

Early development and diets of non-native juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in an invaded river of Patagonia, southern South America

CECILIA YANINA DI PRINZIO^{1*}  AND IVÁN ARISMENDI²

¹*Centro de Investigación en Ecología de Montaña y Estepa Patagónica (CIEMEP)-CONICET, Sarmiento 890, (9200) Esquel, Chubut, Argentina (Email: cydiprinzio@yahoo.com.ar);* ²*Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA*

Abstract Chinook salmon (*Oncorhynchus tshawytscha*) have established populations in both the Atlantic and Pacific basins of southern South America. Yet, basic biological information about these salmon population is absent. Here, we documented relative densities, body size, condition and diet composition of juvenile Chinook Salmon from the Futaleufú River, Argentina. We sampled Chinook Salmon juvenile and environmental variables including daily river discharge, water temperature, electrical conductance, dissolved oxygen and total dissolved solids. We assessed individual variation in the diet of juvenile salmon over time. We estimated the incubation time before fry emergence to be around 101 days under a mean water temperature of 7.5°C. Salmon fry emerged during the Austral Winter (July–August) in off-channel habitats near the redds. Juvenile salmon were between 3.8 and 12.1 cm in length (TL) and their highest body condition occurred early during the Austral summer (December). Juvenile salmon abundances were positively associated with water temperature, but not flow. Diet analyses revealed a specialist feeding behaviour based on food pulses that included both aquatic and terrestrial insects; piscivory was not detected. Juvenile salmon co-occurred with native fishes suggesting a potential for interspecific interference. Our findings provide baseline information for the future management of non-native Chinook Salmon populations in the Southern Hemisphere and elsewhere.

Key words: Chinook fry, diet in early stage, emergence time, feeding strategy, transboundary basin.

INTRODUCTION

Chinook Salmon (*Oncorhynchus tshawytscha*) have successfully established in several regions around the world, including the Great Lakes in North America (Emery 1985), New Zealand (Flain 1981; Quinn & Unwin 1993), and South America (Ciancio *et al.* 2005; Pascual *et al.* 2007; Soto *et al.* 2007; Correa & Gross 2008). In southern South America, Chinook Salmon have been extensively introduced since the last century for recreational fishing purposes and modern aquaculture (Pascual *et al.* 2007; Habit *et al.* 2012; Arismendi *et al.* 2014). However, self-sustaining populations have been documented only during the last few decades (Ciancio *et al.* 2005; Soto *et al.* 2007; Aigo *et al.* 2008; Correa & Gross 2008). Naturalized populations have been reported in basins that drain to the Pacific Ocean from the Pilmaiquen River in Chile (40° 37'S) and southward to the Beagle Channel (54° 50'S) in Argentina (Ciancio *et al.* 2005; Di Prinzio & Pascual 2008; Fernández *et al.* 2010). Similarly, Chinook Salmon populations inhabit rivers that drain to the Atlantic Ocean from the

Caterina River in the Santa Cruz River (Ciancio *et al.* 2005) southward to the Beagle Channel (54° 50'S) in Argentina.

Reasons for the rapid success of Chinook Salmon in southern South America are not well-understood. It has been hypothesized that genetically diverse populations (Becker *et al.* 2007; Astorga *et al.* 2008; Riva Rossi *et al.* 2012) and diverse life histories (Di Prinzio & Pascual 2008) of Chinook Salmon have contributed to their success (Arismendi *et al.* 2014). However, basic information about juvenile Chinook Salmon populations have not been well-documented in Argentina. Hence, this study evaluated and documented different environmental characteristics as well as early development and diets of juvenile Chinook Salmon to explain their success in these environments.

In their natural range along the Pacific coast of North America, there are stream and ocean ecotypes of Chinook Salmon. Spring ecotypes consist of individuals that reside for up to a year in freshwater before migrating to sea. This ecotype includes sub-yearlings that spend a winter in streams before they migrate to the ocean (Chapman & Bjornn 1969; Achord *et al.* 2007). Ocean ecotypes spend a short time period (weeks to months) in freshwater before

*Corresponding author.

Accepted for publication February 2018.

migrating downstream as subyearlings in the spring soon after fry emergence (Healey 1991). In New Zealand, the phenotypic plasticity and rapid evolution of Chinook Salmon has been hypothesized to explain their success (Quinn *et al.* 2001; Kinnison *et al.* 2008, 2011). In this region, a mixture of both stream and ocean ecotypes of Chinook Salmon occur (Unwin & Lucas 1993; Quinn *et al.* 2001). In the Great Lakes in North America, naturalized adfluvial Chinook Salmon populations (Kerr 2006) appear to develop genetic structure after a few generations (Suk *et al.* 2012).

In southern Argentina, there is evidence suggesting that some naturalized populations originated from stocks of the Lower Columbia River, Central Valley of California, Middle Oregon Coast, and Vancouver Island (Di Prinzio *et al.* 2015). Interestingly, the Futaleufú River population has shown similar within-population genetic diversity to those populations from their native range (Di Prinzio *et al.* 2015). Chinook Salmon spawners from this river have a combination of stream and ocean ecotypes (Di Prinzio & Pascual 2008).

Here, we describe the early development and diets of Chinook Salmon in the Futaleufú River, Argentina (Fig. 1). First, we identify freshwater rearing areas and document the environmental conditions of flow and water temperature that out-migrating Chinook Salmon experience. Second, we estimate timing of emergence, body size, condition and relative density of juvenile salmon during their freshwater residence. Third, we describe the diet composition of juvenile salmon across seasons. This baseline information is relevant to identify the diversity of life histories of

Chinook Salmon in the Patagonia, which will be critical for planning and implementing management strategies in the future.

METHODS

Study sites

The Futaleufú River originates in the Chubut province in Argentina (43°08'S; 71°35'W), flows west through Chile, and empties into the Pacific Ocean (Fig. 1). It is a sixth order river with a total length of 246 km and regulated by the Amutui Quimey reservoir (481 m.a.s.l.) in Argentina and then by the Yelcho Lake in Chile. The Futaleufú River supports an important recreational fishery based on introduced Rainbow Trout (*O. mykiss*) and Brown Trout (*Salmo trutta*) with a recent addition of Chinook Salmon.

A pre-sampling effort along 33 km of the Futaleufú River was conducted in 2011 to corroborate the presence of juvenile Chinook Salmon. From this pre-sampling effort, we selected three sites (Table 1) located downstream of the Amutui Quimey reservoir (Fig. 1) that were used consistently by Chinook Salmon spawners to construct redds (C. Di Prinzio unpublished data). At each site, we estimated the sampled reach area (m²) and depth (cm) following Barbour *et al.* (1999) and evaluated substrate composition including boulders (>25 cm), cobbles (6.4–25 cm), pebbles (1.6–6.4 cm), gravel (2–16 mm) and sand (0.25–2 mm) using a 1 m² grid (Ward 1992).

Daily river discharge (annual mean of 300 m³ s⁻³) was provided by the Hydroelectric Futaleufú Reservoir Company; water temperature was recorded continuously at one hour intervals, averaged and stored every 24 h using underwater temperature loggers One Wire Digital Temperature Sensor (DS18B20). Specific conductivity (mS cm⁻¹), pH, dissolved oxygen (mg L⁻¹), total solid dissolved (mg L⁻¹)

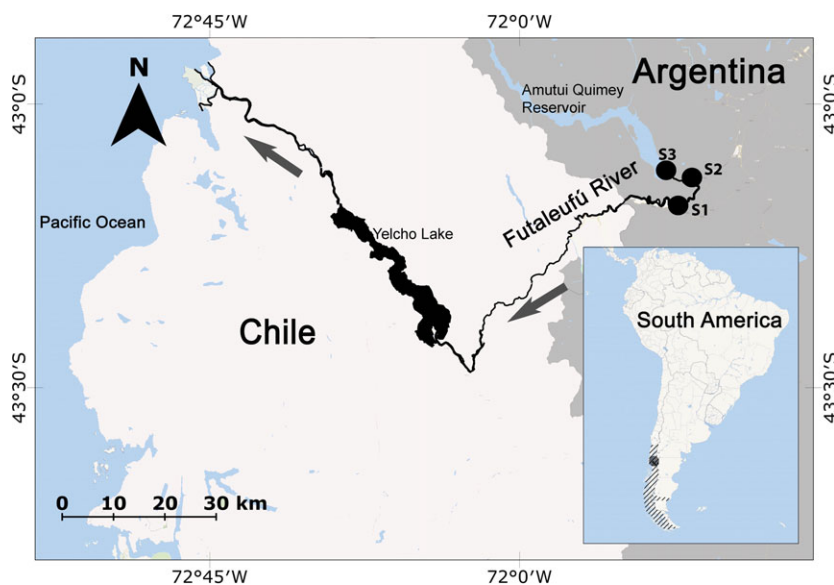


Fig. 1. Map of the study sites in the Futaleufú River basin, South America. Circles are the sampling sites. S1 = site 1; S2 = site 2 and S3 = site 3.

Table 1. Characteristics of the stream reaches sampled at the Futaleufú River, South America

	Site 1	Site 2	Site 3
Latitude (S)	43°10'23"	43°08'28"	43°08'13"
Longitude (W)	71°35'40"	71°35'34"	71°36'27"
Elevation (m.a.s.l)	331	340	357
Distance from the ocean (km)	235	242	244
Stream reach area (m ²)	60	60	60
Mean ± SD of the stream reach depth (cm)	40.7 ± 1.9	30.4 ± 0.9	17.5 ± 0.9
Mean ± SD of electrical conductance (mS cm ⁻¹)	33.4 ± 1.4	30.8 ± 1.7	31.4 ± 1.7
Mean ± SD of pH	6.7 ± 0.5	7.0 ± 0.8	6.6 ± 0.9
Mean ± SD of dissolved oxygen concentration (mg L ⁻¹)	10.6 ± 1.2	10.8 ± 0.9	10.5 ± 0.7
Mean ± SD of total dissolved solids (mg L ⁻¹)	20.2 ± 1.5	20.5 ± 0.9	18.9 ± 0.5
Substrate composition (%)	60% Gravel-40% Sand	70% Pebbles-30% Gravel	40% Cobbles-60% Pebbles

and salinity were measured monthly with a multiparameter probe (Hach sensION 156, Hach Instruments, Lovedale, CO, USA).

Fish sampling

Juvenile Chinook Salmon were collected using a three-pass beach seine (3 mm mesh-size; 5 x 5 m²) along 50 m reaches. We kept similar fishing effort across sites and among dates to compare relative abundances of juvenile salmon. We sampled fish once a month starting at the end of the Austral Winter (August 2012) and finishing at the middle of the Austral Summer (January 2013). In June and July, we did not sample due to high flow conditions.

Because of the lack of information about the timing of fry emergence of Chinook Salmon in these invaded systems, we estimated the duration of eggs spent in the gravel based on the presence of fry in our samples and the theoretical incubation period proposed by Beachman and Murray (1990) as follows:

$$\log_e D = \log_e a - \log_e (T - b)$$

where *D* was the emergence time after fertilization (in days), *T* was the observed mean temperature (°C), $\log_e a$ was a constant (6.872) and *b* was constant (-0.332).

We used Zimmerman *et al.* (2015) to classify juvenile Chinook Salmon sizes into fry (≤45 mm FL), subyearling parr (46–100 mm FL) and yearling smolt (>100 mm FL). All captured salmon were frozen and transported to the lab for posterior analysis; stomach contents were preserved in 90% ethanol.

Laboratory processing

Because Pacific salmon and trout fry can be confounded due to similar morphology, we separated species based on counting anal fin rays (Pollard *et al.* 2011). Identified fishes were counted, weighed (0.001 g nearest unit) and measured (TL; 0.01 mm). Stomach contents were examined under a stereomicroscope and items were classified into Crustacea, Araneae, Cladocera, Plecoptera, Ephemeroptera, Trichoptera, Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera, Thysanoptera, Fish and others.

Data analyses

Because our relatively low sample size and some of our datasets did not meet the assumptions about normality, we used of nonparametric tests. We used a non-parametric ANOVA (Kruskal-Wallis test) and the *post hoc* Dunn test

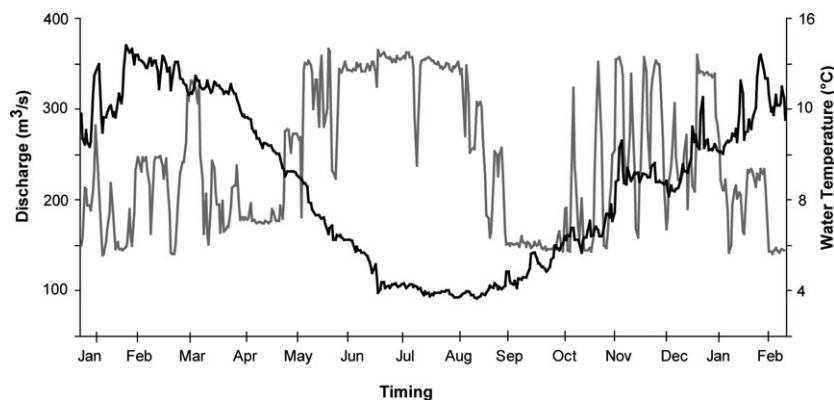


Fig. 2. Daily discharge (m³ s) and water temperature (°C) of the Futaleufú River during 2012–2013. The grey line represents discharge whereas the black line represents water temperature.

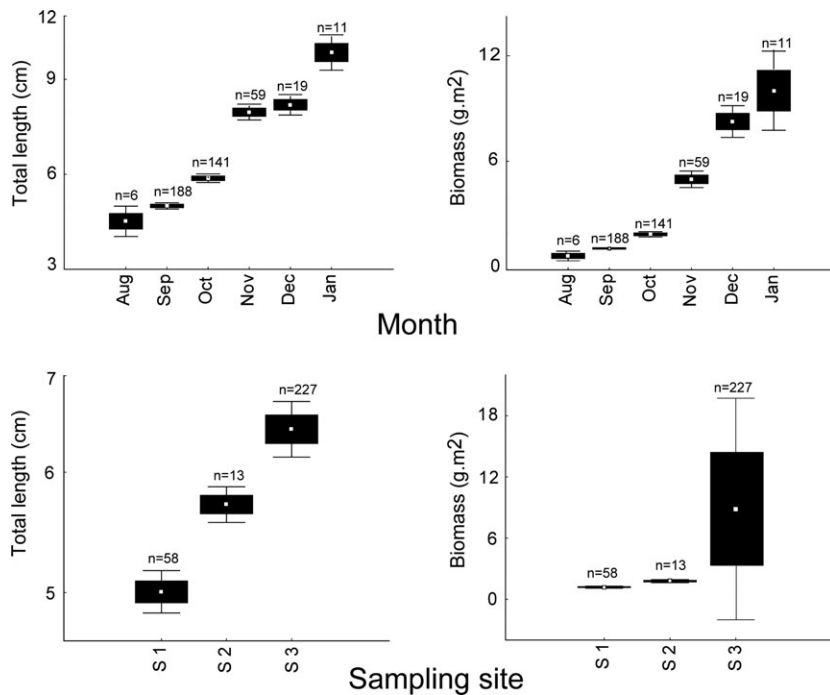


Fig. 3. Box-plots of total length (cm) and biomass (g m⁻²) of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Futaleufú River during the study period (2012–2013) and among our study sites.

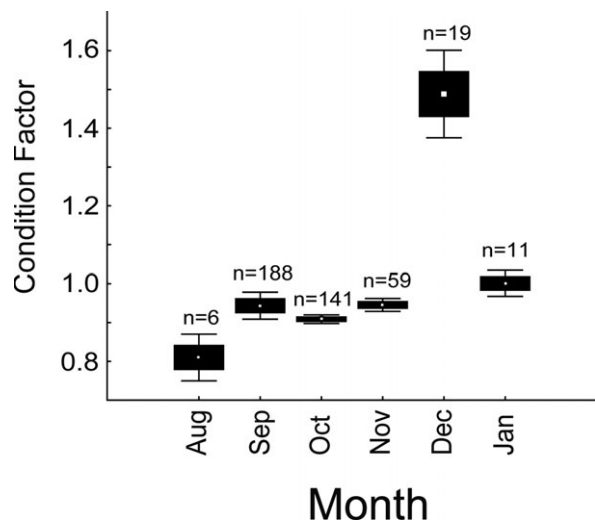


Fig. 4. Fulton's Condition Factor of juvenile Chinook Salmon during the sampling period (2012–2013) in the Futaleufú River, South America.

(Sokal & Rohlf 1995) to compare the size (total length and weight) of juvenile Chinook Salmon across sites and over time. Spearman correlation (non-parametric analysis) was also used to evaluate the association between juvenile Chinook Salmon densities and biomass over time. In addition, we examined differences in juvenile salmon body condition over time using length – weight relationships and estimated the monthly condition factor ($10^5 \times W L^{-3}$, W = weight in g, L = total length in cm).

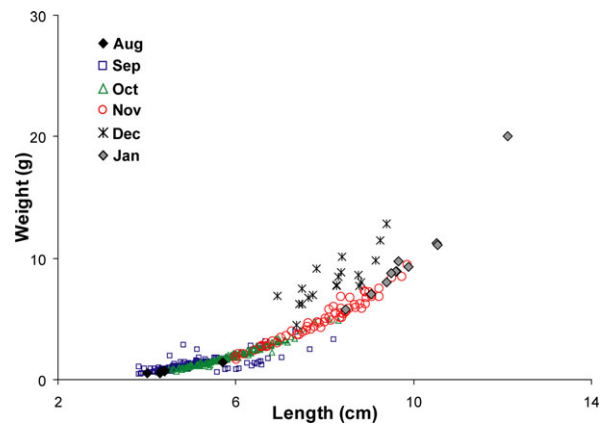


Fig. 5. Length-weight relationship of juvenile Chinook Salmon over time (August 2012–January 2012) in the Futaleufú River, South America.

To evaluate the contribution of each food item to overall diet, we estimated the fish diet coefficient Q (Hureau 1970) using the formula $Q = \%F \times \%M$

where %F is percentage of frequency and %M is percentage of mass of the total individual's stomach captured in the monthly sampled. This coefficient reduced biases associated with the use of numeric or weight based methods because it is the product of the percentage by number (Frequency %) and the percentage by mass (Mass %) of each prey type. Based on the Q index, prey items were classified as main prey ($Q > 200$), secondary prey ($200 > Q > 20$), or occasional prey ($Q < 20$) following Hureau (1970).

The juvenile Chinook Salmon diet breadth (B) was assessed using Levins (1968) index with 95% confidence limits: $B = 1/\sum p_i^2$ $i = 1..n$, where p_i is the fraction of items in the diet that are of category i . Levin's standardized niche breadth from 0 (narrow niche width) state to 1 (broad niche width). Values less than 0.6 indicate that the diet is dominated by few prey items therefore it is a specialist predator and values greater than 0.6 correspond to generalist predator (Krebs 1989). Further, diet diversity of juvenile Chinook Salmon was calculated using the Shannon-Wiener index (Krebs 1989): $H' = -\sum (p_i \ln p_i)$; where p_i is the fraction of items in the fish stomachs that are of category i .

To summarize the monthly variation of fish diets, we performed a Non-Metric Multidimensional Scaling (NMDS) ordination based on the Bray-Curtis similarity coefficient (Clarke & Warwick 1994). Dimension 1 (MDS1) and Dimension 2 (MDS2) were extracted, and the influence of the items prey was assessed with single regression analysis

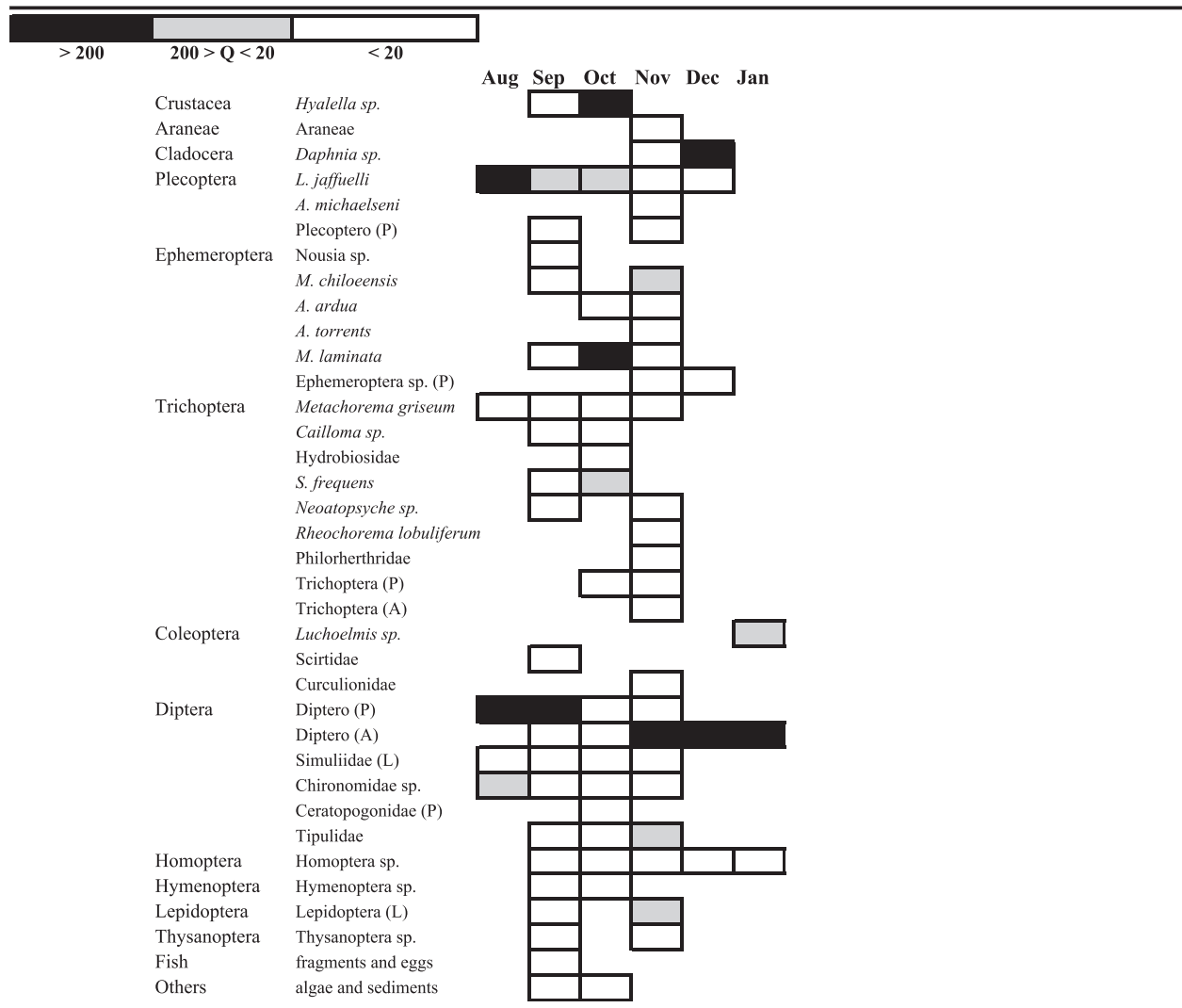
(ter Braak & Smilauer 1998). A similar procedure was employed to relate population attributes with MDS dimensions to determine which item prey best accounted for separation of juvenile salmon in the ordination space.

RESULTS

Habitat conditions and Juvenile Chinook Salmon relative abundances

The three sampling sites showed similar values of conductivity, dissolved oxygen, and total dissolved solids (Table 1) with minor differences in channel depth and streambed substrate. We captured 424 juvenile Chinook Salmon between August and

Table 2. Seasonal diet composition of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Futaleufú River during the study period. Q values >200 represent the main food source whereas Q values between 20 and 200 are secondary food sources. Q values less than 20 represent occasional food sources. P = pupae, L = larvae, A = adult



January. The highest densities were observed in September (3.13 ind. m^{-2}) and the lowest in both August (0.1 ind. m^{-2}) and January (0.18 ind. m^{-2}). Juvenile fish densities were positively associated with temperature ($R_{\text{Spearman correlation}} = -0.844$, $P < 0.05$), but not with flow ($R_{\text{Spearman correlation}} = -0.043$, $P = 0.90$; Fig. 2).

Growth and early development of juvenile Chinook Salmon

Incubation time was estimated as 101 days after the spawning season (we used an observed mean water temperature of 7.5°C). Juvenile Chinook Salmon sizes ranged between 3.8–12.1 cm total length and included 51 fry, 370 parr, and 3 smolts. Both length and weight of juvenile salmon increased from the Austral Winter to the Austral Summer. There were statistically significant differences (Kruskal–Wallis, $P < 0.05$) for length (cm) and weight (g) across sites (Dunn test, $P < 0.05$) and over time (Dunn test, $P < 0.05$; Fig. 3) increasing from August ($4.5 \pm 0.6 \text{ cm}$; $0.8 \pm 0.3 \text{ g}$) to January ($9.8 \pm 0.9 \text{ cm}$; $9.9 \pm 3.7 \text{ g}$). In site 1, total length of juvenile fish was different from site 2 and site 3 (Fig. 3); total length in January, December and November were different from in August, September and October (Fig. 3). Juvenile body condition were variable, with fishes reaching the maximum degree of robustness in December and the minimum in August (Fig. 4). Overall, juvenile Chinook Salmon weights were higher in December than during the rest of the

sampling months, excluding an individual fish sampled in January (Fig. 5).

Juvenile Chinook Salmon diets

Juvenile salmon diets included 77.2% benthic macroinvertebrates and 22.8% terrestrial invertebrates (Homoptera, Hymenoptera, Lepidoptera, Thysanoptera, Araneae, Trichoptera adults, terrestrial Coleoptera, Diptera adults). The main prey ($Q > 200$) varied monthly (Table 2) including Diptera ($Q = 2,988$) and the stonefly larvae *Limnoperla jaffueli* ($Q = 236$) in August, Diptera ($Q = 4,948$) in September, the mayfly larvae *Meridialaris laminata* ($Q = 590$) and the Crustacean *Hyaella* sp. ($Q = 292$) in October. In addition, adults of Diptera ($Q = 2,029$) predominated in the juvenile diets during November, December ($Q = 1,758$) and January ($Q = 7,326$) and the Cladocera *Daphnia* sp. dominated in December ($Q = 1,217$).

The NMDS ordination plot based on diets of juvenile salmon illustrated differences among fish sizes (Fig. 6). Large juvenile salmon (8–12.5 cm TL) were located mainly at the upper right side of the plot while small juvenile salmon (4–6.5 cm TL) were grouped mainly at the lower left side of the plot. Large juvenile salmon were positively correlated with adult Diptera ($R = 0.63$) preys, while smaller fish were positively correlated with pupae dipterans ($R = -0.63$) and larvae of Plecoptera *Limnoperla jaffueli* ($R = -0.54$). Intermediate juvenile salmon (6–9 cm TL) were associated to Chironomids

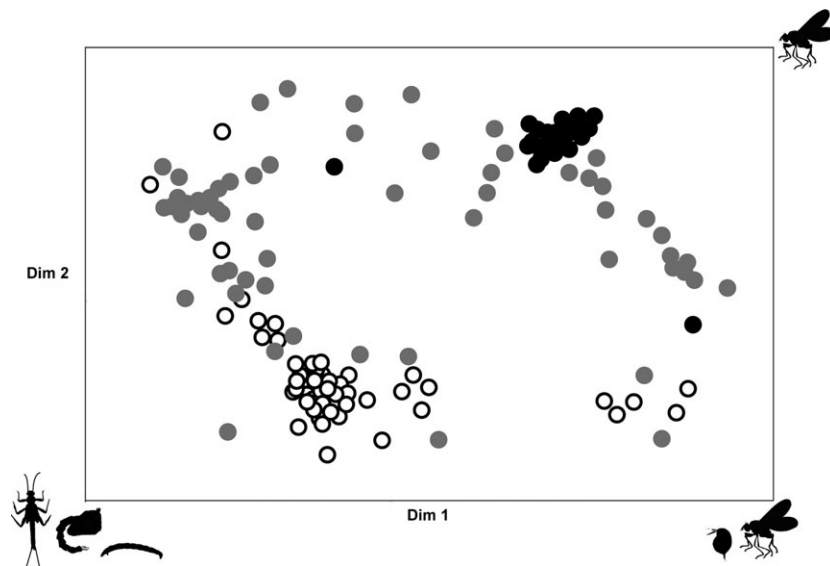


Fig. 6. NMDS ordination plot of diets for juvenile Chinook Salmon in the Futaleufú River, South America. Black circles represent individuals $>10 \text{ cm TL}$ whereas grey circles represent individuals between 6 and 9 cm TL. Open circles represent individuals $<6 \text{ cm TL}$.

($R = -0.60$), pupae Diptera ($R = -0.41$) and copepods ($R = 0.46$). Furthermore, Levin's index (Table 3) values were generally low (0.03 to 0.27) with September having the narrowest niche breadth. Diet diversity values were lower during November, December and January and higher during August, September and October.

DISCUSSION

The presence of juveniles in the Futaleufú River confirms that Chinook Salmon have successfully established naturalized populations in Patagonia, Argentina. As fry, Chinook Salmon remain in off-channel habitats and floodplain areas near spawning grounds. Similar to the Petrohué River in Chile (Soto *et al.* 2007), the highest juvenile densities were observed in spring with the highest proportion of fry occurring in winter; salmon parr are more abundant in spring, and smolts in early summer. In several invaded systems in Chile, juvenile Chinook Salmon have been reported as the ocean ecotype, apparently migrating to sea within the first year of age (Soto *et al.* 2007). However, based on the age structure of stream Chinook Salmon (C.

Di Prinzie unpublished data) and scales (Di Prinzie & Pascual 2008) it seems that the Futaleufú River supports a mixed population of both stream-type and ocean-type.

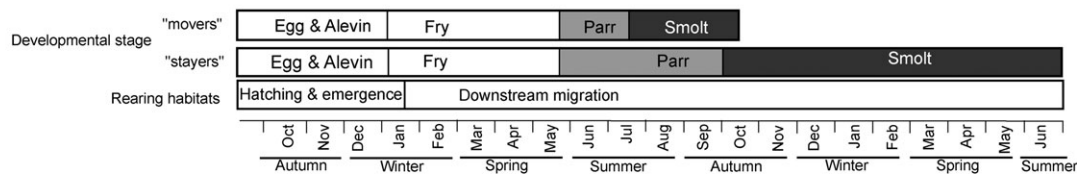
Our findings show that juvenile Chinook Salmon occur between the Austral autumn, spring and summer in the Futaleufú River (April-January; Fig. 7). Likely hatching and emergence happen during winter (up to August) in close proximity to the spawning areas. A few smolts (>10 cm TL) and parr use tributaries and off-channel floodplain habitats downstream from their natal sites between early spring and summer (middle of September to January). In North America, populations are commonly comprised of a mixture of ocean-type and stream-type providing stability to the temporal asynchrony among them (Schroeder *et al.* 2016). A blend of ecotypes offers an advantage to populations because it buffers against environmental variability (Miller *et al.* 2010; Walsworth *et al.* 2014).

Our findings suggest that juvenile Chinook Salmon are not limited by prey availability in the Futaleufú River. Chinook Salmon diets include a variety of prey from both autochthonous (benthic macroinvertebrates) and allochthonous (terrestrial invertebrates) origins. Juvenile salmon can be a specialist predator (narrower niche breadth) with a diet dominated by few prey. Others studies conducted in invaded rivers in New Zealand (i.e. Sagar & Glova 1988; Power 1992), Chile (i.e. Ibarra *et al.* 2011) and North America (Koheler *et al.* 2006; Limm & Marchetti 2009) report juvenile Chinook Salmon as generalists. Some prey are probably consumed opportunistically such as when flooded marginal backwaters rise during storms, during increased flow from reservoir discharge, or during an insect hatch (e.g., Power 1992). For example, populations of adult Diptera peak during spring (ice melt period) and summer and zooplankton peak in summer (peak reservoir releases).

Table 3. Population diet breadth (Levins Index) and diet diversity (Shannon-Weaver Index) of juveniles Chinook Salmon during the sampled period (2012–2013) in the Futaleufú River, South America

Month	Levin Index	Shannon Index
August	0.20	1.28
September	0.03	1.56
October	0.27	2.92
November	0.22	0.84
December	0.10	0.85
January	0.25	0.77

Willamette River, Oregon (Native population)



Futaleufú River, Patagonia (Naturalized population)

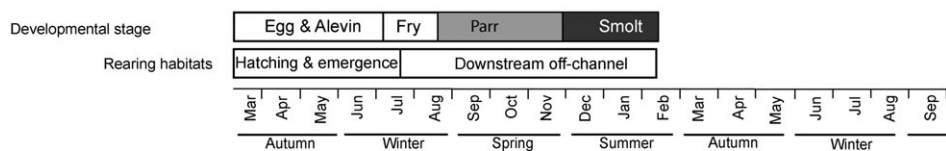


Fig. 7. Schematic diagram illustrating the early life history of juvenile Chinook Salmon during their first stage phase in freshwater residence (0+ years) in the Futaleufú River, South America. The framework is adapted from Bourret, *et al.* (2016) and includes an example of native populations from Oregon (Schroeder *et al.* 2016).

We suspect that Futaleufú River had pulses of food available to juveniles that are supporting the increase in salmon weight during early summer (December). Food pulses have also been documented in Lake Washington, Washington State (Koheler *et al.* 2006) and in Alaska (Armstrong *et al.* 2016), but not in another invaded river of Chile (Ibarra *et al.* 2011). The potential for competition for food between juvenile Chinook Salmon and native species has been overlooked although there is some evidence of habitat overlap with native catfish *Trichomycterus aerolatus* in the Allipen River in Chile (Vargas *et al.* 2010).

In southern South America, managers and policymakers face the complex challenge of protecting economically important salmon populations while minimizing their negative environmental effects. In this region, recreational fisheries based on salmonids provide important revenue for rural communities and angling operators (Vigliano *et al.* 2000; Arismendi & Nahuelhual 2007). However, Chinook Salmon introductions have negative ecological effects in marine (Soto *et al.* 2001) and freshwaters systems (Vargas *et al.* 2010; Arismendi & Soto 2012). In rivers, there is evidence of interactive segregation over habitat processes between juvenile Chinook Salmon and the native catfish *Trichomycterus areolatus* (Vargas *et al.* 2010); marine derived nutrient subsidies from salmon carcasses in rivers have the potential for affecting natural ecosystem functioning (Arismendi & Soto 2012). At present, salmon management alternatives include increasing the harvest limit and extending the fishing seasons in sensitive areas to simultaneously attract anglers and reduce predation/competition pressure with native fishes (Soto *et al.* 2001, 2006; Arismendi & Nahuelhual 2007). However, an effective management of Chinook Salmon require an understanding of their diversity of life history expressions. In particular, a higher proportion of stream ecotype Chinook Salmon inhabiting the Futaleufú River can increase the duration of potential negative interactions with freshwater fishes. Our study provides insights about the early development and freshwater residence of Chinook Salmon in these invaded systems and represent an attempt towards building a baseline of biological information that can support future planning and fisheries management. Ultimately, the management of salmonids will require balancing recreational fisheries, salmonid aquaculture and the conservation of freshwater biodiversity.

ACKNOWLEDGEMENTS

Walter Cerdá, Henry Thomas, Maximiliano Rivadeniera and Luciano Zapata helped during fieldwork. We greatly appreciate Alex Koeberle substantial

comments and language corrections. Lic Luz Manzo for the map design. Supported by CONICET (National Council of Sciences and Technical Research in Argentina) Res.2494/12, Ministerio de Medio Ambiente de la Provincial de Chubut Res. 02/10 and Universidad Nacional de la Patagonia San Juan Bosco R/CIUNPAT N° 252/13. This is the contribution to the Laboratorio de Investigaciones en Ecología y Sistemática Animal (LIESA) N°132.

REFERENCES

- Achord S., Zabel R. W. & Sandford B. P. (2007) Migration timing, growth, and estimated parr-to-smolt survival rates of wild Snake River spring-summer Chinook salmon from the Salmon River basin, Idaho, to the lower Snake River. *Trans. Am. Fish. Soc.* **136**, 142–54.
- Aigo J., Cussac V., Peris S. *et al.* (2008) Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages. *Rev. Fish Biol. Fisheries* **18**, 387–408.
- Arismendi I. & Nahuelhual L. (2007) Non-native salmon and trout recreational fishing in Lake Llanquihue, southern Chile: economic benefits and management implications. *Rev. Fish. Sci.* **15**, 311–25.
- Arismendi I. & Soto D. (2012) Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from Southern Chile. *Knowl. Manag. Aquat. Ecosyst.* **405**, 01.
- Arismendi I., Penaluna B., Dunham J. B. *et al.* (2014) Differential invasion success of salmonids in southern Chile: patterns and hypotheses. *Rev. Fish Biol. Fish* **24**(3), 919–41.
- Armstrong J. B., Takimoto G. T., Schindler D. E., Hayes M. M. & Kauffman M. J. (2016) Resource waves: phenological diversity enhances foraging opportunities for mobile consumers. *Ecology* **97**, 1099–122.
- Astorga M. P., Valenzuela C., Arismendi I. & Iriarte J. L. (2008) Naturalized Chinook Salmon in the northern Chilean Patagonia: do they originate from salmon farming? *Rev. Biol. Mar. Oceanog* **43**, 669–74.
- Barbour M. T., Gerritsen J., Snyder B. D. & Stribling J. B. (1999) *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish*. Environmental Protection Agency (EPA), Washington, DC.
- Beachman T. D. & Murray C. B. (1990) Temperature, egg size, and development of embryos and alevins of five species of Pacific Salmon: A comparative analysis. *Trans. Am. Fish. Soc.* **119**, 927–45.
- Becker L., Pascual M. & Basso N. (2007) Colonization of the southern Patagonia Ocean by exotic Chinook salmon. *Conserv. Biol.* **21**(5), 1347–52.
- Bourret S. L., Caudill C. C. & Keefer M. L. (2016) Diversity of juvenile Chinook salmon life history pathways. *Rev. Fish Biol. Fish.* **26**, 375–403.
- ter Braak C. J. F. & Smilauer P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination*. Microcomputer Power, Ithaca, NY.
- Chapman D. E. W. & Bjornn T. C. (1969) Distribution of salmonids in streams, with special reference of food and

- feeding. In: *Symposium on Salmon and Trout in Streams* (eds T. G. Northcote & H. R. MacMillan) pp. 153–76. Institute of Fisheries, University of British Columbia, Vancouver, BC.
- Ciancio J. E., Pascual M. A., Lancelotti J., Riva Rossi. C. & Botto F. (2005) Natural colonization and establishment of a Chinook salmon, *Oncorhynchus tshawytscha*, population in the Santa Cruz River, an Atlantic basin of Patagonia. *Env. Biol. Fish* **74**, 219–27.
- Clarke K. R. & Warwick R. M. (1994) Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar. Biol.* **118**, 167–76.
- Correa C. & Gross M. R. (2008) Chinook salmon invade southern South America. *Biol. Invasions* **10**, 615–39.
- Di Prinzio C. Y. & Pascual M. A. (2008) The establishment of exotic Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific rivers of Chubut, Patagonia, Argentina. *Ann. Limnol. Int. J. Lim.* **1**, 61–8.
- Di Prinzio C. Y., Riva Rossi. C., Ciancio J., Garza J. & Casaux R. (2015) Disentangling the contributions of ocean ranching and net-pen aquaculture in the successful establishment of Chinook salmon in a Patagonian basin. *Env. Biol. Fish* **98**, 1987–97.
- Emery L. (1985) *Review of Fish Species Introduced Into the Great Lakes, 1819-1974. Great Lakes Fishery Commission Technical Report N° 45.* Great Lakes Fishery Commission, Ann Arbor, MI.
- Fernández D. A., Ciancio J., Ceballos S. G., Riva-Rossi C. & Pascual M. A. (2010) Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum (1792)) in the Beagle Channel, Tierra del Fuego: the onset of an invasion. *Biol. Invasions* **12**, 2991–7.
- Flain M. (1981) Distribution of quinnat salmon, *Oncorhynchus tshawytscha*, off the coast of the South Island, 1925–78. *New Zeal J. Mar. Fresh* **15**(1), 21–4.
- Habit E., Gonzalez J., Ruzzante D. E. & Walde S. J. (2012) Native and introduced fish species richness in Chilean Patagonian lakes: inferences on invasion mechanisms using salmonid-free lakes. *Divers. Distrib.* **18**(12), 1153–65.
- Healey M. C. (1991) Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pacific salmon life histories. In: *Pacific Salmon Life Histories* (eds C. Groot & L. Margolis) pp 311–94. UBC Press, Vancouver, BC.
- Hureau J. (1970) Biologie comparee de quelques poissons antarctiques (Nototheniidae). *Bull. Inst. Oceanogr.* **68**, 1–244.
- Ibarra J., Habit E., Barra R. & Solis K. (2011) Chinook salmon juveniles (*Oncorhynchus tshawytscha* Walbaum, 1792) in rivers and lakes of the Chilean patagonia. *Gayana* **75**(1), 17–25.
- Kerr S. J. (2006) *An Historical Review of Fish Culture, Stocking and Fish Transfers in Ontario, 1865-2004*, 224 pp. Fish and Wildlife Branch, Ontario Ministry of Natural Resources, Peterborough, ON.
- Kinnison M. T., Unwin M. J. & Quinn T. P. (2008) Eco-evolutionary versus habitat contributions to invasion: experimental evaluation in the wild. *Mol. Ecol.* **17**, 405–14.
- Kinnison M. T., Quinn T. P. & Unwin M. J. (2011) Correlated con-temporary evolution of life history traits in New Zealand Chinook Salmon, *Oncorhynchus tshawytscha*. *Heredity* **106**, 448–59.
- Koheler M., Fresh K., Beauchamp D., Condell J., Simenstad C. & Seiler D. (2006) Diet and bioenergetics of lake-rearing juvenile Chinook salmon in Lake Washington. *Trans. Am. Fish. Soc.* **135**, 1580–91.
- Krebs C. J. (1989) *Ecological Methodology*. Harper Collins Publishers, New York, NY.
- Levins R. (1968) *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, NJ.
- Limm M. P. & Marchetti P. M. (2009) Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. *Env. Biol. Fish* **85**, 141–51.
- Miller J. A., Gray A. & Merz J. (2010) Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. *Mar. Ecol. Prog. Ser.* **408**, 227–40.
- Pascual M. A., Cussac V., Dyer B. *et al.* (2007) Freshwater fishes of Patagonia in the 21st century after a hundred years of human settlement, species introductions, and environmental change. *Aquat. Ecosyst. Health* **10**, 212–27.
- Pollard W. R., Hartman G. F., Groot C. & Edgell P. (eds.) (2011) *Field Identification of Coastal Juvenile Salmonids*. Harbour Publishing, Madeira Park, Canada.
- Power G. (1992) Seasonal growth and diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in demonstration channels and the main channel of the Waitaki River, New Zealand, 1982-1983. *Ecol. Freshw. Fish* **1**, 12–25.
- Quinn T. P. & Unwin M. J. (1993) Variation in Life History Patterns among New Zealand Chinook Salmon (*Oncorhynchus tshawytscha*) Populations. *Can. J. Fish Aquat. Sci.* **50**(7), 1414–21.
- Quinn T. P., Kinnison M. T. & Unwin M. J. (2001) Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* **112**, 493.
- Riva Rossi C. M., Pascual M. A., Aedo Marchant E., Basso N. *et al.* (2012) The invasion of Patagonia by Chinook salmon (*Oncorhynchus tshawytscha*): inferences from mitochondrial DNA patterns. *Genetica* **140**(10–12), 439–53.
- Sagar P. M. & Glova G. J. (1988) Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *J. Fish Biol.* **33**, 643–53.
- Schroeder R. K., Whitman L. D., Cannon B. & Olmsted P. (2016) Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. *Can. J. Fish Aquat. Sci.* **73**(6), 921–34.
- Sokal R. R. & Rohlf F. J. (1995) *Biometry*, 3rd edn. W.H. Freeman & Company, New York, NY.
- Soto D., Jara F. & Moreno C. (2001) Escaped Salmon in the Inner Seas, Southern Chile: Facing Ecological and Social Conflicts. *Ecol. Appl.* **11**, 1750–62.
- Soto D., Arismendi I., González J., Sanzana J., Jara F. *et al.* (2006) Sur de Chile, país de truchas y salmones: patrones de invasión y amenazas para las especies nativas. *Rev. Chil. Hist. Nat.* **79**, 97–117.
- Soto D., Arismendi I., Di Prinzio C. & Jara F. (2007) Establishment of Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific basins of southern South America and its potential ecosystem implications. *Rev. Chil. Hist. Nat.* **80**, 81–98.
- Suk H. Y., Neff B. D., Quach K. & Morbey Y. E. (2012) Evolution of introduced Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Huron: emergence of population genetic structure in less than 10 generations. *Ecol. Freshw. Fish* **21**, 235–44.

- Unwin M. J. & Lucas D. H. (1993) Scale Characteristics of Wild and Hatchery Chinook salmon (*Oncorhynchus tshawytscha*) in the Rakaia River, New Zealand, and Their Use in Stock Identification. *Can. J. Fish Aquat. Sci.* **50** (11), 2475–84.
- Vargas P. V., Arismendi I., Lara G., Millar J. & Peredo S. (2010) Evidencia de solapamiento de microhabitat entre juveniles del salmón introducido *Oncorhynchus tshawytscha* y el pez nativo *Trichomycterus areolatus* en el río Allipén, Chile. *Rev. Biol. Marina Oceanogr.* **45**, 285–92.
- Vigliano P. H., Lippolt G., Denegri A., Alonso M., Macchi P. & Odyledye C. (2000) The human factor of the sport and recreational fishery of San Carlos de Bariloche, Río Negro, Argentina. *Fish. Res.* **49**, 141–53.
- Walsworth T. E., Schindler D. E., Griffiths J. R. & Zimmerman C. E. (2014) Diverse juvenile life-history behaviour contribute to the spawning stock of an anadromous fish population. *Ecol. Freshw. Fish* **24**(2), 204–13.
- Ward J. W. (1992) *Aquatic Insect Ecology*. Press Wiley, New York, NY.
- Zimmerman M. S., Kinsel C., Beamer E., Connor E. J. & Pflug D. E. (2015) Abundance, survival and life history strategies of juvenile Chinook salmon in the Skagit River, Washington. *Trans. Am. Fish. Soc.* **144**, 627–41.