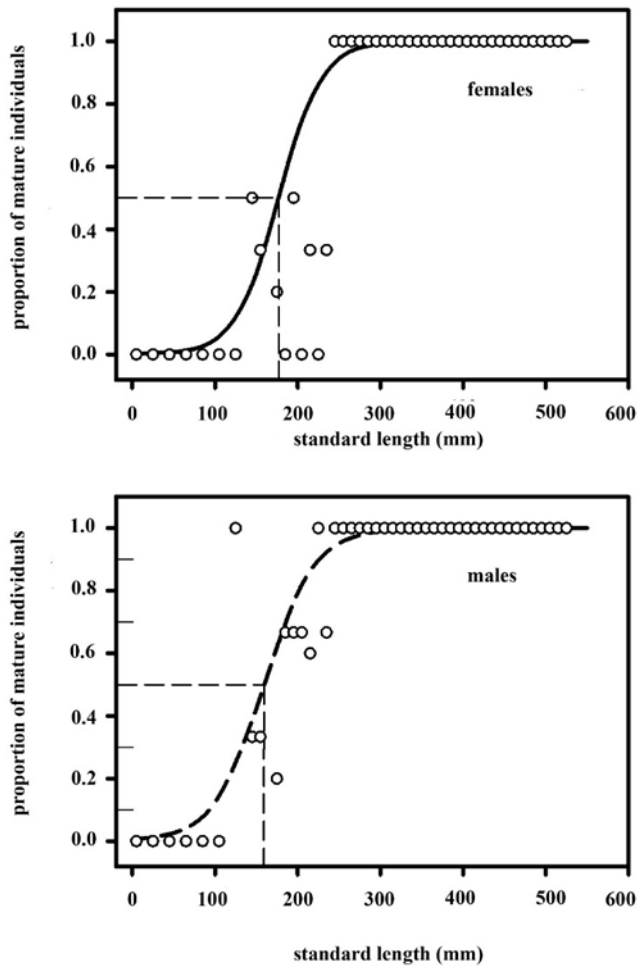


Fig.6. Logistic regression curves for length at first maturity of Creole perch females (top) and males (bottom).

individuals had developing (stage II) or pre-spawning (stage III) gonads; fishes at these stages were found through the years at all depths. Only 9.2% of all catches represented spawning stage individuals (stages IV, V and VI), and those were only found during spring and summer seasons (Table 3).

Virgin juveniles (stage I) and individuals with gonadal stages IV, V and VI, were found principally at shallow depths (0 to 30m), while individuals with gonadal stage II and III, were found at all depths (Fig. 7).

Both males and females showed higher gonadosomatic indices (GSI) during spring (Fig. 8) and at shallow depths (0 to 20m) (Fig. 9). During this season, half (22) of the females showed GSIs ranging

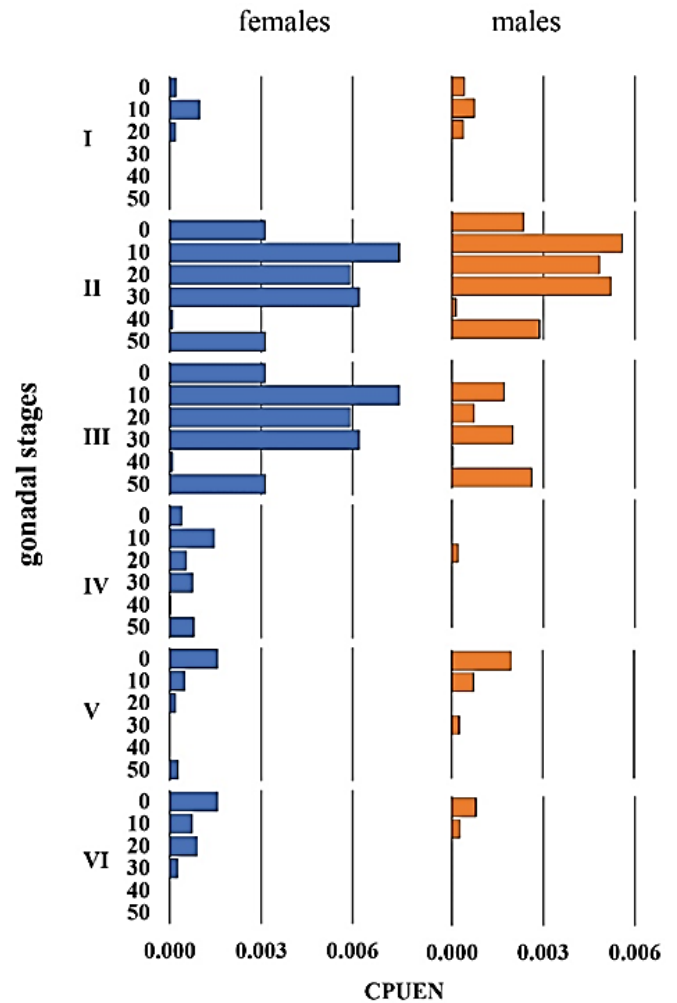


Fig.7. Distribution of gonadal stages by depth stratum and sex.

between 1.68 y 10.53 (mean = 5.57 ± 6.07), while half (8) of the males showed GSIs ranging between 1.38 y 12.01 (mean = 6.08 ± 5.80) (Fig. 8).

Correlations between abundance and environment: Testing for correlation between relative abundance and depth across seasons revealed spatial and temporal differences in the use of the habitat by Creole perches. During the fall, when most fishes were caught at deeper strata (40-50m), a significant positive correlation between male (but not female) abundance and depth was detected ($\rho=0.94$; $p=0.004$). No significant correlations were found for winter catches, though total catches were too few to draw meaningful conclusions. In spring, depth distribution is reversed, showing significant negative correlations between abundance and depth for both

Table 3. Percentages of catches of the different gonadal stages (females + males) in the different seasons of the year.

EG	Winter	Fall	Spring	Summer
I	4%	31%	15%	50%
II	2%	24%	4%	70%
III	11%	51%	6%	32%
IV	16%	16%	32%	37%
V	8%	0%	77%	15%
VI	0%	0%	82%	18%

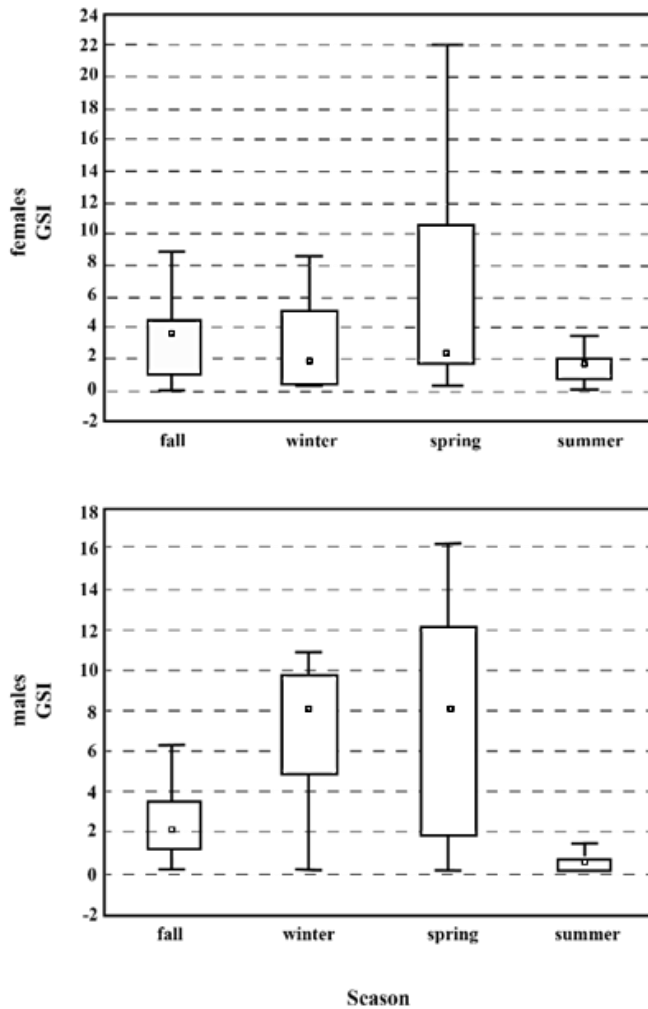


Fig.8. Seasonal distribution of gonadosomatics index values by sex.

females ($\rho=-0.88$; $p=0.02$) and males ($\rho=-0.94$; $p=0.005$). In the summer, linear correlation for adults is absent (since most are found at the 20 m stratum), but there is a significant negative correlation for virgin juveniles ($\rho=-0.88$; $p=0.02$). Interestingly, overall gill net catches were significantly correlated with water temperature ($\rho=0.56$; $p=0.0034$).

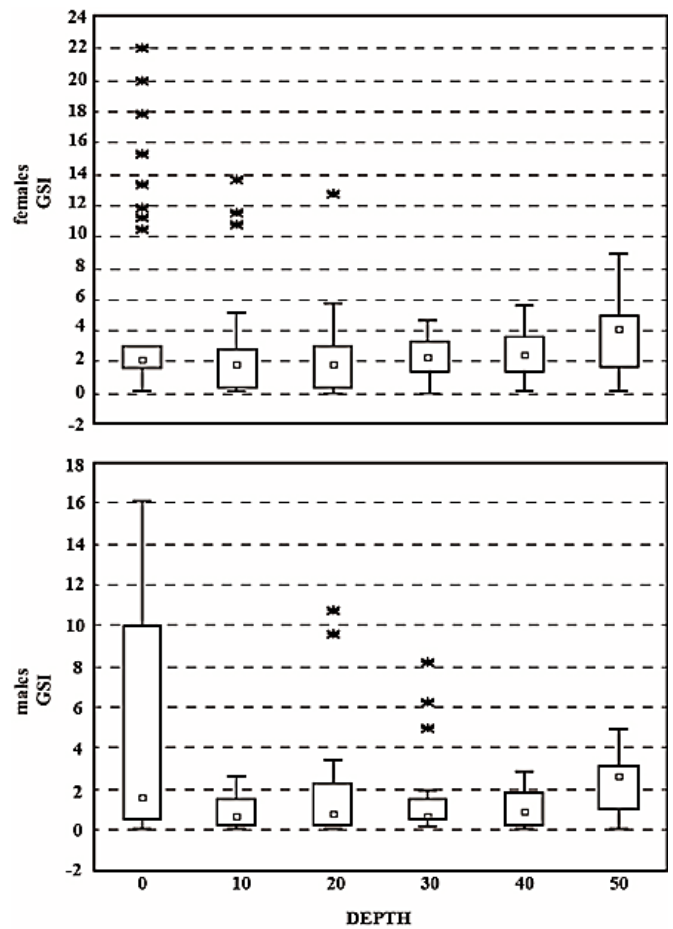


Fig.9. Depth distribution of gonadosomatics index values by sex.

Discussion

Percichthys trucha inhabiting Nahuel Huapi Lake can reach sizes of at least 515 mm (total length) and ages of at least 7 years. This is less than the maximum size and age reported for other water bodies in Patagonia (Guerrero 1991). In this lake, we found adults use all available littoral depth strata. However, they show marked seasonal differences in their depth

distribution. In the fall, they occupy deeper strata; interestingly, there seems to be a sexual depth preference, with males showing a stronger preference for deeper habitat (40+ m). In the winter, catches decrease markedly at all depths sampled, suggesting that Creole perch either move very little during the cold season (thus diminishing gill net catch rate) or migrate to depths deeper than 50 m. In any case, they become more active during spring and summer, and show a clear reversion of their depth preference, being more abundant at shallower depths in spring and then moving to mid-depths (with a peak at the 20 m stratum) during the summer. While half of 1-year-old Creole perch were mature already, and the complete cohort had matured by their third year, less than 10% of perch captured through this study was found to be reproductive adults. Of those, most were caught in spring or summer. Gonadosomatic indices were highest in fish caught in spring, supporting that Creole perch spawns in this season. Spring peak abundances of spawning perch has been reported in other Patagonian water bodies (Amalfi 2009): reproduction is usually concentrated on a specific spring month, which can shift depending on local condition. A similar phenology has been reported for other species in the family, like the Australian Macquarie perch *Macquaria australasica*, that spawns in October-November (Appleford et al. 1998).

Spawning Creole perch did not show uniform spatial distribution: by far most ripe females and males were caught at the Brazo Campanario station, at shallow depths and associated to submerged vegetated shores. Spawning individuals were always caught on vegetated areas rather than sand, gravel or pebble substrates, suggesting *P. trucha* do not lay eggs on bare substrates. While our catches of 1-year-old juveniles were scarce, they have been reportedly seen on Brazo Machete, Victoria Island, Brazo Campanario, Ortiz Basualdo and Club de Caza y Pesca, locations characterized by the presence of submerged vegetation. Similar findings by Juarez (2012) and Schenone (2016) further support our

observations, and indicate that this shallow vegetated beds are the preferred habitat for Creole perch for spawning and early life stages.

Differential distribution of catches according to season and depth show that Creole perch populations in the Nahuel Huapi Lake undergo seasonal migrations, occupying the shallower littoral zones during spring and summer, then moving to the deep littoral zones in the fall and likely deep pelagic zone during the winter, and finally returning to the shallow littoral in the following spring. Similar migration patterns have been described for the yellow perch *Perca flavescens* and the European perch *Perca fluviatilis* in the Northern Hemisphere (Mecozzi 2008). In these species, however, larvae migrate upon hatching to the pelagic zone, where they remain for one or two months before returning to the littoral zone. While sampling for this study did not include the pelagic region, previous work failed to find larva of *P. trucha* among pelagic samples from North Patagonian lakes (Rechencq et al. 2011), suggesting that, unlike their northern counterparts, Creole perch larvae remain in the shallow littoral region, most likely within dense rush beds.

Another intriguing result was the very low abundance of individuals younger than 1 year. A possible reason could be an artifact of sampling bias, as this age category is caught less frequently in gill nets, while fyke traps usually have a low catch rate and seine nets are useless in the dense rush beds where Creole perch larvae are likely most abundant. Nonetheless, much higher abundances have been reported using similar sampling methods at other smaller lakes connected through streams to the Nahuel Huapi lake, including Moreno (Schenone 2016), Correntoso and Espejo Chico lakes (unpublished data), suggesting that our observations of the near absence of young-of-the-year and relatively low abundance of spawning adults are not artifactual. Instead, our data might be indicating that the Nahuel Huapi Lake might not be a preferred spawning habitat for Creole perch. This stands in stark contrast to high abundance of non-spawning

adults in this large water body, and begs the question: is it possible that Creole perches in this lake undergo reproductive migrations to neighboring lakes?

Species of Percichthyidae are known for undergoing both trophic and reproductive migrations between interconnected water bodies, with some species like the Golden perch *Macquaria ambigua* traveling hundreds of kilometers during breeding season (Muncy 1962; Whiteside et al. 1985; Appleford et al. 1998; Buria et al. 2007; Mecozzi 2008; Wesolek 2014; Zampatti et al. 2018). Even *Percichthys trucha* has been reported to migrate between connected Moreno and Morenito lakes, two water bodies hydrologically linked to the Nahuel Huapi system (Buria et al. 2007). Furthermore, the only station within the Nahuel Huapi Lake where we found strong evidence for spawning was Campanario, located in reach that is peculiar relative to other parts of the lake. The Campanario reach is an overall shallower fjord, and its basin connects to the main lake channel through a very shallow pass. Thus, this reach functions in many ways as a smaller water body connected to the rest of the lake. All the above strongly suggests that the Creole perch population of the Nahuel Huapi system undergoes reproductive migration from the larger Nahuel Huapi lake to spawn at smaller lakes connected through tributary streams, and their progeny migrates back as juveniles older than 1 year or young adults.

In summary, our results show that *Percichthys trucha* makes differential use of the littoral zone across the year and along its different life history stages. Juveniles 1-year-old or younger are associated to near-shore habitats with abundant submerged vegetation, and about half of a cohort matures sexually by their first year, with the remaining half maturing in the next two years. Adult perch use all available depth strata, but their depth preferences vary seasonally, preferring shallower zones during the spring and summer, and moving deeper during the fall and winter. Thus, Creole perch have a role in connecting the shallow and deep habitats within the lake. We also found that Creole

perch move during spring to shallow vegetated areas for spawning. Such areas are relatively scarce in the Nahuel Huapi Lake, representing about just 1% of the total shoreline. Accordingly, we found a very low abundance of spawning individuals and young-of-the-year, suggesting that the Nahuel Huapi Creole perch population reproduces mostly outside of the lake.

Studying the natural history of endemic species helps inform sustainable conservation and management practices at multiple spatial scales. Our result highlights two important aspects of the biology of the Creole perch *P. trucha* that should be taken into account for their conservation. At a local scale and given the scarcity of adequate spawning sites along the lakeshore, conservation and management policies should aim to identify such sites and prioritize their protection. At a regional scale and given the current evidence for reproductive migration between water bodies as a key to sustain current Creole perch populations, water basin level management policies should ensure conservation of hydrological connectivity among Patagonian lakes and rivers. These measures would help ensure protect the specific habitat needed for a key stage of Creole perch life history.

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Attached Table:

ID	site	Fall CPUEN			Winter CPUEN			Spring CPUEN			Summer CPUEN		
		H	J	M	H	J	M	H	J	M	H	J	M
1	Arm Ultima Esperanza	0.063	0.000	0.044	0.000		0.014	0.096	0.056	0.000	0.014	0.000	0.000
2	Arm Rincon				0.009		0.000	0.037	0.018	0.000			
3	Arm Machete	0.022	0.000	0.022	0.000		0.000	0.075	0.030	0.000	0.007	0.000	0.000
4	Arm Blest				0.000		0.000	0.076	0.041	0.000			
5	Arm Tristeza	0.036	0.000	0.042	0.000		0.000	0.073	0.055	0.000	0.000	0.000	0.000
6	Arm campanario	0.175	0.061	0.079	0.031		0.010	0.024	0.020	0.007	0.049	0.030	0.005
7	Harvor Isla Victoria				0.000		0.018	0.175	0.110	0.022			
8	Bay Piedras blancas												
9	Arm Huemul	0.012	0.000	0.012	0.007		0.000	0.409	0.379	0.000	0.000	0.000	0.000
10	Bay Ortiz Basualdo	0.054	0.000	0.034	0.006		0.000	0.103	0.021	0.007	0.062	0.029	0.000
11	Club de caza y pesca	0.079	0.004	0.059	0.007		0.007	0.189	0.254	0.007	0.126	0.000	0.000
12	Harvor Americano				0.082		0.041	0.040	0.024	0.000			

مقاله پژوهشی

مهاجرت‌های فصلی و تولید مثلی در سوف ماهی کرئول *Percichthys trucha* (شعاع بالگان): پرسیکتیده) سبب اتصال زیستگاه‌های دررون و برون دریاچه‌ای می‌گردد

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چکیده: در این مطالعه زیست‌شناسی سوف ماهی کرئول *Percichthys trucha* که یکی از بزرگترین ماهیان شکارگر در جوامع آب‌شیرین شمال پاتاگونیا می‌باشد در یک دریاچه الیگوتروف عمیق با تاکید بر: (۱) استفاده تمایزی از بخش‌های عمقی کرانه‌ای برحسب سن، (۲) سن در زمان بلوغ و فصل تخم‌ریزی و (۳) وقوع مهاجرت‌های تولیدمثلی به سواحل دارای پوشش گیاهی، بحث شد. ماهی‌ها از ۱۲ محل مختلف در داخل دریاچه نمونه‌برداری شده و مشخص گردید که *P. trucha* در طی سال و طی مراحل زندگی به‌طور تمایزی از منطقه ساحلی استفاده می‌کند. از زمان تخم‌ریزی و طی سال اول، ماهیان نابالغ نواحی ساحلی کم عمق دارای پوشش گیاهی را ترجیح می‌دهند، ۵۰٪ از افراد در ۱ سالگی به بلوغ رسیده و همه آن‌ها در ۳ سالگی تولیدمثل می‌نمایند. به‌طور کلی، نتایج نشان می‌دهد که رفتار تولیدمثلی *P. trucha* باعث بهبود ارتباط زیستگاه بین مناطق مختلف دریاچه و بین دریاچه و سایر دریاچه‌های متصل به آن توسط انشعاب‌های جویبارهای مختلف می‌شود.

کلمات کلیدی: پاتاگونیا، رفتار تولیدمثلی، فصل تخم‌ریزی، ارتباط زیستگاه‌ها.