Age and growth of diadromous Galaxias *maculatus (Jenyns, 1842) in southernmost South America (54° S) including contribution of age classes to reproduction*

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Age and growth of diadromous *Galaxias maculatus* (Jenyns, 1842) in southernmost South America (54° S) including contribution of age classes to reproduction

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Abstract The population of *Galaxias maculatus* studied here, Arroyo Negro (54° S), is located at the southern extreme of the species distribution. This is the first work on growth and other life history traits of a Fueguian diadromous population based on otoliths study. This species is part of the native fish fauna of Patagonia. Furthermore, studies on the growth and reproduction of *G. maculatus* in South America mostly refer to freshwater populations of Andean-Patagonian lakes and rivers (about 41° S). Size cohorts were studied; age and growth parameters were estimated, the latter using the VBGM. Four size cohorts were established, and 3+ was determined as maximum age class. No differences were found in growth curves between males and females. The 1+ age class was by far not only the most numerous in the population but also the most represented in the reproductive population. The relation between mean TL and latitude was positive ($r = 0.62$) for South American populations; however, further studies are needed to determine whether it is this population's life strategy, the local adaptation of a peripheral population or countergradient growth. The results are interpreted in the context of the information available for other populations, and provide important information about the plasticity in life history traits of this species.

Keywords Maximum size · Otoliths · Patagonia · Puyen · Size-at-age · Tierra del Fuego

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Introduction

Peripheral populations are those populations that are in a geographical (distant from the central population) or ecological (occupying a different environment) edge of the distribution range of a species (Lesica and Allendorf 1995; Bunnell et al. 2004), that generally tend to be more isolated and smaller than central populations and that are located in a more extreme environment. As a consequence, peripheral populations often experience increased genetic drift, selective pressures and genetic bottlenecks. These populations may be important as they might contain a unique genetic diversity or adaptations to a changing environment (Flebbe et al. 2006; Beatty et al. 2008). Peripheral populations are considered to deserve higher priority in conservation because they maximize a species diversity, preserve an important evolutionary legacy and provide the keys to the future speciation (Lesica and Allendorf 1995; Nielsen 1999; Nielsen et al. 2001).

Galaxias maculatus (Jenyns 1842) is one of the most widely distributed freshwater fish in the southern hemisphere, whose current distribution has been explained

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by marine dispersal followed by Gondwanan vicariance (Burridge et al. 2012). Across its wide geographical range, the species exhibits a great plasticity in its life history —including diadromous (amphidromous) and freshwater resident populations—, and size of individuals (e.g. Boy et al. 2009; Barbee et al. 2011; Barriga et al. 2012). In South America, the biology and life history of *G. maculatus* is principally known from freshwater populations of Andean-Patagonian lakes at about 40° S - 41° S (e.g., Campos 1970, 1974; Ferriz 1987; Ferriz and Gómez 2015; Cervellini et al. 1993; Barriga et al. 2002, 2007; Cousseau et al. 2010) and to a lesser extent from the diadromous population from Chile (Campos 1970, 1973, 1974; González-Wevar et al. 2015a, b; Ferriz and Gómez 2015) and Argentina at 54° S and studied here (Boy et al. 2007, 2008, 2009). Given that this species distribution in South America ranges from 32° S (Punta Maitencillo, McDowall 1971) to 55° S, the population studied here locates at the southernmost extreme of its distribution, where seasonal variations in temperature and photoperiod are well marked (Shuter and Post 1990).

The variation among populations in body size and growth rate is influenced by extrinsic factors such as abundance of food, competition, predation and environmental variables and/or intrinsic ones, such as age or genotype (Arnott et al. 2006), and is known from invertebrates to endotherm taxa (Teplitsky and Millien 2013). Countergradient growth is widely recognized in many species of fish as a type of intrinsic factor or phenotypic plasticity in which there is a compensation for length of the growing season (Conover and Present 1990; Venturelli et al. 2010; Rypel 2011) leading to higher somatic growth rate of a population with increasing latitude (Rypel 2012).

Age structure and spawner stock are important in determining long-term sustainable population levels. Larger and older fish are known to produce larger, healthier larvae capable of surviving unfavorable conditions, such as starvation periods or low access to food resources (Hislop 1988; Marteinsdottir and Steinarsson 1998; Closs et al. 2013); and/or a potential higher fecundity of females. For this reason, understanding the proportion of individuals belonging to older age classes would allow fisheries managers to understand the demographic status of the population and to establish conservation plans, since the loss of these age classes may have negative implications for recruitment (Berkeley et al. 2004). On the other hand, it is also important to determine what role the lower age classes have, since they could give an indication of the reproductive capacity or potential of the population (Copp 1990). Most of the age studies on *G. maculatus* focused growth characteristics (e.g., Chapman et al. 2006; Barriga et al. 2007) or its relation to migration (e.g., McDowall et al. 1994), but little is known about the contribution of age cohorts to reproduction. Furthermore, papers on reproduction, in general focus on size at maturity but not age at maturity (e.g., Barriga et al. 2002; Boy et al. 2007, 2009; Chapman et al. 2006; Stevens et al. 2016).

Consequently, *G. maculatus* becomes an interesting species to explore the pattern of variation in size and growth rate, under the general hypothesis that environmental conditions and geographic location influence the adult phenotype related to size. The objectives of this work are a) to study the growth and age structure in a diadromous population of *G. maculatus* located at the southern extreme of this species distribution, b) to study the contribution of the age classes to the reproduction of the population, and c) to identify possible correlations between these traits and the geographic locations of the populations.

Materials and methods

Individuals (adults and juveniles) were collected from Arroyo Negro mouth (54°50'53" S; 68°34'50" W) in Parque Nacional Tierra del Fuego, Argentina. Samples were taken monthly from October 2003 to September 2004, two hours after high tide, using a seine net (10-m long, 1-m deep, 5-mm mesh). Captured fish were taken alive to the laboratory in temperature controlled aerated tanks. Fish were anesthetized with tricaine methanesulfonate (MS-222) to death, measured [±0.01 mm, total length, (TL)] and weighed [±0.01 g, total weight, (W)]. Individuals were dissected in the laboratory to obtain the wet weight of gonads (W_G) and sexed macroscopically. Gonadosomatic index was calculated for each individual by following the equation: $GSI = (W_G/W)100$. Individuals were then classified as spawner ($GSI > 5\%$) or non-spawner ($GSI < 5\%$) (Boy et al. 2007, 2009) in order to study the age and the contribution of age classes to the reproduction of the population.

Length-frequency data of 1246 individuals were analyzed and size cohorts were graphically

identified with FISAT II (version 1.2.2, http://www.fao.org/fi/oldsite/STATIST/fisoft/fisat/index.htm). The mean size-frequency distributions was determined by the Bhattacharya's method (1967) using the following equation: $ln(N_{i+1}) - ln(N_i) = a_j + b_j L_i$ where N_i and N_{i+1} are successive frequencies of the same component of a subset of fish in a sample (i.e. representing age group j) and where L_i is the upper class limit of N_i. From this, the mean of the normal distribution is $L_j = -a_j/b_j$ was estimated (Gayanilo et al. 2005). In addition, the asymptotic length (L_∞) was estimated by the method of Powell (1979) and Wetherall (1986) and the growth coefficient (k) by Shepherd's method (1987). t_0 was calculated by the Pauly equation (1979): $\log_{10}(-t_0) = -0.3922 - (0.2752 \times \log_{10}L_\infty) - (1.038 \times \log_{10}k)$.

The relationship between mean and maximum TL of different populations in South America with latitude, including the population of Arroyo Negro studied here and other Fueguian ones still not published (Rojo pers. obs.), was studied through Pearson correlations since the assumptions of normality and homoscedasticity were met. The TL of the individuals of the Río San Pedro and Lago Gutiérrez (not informed by the authors), was estimated from their standard length, using the equation: $TL = SL \times 1.13$, obtained from TL-TS data of 572 G. maculatus from the diadromous population studied here (Rojo pers. obs.).

From all individuals, both sagittae otoliths were extracted, cleaned and photographed using a binocular microscope with transmitted light. In order to elucidate growth bands, it was not necessary to polish the otoliths and 10 individuals were excluded for having malformations in their otoliths. Then, using an image editing program (Image Pro-Plus v6.0) otoliths were measured [otolith width (OW), otolith length (OL)], circularity index was calculated as $=OW/OL$, and growth bands were identified.

Age was estimated in 556 individuals, considering each band (translucent and opaque) as a growing season, translucent bands for the winter season and opaque ones for the summer season (faster growth). A maximum of seven bands were counted, bands I and II for 0+ age class, bands III and IV for 1+ age class, bands V and VI for 2+ age class and band VII for 3+ age class (Fig. 1). The second read of the otoliths confirmed the first one in most of the cases. In each case when discrepancies occurred, a third read was performed to confirm the second one. Marginal increments (MI) were calculated using the equation: $MI = (R - r_n)/(r_n - r_{n-1})$, where R is
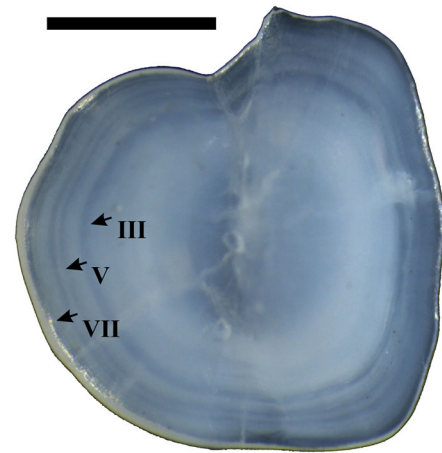

Fig. 1 Image of otolith from 3+ age class Galaxias maculatus from Arroyo Negro, Parque Nacional Tierra del Fuego. The arrows indicate the bands III, V and VII corresponding to the 2nd, 3rd and 4th winter bands respectively. Scale bar: 500 μm

the radius of otolith, r_n the last formed ring radius and r_{n-1} the radius of the penultimate formed ring (Dioses 2013), the individuals of 0+ age class could not be included by having only one or two bands.

The von Bertalanffy growth model or VBGM (von Bertalanffy 1938) was fitted to age-length data using the equation: $L_t = L_\infty\left(1 - e^{(-k(t-t_0))}\right)$, where L_t is the length at age t, L_∞ is the asymptotic length in mm, k is the growth coefficient in year^{-1} and t_0 is the hypothetical age at which the population would have zero length in years. Three growth curves were fitted, one for males ($n = 149$), another for females ($n = 228$) and a third one for both sexes combined ($n = 377$); individuals that could not be sexed were excluded. For a better fit of the model curves, age classes were divided into years, thereby the 0+ age class was divided into 0.5 and 1 years, the 1+ class in 1.5 and 2 years, the 2+ class in 2.5 and 3 years and the 3+ age class in 3.5 years. To compare the growth curves between males and females, an analysis of the residual sum of squares (AoRSS) was employed and the F-statistic was calculated (Chen et al. 1992) as:

$$F = \frac{\dfrac{RSS_p - \sum RSS_i}{3(k-1)}}{\dfrac{\sum RSS_i}{N - 3k}}$$

where RSS_p is the residual sum of square of each VBGM for males and females pooled, ΣRSS_i is the sum of the residual sum of square of each VBGM for each

individual sample, k is the number of categories compared and N is the total sample size. To test whether there was a difference between males and females, the calculated F value was compared with the critical F, with $3(k-1)$ and $N-3k$ degree of freedom of numerator and denominator, respectively. Furthermore, the phi-prime index (Φ') of Munro and Pauly (1983) was calculated to compare the parameters L_∞ and k estimated by VBGM and by the size frequency data: $\Phi' = \log_{10}k + 2 \times \log_{10}L_\infty$, and the criterion of Sparre and Venema (1997) was used to determine the significance of variation among the parameters, where a coefficient of variation (C_v) greater than 4% indicates significant differences.

Statistical analysis

The software R (R Core Team 2015) was used for statistical analyzes. To study differences in size between males and females the nonparametric Kruskal-Wallis test was performed. To study the relationship between TL of individuals and otolith width (OW) and otolith length (OL) linear regressions were performed. In addition, to test the differences between circularity indexes among age classes ANOVA analysis were performed. In order to determine whether significant differences existed between marginal increments throughout the year and among otolith morphometric measures and age classes, a nonparametric Kruskal-Wallis test was used, given that assumptions of the ANOVA could not be met; then Pairwise comparisons using Wilcoxon rank sum test ($P = 0.05$) were used to determine which months differed significantly. To find starting values and parameters for the equation of VBGM and plot its results, the *FSA* (Ogle 2016) and *nlstools* libraries (Baty et al. 2015) were used.

Results

The sizes of *Galaxias maculatus* captured between October 2003 and September 2004 at Arroyo Negro mouth ranged from 50 mm TL (January) to 115 mm TL (October) with males ranging from 51 mm TL to 98 mm TL and females ranging from 50 mm TL to 115 mm TL. A total of 235 females (41.08%), 156 males (27.27%) and 181 individuals (31.64%) that could not be sexed were captured. The total weight of the individuals ranged from 0.34 g (December) to 9.32 g (October).

No differences were found between mean TL of males and females ($\chi^2 = 0.76$, $P = 0.3826$). Two size cohorts were found in October and June, four in April, and three during the remaining months (Table 1). The second and third size cohorts decreased its mean during the beginning of the breeding season (October–January) from 76 to 64 and 86 to 72 mm TL respectively, possibly due to the incorporation of the juveniles (whitebait, i.e., about six months old unpigmented individuals) returning from the sea and the mortality of the longest-lived adults. Then they fluctuated around a value of 67 and 74 mm TL, respectively. The fourth cohort, found only in April and October, had a mean of 88.59 mm TL.

A significant relationship between latitude and mean and maximum TL of South American populations of *G. maculatus* ($r = 0.62$, $t = 4.33$, $P < 0.05$; $r = 0.45$, $t = 2.89$, $P < 0.05$, respectively) was observed. The correlation between latitude and mean and maximum TL was significant among diadromous populations ($r = 0.74$, $t = 3.82$, $P < 0.05$; $r = 0.55$, $t = 2.28$, $P < 0.05$, respectively), but not in the case of landlocked ones ($r = 0.36$, $t = 1.52$, $P = 0.147$; $r = 0.31$, $t = 1.4$, $P = 0.177$, for mean and maximum TL respectively) (Table 2).

Age estimates ranged from 0+ and 3+ years (Fig. 2). Of the 555 fish captured, 16.04% were in their first year of life (0+), while 77.12, 6.30 and 0.54% belonged to the 1+, 2+ and 3+ age classes, respectively. Throughout the year, a preponderance of the 1+ age class (>45% of the individuals) was observed. However, both pigmented (0+) and unpigmented individuals of 0+ age class (Whitebait) increased their representation with the progress of the breeding season. In December, the whitebait represented 77% of the individuals in the 0+ class, and 37% of all individuals of that month. The 2+ age class was poorly represented, with the highest percentage in October and November (<20%). Only three individuals were captured for the 3+ age class.

Morphological differences were observed on otoliths among age classes. The 2+ age class presented the greatest differentiation of the anterior and dorsal edge, otoliths were most circular in 0+ age class (EO = 0.93 ± 0.04) and most elongated in 1+, 2+ and 3+ (EO = 0.91 ± 0.05, 0.89 ± 0.05 and 0.90 ± 0.07 respectively; $F = 4.019$, $P < 0.05$). Significant differences in width and length of otoliths (OW and OL respectively) were found between age classes (OW: $\chi^2 = 187.75$, $P < 0.05$; OL: $\chi^2 = 190.90$, $P < 0.05$). In both cases (OW and OL), 2+ and 3+ age classes did not differ significantly (Pairwise comparisons using Wilcoxon rank sum test, $P = 0.909$

Table 1 Mean ± standard deviation of total length of size cohorts (1st, 2nd, 3rd and 4th) of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004, determined by the method of Bhattacharya

Month	1st TL (mm)	2nd TL (mm)	3rd TL (mm)	4th TL (mm)
October 2003		76.05 ± 4.35	87.02 ± 3.04	
November 2003		74.18 ± 1.01	83.20 ± 2.71	94.33 ± 2.54
December 2003	55.88 ± 3.35	78.00 ± 2.47	89.46 ± 2.79	
January 2004	57.14 ± 2.73	64.43 ± 2.33	72.86 ± 1.59	
February 2004	60.37 ± 1.65	66.02 ± 1.31	75.11 ± 1.70	
March 2004	62.40 ± 3.09	70.19 ± 1.69	79.38 ± 2.01	
April 2004	63.46 ± 3.56	71.57 ± 2.68	77.41 ± 1.37	82.84 ± 0.69
May 2004	58.89 ± 1.29	63.25 ± 1.15	74.00 ± 1.55	
June 2004	60.00 ± 2.13	69.50 ± 1.20		
July 2004	57.50 ± 0.85	62.69 ± 0.90	68.50 ± 0.95	
August 2004	64.17 ± 1.70	71.50 ± 1.04	77.17 ± 1.33	
September 2004	62.00 ± 1.67	68.01 ± 0.67	71.02 ± 1.09	

and $P = 0.606$, respectively), but were higher than 1+ and 0+ age classes, which showed the lowest values (Pairwise comparisons using Wilcoxon rank sum test, all $P < 0.05$). Both increased with TL: $OW = 15.23 + 0.06TL$ ($t = 39.32$, $P < 0.05$) and $OL = 19.60 + 0.05TL$ ($t = 35.14$, $P < 0.05$). The MI in 1+ and 2+ classes differed significantly throughout the months of the year ($\chi^2 = 31.13$, $P < 0.05$ and $\chi^2 = 31.98$, $P < 0.05$, respectively), but only between October and February ($P < 0.05$) and between July and October ($P < 0.05$) for 1+ class, and between November and June ($P < 0.05$) for 2+ class. The 3+ age class did not differ among months ($\chi^2 = 0.8$, $P = 0.8495$) (Fig. 3).

The VBGM parameters (estimated using age data ± standard error) estimated for females: $L_\infty = 127.07 \pm 36.34$ mm, $k = 0.29 \pm 0.19$ year^{-1}, $t_0 = -1.24 \pm 0.66$ years and for males: $L_\infty = 107.97 \pm 23.9$ mm, $k = 0.54 \pm 0.35$ year^{-1}, $t_0 = -0.42 \pm 0.51$ years. No differences in growth curves between males and females were found ($F = 1.19$, $P = 0.3137$). Growth parameters including all males and females were $L_\infty = 123.75 \pm 25.3$ mm, $k = 0.33 \pm 0.16$ year^{-1} and $t_0 = -1.01 \pm 0.45$ years (Fig. 4). The parameters estimated using the length frequency data were $L_\infty = 106.96$ mm, $k = 0.44$ year^{-1} and $t_0 = -0.27$ years. The Φ' indices obtained by VBGM and the length frequency data were 3.703 and 3.702 respectively, where the $C_v = 0.02\%$ indicates that there were no differences between these two methods.

The mean TL of each age class decreased throughout the breeding season and in particular in 0+ class during November–December (Fig. 5). The most represented age classes were 0+ and 1+ during the breeding season, and 1+ during the rest of the year (Fig. 6).

The predominant age class in spawner (found only from October to February, the breeding season) was 1+ for both sexes, which represented 65% in the first four months for females and 75% in the first three months for males of the total of spawner (Fig. 7a, b). For spawner females, 0+ class (excepting whitebait, which is not included in this analysis) was the least represented and 2+ age class decreased the percentage along the breeding season from 25% to 0% of the total. For spawner males, 2+ was also the least represented age class and 0+ was only present in the last three months of the breeding season. Non-spawner individuals (Fig. 7c, d) were observed during the 12 months of the study. Among non-spawner individuals, the mostly represented age classes were 0+ during the breeding season (which decreased its representation progressively to April) and 1+ out of the breeding season.

Discussion

Larger individuals and one more size cohort of *Galaxias maculatus* were found in the Arroyo Negro population compared with the other South American populations. Three cohorts were observed in this population, while only two size cohort were found in continental Patagonia in the Ramos Mexía reservoir, Neuquén (Ferriz 1987), and in the Caleufú River (a cohort composite only for adults and another one for metamorphic larvae, juveniles and adults, Barriga et al. 2007). In another

Table 2 Mean and maximum total length of *Galaxias maculatus* populations from South America

Population	Latitude	Mean total length (mm)	Maximum total length (mm)	n	Life history	Sampling time	Sampling method	References
Río Biobío	−36°48'	54.87	60	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Biobío	−37°25'	55.28	71	120	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río Imperial	−38°36'	55.58	76	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río Imperial	−38°45'	53.32	86	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Toltén	−39°14'	52.67	57	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Toltén	−39°14'	53.58	80	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Ramos Mexía reservoir	−39°15'	45.68	66.5	1757	Landlocked	One year seasonally	1-mm mesh net	Ferriz 1987
Lago Villarrica	−39°15'	43.3	51	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Lago Panguipulli	−39°42'	49.79	66	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río San Pedro	−39°45'	58.76*	109.61*	6956	Landlocked	One year seasonally	Electrofishing and net	Cifuentes et al. 2012
Valdivia and Calle-Calle rivers	−39°51'	54	116	–	Both	One year monthly	2-mm mesh net	Campos 1973
Río Valdivia	−39°51'	43.14	56	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Valdivia	−39°51'	47.41	74	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río Bueno	−40.10'	54	100	306	Landlocked	Summer and autumn	Electrofishing	Penaluna et al. 2009
Río Bueno	−40°14'	48.46	88	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río Caleufú	−40°25'	57.88	80	46	Landlocked	One year monthly	Electrofishing	Barriga et al. 2007
Piedra del Águila reservoir	−40°30'	42.47	–	31	Landlocked	One year monthly	Electrofishing	Barriga et al. 2007
Lago Rupanco	−40°49'	52.02	65	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Laguna Ezquerra	−41°03'	–	74	–	Landlocked	One year seasonally	Baited traps	Cussac et al. 1992
Lago Todos los Santos	−41°08'	50.89	71	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Lago Gutiérrez	−41°12'	–	69.83*	1195	Landlocked	One year monthly	Baited traps	Barriga et al. 2002
Bahía Ralún	−41°23'	63.59	84	85	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Puelo	−41°39'	56.83	98	66	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Bahía Sotomó	−41°39'	53.24	75	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Río Cisnes	−44°45'	55.32	88	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Bahía Aysén	−45°24'	41.86	78	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**
Lago Vargas	−47°40'	35.84	48	100	Landlocked	Autumn	10-mm mesh net	Górski et al. 2015**
Río Baker	−47°47'	56.52	98	100	Diadromous	Autumn	10-mm mesh net	Górski et al. 2015**

Table 2 (continued)

Population	Latitude	Mean total length (mm)	Maximum total length (mm)	n	Life history	Sampling time	Sampling method	References
Río Santa Cruz	−50°12'	–	90	1183	Landlocked	Spring	Electrofishing	Tagliaferro et al. 2014
Río Grande	−53°49'	64.16	84.15	42	Diadromous	Autumn	Electrofishing	Rojo pers. obs.
Isla de los Estados	−54°46'	69.33	91	3	Diadromous	Summer	Entomological net	Gosztonyi 1970
Laguna Cecilia	−54°49'	61.28	103.4	203	Landlocked	Summer	Electrofishing	Rojo pers. obs.
Laguna Negra	−54°50'	63.69	116	735	Landlocked	One year seasonally	Electrofishing	Rojo pers. obs.
Arroyo Negro	−54°51'	67.79	115	572	Diadromous	One year seasonally	5-mm mesh net	Boy et al. 2009; This work
Bahía Varela	−54°52'	79.91	113	357	Diadromous	Spring-Summer	5-mm mesh net	Rojo pers. obs.

* TL estimated from SL (see Material and Methods). ** The sampling carried out by Górsky et al. (2015) only considered the first 100 specimens collected for the calculation of mean and maximum total lengths, therefore maximum length would be underestimated
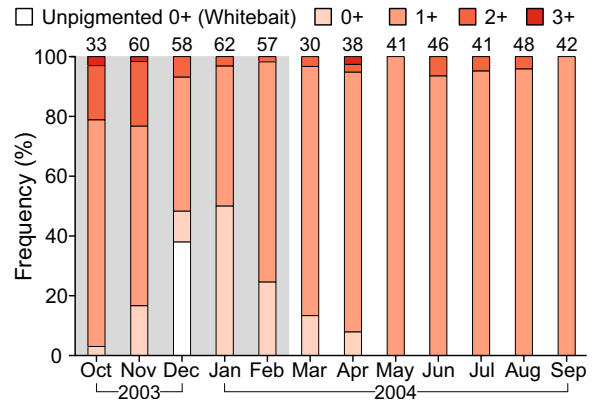

Fig. 2 Relative frequency of estimated ages in otoliths of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004, $n = 556$. The grey shaded area indicates breeding season. Whitebait (juveniles) belong to 0+ age class but were separated for clarity purposes only (see Results section). The numbers over the bars indicate monthly sample size

continent, Chapman et al. (2006) attribute the smallest maximum sizes between western and eastern Australian populations of *G. maculatus* to the lower primary productivity of the systems in western ones, also in some populations to better predation evasion, given that the smallest individuals are less conspicuous and more agile. The maximum TL for this population (115 mm) was not the maximum found for the species, since in Australian eastern populations the maximum size was 148 mm in Merri River, 132 mm in Bullen Merri Lake (Laurenson et al. 2012) and 138 mm in Modewarre Lake (Pollard 1971a). Geographical differences in sizes could be the result of various factors including the lower presence of predators, a higher productivity of
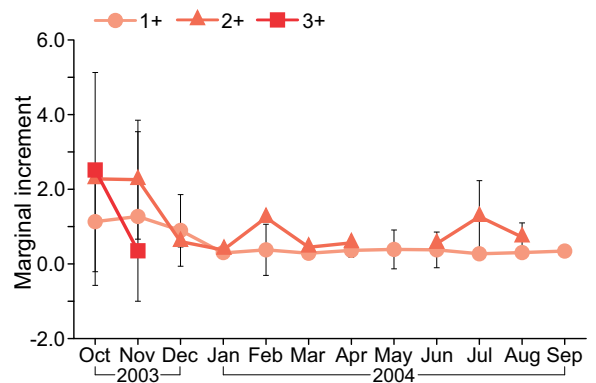

Fig. 3 Marginal increments ± standard deviation for each age class from otoliths of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004. $n = 444$

Fig. 4 von Bertalanffy model fitted for males and females (*n* = 377) of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004
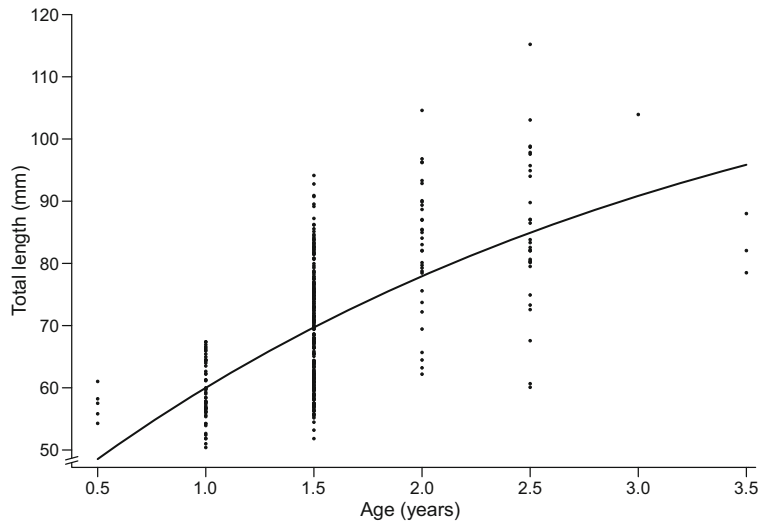
waterbodies or a more benign climate than in South America. In accordance with Jordan (1891), the number of vertebrae in fish populations increases with latitude (Jordan's rule; McDowall 2008), the individuals studied here would have the largest maximum sizes owing to an increased number of vertebrae. The diadromous life history of Arroyo Negro would also have implications for the number of vertebrae since diadromous individuals generally have a higher vertebral count than landlocked ones (McDowall 2003). In addition, we hypothesize that the protecting effect of whitebait translucency against predators would have a positive selective value. The decrease in TL in the cohorts estimated by the Bhattacharya's method could take place due to the recruitment of unpigmented individuals (whitebait) to the population in December and their metamorphosis to juveniles in January. In order to achieve a broader

Fig. 5 Mean ± standard deviation of total length of each age class of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004. n = 556

understanding of the factors that influence final size on South American *G. maculatus*, further studies should include the study of vertebral counts, primary productivity, predation pressure, hatch size, the relationship between size at whitebait-pigmented individual transition and maximum size attained, and growth rates within the context of diadromic-landlocked life strategies and latitudinal location of its South American populations. Furthermore, in several fish species the importance of being large to winter survival increases with latitude whereas the length of the growing season simultaneously decreases, as an adaptive response to size-selective winter mortality. The result is a counter-gradient variation in growth rate (Conover 1990; Conover and Present 1990). In somatic growth, fast-growing genotypes have a higher fitness in places where the environment promotes a slow growth, for example in areas located at high latitudes where winters tend to be harsher than at lower latitudes (Conover 1990).
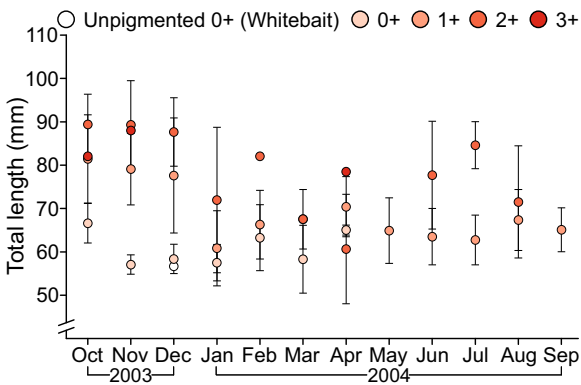
Although greater female size has been proposed by several authors for different populations of *G. maculatus* (McDowall 1968; Pollard 1971b; Ferriz 1987; Chapman et al. 2006; Laurenson et al. 2012), we propose here a general growth model ($L_\infty = 123.75 \pm 25.3$ mm, $k = 0.33 \pm 0.16$ year^{-1} and $t_0 = -1.01 \pm 0.45$ years) for the Arroyo Negro diadromous population, given that sex differences were not observed. Furthermore, the asymptotic length (L_∞) found here is larger than the one found in landlocked populations from South America: in Laguna Ezquerra, 97.2 mm (Cussac et al. 1992); in the Caleufú River, 54.14 mm (for the second cohort composed of metamorphic larvae,
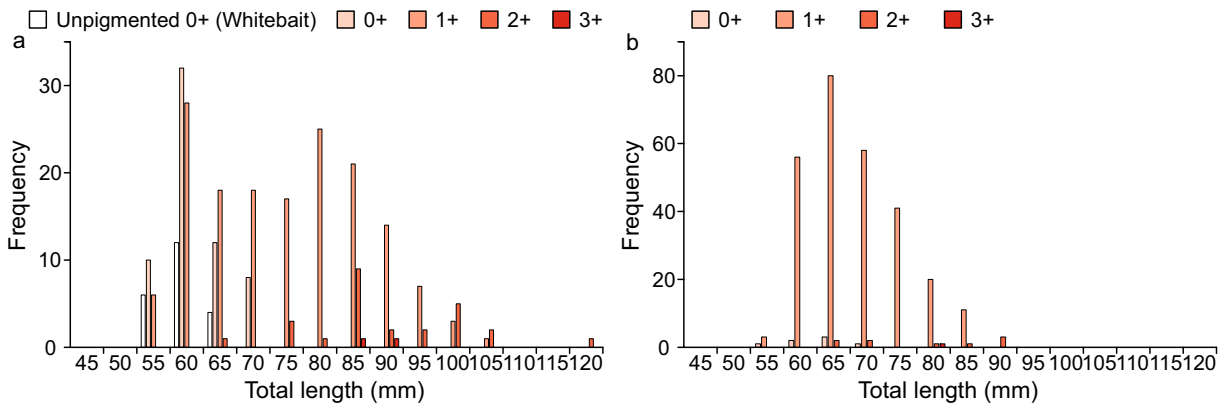
Fig. 6 Size frequency distribution for each age class of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004. **a** Breeding season (October to February), $n = 270$. **b** March to September, $n = 286$

juveniles and adults, Barriga et al. 2007); and from Australia, in Moates Lake, 83 mm and 91 mm for females and males respectively (Chapman et al. 2006).

The reason for the larger size found here does not seem to lie in the lifespan of the individuals, being that the maximum age of three years found in the Arroyo Negro population is consistent with other populations of *G. maculatus* from South America in Chile (Vega et al. 2013), from west of Australia in Moates lake (Chapman et al. 2006) and from New Zealand (McDowall 1968).

Unlike the age observed under this study, an annual life cycle in the Ramos Mexía reservoir, Neuquén (Ferriz 1987), and a one-year life cycle in the diadromous population of Jerdacuttup river, Australia, (Chapman et al. 2006) were suggested from the progression of size cohorts. The highest MI was observed in October and November, especially in 2+ age class. In addition, it was observed that the MI was not uniform along the entire perimeter of the otolith, given the change of shape observed between age classes.
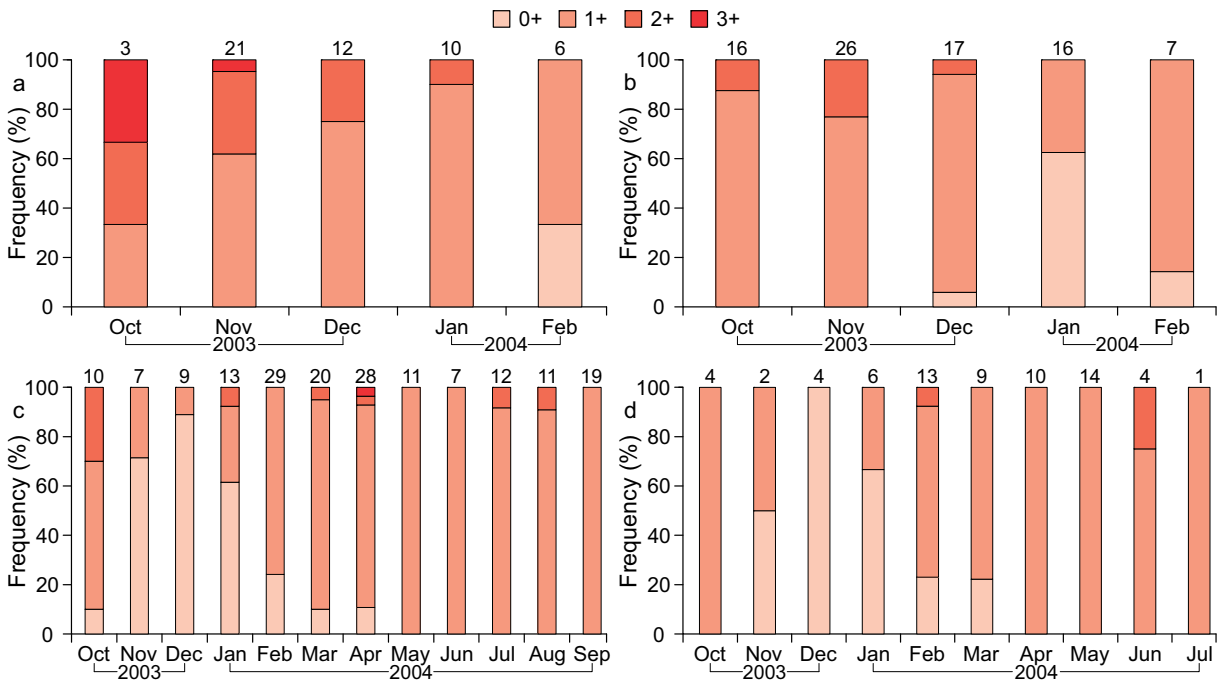

Fig. 7 Age composition of spawner and non-spawner individuals of *Galaxias maculatus* from Arroyo Negro, Parque Nacional Tierra del Fuego, between October 2003 and September 2004.

a spawner females, $n = 52$. **b** spawner males, $n = 82$. **c** non-spawner females, $n = 176$. **d** non-spawner males, $n = 67$. The numbers over the bars indicate monthly sample size

The integrated results about age and spawner/ non spawner condition of the individuals shows that the 1+ age class is the main contributor to the reproduction of the population (70–77%), followed by 2+ in females (17%) and by 0+ in males (19%). The contribution of the 2+ age class is focused on the first months of the breeding season; and the 0+ was only observed at the end of this season, what is more, in 0+ females only at the last month. These differences in the contribution of 0+ age class might be a consequence of the cost of sexual maturation, suggesting an energy compromise between growth and reproduction in the youngest females, which would prioritize somatic growth. Moreover, this would explain the decline in the mean size of spawner females throughout breeding season previously observed (Boy et al. 2007), since towards the end of the season, younger females are recruited as reproductive females and older ones are no longer observed. The higher proportion of the longest-lived individuals observed in AN than in other populations of the species, together with the finding that they represent about 17% of the spawners, could be a consequence of selection resulting in an increased larval survival and/or enhance greater recruitment in a population under strong environmental conditions.

In summary, fish from a diadromous population of *Galaxias maculatus* at the southern world extreme of this species distribution are larger than those from other populations in South America. Further studies are needed in order to elucidate if the largest final size is a consequence of the diadromous life strategy of the population studied, a local adaptation of a peripheral population or countergradient growth. Though the available information about size and growth in South American populations of *G. maculatus* is not standardized, these differences in body length and maximum age demonstrate the plasticity of life history strategies, maybe as adaptation to the different and/or unpredictable environments (Chapman et al. 2006). The high proportion of one-year-old individuals and their high contribution to the reproduction (typical of a fast growing species) together with the largest final size of this population can be interpreted in the context of the plasticity of life history traits of this species.

Compliance with ethical standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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