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PATAGONIAN LAKES

Review Paper

Climate change impacts on freshwater fishes: a Patagonian perspective

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Abstract The fish fauna of Patagonian lakes comprises a small, unique group of native species and several exotic ones. The consequences of environmental changes for Patagonian fish populations vary according to the physiology of the species considered. Several previously predicted facts such as extirpations, extinctions, and translocations have occurred and human actions such as transport, introduction, and stocking of exotic species suggest a more complex future. We discuss the historical biogeography of Patagonian freshwater ichthyofauna to help us better understand their present adaptations and physiological ecology. We also address potential interactions between climate change and processes such as migration, species introductions, and invasions. There is still much to learn from Patagonian fishes to comprehend how these species will endure environmental changes.

Keywords Climate change · Fish · Freshwater · Patagonia · Temperature

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Introduction

Patagonia is the southernmost region of South America, extending down the Barrancas and Colorado rivers in Argentina, and south from the Puelo River basin in Chile (Cussac et al., 2016). Patagonian freshwaters are shaped by the Andean Range that runs in a north–south axis on the west side and by the plateau that extends towards the east side, encompassing many glacial deep Andean lakes, a few shallow plateau lakes, some artificial reservoirs, and both short, steep Pacific and long, flat Atlantic drainage rivers. The freshwater ichthyofauna presents an ensemble of 29 fish species comprising Neotropical fishes (siluriformes and characids), marine dispersants (galaxiids), oceanic elements of local origin (percichthyids, atherinopsids, and mugilids), the only two species of lampreys of South America, several exotic salmonids, and one exotic cyprinid (Fig. 1; Table 1; Pascual et al., 2007; Cussac et al., 2016). This ensemble occurs over a wide thermal gradient due to the broad latitudinal and altitudinal range of the region, having its habitat and connectivity regulated by rainfall (Aigo et al., 2008; Cussac et al., 2009).

Changes in ecologically important climate variables for these freshwater fishes have been registered in Argentinean Patagonia from year 1961 to 2016. Precipitations have diminished in center–south of the region; Mean Annual Air Temperature (MAAT), an estimator of lake water bottom temperature, has

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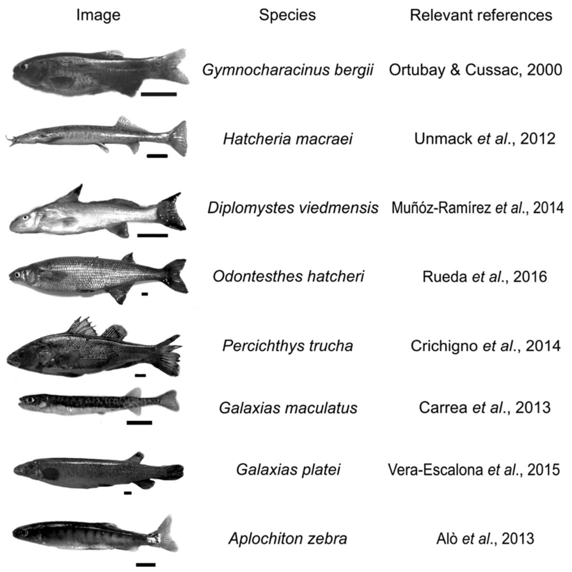

Image	Species	Relevant references
	Gymnocharacinus bergii	Ortubay & Cussac, 2000
	Hatcheria macraei	Unmack *et al.*, 2012
	Diplomystes viedmensis	Muñóz-Ramírez *et al.*, 2014
	Odontesthes hatcheri	Rueda *et al.*, 2016
	Percichthys trucha	Crichigno *et al.*, 2014
	Galaxias maculatus	Carrea *et al.*, 2013
	Galaxias platei	Vera-Escalona *et al.*, 2015
	Aplochiton zebra	Alò *et al.*, 2013

Fig. 1 Main basins in Argentine Patagonia: *A* Colorado; *B* Negro; *C* Chubut; *D* Deseado; *E* Chico-Santa Cruz; *F* Coyle; *G* Gallegos; *H* Grande

increased in northern Patagonia up to 1.5°C; and Mean Summer Air Temperature (MSAT), an estimator of summer surface water temperature, has increased up to 2.5°C (http://www.smn.gov.ar/serviciosclimaticos/?mod=cambioclim&id=7, Quirós & Drago, 1985; Quirós, 1991; Livingstone & Lotter, 1998; Cussac et al., 2009; Báez et al., 2011).

How fishes can respond to climate change is an open research topic. On a global scale, it is generally agreed that distributional shifts, local extirpations, and species extinctions are expected to occur, but data to validate these predictions are relatively scarce (Sinervo et al., 2010). Assuming that during the Pleistocene, North Hemisphere fish moved along a north–south axis in order to seek refuge from glaciations, Oberdorff et al. (1997) expected that less climatically driven extinctions occurred in rivers having a north–south orientation (North American rivers) than in rivers having an east–west orientation (European rivers). In the same way, though most of the main Patagonian rivers east of the Andes run from west-to-east (Fig. 2), the two northernmost basins (Colorado and Negro) have tributaries with a wide north-to-south (Colorado) and south-to-north (Negro) development, so the greatest effects of climate change would be expected in the upper Colorado basin and in the lower Negro basin. Consistent with observed changes, the northern border of the Patagonian Province (Colorado basin, Ringuelet, 1975) was shifted southward (Negro basin) by Arratia et al. (1983) and Almiron et al. (1997). The effects of climate change on fish and fisheries around the world have been comprehensively reviewed by several authors (Allan et al., 2005; Ficke et al., 2007; Lynch et al., 2010; Woodward et al., 2010; Harrod, 2015; Poesch et al., 2016), including those regarding ultraviolet radiation, rainfall, and temperature changes on Patagonian freshwater fishes (Aigo et al., 2008; Cussac et al., 2009, 2016; Gonçalves et al., 2010; Báez et al., 2011).

Environmental changes can affect both development and homeostasis, thereby disrupting the match between an individual's phenotype and the environment (Whitman & Agrawal, 2009), making the persistence of a species to depend ultimately on its capacity to change its phenotype through adaptive responses. Both between and within generations, adaptive variation allows organisms to withstand environmental challenges (Meyers & Bull, 2002). The former involves microevolutionary changes (i.e., allele frequency shifts) in the population in response to natural selection (Charmantier et al., 2008), which will only occur if populations bear significant genetic variation and have connectivity among them to allow the exchange of alleles at adaptive loci. The latter, on the other hand, acts within any given generation at an individual level through phenotypic plasticity (Guntrip & Sibly, 1998; Pigliucci, 2001; Pigliucci et al., 2006), and if there is an additive genetic component, it may be favored by selection and eventually become fixed in the population over time (West-Eberhard, 2003; Williams et al., 2008). Adaptive plasticity may be fundamental for organisms with long generation times, as is the case in most Patagonian fishes, and it can be viewed as an adaptation not only to current but also to past selection regimes (Ghalambor et al., 2007), hence the importance to look at the historical environmental changes that have occurred in Patagonia to understand current adaptations. Though the capacity for evolutionary adaptation is probably the most difficult trait to quantify across species (Williams et al., 2008), understanding the role of plasticity in evolutionary responses is crucial for predicting the short- and long-term effects of environmental change on Patagonian freshwater fishes.

Historical events thought to influence present distributions of fish were of little assistance in

Table 1 Patagonian fishes (*sensu* Cussac et al., 2016), origin (native, non-native, marine), present distribution, and main pressures impacting native populations (after Cussac et al., 2004; Pascual et al., 2007; Aigo et al., 2008)

Order	Family	Species	Origin	Present distribution	Main pressures
Petromyzontiformes	Petromyzontidae	*Geotria australis* Gray, 1851	Native	Negro and Limay basins	Damming
		Mordacia lapicida Gray, 1851	Native	Rivers of southern Chile	Damming
Cypriniformes	Cyprinidae	*Cyprinus carpio* Linnaeus, 1758	Non-Native	Colorado, Negro, and Limay basins	
Characiformes	Characidae	*Astyanax eigenmanniorum* (Cope, 1894)	Non-Native	Colorado and Negro basins.	
		Cheirodon interruptus (Jenyns, 1842)	Non-Native	Colorado and Negro basins. Valcheta stream.	
		Gymnocharacinus bergii Steindachner, 1903	Native	Upper Valcheta stream	Salmonid predation and salmonid and *Cheirodon* competition. Habitat modification.
		Oligosarcus jenynsii (Günther, 1864)	Non-Native	Colorado and Negro basins.	
Siluriformes	Diplomystidae	*Olivaichthys viedmensis* MacDonagh, 1931 (including other nominal species according to Muñoz-Ramírez et al., 2014 and Arratia & Quezada-Romegialli, 2017)	Native	Colorado, Negro, Chubut, and Baker basins.	Salmonid predation and competition. Habitat modification.
	Callichthyidae	*Corydoras paleatus* (Jenyns, 1842)	Non-Native	Colorado and Negro basins.	
	Trichomycteridae	*Hatcheria macraei* (Girard, 1855)	Native	Colorado, Negro, Chubut, Deseado, Puelo, Futaleufú, Yelcho, Palena, Aysén, and Baker basins.	Salmonid predation and competition. Habitat modification.
Osmeriformes	Galaxiidae	*Aplochiton taeniatus Jenyns, 1842*	Native	Pacific drainages from Lake Lacar to Tierra del Fuego, excluding Manso basin.	Salmonid predation and competition. Habitat modification. Damming. Climate warming.
		A. zebra Jenyns, 1842	Native	Pacific drainages from Lake Lacar to Tierra del Fuego, excluding Manso basin.	Salmonid predation and competition. Habitat modification. Damming. Climate warming.
		Galaxias maculatus (Jenyns, 1842)	Native	Atlantic and Pacific drainages from Lake Pellegrini to Tierra del Fuego	Salmonid predation and competition. Habitat modification. Damming. Climate warming.
		G. platei (Steindachner, 1898)	Native	Atlantic and Pacific drainages from Negro River to Tierra del Fuego	Salmonid predation and competition. Habitat modification. Damming. Climate warming.

Table 1 continued

Order	Family	Species	Origin	Present distribution	Main pressures
Salmoniformes	Salmonidae	*Salvelinus fontinalis* (Mitchill 1814)	Non-Native	Atlantic and Pacific drainages from Limay River (Piedra del Águila Reservoir) to Tierra del Fuego (Escondido Lake).	Climate warming.
		S. namaycush (Walbaum, 1792)	Non-Native	Lake Burmeister and Santa Cruz basin.	Climate warming.
		Salmo salar Linnaeus, 1758	Non-Native	Limay and Futaleufú basins.	Climate warming.
		S. trutta (Linnaeus, 1758)	Non-Native	Atlantic and Pacific drainages from Limay River to Tierra del Fuego.	Climate warming.
		Oncorhynchus mykiss (Walbaum, 1792)	Non-Native	Atlantic and Pacific drainages from Negro River to Tierra del Fuego.	Climate warming.
		O. kisutch (Walbaum, 1792)	Non-Native	Pacific drainages and Santa Cruz basin.	Climate warming.
		O. tshawytscha (Walbaum, 1792)	Non-Native	Pacific drainages and Santa Cruz basin.	Climate warming.
Atheriniformes	Atherinopsidae	*Odontesthes hatcheri* (Eigenmann, 1909)	Native	Colorado, Negro, Chubut, Puelo, Futaleufú, and Baker basins.	Salmonid predation and competition. Habitat modification. Genetic introgression.
		O. bonariensis (Valenciennes, 1835)	Non-Native	Colorado, Negro, and Chubut basins.	
		O. argentinensis (Valenciennes, 1835)	Marine	Estuaries of Colorado, Negro, and Chubut rivers.	
Cyprinodontiformes	Poeciliidae	*Cnesterodon decemmaculatus* (Jenyns, 1842)	Non-Native	Colorado and Negro basins, Curicó Lake and Valcheta stream.	
	Anablepidae	*Jenynsia multidentata* (Jenyns, 1842)	Native	Colorado and Negro basins, Curicó Lake, and Valcheta stream.	Salmonid predation and competition. Habitat modification.
Mugiliformes	Mugilidae	*Mugil liza* Valenciennes, 1836	Marine	Estuaries of Colorado, Negro, and Chubut rivers.	
Pleuronectiformes	Paralichthydae	*Paralichthys brasiliensis* Ranzani, 1842	Marine	Estuaries of Colorado, Negro, and Chubut rivers.	
Perciformes	Percichthyidae	*Percichthys trucha* (Valenciennes, 1833) [including other nominal species according to Ruzzante et al. (2011) and Crichigno et al. (2014)]	Native	Colorado, Negro, Chubut, Puelo, Futaleufú, Baker, Deseado, and Santa Cruz basins.	Salmonid predation and competition. Common carp invasion.

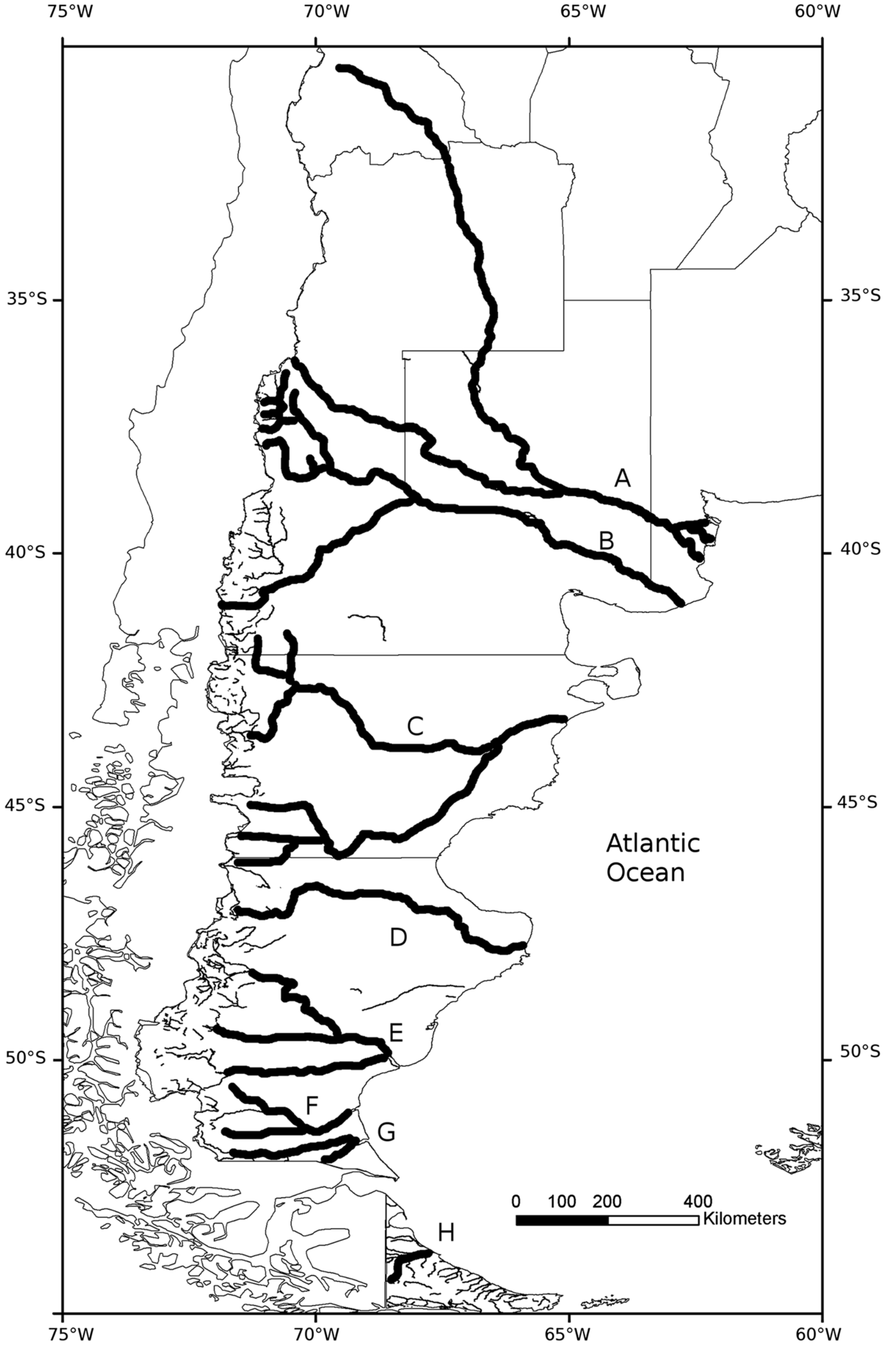

Fig. 2 Main native Patagonian species (bar = 10 mm) and relevant references

explaining variations in fish species richness at the global scale (Oberdorff et al., 1995). However, continental effects on contemporary fish species richness, though less explicative than ecological factors, was highly significant, not excluding historical influences in generating different overall species richness levels for rivers of Western Europe and North America (Oberdorff et al., 1997). In particular, Patagonia has a long history of environmental changes due to geological events at regional and global scales

Table 2 Epoch and time when Andean fish fauna were exposed to environmental changes according to fossil records and genetic evidence

Epoch/change	Time	Taxa	Evidence	References
Eocene/from warming to cooling	−58.8 to −33.9 mya	Siluriformes Characiformes Percichthyidae	Fossil record	Cione & Báez (2007)
Oligocene/cooling	−33.9 to −23 mya	*Galaxias platei*	Genetics	Burridge et al. (2012)
Miocene/aridization and marine incursions	−23 to −5.3 mya	Loricariidae Pimelodidae *Odontesthes* Percichthyidae *Galaxias platei*	Fossil record and genetics	Ruzzante et al. (2006), Cione & Báez (2007), Zemlak et al. (2008), and Cione et al. (2011)
Pliocene/change to a cooler, dry, seasonal climate	−5.3 to −1.8 mya	Siluriformes Percichthyidae	Fossil record and genetics	Ruzzante et al. (2006, 2011) and Cione & Báez (2007)
Pleistocene/glaciations	−1.8 mya to −11500 ya	*Callichthys* *Pimelodella* *Corydoras* Percichthyidae *Galaxias platei*	Fossil record and genetics	Ruzzante et al. (2006, 2011), Cione & Báez (2007), and Zemlak et al. (2008)

that shaped the evolutionary history of the different groups (Ruzzante et al., 2008; Barber et al., 2011). These events show, over time spans of thousands to millions of years, magnitudes of change that modeled the physiological capabilities of present species with adaptations that can be seen nowadays (Menni, 2004; Cussac et al., 2009). The aim of this work is to review the data regarding the adaptation of Patagonian fishes to past and present environmental conditions and discuss the expectations about their future in the context of contemporary climate change.

Historical biogeography

The first integrative outline of Patagonian fish fauna was performed by McDowall (1971a). He clearly recognized "(1) Primary and secondary fishes: Trichomycteridae and other catfishes, Characidae, Poeciliidae" as having a South American origin or having entered South America from other land areas, and "(2) Peripheral fishes: Atherinidae, Serranidae, Galaxiidae, Aplochitonidae, Geotriinae, and a few other odd forms which enter fresh waters." Historical biogeography on Patagonian fishes, supported by fossil records and phylogeography (see http://patagonia.byu.edu/), has usually been visualized within the framework of the effects of Quaternary glaciations on populations of marine-related species like the perch *Percichthys trucha* (Valenciennes, 1833), the puyen *Galaxias maculatus* (Jenyns, 1842), and the big puyen *Galaxias platei* (Steindachner, 1898) (Table 2; Ruzzante et al., 2006, 2008, 2011; Zemlak et al., 2008, 2010; Carrea et al., 2012, 2013). In some cases, the permanence over thousands of years of the physiological adaptations involved can be assumed. For instance, Ruzzante et al. (2008) found past demographic changes for big puyen and perca coincident with significant Andean glaciations. The most recent glacial advance (c. 15,000–35,000 years ago) produced a marked population bottleneck in "the cold-water adapted" *G. platei,* and an earlier large glacial expansion (c. 140,000–180,000 years ago) had the greatest impact on the demographic history of "the more warm-adapted" perca, greatly reducing populations east and west of the Andes. These demographic responses have been attributed to different ecological traits based on knowledge of the present physiological ecology of the species (Milano, 2003; Cussac et al., 2004; Aigo, 2010; Aigo et al., 2014).

Moreover, long-term (millions of years) maintenance of physiological traits by Neotropical Ostariophysi (characinids and catfishes) living under the warmer climatic conditions registered in Patagonia during the Tertiary (Menni & Gómez, 1995; Ortubay et al., 1997; Cione et al., 2005; Cione & Báez, 2007; Unmack et al., 2009, 2012; Muñoz-Ramirez et al., 2014) can be inferred. At the present time, lower lethal temperatures correlate with the southern limit of the geographical distribution of several Neotropical species (Gómez, 1996, 2014; González Naya et al., 2011) and the southward decrease in diversity correlates with water temperature (Menni & Gómez, 1995).

Worthy of note is the progressive southward disappearance of several catfishes; the bagre pintado *Trichomycterus areolatus* (Valenciennes, 1840), reaching its southernmost record at 42°22′S on Chiloe island (Unmack et al., 2009), the otuno *Olivaichthys viedmensis* MacDonagh, 1931 up to 47°19′S (Muñoz-Ramirez et al., 2014; Arratia & Quezada-Romegialli, 2017), and the bagre de torrente *Hatcheria macraei* (Girard, 1855) up to 47°34′S (Unmack et al., 2012). In Lake Buenos Aires (46°32′S), the latter presents a lethal temperature (31°C) similar to that of a warm water fish, suggesting a physiological relic related to previous warm water adaptation (Gómez, 1990).

In the same way, resource-related ecological factors and acute physiological limits seem to have been integrated in order to shape the process of decreasing diversity of characins west of the Andes. The species belonging to the genus *Cheirodon* are allopatrically distributed southward in Chile, with some species present above the Patagonia region: *Cheirodon pisciculus* Girard, 1855 (Maipo river, 33°52′S), *Cheirodon galusdai* Eigenmann, 1928 (Itata, Andalién, and Bío-Bío rivers, 36°46′–37°46′S), *Cheirodon kiliani* Campos, 1982 (Lanalhue lake up to Valdivia river, 37°55′S), and *Cheirodon australe* Eigenmann, 1928 (Imperial, Toltén, Valdivia, Bueno and Maullín rivers, 37°55–41°08′) (Habit et al., 2006). On either side of the Andean Range, the presence of *C. australe* in Lake Tarahuin, Chile (42°40′S, 73°56′W, Campos et al., 1996) and the extreme endemism of the scaleless characin *Gymnocharacinus bergii* Steindachner, 1903 in the endorheic Valcheta stream in Argentina (40°51′S, 66°34′W) represent the southernmost distribution of the order Characiformes (Menni & Gómez, 1995). The case of *G. bergii* was interpreted as a consequence of the thermal character of the Valcheta stream (Menni & Gómez, 1995; Ortubay et al., 1997), and its isolation may be explained by the minimum area necessary for one species, excluding others by competition (Menni & Gómez, 1995). Cussac & Ortubay (2002) described life history traits in *G. bergii* related to its restricted environment; Ortubay et al. (2002) found a high aggressiveness against *Jenynsia multidentata* (Jenyns, 1842), a common inhabitant of the lower limit of the Brazilian Subregion; and Miquelarena et al. (2005) considered the morphological reductions described for adult individuals to be a consequence of low inter-specific competition, low predation, and small population size, allowing regression phenomena in this unique population. Therefore, *G. bergii* has maintained physiological traits adapted to warm water and evolved morphological reductions as a consequence of its isolation. Interestingly, a recent human-mediated translocation of *Cheirodon interruptus* (Jenyns, 1842) has been reported in the lower reaches of Valcheta stream, imposing a new challenge for the conservation of *G. bergii* due to the presence of a possible new competitor (López et al., 2013).

Ostariophysan fishes were not the only old inhabitants of Patagonia. Fossil records indicate the presence of Percichthyidae in Southern South America from the Eocene (Cione & Báez, 2007), having originated in fresh water as a secondary radiation from marine protopercoid ancestors (Jerry et al., 2001). Similarly, marine-to-freshwater transitions have occurred in several Atheriniform lineages such as *Odontesthes* in Southern Brazil during the Miocene (Campanella et al., 2015). The adaptive potential of estuarine fishes to invade freshwater has been emphasized for Atherinopsidae (Beheregaray & Sunnucks, 2001; Beheregaray et al., 2002), and regulatory modifications of gene expression in freshwater and marine morphs of the clupeid *Alosa pseudoharengus* (Wilson, 1811) were documented (Czesny et al., 2012). In agreement with this adaptive potential, the magnitude of the phenotypic plasticity of *P. trucha* and the Patagonian silverside *Odontesthes hatcheri* (Eigenmann, 1909) was evaluated at a morphological level, explaining a great proportion of the morphological variation observed in the wild (Crichigno et al., 2012, 2014).

Recent genetic studies have positioned landlocked *G. platei* far from the facultative diadromous *G. maculatus,* placing it close to the mostly landlocked *Neochana* species (Burridge et al., 2012), or close to two landlocked New Zealand Galaxiidae; *Galaxias sp.* and *G. gollumoides* McDowall & Chadderton, 1999 (Vera-Escalona et al., 2015). Genetic estimates of divergence times suggest the presence of *G. platei* in South America not just before the Andes uprise, in the Miocene (Zemlak et al., 2008), but even before the separation of Australia and South America, in the Oligocene (Burridge et al., 2012). *Galaxias platei* is mostly restricted to montane lakes and streams of Patagonia, and shows extremely high endurance to low temperature and low oxygen availability (Milano, 2003; Cussac et al., 2004; Barrantes et al., 2017). When exposed to competition and predation by other fishes, it seems to exploit the lake bottom, also changing its trophic niche (Milano, 2003; Cussac et al., 2004; Belk et al., 2014; Sobenes et al., 2013).

In brief, historical changes pauperized the ostariophysan diversity in Patagonia and favored the invasion of freshwater by marine-related taxa (Galaxiidae, Percichthyidae, Atherinopsidae), leaving relic traits that can be helpful to interpret and predict the effects of climate change on present fish populations.

Ecological physiology

The environmental changes that affected Patagonia in the past, such as cooling from the late Eocene, which restricted the tropical climate to lower latitudes (Cione & Báez, 2007; Cione et al., 2007), the uprising of the Andes and the consequent aridization, marine transgressions and regressions (Hubert & Renno, 2006), glaciations (Ruzzante et al., 2006, 2008, 2011; Fraser et al., 2012), and hydrological variability (Piovano et al., 2009) modeled Patagonian fish adaptations. Among those we can mention the following: (a) trophic polymorphism and phenotypic plasticity of the oropharyngeal apparatus in *P. trucha* and *O. hatchery,* regarding open trophic niches in new postglacial lakes (Ruzzante et al., 1998, 2003; Crichigno et al., 2012, 2014); (b) cephalic lateral line in *P. trucha* (Vega & Viozzi, 2016) and cephalic sensorial pores in *G. platei*, regarding darkness and the use of the bottom of deep lakes (Sáez & Pequeño, 2014), (c) variation in eye diameter in relation to lakes of different water transparency in the peladilla *Aplochiton zebra* Jenyns, 1842 (McDowall, 1971b; McDowall & Pankhurst, 2005; Lattuca et al., 2007), (d) facultative diadromy in *G. maculatus,* regarding avoidance of cold Pleistocene winters (McDowall, 1980; Carrea et al., 2013), (e) tolerance to high temperature in *G. bergii, H. macraei, P. trucha,* and *O. hatcheri* (Ortubay et al., 1997; Aigo et al., 2008; 2014; Cussac et al., 2009), coincident with the fossil record of Siluriformes and Percichthyidae from the Eocene (Table 2, Cione & Báez, 2007), and f) tolerance to extremely low temperature and to low oxygen availability, improved vision in darkness, and gill protection against abrasion in *G. platei*, regarding endurance in glacial refuges and periglacial environment (Cussac et al., 2004; Zemlak et al., 2008; Barrantes et al., 2017). Particularly, thermal tolerance is central to the concept of the thermal niche of fishes, i.e., thinking of temperature as an ecological resource in addition to thinking of temperature as a physiological factor (Magnuson, 2010).

Contemporary climate change is expected to affect the physiology of freshwater fishes as this is greatly influenced by their thermal environment (McNab, 2002; Abrahams, 2006). Indeed, the role of temperature in ectothermic poikilotherms seems to be the main factor regulating the life of fishes (Cussac et al., 2009; Magnuson, 2010). Lower limits of temperature tolerance are often associated with the freezing temperature of water, and upper limits are explained by irreversible denaturalization of enzymes critical for survival (McNab, 2002). More precisely, the mismatch between the demand for and the supply of oxygen by the respiratory system is the primary mechanism that restricts an animal's tolerance to upper thermal extremes (Pörtner & Knust, 2007).

Fish kills are well documented in the southern limit of the Neotropical Region (González Naya et al., 2011; Gómez, 2014). Furthermore, temperature also affects fish viability between lethal limits (Fry, 1971), either through constraints to body size imposed by winter starvation at high latitudes or altitudes (Shuter & Post, 1990), by increased vulnerability to predation by sub-lethal heat shocks (Coutant, 1973; Yokum & Edsall, 1974), or by reduced availability of littoral habitats due to elevated water temperatures (Jansen & Hesslein, 2004). Indeed, species have their own optimal temperatures and intra-specific differences may arise due to local conditions (e.g., species or age groups that occupy similar thermal habitats differ more in prey types, whereas those eating more similar prey types tend to occupy more different thermal habitats), provoking distinct responses to temperature changes. Thus, temperature may be considered both as an ecological resource and as a physiological factor (Magnuson & De Stasio, 1997; Magnuson, 2010).

The preferred temperature of *O. hatcheri* (17°C) is close to that of *P. trucha* (20.4°C), whereas those of *G. maculatus* and *A. zebra* (10 and 13°C, respectively) are lower and more similar to that of the exotic rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) (13.5°C). Furthermore, the loss of equilibrium temperature and the upper lethal temperature have shown inter-specific differences similar to those observed in temperature preferences. *Percichthys trucha*, *O. hatcheri*, and *G. platei* displayed higher values (27–31°C) than *G. maculatus*, *A. zebra*, and the exotic *O. mykiss* (25–30°C) (Milano, 2003; Lattuca, 2006; Aigo, 2010; Aigo et al., 2014). In consequence, there are three possible situations: (a) Expansion ranges; species limited in their southward distribution by low temperatures, characins (*G. bergii* and *C. interruptus)* and catfishes (*T. areolatus, H. macraei,* and *O. viedmensis*), expected to expand their range southward; (b) Evasion to colder regions; marine-related species (*O. hatcheri* and *P. trucha*) limited both southward and northward, expected to move southward; and (c) Extirpations; marine-related species (*G. maculatus, G. platei*, and exotic salmonid fishes) limited in their northward distribution by high temperatures, expected to be extirpated in its northernmost distribution (Gonçalves et al., 2010).

Southward dispersion of Neotropical species into the Andean Region has already been observed (Aigo et al., 2008; Cussac et al., 2009, 2016). Canal construction, weirs, and the transport of fish to be used as bait facilitate the movement of fishes out of their natural range (Alvear et al., 2007; Crichigno et al., 2016a). However, the potential for such landscape changes and transport to cause range expansion needs suitable conditions. Hoffmann (1989) reported an important change in the position of the 800 mm isohyets before and after 1959 in the south of the Brazilian Subregion. During the year 2000, new wetlands with nine species of Brazilian fishes were recorded there, in the formerly called ‘‘pampeana’’ dry zone (Canevari et al., 1998). This transition between the Neotropical and the Andean Region is not new. The presence of the Andean *Percichthys* in the Neotropical region, and of *Corydoras* and other Neotropical fishes in the Andean region has long been recognized (Table 2; Almirón et al., 1997; Bruno et al., 2013, 2015, 2016).

Conversely, population decline and extirpations of cold water species were observed in Northern Patagonia. The native *G. maculatus* was found to be at low abundance in the Negro River, the northernmost limit of its distribution in Argentina (Alvear et al., 2007) and extirpations have already been observed by Habit et al. (2010) in the northernmost populations of the species in Chile (Cussac et al., 2004). In the same area, two related species, *Brachygalaxias gothei* Busse, 1983 and *Galaxias globiceps* Eigenmann, 1928 seem to be completely extinct (Habit et al., 2006, 2010).

Fish migration

The trade-off between food availability and predation risk is among the causes that result in diadromous/landlocked or lacustrine/riverine patterns, and intra-lacustrine or intra-riverine movements of migratory fish (Gross et al., 1988; McDowall, 2008). Intra-lacustrine movements (Cussac et al., 1992; Barriga et al., 2002; Buria et al., 2007), migratory movements associated with rivers (Menni, 2004; Barriga et al., 2007), diadromy (Cussac et al., 2004), and anadromy (Pascual et al., 2001; Di Prinzio & Pascual, 2008) have been observed in both native and exotic Patagonian fishes. McDowall (1980) proposed that the adaptive value of anadromy was to escape from the cold Pleistocene winters. In fact, seasonal thermal fluctuations generate different temperatures in fresh and marine waters due to their differential thermal inertia, determining aquatic primary production and opportunities for planktonic feeding. Thus, winter feeding of the marine diadromous larvae of *G. maculatus* and *Aplochiton* spp. is favored poleward (Gross et al., 1988; McNab, 2002). Interestingly, diadromous individuals of *G. maculatus* originally reported by Azpelicueta et al. (1996) in the Negro River (northern Patagonia) were absent two decades later (Carrea et al. 2013). Moreover, their higher degree of genetic structure with respect to the Santa Cruz River basin (southern Patagonia) populations reflects the adoption of a resident life history at low latitude (Carrea et al., 2013). Further studies are necessary to assess whether the ability of the South American species of Galaxiidae to display diadromous or landlocked life history patterns across large latitudinal ranges (McDowall, 1971a; Cussac et al., 2004; Barriga et al., 2007; Boy et al., 2007; Lattuca et al., 2007) is being modified by climate change, probably through changes in aquatic primary production.

Migration can expose fish to harmful conditions of temperature and low oxygen concentration. Similarly to North American and Australian Percichthyidae (Cadawallader & Rogan, 1977; Beck & Willis, 2000; Jackson & Hightower, 2001; Simpson & Mapleston, 2002; Crook, 2004; O'Connor et al., 2005), the native *P. trucha* was found to move throughout a set of interconnected mountain lakes in northern Patagonia and to use a small, shallow, connected lake as a principal spawning area (Fuster de Plaza & Plaza, 1955; Buria et al., 2007). Massive deaths of *P. trucha* have been observed during the breeding period (summer) in an inlet river (Collón Curá River) to Piedra del Águila reservoir (40°25′S, 70°39′W) in the upper Negro basin. Taking into account the 1.5–2.5°C increment (1961–2015) in the local MSAT along with the consequences of damming (i.e., lack of shelter in the littoral zone of the reservoir and the elimination of inlet streams used by *P. trucha* as spawning sites), these massive deaths related to exceptionally high breeding concentration, high temperature, and oxygen depletion, are likely to be more frequent in the near future.

Non-native species introductions and invasions

Southern South America is one of the six global hot spots of freshwater fish invasions (Leprieur et al., 2008) showing significant homogenization of its fish fauna (Villéger et al., 2011). In particular, Patagonia possesses a small native freshwater fish fauna and proportionally one of the highest rates of fish species introduced. Several species of salmonids were introduced into Patagonia during the XX century focussing on increasing diversity and sport fishery opportunities: *Salvelinus fontinalis* (Mitchill, 1814), *S. namaycush* (Walbaum, 1792), *Salmo salar* Linnaeus, 1758, *S. trutta* (Linnaeus, 1758), *Oncorhynchus masou* (Brevoort, 1856), *O. mykiss, O. kisutch* (Walbaum, 1792), and *O. tshawytscha* (Walbaum, 1792) (Pascual et al., 2007; Macchi et al., 2008). Decades later, most of these exotic species have expanded their range from the release sites by invading and colonizing new basins, even through transoceanic routes, as in the case of *O. tshawytscha*, which has reached Atlantic rivers from the Pacific Ocean (Becker et al., 2007). In addition, *O. mykiss* and *O. tshawytscha* showed spontaneous establishment of anadromous populations in the southernmost Patagonian basins (Pascual et al., 2001; Ciancio et al., 2005; Soto et al., 2007).

All in all, these introductions have resulted in the partial displacement of several native Patagonian species from historical territories due to competition and predation (Lattuca et al., 2008; Macchi et al., 1999). Although salmonids have been found strongly present both in lakes and streams, the Zoogeographic Integrity Coefficient (Elvira, 1995), which refers to the number of native species per total number of species, revealed that Patagonian rivers showed lower integrity than lakes (Aigo et al., 2008).

Salmonids are regarded as highly vulnerable to increasing temperatures (Keleher & Rahel, 1996; Carveth et al., 2006) through direct mortality or physiological and ecological impairment, as compared to other species adapted to warmer water temperatures (Bear et al., 2007). Their abundance showed negative relationships with climate changes (Bryant, 2009), particularly with increasing temperature in the northern hemisphere (Nakano et al., 1996; Boylan & Adams, 2006; Reist et al., 2006a, b; Graham & Harrod, 2009). The decrease in littoral relative abundances of exotic salmonid fishes in Andean Patagonian lakes resembles this situation (Aigo et al., 2008; 2014). Just as proposed by Ficke et al. (2007), the increase of surface water temperature and the different preferred temperatures of *O. mykiss* (lower) and the native *P. trucha* (higher) may explain the decrease in the relative abundance of salmonids in littoral captures in Patagonian lakes over recent years (Aigo et al., 2008, 2014). In lake Blanca, the records of Quirós (1991) showed near 50% of salmonids and 50% of *P. trucha* in 1984–1987 samplings. After 20 years, capture of *P. trucha* was the highest recorded in all Patagonian lakes and reservoirs, and salmonids were nearly undetectable (Ortubay et al., 2006). In the same way, the results of Alonso (2003) and Vigliano & Alonso (2007) signaled a significant reduction on the abundance of wild salmonid populations in three reservoirs in the Limay river (upper Negro basin). Their decrease in the littoral of lakes and reservoirs could be the consequence of a pioneer effect and its subsequent stabilization (Macchi et al., 2007), and also of the exclusion of salmonids from the littoral zone observed by Jansen & Hesslein (2004) in relation to an increase in water temperature at lake shores.

Contemporary evolution (Stockwell et al., 2003) involving salmonid fishes must be considered as well, as it has been already observed (Primmer, 2011; Fraser et al., 2012). In rainbow trout, thermal tolerance can be selected for (Myrick & Cech, 2000; Molony, 2001; Ineno et al., 2005; Perry et al., 2005) which has been associated with expression of certain heat shock proteins (HSPs, Heredia-Middleton et al., 2008; Feldhaus et al., 2010; Narum & Campbell, 2010), and quantitative traits loci (QTL; Jackson et al., 1998). In addition, single nucleotide polymorphisms (SNPs) have been associated with temperature preference (Narum et al., 2010). In this way, the ability for rapid local adaptation seems to be the basis of the upstream range expansion in the thermal Valcheta stream in Northern Patagonia since its introduction at the beginning of the XX century (Kacoliris et al., 2015). Preliminary results of Crichigno (Pers. Obs.) suggest heritability of the preference for higher temperatures in rainbow trout juveniles of this population.

Temperature is also affecting the reproduction of farmed rainbow trout in the Alicurá Reservoir in northern Patagonia through lack of ovulation, atresia, and a partial or total absence of spawning during the breeding season (Pankhurst et al., 1996; Pankhurst & King, 2010; Báez et al., 2011). Lakes and artificial reservoirs in northern Patagonia are suitable for aquaculture given their high water quality of glacial origin and, since 1969, salmonid aquaculture of rainbow trout began to rise (Wicki & Luchini, 2002; Macchi et al., 2008). Rainbow trout cage culture is primarily developed in the Alicurá Reservoir, in the upper Negro basin, with its fish production reaching 1,800 ton year^{-1} in 2009 (Zeller et al., 2009). Although this activity is still incipient, escaped fish in Alicurá Reservoir have been shown to affect not only the reservoir fish population but also those of headwater lakes and rivers (Cussac et al., 2014). Although Patagonian lakes and reservoirs have well-oxygenated waters (Pérez et al., 2002), the decrease in dissolved oxygen and increase in biological oxygen demand and nutrient concentration (Phosphorus, organic and inorganic Nitrogen, and total Carbon), generally found in the water column around fish farms (Wu, 1995) and enhanced by higher temperature, might be the reason for the anomalous composition of current gillnet littoral captures in the Alicurá Reservoir (Cussac et al., 2014), as well as the spatial segregation of the native *P. trucha* towards deep waters (Nabaes Jodar et al., 2017).

More recently, the common carp *Cyprinus carpio* Linnaeus, 1758, formerly introduced in the lower Colorado river in the mid-1980s, has invaded other rivers to the south (Negro river), displacing the native perca from its northern distributional range (Maiztegui et al., 2016). Although *P. trucha* has shown strong adaptability through geological history in relation to climatic changes (Ruzzante et al. 2008), the probable greater tolerance of *C. carpio* to benthic low oxygen availability has favored its invasiveness, adding new locations to its range in the Andean region (Crichigno et al., 2016a). Annual maximum air temperature and concentration of chlorophyll-a were the main variables that explained *C. carpio* presence along North and South America (Zambrano et al., 2006) and temperature and chlorophyll-a were important variables for predicting the presence of *C. carpio* in Argentina. The lakes and reservoirs with *C. carpio* have MAAT higher than 10°C. Present capture data for the Negro River show water temperatures below preference and optimum growth temperatures, but climate warming could help future advances in the area from north to south, along Limay river in the upper Negro basin (Crichigno et al., 2016a).

The composition of native fish assemblages is related to the presence and type of non-native species (Giacomini et al., 2011). Translocations also contribute to extirpations of native populations, as is the case with the native *O. hatcheri,* present in the Andean Cuyan and Patagonian Provinces (Ringuelet et al., 1967; Menni, 2004; López et al., 2008). Stocking practices of *Odontesthes bonariensis* (Valenciennes, 1835) in the original *O. hatcheri* distribution area, and their ability to hybridize (Crichigno et al., 2016b) led to the establishment of a hybrid zone across northern Patagonia (Crichigno et al., 2013, 2016b; Conte-Grand et al., 2015; Rueda et al., 2016). Although *O. bonariensis* has replaced *O. hatcheri* populations almost completely at their northern distributional limit (Aigo et al., 2008), it has not overlapped the entire geographic range of *O. hatcheri* due to its different degree of temperature-dependent sex determination (TSD, Strüssmann et al., 1997). TSD could thus represent a differential constraint for both species, climate dependent, as reported values of TSD show high agreement between summer water temperatures and the distribution area of each species (Cussac et al., 2009; Conte-Grand et al., 2015).

Concluding remarks

Patagonian freshwater fishes have historically been exposed to environmental changes, leading to several adaptations observed in present species. The consequences of climate change for Patagonian fish populations will vary with the degree of local environmental shifts as well as the ecological physiology and evolutionary history of the species considered. Previously predicted extirpations, extinctions, and translocations can already be observed. Further human actions such as species transport, exotic species introductions, and fish stocking seem to lay a more complex future. As fish populations are important for the generation of aquatic ecosystem services (Holmlund & Hammer, 1999), fish biodiversity becomes crucial to maintain the services provided (Harrison et al., 2014). More research is needed on Patagonian native fishes to successfully contribute to their conservation.

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