

Fishes of southern South America: a story driven by temperature

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Abstract The latitudinal extension of southern South America imposes a thermal gradient that affects the structure of marine and freshwater fish assemblages and the biology of the species through direct exposure to the temperature gradients or by means of a web of historical and ecological relationships. We have reviewed biological and ecological data of marine and freshwater fishes from the southern Neotropics, including Patagonia, and report several examples of dependence on temperature, from glacial times to today's climate change. We were able to identify historic and present effects on the diversity of fish assemblages, isolation, southern limits for the distribution of species, and

morphological variation among populations. There is a wide range of characteristics that exemplify an adaptation to low temperatures, including biochemical peculiarities, physiological adjustments, and alternative life history patterns, and these appear in both freshwater and marine, and native and exotic fishes. The consequences of stable temperature regimes in both the ocean and thermal streams deserve special mention as these shape specialists under conditions of low selective pressure. At present, habitat use and interactions among species are being subject to changes as consequences of water temperature, and some of these are already evident in the northern and southern hemispheres.

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Fishes of southern South America: an overview

Our knowledge of marine and freshwater fishes of southern South America has increased significantly in recent years (Menni et al. 1984; López et al. 2002; Baigún and Ferriz 2003; Menni 2004; López and Miquelarena 2005; Hubert and Renno 2006; Pascual et al. 2007; Aigo et al. 2008). A complete comprehension of their present status involves an understanding of tectonic plates, geological history (Cussac et al. 2004; Ruzzante et al. 2006), physiological constraints

(Gómez 1996; Fernández et al. 2000; Johnston et al. 2003; Fernández et al. 2005), ecological interactions (Milano et al. 2002, 2006), alien species (Macchi et al. 1999, 2007), human impacts (Pascual et al. 2002; Ortubay et al. 2006), phylogeography, and molecular phylogeny (Johnston et al. 2003; Near et al. 2004; Zattara and Premoli 2005; Ruzzante et al. 2006).

Argentina has 47 freshwater native fish families, 184 genera (four endemic, one in the Parano-Platensean Province), and 461 species (94 endemic) (Fig. 1). When political borders are ignored, more than 90% of the genera (170) are shared with Brazil, nearly 75% (139) with Paraguay, 70% (133) with Bolivia, and 60% (114) with Uruguay. However, when diversity is compared between Chile and Argentina, we can see the large effect of isolation due to the Andean orogeny northward of Chiloé Island (Dyer 2000) and the effect of homogenization produced southward of Chiloé (Cussac et al. 2004; Ruzzante et al. 2006; Pascual et al. 2007) due to extirpation, drainage change, and basin capture phenomena produced by glacial activity (Gagnon and Angers 2006).

The most dominant fishes among the many marine species present in the continental shelf of the Southern Ocean belong to sub-order Notothenioidei. These fishes have undergone an impressive adaptive radiation in Antarctic waters and currently comprise eight families and 129 species that inhabit Antarctic and sub-Antarctic waters (Eastman 1993, 2005). Outside of Antarctic waters, there are currently 28 species living in Patagonian, New Zealand, and Australian waters, with some species reaching as far north as 39°S (Buenos Aires Province) along the Atlantic Argentinean coast and 33°S (Valparaíso) along the Pacific Coast (Gosztonyi 1974; Pequeño 1989; Eastman 1993). The ancestral forms of the notothenioids are generally considered to have been a small temperate bottom-living species that lacked a swim bladder (Eastman 1993).

It is of course much to narrow a view to attempt to identify a common cause for this scenario—the adaptive radiation of these fishes. However, temperature has been recognized as one of the main cues to gaining an understanding of fish biogeography in southern South America (Ringuelet 1975; Quirós 1991; Menni and Gómez 1995; Gómez 1996). Life in water exists in a range of -2 to 50°C , and no fish can avoid the effect of temperature on its metabolic rate

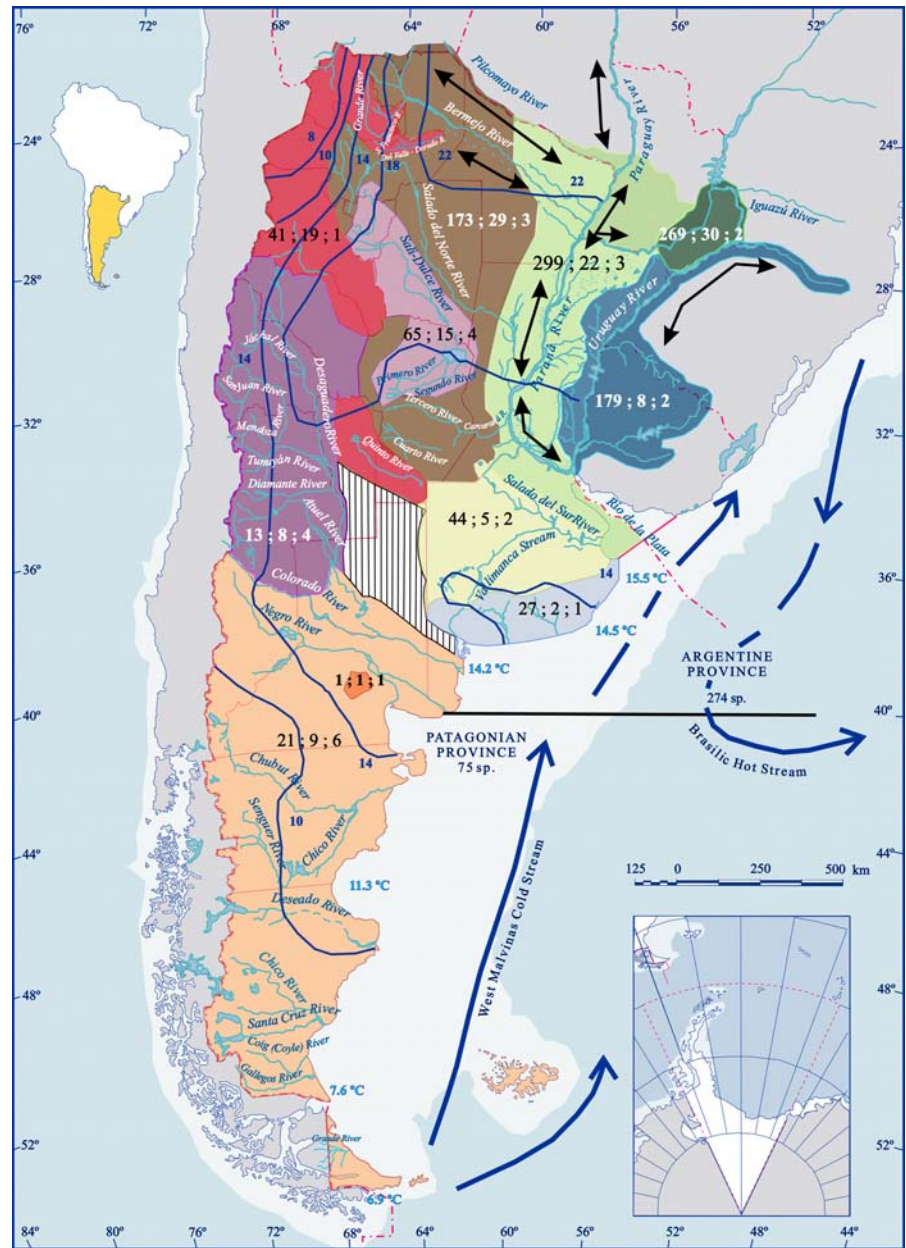
(Hill et al. 2006). Higher temperature enhances algal blooms, diminishes the concentration of oxygen in water, and increases the rate of organic matter degradation, thereby decreasing organisms' oxygen capacity and increasing oxygen demands (Wetzel 1983; Portner and Knust 2007). Integrating the growing amount of knowledge on South American fishes around such a causal factor with such a clear biological meaning could be useful. Consequently, the aim of this article is to review the influence of temperature in shaping fish communities along the climatic gradient in southern Argentina. The structure of this review is organized around six ecological and evolutionary processes: (1) physiological adaptation to extreme conditions, (2) decreasing freshwater fish diversity along a southward gradient, (3) life history variations throughout the gradient, (4) influence of temporal changes in climate on geological scales, (5) distribution, breeding, and temperature, and (6) global changes and climate warming.

Physiological adaptation to extreme conditions

Mean annual air temperature (www.smn.gov.ar) and surface seawater mean annual temperature (www.hidro.gov.ar) decrease by more than 13°C from latitude 25 to 55°S (Fig. 1), without any major differences arising between them. In lotic freshwater environments, the relationship between air temperature and water temperature is much more complex. For example, due to the drainage of freshwater from lower to higher latitudes, water temperature is $2\text{--}4^{\circ}\text{C}$ warmer than air temperature in the Paraná-Paraguay basin (Menni and Gómez 1995), while Andean streams can be cooler than air due to their glacial origin. In lentic water bodies, when only local climate factors determine water temperature, positive linear relationships can be established between bottom water and mean annual air temperature (Quirós and Drago 1985; Quirós 1991).

Temperature affects the viability of populations at high latitudes or altitudes either through constraints to body size imposed by winter starvation conditions (Shuter and Post 1990) or directly by lethality (Fry 1971). The mismatch between the demand for oxygen and the capacity of the oxygen system to supply tissues is the primary mechanism that restricts an animal's tolerance to thermal extremes

Fig. 1 Ichthyological ecoregions of Argentina (López et al. 2002). The groups of three black or white numbers are, respectively, autochthonous, endemic, and exotic fishes. Blue numbers and solid lines are isotherms of annual mean air temperatures (www.smn.gov.ar). Marine references in blue numbers are annual mean surface water temperatures (www.hidro.gov.ar). Data on species numbers of marine ecoregions were kindly provided by Juan Martín Díaz de Astarloa. Parano-platensean Province: ■, Misionerean ecoregion; ■, lower Uruguay River ecoregion; ■, subtropical Potamic Axis ecoregion; ■, eastern Parano-platensean ecoregion; ■, central Endorreic ecoregion; ■, western Parano-platensean ecoregion; ■, Salado del Sur-Vallimanca ecoregion; ■, Bonaerensean Atlantic ecoregion. Subandean-Cuyan Province: ■, subAndean-Cuyan ecoregion. Patagonian Province: ■, Patagonian ecoregion; ■, Somuncurá ecoregion; ■, area without records; ↔, migratory displacement; —, isotherms



(Portner and Knust 2007). The metabolic rate of ectothermic organisms depends on temperature and body size; this is particularly true for aquatic organisms since the change rate in the environmental temperatures experienced by them is buffered by the large thermal mass of water (Clarke and Johnston 1999). Temperature gradients produced by latitudinal or altitudinal changes create advantageous scenarios for geographic variations in metabolic rate (Conover and Schultz 1995).

Ringuélet (1975) proposed that the impoverishment of fish fauna in the south of the Brazilic subregion was due to low temperature and high salinity. Lethal levels of low temperature correlate with the southern limit of the geographical distribution of several fish species (Gómez 1996). Moreover, the southward decrease of diversity correlates with water temperature (Menni and Gómez 1995). In restricted areas, the number of species correlates with salinity (Gómez and Ferriz 1998). The cichlids,

which are very common in southern South America, tolerate high salinity. However, given the low salinity values of the Neotropical freshwaters where they live, their high tolerance to salinity ($>20 \text{ g l}^{-1}$) is a 'relic' character of low or no adaptive value (Gómez and González Naya 2007). Similarly, in Lake Buenos Aires ($46^{\circ}32' \text{ S}$, Fig. 1), the 'bagre' *Hatcheria macraei* shows a death temperature (31°C) similar to that of a warm water fish, but a low equilibrium loss temperature (22°C), suggesting that the high death temperature of *H. macraei* is a 'physiologic relic' related to previous warm water adaptation. A low equilibrium loss temperature can be seen as a product of the present thermal condition (Gómez 1990).

Early studies on Arctic and Antarctic fishes found resting metabolic rates that were greater than those predicted by extrapolation of the resting metabolic rate of temperate or tropical fish to polar temperatures. This was the origin of the concept of metabolic cold adaptation. However, there is no convincing evidence for such an elevated metabolic rate in polar fish (Steffensen 2002). Polar fish need long periods of time to acclimate to experimental apparatus and also to normalize oxygen consumption after post-prandial increases in oxygen consumption (Clarke and Johnston 1999). Similar long post-prandial times and not so high oxygen consumption values have been found in sub-Antarctic notothenioids (F. Vanella, personal communication).

Johnston et al. (2003) have shown that the radiation of Antarctic and sub-Antarctic notothenioids was associated with a progressive decrease in the body size-specific maximum number of fast fibers in the myotomal muscles of the more derived species, but not with a reduction in body size. Thus, if fiber size—but not body size—is reduced, there should be an increase in the size of the muscle fibers. In actual fact, this group does have unusually large muscle fibers, with diameters that can reach $100 \mu\text{m}$ in slow muscle and $500 \mu\text{m}$ in fast muscle (Smialowska and Kilarsky 1981; Dunn et al. 1989; Battram and Johnston 1991; Fernández et al. 2000; Johnston et al. 2003; Fernández et al. 2005). This characteristic imposes obvious constraints in terms of oxygen diffusion and important metabolites, such as ATP, restricting muscle fiber size at least in aerobic fibers (slow twitch muscle fibers). Even if anaerobic muscle fibers (fast twitch muscle fibers) are powered by phosphagen hydrolysis and glycogenolysis—and therefore do not depend

directly on diffusive fluxes—recovery is an aerobic process, and the rate of recovery will determine how quickly a new cycle of contraction and relaxation can occur. Large muscle fibers could have been favored in the evolution of notothenioids, since the decrease in the fiber surface to volume ratio will decrease the cost of maintaining ion homeostasis in these fibers. This idea, called the 'optimal fiber size hypothesis', was proposed by Johnston et al. (2003, 2004) for notothenioids and Arctic char evolution and by Kinsey et al. (2005) for blue crabs.

The mitochondrial volume density of mammalian skeletal muscles is normally below 10%, but in fish this value can be more than 50% (Guderley 2004). Fish living in cold temperatures have higher mitochondrial contents in their muscles than those living in warmer temperatures, with values reaching 60% in some Antarctic species (Johnston et al. 1988). Oxidative muscle fibers from species with similar life history traits show a significant negative relationship between mitochondrial volume density and habitat temperature; this is especially evident in demersal and moderately active species (Johnston et al. 1998). Thus, the primary mechanism for enhancing the aerobic capacity of muscle in cold-water fish is to increase the volume density of mitochondrial clusters (Johnston et al. 1998).

The decrease in the South American freshwater fish diversity

A decrease in fish diversity can be observed both from east to west and from north to south. Westward, fish diversity decreases from 79 to 41 species due to the absence of the Gymnotidae, Hemiodidae, Crenuchidae, Trichomycteridae, Lebiasinidae, and Aspredinidae families. In particular, the endorheic Salí-Dulce basin contains only 20% of the Parano-Platensean species (e.g., Clupeiformes and Belontiiformes) and none of the big pimelodids (e.g., the 'surubíes' of the genus *Pseudoplatystoma*). Southward, the River de la Plata contains only 30% of the species of the Parano-Platensean Province. The Salado basin (Buenos Aires), being the southernmost limit of curimatids and loricarids, has only 10% of the species of the Parano-Platensean Province (Ringuelet 1955; López and Miquelarena 2005). This basin is a mixture of lentic and lotic water bodies and is

characterized by a high variability and instability. Brazilian euryoic species of the families Clupeidae, Characidae, Pimelodidae, Callichthyidae, Anablepidae, Cichlidae, and Synbranchidae remain between 37°S and 39°S (Menni 2004). The great sea shore extension and the associated lentic and lotic water bodies allow for the presence of several euryhaline species. At a specific level, endemism is high in the Parano-Platensean Province, along the Paraná and de la Plata rivers. The highest number of endemic species has been described in the Iguazú basin, Alto Paraná Province (López et al. 2005).

Many different types of water bodies are present in Parano-Platense Province (Fig. 1), including large flood plain rivers (Pilcomayo and Bermejo, both of Andean origin, Paraguay, Paraná, and Uruguay), reservoirs, Pampasic and altiplanic ‘lagunas’, wetlands, deltas, endorheic basins, salt lakes, salt marshes, and estuaries (López and Miquelarena 2005). This province contains most of the species, genera, and families of Argentinean fauna, with a great variety of morphologies and life history traits and high endemism. The ‘Pampa húmeda’ is an extensive loess plain under an east–west climate gradient of decreasing rainfall westward of La Plata River and the Atlantic Ocean (about 63°W, from 33°30′ to 38°30′ S). The most common lentic water bodies in this region are ‘lagunas’. These third-order lakes maintain high salinity levels because of their marine origin or the increased east–west aridity gradient. They lack thermal stratification and show wide ranges of physical and chemical variables (Ringuelet 1962; Ringuelet et al. 1967; Gómez et al. 2007). The Paraguay, Paraná, and Uruguay rivers are faunal corridors that allow the southward dispersion of tropical and subtropical species (López and Miquelarena 2005), with triangle-like distribution areas (e.g., Anostomidae). Some places, such as headwaters, are characterized by the absence of some groups (e.g., Myliobatiformes, Clupeiformes, and Pleuronectiformes) that are usually present in the big rivers. Conversely, there are genera distributed only along the Paraguay–Paraná, Uruguay, and de la Plata rivers, such as the ‘viejas’ of the genus *Hypoptopoma* (Loricariidae) and the ‘mojarra’ of the genus *Hyphessobrycon* (Characidae).

We should be aware of the fact that the southward tendency of diversity decrease changes in Patagonia due to the presence of austral species of Galaxiidae and Percichthyidae and the presence of several species of

salmonids (Pascual et al. 2007). However, the progressive southward disappearance of the ‘otunos’ *Diplomystes cuyanus*, *D. viedmensis*, and *D. mesembrianus*, the ‘bagre’ *Trichomycterus areolatus*, *H. macraei*, the Patagonian ‘pejerrey’ *Odontesthes hatcheri* and, finally, the ‘perca’ *Percichthys trucha* is noticeable. The lowest diversity occurs on Tierra del Fuego Island, the southernmost (54°S) area of the world with freshwater fish fauna, where only salmonids (Becker et al. 2007; Pascual and Ciancio 2007) and four native species of the Galaxiidae family are found (Cussac et al. 2004; Liotta 2006; Milano et al. 2006).

Life history variations throughout the gradient

Temperature is not a significant cue for the migration of tropical freshwater fishes and seems to be related with migrations along La Plata basin only indirectly, mainly through food availability and gonadal cycles (see Menni 2004 for a review). Approximately ten Paranensean fishes are migratory, with movements of more than 500 km between 24 and 34°S (Fig. 1). The main species, the ‘sábalo’ *Prochilodus lineatus*, comprise 50% of the fish biomass of the basin (Sverlij et al. 1993), and they have retained their original seasonal pattern despite damming and changes in water discharge (Quirós and Vidal 2000).

A clear relationship between landlocked and diadromous life histories and latitude can be established for salmonids and galaxiids along a southward vector. The causes that favored these alternative life patterns seem to rely on the different thermal inertia of freshwater bodies and oceans. Consequently, low temperature has differential effects on freshwater and marine aquatic primary production and the opportunities for planktonic feeding (Gross et al. 1988), thereby favoring landlocked life at low latitudes and diadromy southward. The ability of the South American species of Galaxiidae to display diadromous or landlocked life history patterns along large latitudinal and altitudinal ranges (McDowall 1971; Cussac et al. 2004; Barriga et al. 2007; Boy et al. 2007; Lattuca et al. 2007) deserves attention. McDowall (1980) proposed that the adaptive value of anadromy was the escape from the cold Pleistocene winters. We should not expect that winter temperatures imply the same constraint for lacustrine (landlocked) or marine

(diadromous) larvae. Unfortunately, the landlocked or diadromous character of galaxiids' populations has been clearly stated in only a few cases (Cussac et al. 2004; Boy et al. 2007; Lattuca et al. 2008). For example, McDowall (2003) reports only six lacustrine populations of the small 'puyen' *Galaxias maculatus* in South America and six in the Malvinas Islands. As McDowall (2001) pointed out, diadromy favors dispersion on the basis of straying and a lack of homing behavior, and landlocking favors speciation through local adaptation. However, landlocked *G. maculatus* has retained the ability to display several alternative life history patterns in relation to migration and the choice of reproduction sites (Chapman et al. 2006; Barriga et al. 2007; Boy et al. 2007). The salmonid species introduced into Patagonia (Pascual and Ciancio 2007) seem to follow the same pattern, with a 'spontaneous' establishment of anadromous populations of *O. mykiss* and chinook salmon *Oncorhynchus tshawytscha* (Pascual et al. 2001; Ciancio et al. 2005; Soto et al. 2007; D. Fernández et al., personal communication).

Influence of temporal changes in climate on geological scales

Isolation, empty niches, and thermal stability

Antarctica was affected by tectonic and oceanographic events that resulted in it becoming gradually isolated and colder and losing inshore shallow habitats due to the expansion of the ice sheet (Eastman 1993; Clarke and Johnston 1996). These events could have caused local extinctions of many of the Eocene components of the fish fauna, thereby reducing its diversity and leaving empty niches available to be occupied by groups that diversified in situ (notothenioids) or immigrated into this modified ecosystem (liparids and zoarcids) (Eastman 2005). There were, therefore, two main factors associated to diversification in Antarctic waters: fairly constant cold temperature and empty niches.

The evolution of antifreeze glycoproteins (17 million years ago according to Near 2004) is the most commonly accepted explanation for the success of the radiation of the Antarctic notothenioids, as these glycoproteins would have enabled the notothenioids to adjust to the climatic cooling that followed

the opening of the Drake passage and the establishment of the Antarctic Polar Front some 20–25 million years ago (Cheng and DeVries 1991; Eastman 1993; Clarke and Johnston 1996). In agreement with this hypothesis are the findings that the most basal notothenioid families (Bovichtidae, Pseudaphritidae and Eleginopidae) are represented by non-Antarctic species (except for a single Antarctic bovichtid) with the plesiomorphic condition of lacking antifreeze glycoproteins (Eastman and Eakin 2000). Therefore, it is quite well established that a constantly cold environment was a characteristic predating the adaptive radiation of the notothenioids.

Similarly, lake populations in southwestern Argentina were established after the retreat of Pleistocene glaciers, probably after their last advance between 15,000 and 14,500 years B.P. Post-glacial lakes are relatively young environments where available ecological niches are likely to be present. Such lakes tend to have few species, partly because there has been little time or opportunity for colonization and partly because there has been even less time for in situ speciation to have occurred. Consequently, the organisms that do colonize these lakes are likely to encounter under- or unexploited resources and few competitors (see Ruzzante et al. 1998 for a review).

The 'perca' is widely distributed all along the Southern Andean and Patagonian regions of southern South America (López Arbarello 2004). The nominal species show a conspicuous morphological variation of the oropharyngeal apparatus—large and small mouths, and long and short gill rakes (Ruzzante et al. 1998)—that are related to resource use (Logan 2000). The variation patterns are different in different lakes (Ruzzante et al. 2003). Genetic studies have not yet found evidence of either specific differences or reproductive isolation between morphs (Ruzzante et al. 2006), and some findings suggest that environmental cues plays a major role in determining oropharyngeal development. This variation can be identified during the juvenile period (Ruzzante et al. 2003) and can also be observed among sibling larvae breeding in captivity, seemingly related with yolk amount (S. Crichigno, personal communication). Populations of 'perca' upstream and downstream of a hydroelectric dam can also show oropharyngeal differences, and these differences were identified within only a few years of the dam being built (Cussac et al. 1998). Similarly, 'perca' stocked in a

fishless lake were successively named as different species throughout a 40-year period due to changes in their mouth shape, during which time drastic changes occurred in the lake's trophic web (Ortubay et al. 2006).

The case of the big 'puyen' *Galaxias platei* is different. This species is mostly restricted to montane lakes and streams of Patagonia, and it shows an extremely high endurance to low temperature and low oxygen availability (Milano 2003; Cussac et al. 2004) as well as major between-lakes variations in the morphology of the caudal peduncle. This variation can be correlated with the predation risk observed within each lake (Milano et al. 2002, 2006). Within the tolerance range, the capability to endure cold winters depends on being able to endure starvation (Shutter and Post 1990). In this context, *G. platei* seems to exploit the deep bottom of the lakes with scarce trophic competition or predation by other Patagonian fishes (Milano 2003; Cussac et al. 2004).

In accordance with their physiological and ecological distinctiveness, it would seem that glaciations affected *P. trucha* and *G. platei* in two different ways. 'Perca' distribution encompasses all Patagonian areas around the last glacial maximum (LGM) and *G. platei* is found deep inside this area. The colder water inhabitant, *G. platei*, underwent a strong bottleneck during the LGM. In contrast, the more warm-adapted and widely distributed *P. trucha* showed continuous population growth through the last two glacial cycles but went through an important bottleneck approximately 180 ka, which may have eliminated the eastern populations (Ruzzante et al. 2008).

Thermal stability, morphological reduction, and disaptation

Climate cooling has been a determinant factor for freshwater fish distribution in temperate areas. Following the Pleistocene glaciations, the Brazilian fish fauna of Patagonia was restricted to the thermal Valcheta Stream basin, in the Somuncurá Plateau (Menni and Gómez 1995). The Valcheta basin consists of two branches, both of which show a strong temperature gradient from the headwaters (20–26°C) to the downstream waters (17–18°C). Five species currently occur in the basin: the 'mojarra' *Gymnocharacinus bergii* (Characidae), which is one of the southernmost characids in the world and one of

the two Characiformes present in Patagonia (Ringuelet 1975; Campos et al. 1996; Körber and Ortubay 2004), the southernmost populations of two mosquito fish, *Cnesterodon decemmaculatus* (Poeciliidae) and *Jenynsia multidentata* (Anablepidae), and two exotic salmonids, the rainbow trout *Oncorhynchus mykiss* and the brook trout *Salvelinus fontinalis* (Ortubay et al. 1997). *Gymnocharacinus bergii* is a warm stenothermal fish that is on the endangered list (Ortubay et al. 1997; Ortubay and Cussac 2000) and, interestingly, none of the remaining four species occur in the headwaters of the stream (Miquelarena and Arámburu 1983). Although the high temperature might explain the absence of introduced salmonids, warm water conditions cannot account for the absence of the extremely eurytopic *C. decemmaculatus* and *J. multidentata* (Menni and Gómez 1995; Menni et al. 1996; Ortubay et al. 1997). Moreover, *J. multidentata* is known to coexist with several characin species in other small thermal springs (Menni et al. 1998). As an example of how behavioural traits and functional abilities interact with the thermal landscape, laboratory observations have revealed that the exclusion of *J. multidentata* from the headwaters of the Valcheta Stream seems to be due to the aggressive behavior of *G. bergii*, which is elicited to a large extent by *J. multidentata*'s own agonistic behavior (Ortubay et al. 2002). The absence of *C. decemmaculatus* from the Valcheta headwaters could be related with their poor swimming capacity that places them at a disadvantage in the high-speed water current of these waters (Trenti et al. 1999).

Several adult structures have been reduced or modified in *G. bergii*, setting it apart from other characids as a monotypic subfamily (Miquelarena 1982). The reduction and loss of scales in adults is almost complete (Miquelarena and Arámburu 1983; Miquelarena et al. 2005) and the fright reaction has been modified (Lozada et al. 2000; Cordi et al. 2005). Stability and predictability of the environment favor specialization (Balon 1990), and low competition and low predation could diminish the negative selection pressure for any degenerative alleles, allowing important regressions in the structure and bodily functions (Peters and Peters 1983; Peters 1990; Peters et al. 1993). For example, studies of cave environments reveal the occurrence of morphological regression in species such as the cave-dwelling form of *Astyanax mexicanus* and the blind

cave catfishes *Trogloglanis pattersoni*, *Satan eurystomus*, and *Pimelodella kronei* (Langecker and Longley 1993; Trajano 1997). Examples of major regression phenomena in these Ostariophysi, in addition to the lack of pigmentation of cave dwelling *Rhamdia quelen* (Romero et al. 2002), suggest that regressive mutations could also have developed in particularly permissive habitats, such as the thermal Valcheta Stream (Miquelarena et al. 2005).

Notothenioids have unusual characteristics, including some events of disaptations (loss of evolutionary function) and adaptive recoveries (Montgomery and Clements 2000), that are associated to the successful adaptive radiation this group has undergone and to the special thermal conditions they experienced. The presence of these characteristics reinforces the theory of the radiation taking place inside Antarctic waters. For example, the Antarctic *Trematomus bernachii* and the sub-Antarctic (but with Antarctic origin) black cod *Notothenia augustata* lack the heat shock response, a set of genes that is activated in response to high temperature stress (Hofmann et al. 2000). Another example of disaptation—and one that was only possible due to the unusually cold and constant conditions of the Southern Ocean—is found in members of the Channichthyidae family, which has suffered the loss of the expression of significant quantities of hemoglobin and myoglobin (Cocca et al. 1995; Moylan and Sidell 2000; di Prisco et al. 2002; Cheng and Detrich 2007). All 16 species have lost most of the adult $\alpha\beta$ -globin locus, retaining only a small fragment of the α -globin gene, with the only exception being *Neopagetopsis ionah*, which possesses a disrupted $\alpha\beta$ -globin gene complex that is non-functional (Near et al. 2006). Six of the icefish species fail to express myoglobin (Moylan and Sidell 2000). This loss of the respiratory hemoproteins was initially suggested to be a selectively neutral or even advantageous mutation if it resulted only in a reduction of the energy cost for blood circulation. Nevertheless, these losses have been determined to lead to a higher energetic cost for blood circulation and reduced cardiac performance (Sidell and O'Brien 2006). Moreover, the loss of respiratory pigments is associated with a set of compensatory adaptations in the heart and peripheral circulatory system (Tota et al. 1997), including a relatively large ventricular muscle mass (Johnston 1993) and a high blood volume (Acierno et al. 1995)

coupled to a high-output cardiac pump operating at low frequencies and pressures (Tota et al. 1997). The development of compensatory physiological and circulatory adaptations in icefishes reinforces the hypothesis that the loss was probably maladaptive (di Prisco et al. 2002). Egginton et al. (2002) showed that structural adaptations in the circulatory system potentially enable a similar degree of tissue oxygenation over a 20°C range of environmental temperature in the nototheniids that would be overwhelming in the channichthyids due to the lack of respiratory pigments.

The ability to maximize performance in one environment was likely only be achieved at the cost of diminishing performance over a wider range of environments—i.e., a trade-off between generalist and specialist phenotypes (Wilson et al. 2002). Therefore, ectotherms from highly stable thermal environments, such as the Antarctic, should have a specialist phenotype that allow them to maximize performance at one temperature, while ectotherms from more variable thermal environments should possess more generalist phenotypes that maximize performance breadth. However, when the burst swimming performance in three species of Antarctic notothenioids was analyzed, Wilson et al. (2001) found a thermal performance breadth of at least 11°C, which is similar to those shown by temperate fish species. In contrast, when these researchers analyzed sustained swimming in one of these Antarctic species, the performance breadth was only 5°C (Wilson et al. 2002). It is likely that the predicted trade-off only occurs for some key physiological process that is probably related to oxidative metabolism, such as sustained swimming, which relies on an adequate supply of O₂ to the tissues. In contrast, burst swimming, which only involves oxidative steps in the recovery phase, is not affected by the trade-off. A more sophisticated analysis, however, showed a smaller thermal performance breadth in burst swimming for a sub-Antarctic notothenioid (Fernández et al. 2002).

Distribution, breeding, and temperature

The Bonaerensean 'pejerrey' *Odontesthes bonariensis* is a dominant species in the limnetic zone of the 'lagunas'. This ubiquitous species is highly valued as

food and as a sport fish and has been introduced in natural and man-made water bodies in Argentina, Chile, Japan, and Italy since the beginning of the twentieth century (López et al. 1991). Gómez et al. (2007) defined the ranges and optimum values for water temperature and 16 water physical and chemical variables in relation to the geographical distribution of the species. The ‘pejerrey’ is a limnetic swimmer (Freyre and Protogino 1993), with a swimming speed estimated as three standard length seg^{-1} and a high metabolic rate (Gómez and Ferriz 2001). Similarly to the Patagonian ‘pejerrey’ *O. hatcheri* (Cussac et al. 1992; Cervellini et al. 1993), it shows spatial and trophic ontogenetic niche shifts (S. Gómez and R. Ferriz, personal communication).

It is appealing to analyze the relationships between the Bonaerense and the Patagonian ‘pejerrey’. Both species have a remarkable tolerance to high salinity but not to sea water (Tsuzuki et al. 2000; Gómez and Ferriz 2001). Dyer (2000) and Menni (2004) agree in their view that both species were isolated by marine incursions several millions of years ago (Hubert and Renno 2006). At the present time, the distribution of these species overlaps due to the stocking of *O. bonariensis* in Patagonian and Andean lakes and reservoirs in the north of the distribution range of *O. hatcheri* (Liotta 2006). Both species hybridize in captivity (Strüssmann et al. 1997a) and, probably, also in the wild.

Could *O. bonariensis* overlap all of the distribution range of *O. hatcheri*? It must be noted that these species show a different degree of temperature-dependent sex determination (TSD; Strüssmann et al. 1997b), which supposedly confers an adaptive advantage to some species in a trade-off between intraspecific competition and genetic diversity (Hattori et al. 2007). Temperature-dependent sex determination could represent a differential constraint for both species, within the biogeographical range established by thermal tolerance and body size during the first winter.

Odontesthes bonariensis larvae survive at temperatures between 13 and 29°C, but growth is negligible at 13 and 15°C, and prolonged exposure to 29°C causes the disappearance of germ cells. In *O. bonariensis*, groups of fish exposed to about 17°C from the hatching to the juvenile stage become all-female, whereas groups exposed to about 25°C become male-biased. The proportions of females

are 100% at 13–19°C, 95% at 21°C, 81.2% at 23°C, 29.4% at 25°C, 10% at 27°C, and 0% at 29°C. The survival of *O. hatcheri* is limited to temperatures between 13 and 27°C (only 8.7% at the latter temperature), with slow but steady growth at 13 and 15°C. Strüssmann et al. (1997b) reported that the proportions of females were 88.9 and 89.5% at 13 and 15°C, respectively, about 50% at temperatures between 17 and 23°C, and 30.8% at 25°C. It must be noted that these values show high agreement with the summer mean air temperatures (www.smn.gov.ar) of the distribution areas of each species (Liotta 2006).

Global changes and climate warming

The temperature increase attributable to the global change is considered one of the most important factors affecting the modification of freshwater systems (Roessig et al. 2004; Gooseff et al. 2005; Ficke et al. 2007). In some cases, global heating has produced an increment in mass deaths and a significant reduction of the fishing stocks (Kangur et al. 2007). During the last 40 years, the minimum mean annual temperature increased from 8.9 to 10.1°C in the the Salado River basin (36°S), and the annual mean rainfall increased from 700 to 950 mm (Gómez and Menni 2005). The effects of these changes have been clearly observed in the formation of new communities of fish in areas that were formerly dry (Gómez et al. 2004). Conversely, decreases in the flow of the tropical rivers (Meisner and Shuter 1992) could affect the extension of flood plains, with a loss of breeding areas and an increase in mass fish deaths.

The exclusion of salmonids from the littoral zone due to an increase in water temperature at lake shores (Elliot 1981; Jansen and Hesslein 2004) seems to have occurred in Patagonia during the last 20 years—to the benefit of *P. trucha* and the detriment of salmonid fish (Quirós 1991; Aigo et al. 2008). Salmonids are usually found both in littoral and limnetic zones, and *P. trucha* is usually found in the littoral zone (Macchi et al. 1999, 2007; Buria et al. 2007). Thus, interactions between salmonids and native Patagonian fishes, including trophic competition and predation, seem to be played out in the littoral zone of the lakes (Macchi et al. 1999). Thermal preferences of native Patagonian fishes are currently being studied.

Conclusion

The examples we have reviewed show how temperature, through biochemical processes and ecological relationships, have affected and continue to affect fish evolution, distribution, and life history in the southern region of South America, explaining a great part of the present distribution and biological traits of extant species. We propose that these pieces of knowledge provide a palpable measure of the diversity and magnitude of the causal relationships between environmental temperature and individual fish and fish populations. Twenty thousand years after the last glaciation, climate change is currently presenting a new and faster thermal challenge to the fishes of southern South America, but now we know the causes and can—possibly—visualize the consequences.

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