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Early migration and estuary stopover of introduced chinook salmon population in the Lapataia River Basin, southern Tierra del Fuego Island

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ABSTRACT

Established populations of chinook salmon (*Oncorhynchus tshawytscha*) have recently been reported in South America, at both Atlantic and Pacific basins. Several studies have evaluated different aspects of their life histories; however, little is known about the use of the estuaries by the juveniles of these populations. We examined spawning time, seaward migration timing, growth rate, scale patterns, diet, and geometric morphometric, contrasting the early life history during freshwater and estuary residence of a chinook population established in Lapataia Basin. Fall run spawning took place in March–April and the parr emerged in September. Two distinct seaward migration patterns were identified from sein net fishing records: one population segment migrating earlier to the estuary in October and a second group migrating later in February. The growth rate of fish captured at the estuary was significantly higher than the fish captured in freshwater. In addition, higher scale intercirculi distances were observed in estuary fish showing differences in growth rate. The feeding habitat in fish captured in both environments changed through time from bottom feeding to surface feeding and from significant diet overlap to no overlap. The morphology of the fish captured at the estuary was associated with the elongation of the caudal peduncle and a decrease in the condition factor index, both changes related to smolt transformation. The earlier migration and the higher growth rate of juveniles in the estuary together with fish of 1 + yo captured in this environment reveal that the estuary of Lapataia Basin is not only a stopover for the chinook salmon, but also a key habitat to reside and feed previous to the final seaward migration.

1. Introduction

Tierra del Fuego Island, at the southern South America (52°S-55°S), is one of the few regions in the world where the number of freshwater fish introduced is greater than the number of native fish species (Leprieur et al., 2008; Cussac et al., 2009). The only native fish species inhabiting the inland waters of this island are the galaxiid fishes *Galaxias maculatus*, with diadromous and landlocked populations, and *G. platei*, with landlocked populations only (Cussac et al., 2004). In addition, there are some historical records of two other galaxiids of the genus *Aplochiton*, but their current status is unknown (Cussac et al., 2004). Since the beginning of the 20th century, different salmonid species such as brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) have been introduced in Patagonia, Argentina (Pascual et al., 2007). In contrast to the long history of introductions of trout, the chinook salmon (*Oncorhynchus tshawytscha*) has recently been introduced in Patagonia. The first established population of this species was recorded in 1989 in a Pacific basin (Grosman, 1991), while the first record in an Atlantic basin was found in 2002 by Ciancio et al. (2005). The last established population of chinook salmon in Patagonia was

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reported in 2007 by Fernández et al. (2010) in Lapataia Basin flowing into the Beagle Channel, South Tierra del Fuego Island.

Salmonids exhibit a great phenotypic plasticity and a wide variety of life histories that allow them to use different environments (Gross, 1987). The migration behavior of salmonid populations is one of the most important aspects to describe the plasticity of this species (Gross, 1987). Most salmonids introduced in Patagonia established wild landlocked populations; nevertheless, there have been some successful anadromous populations of brown trout (O'Neal and Stanford, 2011) and rainbow trout (Pascual et al., 2001). Anadromy is explained as a fish born in freshwater that migrates to the ocean to grow and then returns to freshwater to spawn (Gross et al., 1988). Salmonids develop this life history trait as a gain to individual fitness associated with movement across the freshwater-ocean salinity (Gross, 1987). Unlike other salmonids, the life history of chinook salmon is extensively diverse, showing a wide range of alternative migration patterns. In this regard, the populations of chinook salmon can be divided into stream-type and ocean-type according to the length of their freshwater residence in the rivers and their age at seaward migration (Gilbert, 1913; Healey, 1991). The stream-type spends at least one year in freshwater before smoltification, while the ocean-type migrates to the sea during the first year of life (Healey, 1991). After seaward migration, both ecotypes show differences in the amount of time they remain in brackish waters, with ocean-type spending a longer period than stream-type (Quinn and Myers, 2004).

Salmonids growth, age and migration pathways have been widely studied by scale analysis (Gilbert, 1913; Koo and Isarankura, 1967; Unwin and Lucas, 1993; Ruggerone et al., 2009). Although this technique has proven useful to describe the life history of many chinook populations, it may not be so useful to study small differences due to alternative development pathways of the emerging fry. For instance, classification as stream- or ocean-type population not always shows all the phenotypic variation within or between the ecotypes (Bourret et al., 2016) and also might downplay the role of the estuary as a key environment during salmon migration. In this regard, the anadromous fish not only use freshwater and ocean habitats to complete their life cycle, but also need the estuary as a stopover for feeding and residence during transition between environments (Weitkamp et al., 2014). It has been reported that several chinook salmon populations spend from few weeks up to several months in the estuary, being it an indispensable environment prior to final migration to the ocean (Reimers, 1973; Bottom et al., 2005; Duffy et al., 2005). However, despite the importance of estuaries as nursery habitat for salmonids, the majority of research has been focused on freshwater and marine environments (Weitkamp et al., 2014).

Several works have described the life history, genetic stock, and distribution of chinook salmon populations established in Patagonia since their first record (Grosman, 1991; Ciancio et al., 2005, 2015; Becker et al., 2007; Correa and Gross, 2008; Di Prinzio and Pascual, 2008; Fernández et al., 2010; Riva Rossi et al., 2012; Araya et al., 2014; Narum et al., 2017). Nevertheless, there are scarce and fragmented data evaluating the early stages or the use of estuary by these populations. So far, life history characterization of chinook salmon populations invading Pacific and Atlantic basins in Patagonia have been carried out studying mainly the adult portion of these populations. The aim of this work is to examine the spawning, hatching and emergence timing and the juvenile life history alternatives in a fall chinook population. Migration timing, growth rate, scale analysis, diet, and geometric morphometric technique were used to compare juveniles during freshwater and estuary residence. We considered the hypothesis that the juveniles used the estuary of Lapataia basin before the final sea migration.

2. Materials and methods

2.1. Study area

The study was conducted at the Lapataia Basin and its estuary in the Tierra del Fuego National Park (TFNP), located at the extreme South of Patagonia (Fig. 1). Lapataia Basin is a 540 km^2 area located from the parallels 54°38′S in Chile to 54°51′S in Argentina. The river has it sources in a glacier, drains into the Acigami Lake of 22 km^2 and then out flows from the lake to the Lapataia and Ovando Rivers across 2 km to the estuary at the Beagle Channel (Fig. 1). The river is a snowmelt flood-dominated system, and flood events typically occur between October and December (Niemeyer, 1980; Iturraspe et al., 1989). No tributaries flow into the main stream. Historical discharge data (1985–1987) was obtained from Iturraspe et al.

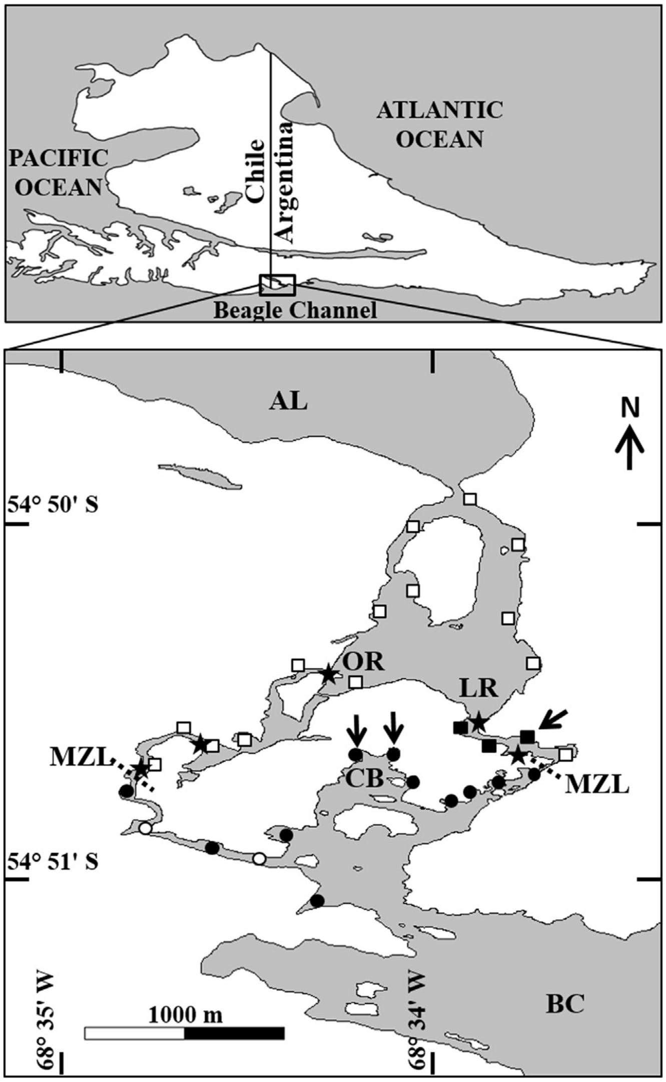

Fig. 1. Tierra del Fuego Island (upper panel) and location of Lapataia Basin and Estuary (lower panel). The sampling locations are identified as follows: Squares indicate 17 freshwater sampling sites (3 full squares: positive *O. tshawytscha* fishing and 14 empty squares: negative *O. tshawytscha* fishing) and circles indicate 13 estuary sample sites (11 full circles: positive *O. tshawytscha* fishing and 2 empty circles: negative *O. tshawytscha* fishing). Asterisks indicate identified spawning areas. Arrows show the sites were the fish were sampled regularly. The mixing zones limits (MZL, indicated by dashed lines) were assigned following the limits proposed by Vanella et al. (2016). AL: Acigami Lake, LR: Lapataia River, OR: Ovando River, CB: Cormoranes Bay; BC: Beagle Channel.

(1989) and daily mean air temperature data (2014- 2015–2016) were provided by the Environmental and Geographic Information Service of the Austral Center for Scientific Research (CADIC-CONICET).

2.2. *Spawning run timing and beds distribution*

Daily field surveys were conducted from November 1st, 2011 to April 30th, 2012 recording the presence of adult salmon in Lapataia and Ovando Rivers from the outlet of Acigami Lake to the estuary. During this period flyers reporting the presence of chinook salmon were given to visitors to the National Park and anglers, and the latter were also interviewed to record information about the dates of their personal observations and captures of salmon in the rivers. Furthermore, adult fish were captured using three gill nets (50 × 2.5 m; 10.1 cm stretch mesh) settled periodically (once to three times per week) from late February to early May of 2015. Additionally, a trap was designed to be set into the Ovando River 100 m downstream of the mixing fresh and sea water zone limit, at a narrow area covering the entire section of the river.

Each adult salmon was sexed and measured (fork length, ± 0.5 cm and total weight, ± 1 g), and scales located above the lateral line and near the anterior margin of the dorsal fin were extracted and stored. Five scales of each fish were cleaned, impressed on acetate cards and inspected on stereomicroscope connected to a digital camera. The scales radius and circuli were measured and counted on digital images using the Image-pro plus 4.5 Software (www.mediacy.com/imageproplus). In order to distinguish among circuli formed in different environmental conditions, differences in growth of fish were assumed to be reflected on their scales according to Rich (1920) and Reimers (1973) interpretations. Slower growth, during fresh water residence, was expected to be represented by narrow circuli spacing while faster growth, during estuary and ocean residence, was expected to be represented by wide circuli spacing. Additionally, the life history of adult fish was studied by comparing their scales patterns with that of juveniles with known life history described later in this work.

The spawning beds were recorded along all the river length during three consecutive falls and winters (2014–2016), taking advantage of the low discharge during these seasons. Each bed was georeferenced and classified as active if the substrate color was clear or inactive if the substrate color was dark.

2.3. *Hatching, timing of fry emergence and juveniles sampled*

The log-inverse Belehradek model and the unmodified thermal sum hypothesis were used to estimate the range of accumulated temperature units (ATUs) for hatching time (Alderdice and Velsen, 1978). The range of ATUs for the estimation of chinook salmon emergence timing was obtained from Geist et al. (2006). Water temperature was recorded on the river every hour using waterproof electronic data-loggers (Thermochron® iButton, CA, USA) placed on the spawning area and mean daily water temperatures were used to calculate ATUs. Under-gravel fry and emerged parr were captured on the spawning bed area with backpack electro-fishing gear (LR-24 Electrofisher, Smith Root Inc, WA, USA).

In order to identify juvenile rearing areas in fresh and brackish water, a total of 17 sites at Lapataia and Ovando Rivers were surveyed from April 2014 to May 2015 and 12 sites were surveyed at estuary from November 2014 to March 2015 (Fig. 1). The juveniles were captured in both environments by a seine net (30 × 1.5 m; 3.2 mm stretch mesh). The sample sites in the rivers were selected in order to include different environments regarding substrate type, presence of aquatic vegetation, refuge, flow velocity and depth. In addition, a drifting tangle net (20 × 1.5 m; 12 mm stretch mesh) was used to sample deeper zones in the rivers. One site of each environment was selected to be sampled once a month from September 2015 to April 2016 for all subsequent fish analysis (see Fig. 1 for localization). During this period, water temperatures of these areas were recorded every hour using waterproof electronic data-loggers (Thermochron® iButton, CA, USA) and conductivity was recorded with a Hanna HI 9828 multi-parameter.

Fish were measured (fork length, ± 0.1 mm and total weight, ± 0.01 g), and the weight-length relation was estimated in accordance with Froese (2006) as $W_{(g)} = a{*}LF^{b}_{(mm)}$. The condition factor was estimated as the relative condition factor (Kn) following Anderson and Neumann (1996): $Kn = W/W'$ where W is the weight of the individual and W′ is the length-specific mean weight for the Lapataia Basin population, including the fish captured at the estuary, as predicted by the weight-length equation estimated for it.

Scales located above the lateral line and near the anterior margin of the dorsal fin were extracted and stored. Three scales of each fish were cleaned, inspected on a stereomicroscope and photographed to measure scale radius and to count circuli. The relationships between scale radius to fork length and number of circuli to scale radius for fish collected from Lapataia River and Cormoranes Bay were described with linear regression models: $[Scale\ radius = intercept + slope{*}fork\ length]$ and $[N^{o}\ of circuli = intercept + slope{*}scale\ radius]$. The homogeneity in slope and intercept between sites was tested. The distance between the first ten circulus pair was used to classified growth patterns of fish living in freshwater and estuary, following Rich (1920) and Reimers (1973).

The data were checked for normal distribution with the Kolmogorov–Smirnoff test. The effects of site and time on each variable were tested using two-way ANOVA and post hoc Tukey's HSD test ($p < 0.05$).

2.4. *Diet analysis*

The gut contents of *O. tshawytscha* juveniles from LR ($n = 30$) and CB ($n = 30$), collected on November 11th and February 15th, were analyzed. This analysis was restricted to prey items found in the anterior part of the gut to increase the likelihood that the prey had been eaten recently. Prey categories were identified to the lowest possible taxonomic level and counted within each prey category under a stereomicroscope. The total weight of each prey category per gut was measured at the nearest 0.01 mg in an analytical scale. Percent of frequency of occurrence ($\%F_i$), percentage of total prey number ($\%N_i$) and percentage of total stomach content weight ($\%W_i$) were calculated in order to estimate the Index of Relative Importance $[IRI = \%F_i{*}(\%N_i + \%W_i)]$ for each category of prey items (Pinkas et al., 1971). Food ration was expressed as total stomach content weight of each item divided by fish weight. Non-parametric Mann–Whitney *t*-test was used to compare food ration of each item between fish captured at both sites ($p < 0.05$). To evaluate dietary overlap, the Schoener's Index (α) was used: $[\alpha = 1 - 0.5\ (\sum_{i=1}^{n} |P_{xi} - P_{yi}|)]$ where P_{xi} is the proportion of food category i in the diet of fish group x, P_{yi} is the proportion of food category i in the diet of fish group y, and n is the number of food categories (Wallace, 1981). Overlap was considered to be biologically significant when the Schoener's Index value exceeded 0.60 (Zaret and Rand, 1971).

2.5. *Geometric morphometric*

Geometric morphometric procedures were applied to discriminate between the shapes of fishes captured in February 15th at LR ($n = 32$) and CB ($n = 55$). Fish were anesthetized with tricaine methanesulfonate (MS-222) before obtaining fork lengths, weights, and digital photographs of their left side. The freeware program

TpsDig (Rohlf, 2010) was used to digitize 17 homologous and conserved landmarks within the species (Fig. 2), and commonly employed in previews morphology studies of chinook salmon juveniles (Billman et al., 2014; Bowen and Marchetti, 2015). The unbend application of the tpsUtil software (Rohlf, 2013) was employed to correct for possible bias due to body bending, using three additional landmarks along the lateral line to generate corrected landmark coordinates. The freeware program MorphoJ (Klingenberg, 2011) was used for the shapes analyses. The landmarks were converted to shape coordinates using Procrustes superimposition (Rohlf and Slice, 1990). In order to avoid allometry effects, residuals of the allometric regression were used for statistical analysis and investigation of shape variation according to the procedure proposed by Sidlauskas et al. (2011). Canonical Variate Analysis (CVA) and T-square test were carried out to investigate the difference between group mean.

3. Results

3.1. Adult runs and spawning

The first adults in the river during 2011–2012 daily survey were observed on March 4th and the last one on April 12th. The captures of adult fish in the rivers by gill nets and trap during 2015 were conducted from March 20th to April 6th. During this period, a total of 9 individuals (4 females and 5 males) were captured (Table 1). Except for a young male of 2 + years old (yo), all males and females age ranged between 3 + and 4 + yo. The macroscopic analysis of the gonads showed that the testes were fluent and the ovaries were ovulated, loosing oocytes easily at handling pressure.

A total of ten active spawning beds were identified in the Lapataia River distributed in two different areas, and nine active spawning beds in the Ovando River distributed in three areas (Fig. 1). All beds were located in transitional areas between pools and riffles with acceleration of the water flow rate and shallow depths. The spawning beds that were closest to the limit between the fresh and brackish water were located at 100 m into the Lapataia River, while the farthest ones were located at 1100 m in the Ovando River.

3.2. Hatch and emergence time

The time of spawning was defined as April 1st based on the period of time when adult females were observed and captured on bed grounds during the 2015 run described above. Therefore, hatching and emergence time estimated from ATUs would take place in early June (65–74 days post spawning) and from late September to early October (163–190 days post spawning) in the Lapataia River, respectively (Fig. 3). Spawning activity took place during the period when flow discharge, photoperiod and temperature decreased, while emergence was recorded when these variables increased (Fig. 3). The predicted timing of fry emergence, between September 10th and October 10th, was consistent with the timing of under-gravel fry captured on September 27th ($L_F = 35.8 \pm 0.3$ mm; $W = 0.34 \pm 0.01$ g; $n = 30$) and emerged fry captured at the same site on October 8th ($L_F = 36.6 \pm 0.6$ mm; $W = 0.43 \pm 0.03$ g; $n = 9$).

3.3. Rearing habitats of juveniles

One rearing area with a high density of juveniles was identified in fresh water and two in brackish water, and were called LR for Lapataia River and CB for Cormoranes Bay, respectively (see Fig. 1 for localization). The LR rearing habitat was characterized by flood plain zones (total area: 5833 m^2) that were wet only during spring and summer, with shallow water (5–30 cm depth) and sand or grass as substrate and grass as riparian vegetation. The estuary rearing area (total area: 2070 m^2) was characterized by an intertidal zone during high tidal events, with sand and silt as substrate and riparian forest of *Nothofagus* spp. Fig. 4 shows the temperature and conductivity registered in these areas during the sampled period.

Fish were caught in both environments from October 8th to February 15th. From that time to April 11th fish in LR were absent at all subsequent samples and were only captured in CB. Together with juvenile salmons, *G. maculatus* in LR and *G. maculatus* with *Eleginops maclovinus* were captured in CB.

3.4. Growth

A total of 1209 young-of-the-year fish were captured in LR ($n = 668$) and in CB ($n = 541$). The fork length and weight of the emerged fry captured on October 8th in LR were not significantly different from fish captured in CB at the same time (Fig. 5a and b). The length and weight of fish caught in December, January and February were significantly higher ($p < 0.001$) in CB than in LR (Fig. 5a and b). The weight-length equation estimated for all captured fish at both environments was $W_{(g)} = 0.000003*LF_{(mm)}^{3.326}$; $R^2 = 0.9726$. The relative condition factor of fish predicted by the weight-length equation estimated was not different between sites from October to January ($p > 0.05$), while in February it showed higher values ($p < 0.001$) in LR than in CB (Fig. 5c). The L_F, W and Kn of fish captured in CB in March and April (absent in LR during these months), is also shown in Fig. 5. Seven fishes captured in CB in March (4.1% of total fish captured) showed vertebral deformities and were excluded from the analysis.

Besides the periodic catches of young-of-the-year fish described above, we did also catch 15 fish of 1 + yo age in CB ($L_F = 202.2 \pm 5.3$ mm; $W = 91.5 \pm 8.2$ g) on February 15th.

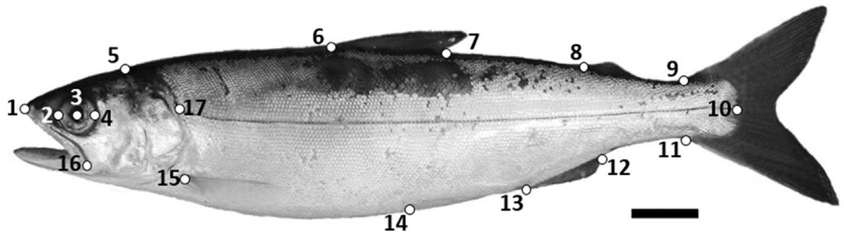

Fig. 2. Landmarks (white circles) digitized on juvenile chinook salmon photograph used for geometric morphometric analysis: (1) anterior tip of snout, (2) anterior tip of the eye, (3) middle of the eye, (4) back tip of the eye, (5) uppermost point of operculum, (6) origin of dorsal fin, (7) insertion of dorsal fin, (8) origin of adipose fin, (9) anterior attachment of dorsal membrane from caudal fin, (10) base of middle caudal rays, (11) anterior attachment of ventral membrane from caudal fin, (12) insertion of anal fin, (13) origin of anal fin, (14) origin of pelvic fin, (15) origin of pectoral fin, (16) most posterior point of maxillary, and (17) origin of lateral line. Scale bar = 1 cm.

Table 1
Sex, average size, age and reproductive status of adult migrants caught in the Lapataia basin between March 20th and April 6th, 2015.

Sex	Fork length (cm)	Weight (kg)	Age (years)	Reproductive status	
				Gonad	Oocyte diameter (mm)
Male (n = 5)	83.3 ± 6.0	7.3 ± 1.4	3.4 (2–4)	Fluent	–
Female (n = 4)	94.9 ± 3.9	9.9 ± 1.5	3.5 (3–4)	Ovulated	7.98 ± 0.19

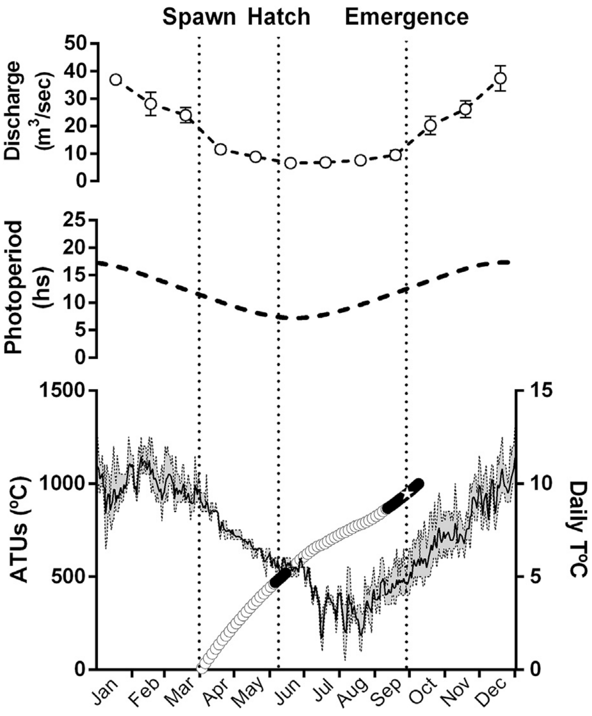

Fig. 3. Monthly mean (±SEM) of water discharge (m^3/sec) recorded during 1985–1987 in Lapataia River by Iturraspe et al. (1989) and photoperiod is shown at the top and middle of the figure. Mean daily water temperature (solid line) with maximum and minimum (dashed lines) registered throughout 2015 year is shown at the bottom of the figure together with the accumulated temperature units (ATUs °C) calculated during under-gravel life time (white circles). The black circles represent the range of ATUs for hatching and for emergence estimated following Alderdice and Velsen (1978) and Geist et al. (2006), respectively. The white asterisk indicates the emergence time detected by direct observation.

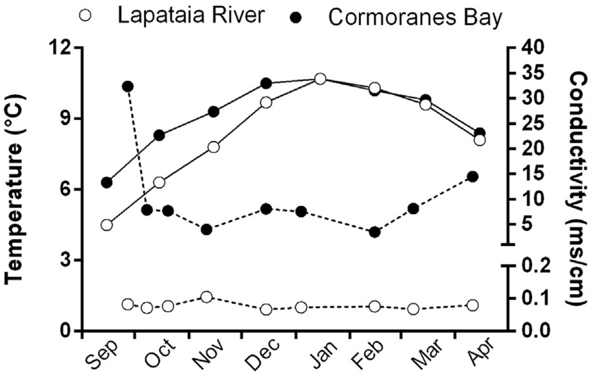

Fig. 4. Monthly mean temperature (solid line) and conductivity (dashed line) registered in Lapataia River (white circles) and Cormoranes Bay (black circles) during the months when fish were captured.

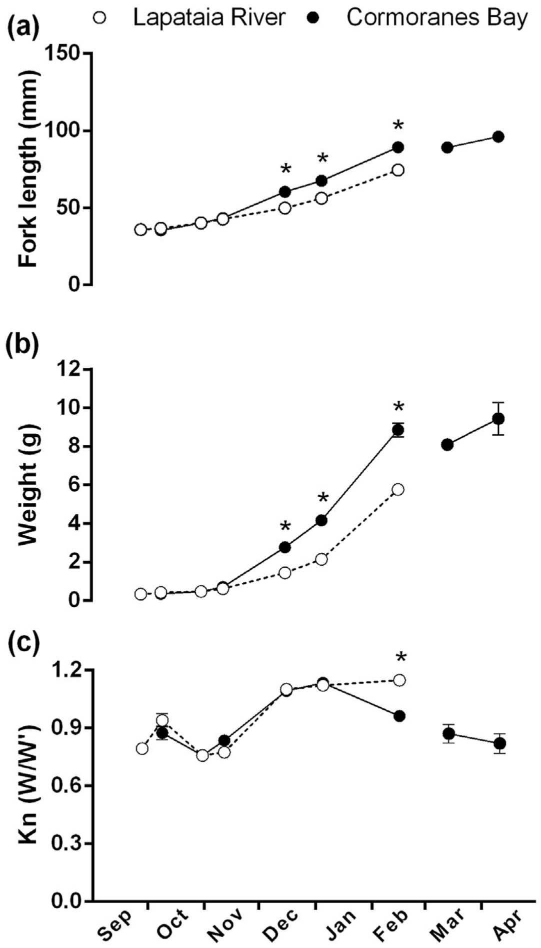

Fig. 5. Mean (±SEM) of (a) Fork length (mm), (b) weight (g), and (c), condition factor (Kn) for young-of-the-year chinook salmon sampled from September 27th to April 11th in Lapataia River (white circles; n = 668) and Cormoranes Bay (black circles; n = 541). The data from March and April are fish captured in CB when no fish were found in LR. Asterisks represent significant differences between sites at same time resulting from Tukey's post hoc tests ($p < 0.05$).

3.5. Scale analysis

The fork length of fish with only one circulus captured in LR and CB were 43.9 ± 1.7 mm and 45.6 ± 0.9 mm, respectively. The analysis of the scales of the fish showed that their fork length was positively and linearly related to scale radius (LR: $L_F = 5.639*Scale\ radius - 129.5$, $R^2 = 0.8383$; CB: $L_F = 5.807*Scale\ radius - 153.6$, $R^2 = 0.8805$; Fig. 6a). The slopes of these relationships were not significantly different between LR and CB fish ($F_{1,\ 199} = 2.337$; $p > 0.05$), while the intercept of these relationships was significantly higher for LR fish than CB fish ($F_{1,\ 200} = 6.634$: $p < 0.01$). The relationship between number of circuli and scale radius was also positively and linearly related for LR and CB fish (LR: $No\ of\ Circuli = 0.03069*L_f - 1.363$, $R^2 = 0.9001$; CB: $No\ of\ Circuli = 0.03002*L_f - 0.8211$, $R^2 = 0.9015$; Fig. 6b). The slopes of both relationships were not significantly

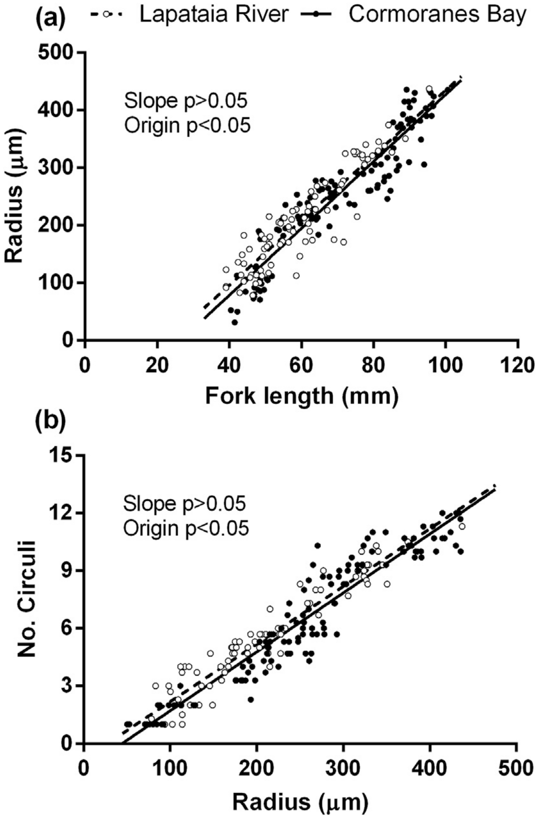

Fig. 6. Linear model with regression line for the relationships between (a) scale radius to fork length and (b) number of circuli to scale radius for fish collected from Lapataia River (white circles) and Cormoranes Bay (black circles). L_F vs Radius: LR: $L_F = 5.639$ (±0.2769) * Radius − 129.5 (±17.08); r = 0.9156; p < 0.0001; n = 82. CB: $L_F = 5.807$ (±0.1961) * Radius − 153.6 (±14.17); r = 0.9384; p < 0.0001; n = 121. Slope equal p = 0.6293; intercept different p = 0.01072. Radius vs Circuli: LR: Radius = 0.0300 (±0.0011) * Radius − 0.8211 (±0.2552); r = 0.9487; p < 0.0001; n = 82. CB: $L_F = 0.03069$ (±0.00093) * Radius − 1.363 (±0.2577); r = 0.9495; p < 0.0001; n = 121. Slope equal p = 0.6664; intercept different p = 0.0065.

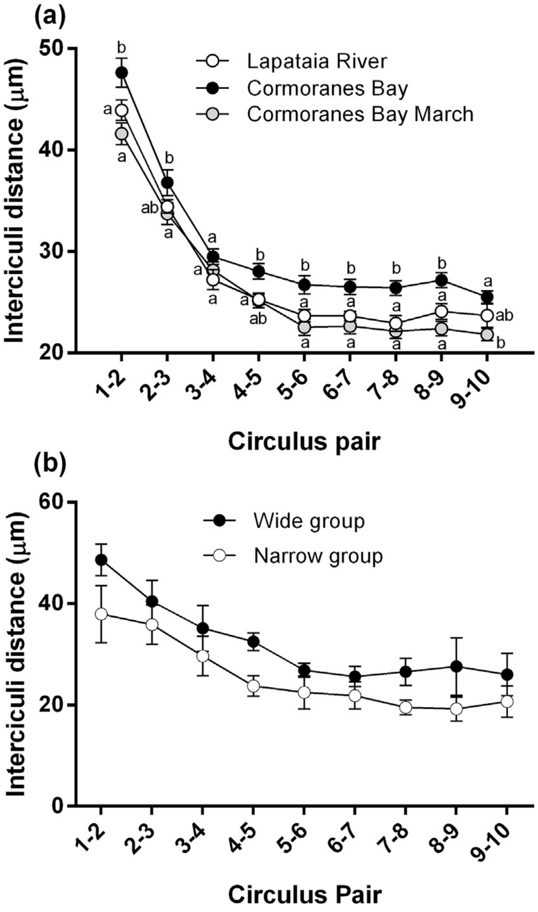

Fig. 7. Mean (±SEM) of circulus spacing for each circulus pair measured from the scales of (a) juvenile chinook salmon collected in February from Lapataia River (white circles; n = 25), Cormoranes Bay (black circles; n = 25) and fish captured in Cormoranes Bay in March (grey circles; n = 25) and (b) scales of adult chinook salmon grouped as narrow group (white circles; n = 6) and wide group (black circles; n = 3). Different letters represent significant differences of intercirculi distances between fish groups at same cirulus pair resulting from Tukey's *post hoc* tests (p < 0.05).

different between LR and CB fish ($F_{1,\,197} = 0.186$; $p > 0.05$), while the intercept of these relationships was significantly higher for LR fish than CB fish ($F_{1,\,198} = 7.577$; $p < 0.01$).

The analysis of the scales of fish captured in February in LR and CB and in March in CB showed significant effects of site on scale intercirculi distance ($F_{2,\,620} = 49.7$; $p < 0.0001$; Fig. 7a). Tukey's *post hoc* test for two-way ANOVA indicated that the intercirculi distance of seven out of nine interciculus pair of the scales of fish captured in February in LR was lower than in scales of fish captured in CB at the same time. On the other hand, no differences were found between the intercirculi distance of fish captured in LR in February and CB in March (Fig. 7a). According to the first ten circuli aspect of scales of adults captured in the Lapataia River Basin between March 20th and April 6th, 2015, it was possible to distinguish between a group of fishes with narrow intercirculi space and a group with wide intercirculi space. Further measurements of this distance showed significant effects of group on scale intercirculi distance ($F_{1,\,63} = 65.3$; $p < 0.0001$; Fig. 7b).

3.6. Diet

Fig. 8 shows the diet analysis of salmon captured in November and February in both sites. The index of relative importance of diet items of fish captured in November in LR (Fig. 8a) was represented by 56.7% of autochthon items (Plecoptera 48.7%; pupa of Diptera 7.9% and Coleoptera 0.1%), whereas allochthonous preys represented 43.3% (Arachinda 36.0% and adults of Hemiptera 7.3%). The stomach content of fish captured in CB at the same time was highly dominated (99.3%) by autochthon items (Amphipoda 87.3%; pupa of Diptera 9% and larvae of Diptera 3.1%), and only 0.6% of allochthonous items (adults of Diptera 0.4%; Arachinda 0.1% and Collembola 0.1%). The overlap index value was lower than the threshold value of 0.6 (α = 0.38) indicating that there was a difference in feeding habitat between chinook juveniles captured at LR and at CB in November. Also, fish groups showed significant difference in their total food ration, with significantly higher value ($p < 0.0001$) in fish captured in CB (Fig. 8b).

The index of relative importance of diet items of fish captured in February (Fig. 8c) was highly dominated by allochthonous preys in Lapataia River (adult of Diptera 66.9%; Hemiptera 4.1% and 1.1% of adult of Trichoptera, Ephemeroptera, Hymenoptera and Arachinda) and in the CB (adult of Diptera 90.9% and Hemiptera 0.7%); meanwhile autochthon preys represented only 27.9% in LR (pupa of Diptera 16.9%; larvae of Diptera 9.7% and 1.3% of pupae of Trichoptera, Amphipoda and Nematode) and 8.4% in CB (pupa of Diptera 7.9%; larvae of Diptera 0.3%; Tainacea 0.1% and fish eggs 0.1). According to size, presence of adhesive disc, environment and season of the year, it is possible that the fish eggs observed in the diet were of puyen *G. maculatus*. The overlap index values were

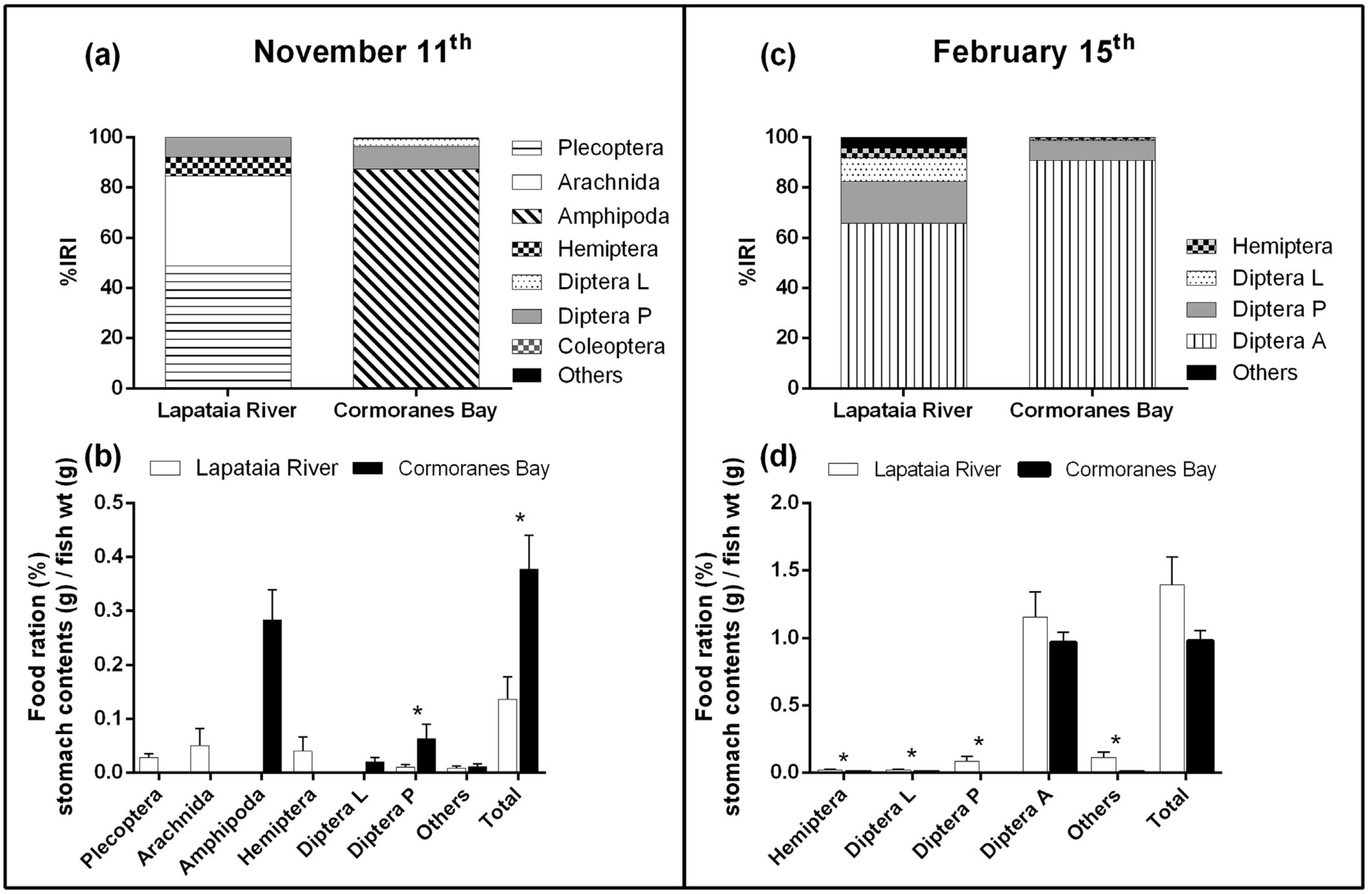

Fig. 8. Index of relative importance (a, c) and mean (±SEM) of food ration (b, d) of juvenile chinook salmon captured in November (left panel) and February (right panel) in Lapataia River and Cormoranes Bay. L: larvae; P: pupae; A: adult. Others in left panel: Plecoptera in LR and None in CB. Others in right panel: Trichoptera, Amphipoda, Nematoda, Arachnida (Araneae), Hymenoptera and Ephemeroptera in LR and Tanaidacea, fish eggs and Nematoda in CB. Asterisks represent significant differences of food ration between sites at the same time resulting from Tukey's *post hoc* tests ($p < 0.05$).

higher than the threshold value of 0.6 ($\alpha = 0.66$) at both environments indicating that there was no difference in feeding prey between chinook juveniles captured at LR and CB in February. Also, fish groups did not show significant difference in their total food ration (Fig. 8d).

The diet of 1 + yo fish captured in CB in March showed that 13 stomachs were empty or practically empty with only 1–3 dipterans pupa and 2 stomachs with 1 and 3 *G. maculatus* of 50–60 mm body length each.

3.7. Morphometry

Since allometry dependence was detected ($p < 0.01$; predicted = 7.03%), residuals of the allometric regression were used for further comparison analysis. Canonical variate analysis revealed that fish captured in LR and CB in February could be separated in two different groups by shape (Procrustes distance = 0.0116; Mahalanobis distance = 3.7221; T-square = 274.7; $p < 0.0001$; Fig. 9). The comparison of body morphology showed that caudal peduncle was more elongated in fish captured in CB compared to fish captured in LR at the same time (Fig. 9).

4. Discussion

The first study of chinook salmon population in Lapataia and Ovando Rivers by Fernández et al. (2010) showed that the scale pattern of adult fish corresponded to a stream-type population, contrasting with the ocean-type registered in this work. This difference may be due to a phenotypic response to environmental factors acting on and controlling early life history. A similar shift from one ecotype into another was observed in rivers of New Zealand (Parrott, 1971), suggesting an early phenotypic change due to variations in juvenile growth and life history (Quinn et al., 2001).

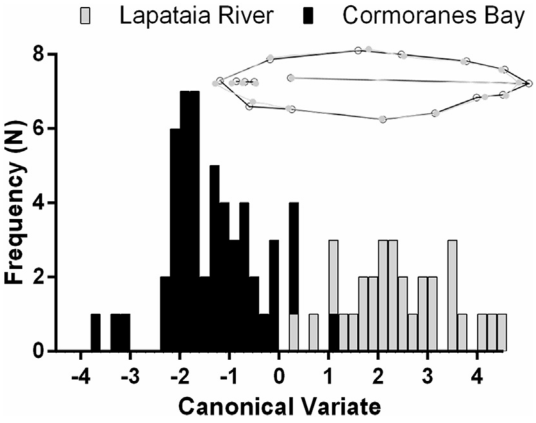

Fig. 9. (a) Distribution of CV scores among Lapataia River fish (open bars, n = 32) and Cormoranes Bay migrant fish (solid bars, n = 55) and wireframe visualizations of both shapes. Difference between means: Procrustes distance: 0.01160106; Mahalanobis distance: 3.7221; T-square: 274.6679; p < 0001.

Another possibility, although less probable, is that there may be differences in the interpretations of their life history due to the methodology used. In this regard, different results could be obtained from scale analysis of adult or from direct observation of juvenile migration as it was extensively discussed by Reimers (1973). For instance, analysis of adult scales from Willamette River showed that most spring chinook salmon resided a year in freshwater (Mattson, 1963), but juvenile sampling showed that fish went downstream as fry (Mattson, 1962).

Reproductive activity was observed during April (early Fall), with a decline in photoperiod and water temperature conditions (below 11 h light and 9 °C), which would be the trigger conditions of final maturation and spawning (Nagahama, 1994; Pankhurst and Porter, 2003; Migaud et al., 2010). Water temperature found in this watershed during upstream migration of adults was at the lower limit of the preferred temperature range (10.6–19.4 °C) for fall chinook salmon proposed by Bell (1991). The fall run fish captured in the Lapataia and Ovando Rivers and the narrow distance that separates the spawning areas from the ocean is consistent with the ocean phenotype described by Healey (1991). Regardless of the date of migration from the sea, similar period of spawning (late March to early May) was observed in others basin of Patagonia, both Pacific: Petrohué River 42°S (Soto et al., 2007); Futaleufú and Corcovado Rivers 43°S (Di Prinzio and Pascual, 2008), Aysén River 45°S (Niklitschek and Aedo, 2002), and Atlantic: Caterina River 50°S (Ciancio et al., 2005), Grande River 53°S (Chalde et al., 2016).

Water temperature registered during incubation time was between 5 °C and 10 °C, which is within the limits of the optimum range for early development proposed by Bell (1991). Chinook salmon are known to spawn in the same areas throughout years and redds are distributed in distinct aggregations throughout the rivers (Klett et al., 2013). The location of spawning beds was restricted to the five hyporheic zones identified in the rivers, which are typical selected areas for fall chinook spawning (Geist and Dauble, 1998). These areas were located in transitional zones between pools and riffles where a change in depth was associated with increased hyporheic–surface water exchange. These data allow us to hypothesize that the number of beds in Lapataia Basin could be limited by the quantity of suitable areas available for spawning as it was studied by Levy and Slaney (1993) in rivers of British Columbia.

Rivers with a glacial regime like Lapataia are characterized by seasonal flows during the warm season, with high discharge in summer after ice melting and low discharge from the end of autumn to early spring (Leopold et al., 1964). Therefore, the seasonality of discharge measured in Lapataia River by Iturraspe et al. (1989) showed that egg incubation and under gravel period post hatching (April–September) may overlap with the period of low discharge, while fry emergence and freshwater residence (until mid-February) may take place at the beginning of the high discharge season. This overflow event, at the emergence time, provides floodplain areas with optimal rearing habitat for juvenile chinook salmon (Jeffres et al., 2008). The effects of flooded areas improving chinook growth and survival may be due to increasing habitat diversity (Junk et al., 1989), higher productivity (Sommer et al., 2001), and decreased predation or competition (Corti et al., 1997).

The juvenile migration pattern showed that the chinook salmon population of the Lapataia Basin comprises two migratory phenotypes: early ocean-type fish (EOT) that migrate to the estuary a few days after emergence, and late ocean-type fish (LOT) that stay 4–5 months in freshwater after estuary migration. The main differences observed between these phenotypes of chinook salmon established in Lapataia basin are summarized in Table 2. This migration pattern showed similarities with the fall-run population of Petrohué River described by Soto et al. (2007) where some juveniles migrate to the estuary before November (as small as 50–70 mm fork length) and a second migration takes place in February (as large as 100 mm fork length).

Table 2
Principal features of the life histories of juvenile ocean types of fall chinook salmon in the Lapataia River basin.

	Sample Site	
	Lapataia river	Cormoranes bay
Spawning date	Early April	Early April
Hatching date	Mid September	Mid September
Outmigration date	Late February	Mid October
Outmigration size (mm)[a]	75.9 ± 1.9–81.5 ± 10.1	35.7 ± 0.5
Fork length (mm) at first circulii	43.9 ± 1.7	45.6 ± 0.9
FW radius at Outmigration (μm)[a]	316.5 ± 8.2–361.2 ± 8.1	No scale
FW circulii at Outmigration[a]	8.8 ± 0.2–11.1 ± 0.2	No scale

[a] The size, FW radius and circulii are expressed as the range registered in the last fishes captured in Lapataia River on February 15th and the first fishes captured in Cormoranes Bay on March 4th.

Carrying capacity, as determined by habitat features (Armstrong et al., 2003), establishes a bottleneck which increases competition, leading to density-dependent effects. Key periods where bottlenecks have been previously demonstrated in chinook salmon are at spawning time when availability of spawning gravel can cause density dependent regulation of breeding and the early post-emergent fry stage (Milner et al., 2003). In this regard, two potential habitat space bottlenecks were identified in Lapataia Basin acting at two different moments in the life history of the chinook salmon. First, the reduced number of spawning areas that was previously described could be acting as a limitation factor of the offspring number. Second, a density dependent regulation could be acting on fish abundance during early life stages in Lapataia River due to the limited nursery areas available. Both restrictions for population size were identified in chinook salmon introduced in New Zealand where suitable spawning and rearing areas in streams are limited (Waugh, 1980). In this regard, fish were captured in Lapataia River only in three flood plain zones that were wet only during spring and summer, with shallow water and sand or grass as substrate. This limitation could not only be affecting the density during freshwater period, but may also influence the decision of fry to early migration to the estuary. Thus, the separation of the population in two different migrant strategies could be thought as the result of adaptive strategies maximizing their opportunities under population numerical pressure.

In addition to the distinct migration timing displayed by juveniles, growth differences were found between EOT and LOT fish groups. The EOT showed higher growth in length and weight than LOT, at least while they were segregated. The higher water temperature registered in the estuary and the different diet of juveniles observed in November could be factors that explain the higher growth rate of EOT fish. It should be noted that the tendency of growth curves of fish captured at the estuary from February onward decreased, which seems to be the effect of the migration of smaller fish belonging to the LOT group.

In terms of food habits, a clear change in the index of relative importance through time from bottom feeding items in November to surface feeding items in February was observed. Moreover, the analyzed diet of 1 + yo fish showed that chinook salmon became ichthyophagous, as it was observed in other estuaries (Healey, 1980). In a context of the biological invasion by chinook salmon, this is the first report of predation on native fish *G. maculatus*, which is a species of great interest for conservation in Patagonia. The highest growth rate of EOT juvenile in CB together with the fish of 1 + yo captured in this environment reveal that the estuary of

Lapataia Basin is not only a stopover for the chinook salmon on their way to the ocean, but also a key habitat to reside and feed previous to the final seaward migration.

Losses due to fish spinal deformities are widespread in aquaculture production of many species, including chinook salmon (Evans and Neff, 2009). Proportion of fishes with vertebral deformities captured in this study was in accordance with the level of incidence showed for wild and captive Atlantic salmon (Gjerde et al., 2005). Since the population under study was established as a consequence of escapes from fish farms (Riva Rossi et al., 2012), it would be possible to assign these vertebral deformities to the persistence of inbreeding factors (Gjerde et al., 2005).

The comparisons of scale circuli spacing between and within populations of fish at a specific time can be used to infer that fishes displaying the same scale circulus patterns inhabit similar environments and show similar growth rate (Fisher and Pearcy, 1990; Fukuwaka and Kaeriyama, 1997; Fukuwaka, 1998; Hubley et al., 2008). In this work, circulus spacing for chinook salmon captured in LR and CB reveals spatial differences in freshwater and estuary growth rate. Moreover, since circulus spacing of each group of fish in the same period of time was significantly different, it is possible to assume that they did not mix, and that their migration timing was different. Furthermore, the analysis of circulus spacing of the spawning salmon showed a mixed reproductive stock, with 6 scale pattern matching like EOT fish and 3 like LOT.

Juvenile salmonids undergo significant physiological and morphological changes during their early life history, shifting from freshwater parr form to smolt allowing the out migration (Björnsson et al., 2011; McCormick, 2013). A clear morphological change during this transformation is the elongation of the caudal peduncle (Beeman et al., 1994), as it was observed by geometric morphometric analysis in the fish captured in February at CB. Besides, this elongation of the body was reflected by a decrease in the condition factor index of these fish which is a typical change during smoltification (Folmar and Dickhoff, 1980; Winans, 1984). It has been proposed that this streamlined body shape is related with swimming in open water habitats (Winans and Nishioka, 1987; Morinville and Rasmussen, 2008).

The high colonizing ability of chinook salmon is related with its phenotypic plasticity, which was clearly observed in this study, since a single population develop two different strategies of life during the juvenile stage only about ten years after successfully colonize the Lapataia Basin. It is known that there are at least two other chinook salmon populations established in TDF (Chalde et al., 2016), which may have different life histories than those presented in this work. In the context of this chinook invasion that include different basins in Tierra del Fuego, the current challenge is to describe the life histories traits of all these new populations to understand the plasticity of this species under different environmental conditions.

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