Journal of FISH BIOLOGY

Journal of Fish Biology (2016)
doi:10.1111/jfb.13008, available online at wileyonlinelibrary.com

Freshwater fishes of Patagonia: conservation and fisheries

V. E. Cussac*†, E. Habit‡, J. Ciancio§, M. A. Battini*, C. Riva Rossi§, J. P. Barriga*, C. Baigún|| and S. Crichigno*

**Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue, Argentina, ‡Facultad de Ciencias Ambientales& Centro EULA-Chile, Universidad de Concepción, Barrio Universitario s/n, Concepción, Chile, §Centro Nacional Patagónico (CENPAT), CONICET, Argentina and ||Instituto de Investigaciones Biotecnológicas de Chascomús (IIB-INTECH), CONICET, Argentina*

The absence of much literature on the Patagonian fish fauna in comparison with that of the neotropics, has previously been blamed on its poor species diversity. Knowledge of the fishes of Patagonia, however, rose sharply at the beginning of the present century, allowing for an understanding of the complex biogeographical history that has led to the present diversity and distribution patterns. There are several new and potential threats to biodiversity and conservation of Patagonian fishes, such as the introduction of exotic species, damming, climate change and changes geared to safeguard economic interests, often acting synergistically. A great amount of new information is now available and the aim of the present review is to articulate this knowledge in a comprehensive way in order to aid in the development of tools to face the increasing challenges posed by environmental change and human activity. Knowledge about fishes of Patagonia has grown at the same time as human actions, and presence.

Key words: fishes; lakes; reservoirs; rivers; salmonids; southern South America.

INTRODUCTION

The Patagonian Province is a biogeographical area (Dyer, 2000) that has two parts, that between the Atlantic Ocean and the Andes, described as east Patagonia, and that between the Andes and the Pacific Ocean known as west Patagonia (Fig. 1). The poor diversity of the Patagonian fish fauna (Ringuelet *et al.*, 1967; McDowall, 1971) in comparison with the exuberant diversity of the neotropics, is one of the reasons for its poor representation in the literature (Hubert & Renno, 2006; Barletta *et al.*, 2010). Knowledge of fishes in Patagonia, however, rose sharply at the beginning of the present century thanks to several review papers on species distribution (Baigún & Ferriz, 2003), biogeography of the family Galaxiidae (Cussac *et al.*, 2004), an exhaustive revision of the fishes of Argentina (Menni, 2004), updates on Patagonian species (Habit *et al.*, 2006; Pascual *et al.*, 2007), a conceptual rearrangement of zoogeographic provinces of Argentina (López *et al.*, 2008), discussions about the role of temperature in the biogeographic history of southern South American fishes

---

†Author to whom correspondence should be addressed: Tel.: +54 294 4428505; email: victor.cussac@crub.uncoma.edu.ar

(Cussac *et al.*, 2009), the effects of ultraviolet radiation and temperature on temperate aquatic organisms (Gonçalves *et al.*, 2010), and two notable books on salmonids in Patagonia (Wegrzyn & Ortubay, 2009*a*, *b*).

Notwithstanding the brief lapse of time, a great amount of new information is now available, and the aim of the present review is to articulate this knowledge in a comprehensive way in order to aid the development of tools needed to face the increasing challenges of environmental change and human actions.

THE INCREASING COMPLEXITY OF ANTHROPOGENIC PERTURBATIONS

A major update that needs to be considered is that of renewed threats to fish biodiversity in Patagonia, such as introduction of exotic species, damming, global change and changes geared to safeguard economic interests (Hulme, 2005), all of which may act synergistically (Vince, 2010*a*, *b*).

The effects of resident, escaped and anadromous salmonid populations on freshwater communities have been studied around the world (McDowall, 2006). In Patagonia, the process of salmonid introduction, well documented by Macchi *et al.* (2008), resulted in severe impacts on native fish populations (Quirós *et al.*, 1986; Quirós, 1991; Baigún *et al.*, 2007; Aigo *et al.*, 2008; Arismendi *et al.*, 2009, 2014; Vigliano *et al.*, 2009; Habit *et al.*, 2010, 2012; Young *et al.*, 2010; Correa & Hendry, 2012; Correa *et al.*, 2012; González, 2012). Beginning in the 1980s, the marine cage culture of salmonids in Chile grew sharply, from 53 t harvested in 1981 to well over 600 000 t year^{-1} today. The dominant species is Atlantic salmon *Salmo salar* L.1758 (over 60%), followed by rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) (20%), coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (17%) and Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (<1%). Intriguingly, the species that was farmed the least, *O. tshawytscha*, had invaded almost every major basin in Patagonia (Fig. 2).

Several negative effects are associated with this industry in different areas: wastes, chemicals, diseases and escapees straying into rivers in Chilean and Argentine Patagonia (Correa & Gross, 2007; Soto *et al.*, 2007; Pascual *et al.*, 2009; García de Leaniz *et al.*, 2010; Montory *et al.*, 2010, 2011; Consuegra *et al.*, 2011; Elgueta *et al.*, 2013). Salmonid aquaculture has developed into a highly globalized trade-dependent industry, where fish meal and fish oil, produced in fisheries around the world, are key inputs to produce the feed for farmed fishes, transforming schooling fishes into salmonids flesh (Deutsch *et al.*, 2007). Although salmonid cage culture in Patagonian reservoirs is subjected to the negative effects of global warming (Báez *et al.*, 2011), *O. mykiss* farming activities have increased and impose the threat of fish escapes both on native fish populations and on the wild salmonid sport fishery (Cussac *et al.*, 2014). The impacts may not only be in the reservoirs where the farms are placed (*e.g.* Alicura Reservoir) but also in headwater lakes (*e.g.* Traful) (Vigliano *et al.*, 2008*a*, *b*).

THE FISHES IN THE STREAMS OF PATAGONIA

East and west of the Andes, Patagonia comprises a diverse hydrographical network draining into the Pacific and Atlantic Oceans as well as endorheic drainages

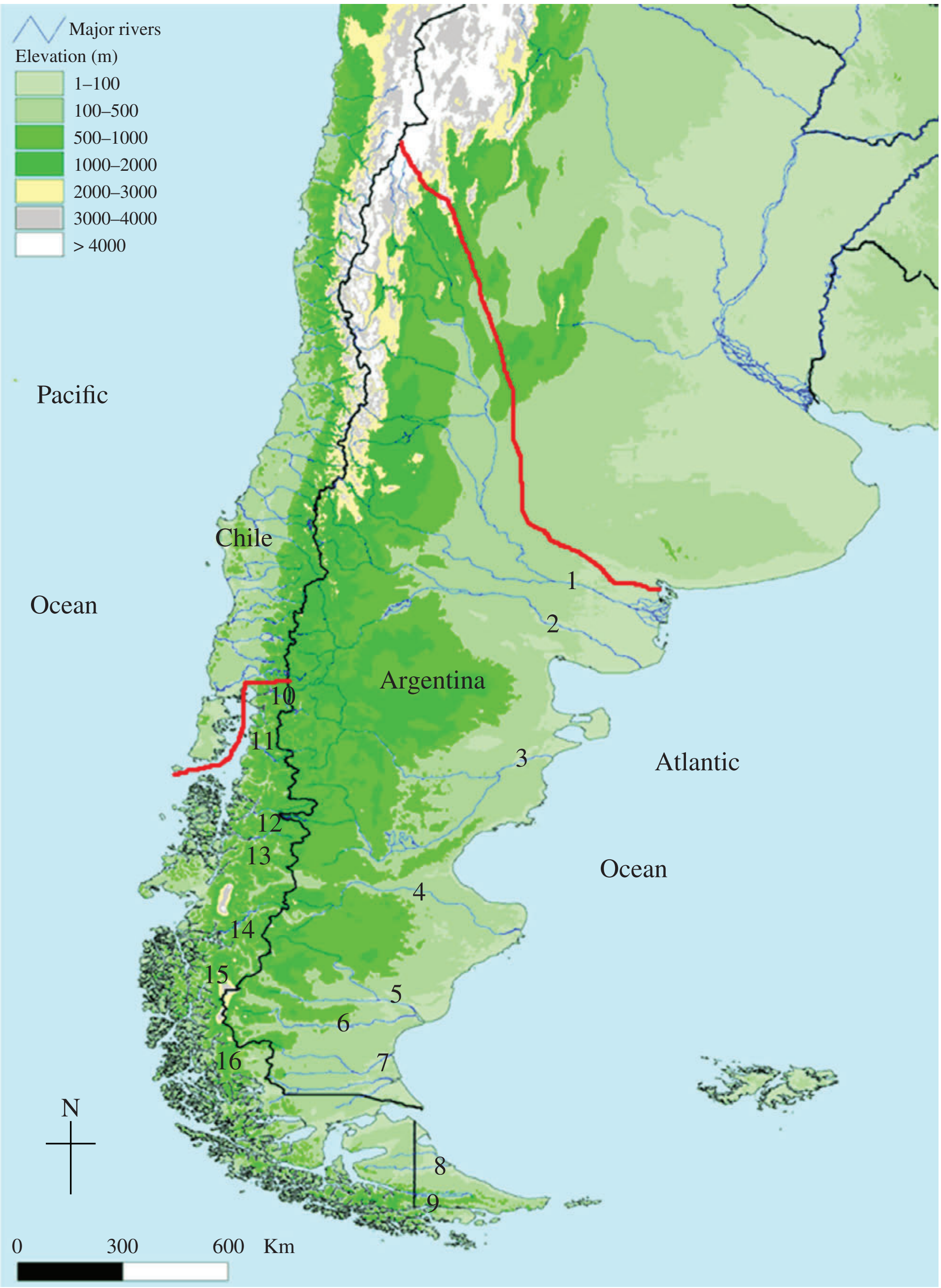

FIG. 1. Principal basins of southern South America: 1, Colorado; 2, Negro; 3, Chubut; 4, Deseado; 5, Chico; 6, Santa Cruz; 7, Coyle; 8, Grande; 9, Ovando; 10, Puelo; 11, Futaleufu; 12, Palena; 13, Aysén; 14, Baker; 15, Pascua; 16, Serrano. Red lines indicate the northern limits of Andean Region (Andean Cuyan and Patagonian Provinces of López *et al.*, 2008) in Argentina and the northern limit of the Patagonian Province (Dyer, 2000) in Chile (modified after http://patagonia.byu.edu/es/areas/general.aspx).

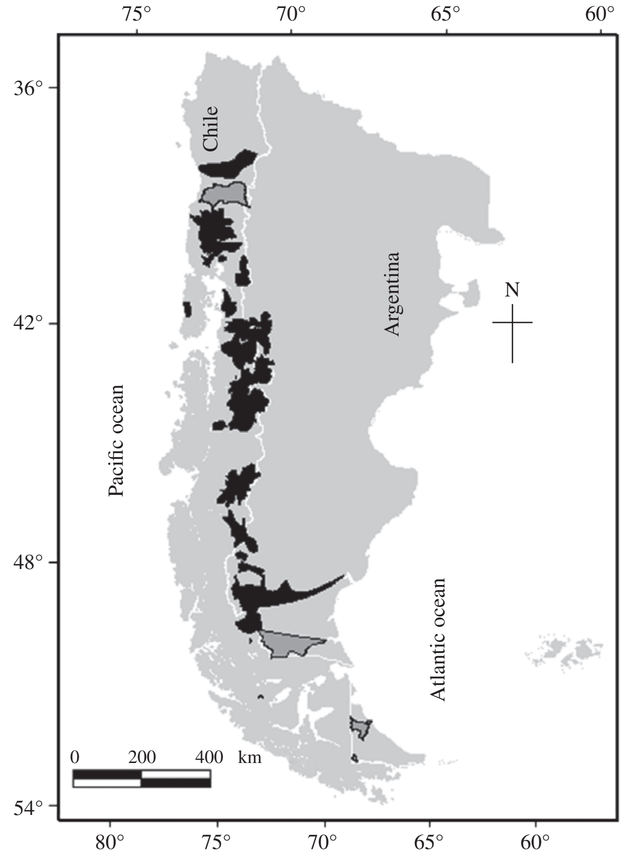

FIG. 2. *Oncorhynchus tshawytscha* invaded geographic range in Patagonia. River basins where self-sustaining populations were established (■). Basins where free-ranging individuals of *O. tshawytscha* were recorded, but not establishment probed are also shown (▨). Presence data derived from Correa & Gross (2007) and Riva Rossi *et al.* (2012).

(Pascual *et al.*, 2002; Habit *et al.*, 2010). Knowledge about stream fishes is much scarcer than that of corresponding lake-inhabiting fishes. Even the fishes of Negro River, one of the most important rivers in terms of basin size and socioeconomic importance, have been surveyed only recently (Alvear *et al.*, 2007), and new locations for riverine native fishes (Table I) continue to be reported since the review of Aigo *et al.* (2008).

Composition and distribution of fish assemblages along rivers varies between headwaters and lower zones (Habit *et al.*, 2007). In both east and west Patagonia, fish communities vary from north to south, showing a general decline southwards in species richness, dominated by a steep decline of non-diadromous species (Cussac *et al.*, 2009; Habit *et al.*, 2012).

Non diadromous species in Chilean streams are represented by perca *Percichthys trucha* (Valenciennes 1833) and *Percichthys melanops* Girard 1855, pejerrey *Odontesthes hatcheri* (Eigenmann 1909), catfish *Hatcheria macraei* (Girard 1855), recently found Diplomystidae individuals in the Baker River (Muñoz-Ramírez *et al.*, 2014) and

TABLE I. New localities for Patagonian fishes (Liotta, 2006; Pascual *et al.*, 2007; Aigo *et al.*, 2008)

Species	Collection site	Coordinates	Basin	Ocean drainage
Odontesthes hatcheri	El Porteño Creek[1]	41°12′14S; 70°40′46″W	Limay	Atlantic
Jenynsia multidentata	Agrio River[1]	36°48′30″S; 69°53′36″W	Neuquén	Atlantic
Aplochiton zebra	Centinela Creek[1]	42°48′31″S; 71°38′55″W	Futaleufú	Pacific
	Carrileufú River[1]	42°28′53″S; 71°34′02″W	Futaleufú	Pacific
Cheirodon interruptus	Valchetta Stream[5]	40°43′52″S; 66°19′25″W	Curicó	Endorheic
Hatcheria macraei	Chacay Melehue Creek[1]	37°15′30″S; 70°27′57″W	Neuquén	Atlantic
	Nahueve River[1]	37°04′55″S; 70°46′11″W	Neuquén	Atlantic
	Malleo River[1]	39°46′59″S; 71°02′06″W	Neuquén	Atlantic
	Comallo Creek[2]	41°04′11″S; 70°20′18″W	Limay	Atlantic
	Las Bayas Creek[2]	41°27′40″S; 70°39’24″W	Chubut	Atlantic
	Lake Fontana[1]	44°55′26″S; 71°32′12″W	Senguerr	Atlantic
	Mayo River[2]	45°40′58″S; 70°15′55″W	Senguerr	Atlantic
	Telken Creek[2]	46°52′52″S; 70°44′02″W	Deseado	Atlantic
	Lake Mascardi	41°21′03″S; 71°32′45″W	Manso	Pacific
	Lake Epuyen[3]	42°11′22″S; 71°30′49″W	Puelo	Pacific
	Lake Rivadavia[1]	42°36′36″S; 71°40′00″W	Futaleufu	Pacific
	Nant y Fall Creek[2]	43°13′22″S; 71°25’17″W	Futaleufu	Pacific
	Corintos Creek[2]	43°07′48″S; 71°26′24″W	Futaleufu	Pacific
	Cabeza de Vaca Creek[2]	43°29′59″S; 71°20′52″W	Corcovado	Pacific
	Frío Creek[2]	43°18′34″S; 71°26′33″W	Corcovado	Pacific
Olivaichthys cuyanus	Barrancas River[1]	36°48′30″S 69°53′36″W	Colorado	Atlantic
Olivaichthys viedmensis	Agrio River[1]	36°48′30″S 69°53′36″W	Neuquén	Atlantic
	Lake Ruca Choroi[1]	39°12′24″S 70°55′18″W	Limay	Atlantic
	Caleufú River[4]	40°23′58″S 70°44′34″W	Limay	Atlantic

[1] M. Battini & J. Barriga pers.obs., [2] Battini *et al.* (2008), [3] G. Viozzi pers.obs., [4] Barriga & Battini, 2009, [5] López *et al.* (2013).

big puyen *Galaxias platei* Steindachner 1898. New studies including comprehensive sampling throughout Patagonia have described changes in the distribution and abundance of some of these species (Habit *et al.*, 2010; Zemlak *et al.*, 2010, 2011; Habit *et al.*, 2012).

Distribution of *P. trucha* in Chile has been historically described from Aconcagua to the Strait of Magellan (Arratia *et al.*, 1981; Arratia, 1982; Campos & Gavilán, 1996; Dyer, 2000), but it is absent south of the Baker River basin. Moreover, in west Patagonia, it shows a gap in its distribution, being present from the Puelo to Futaleufú catchments, and to the south only in the Baker system. As indicated by the phylogeographic studies of Ruzzante *et al.* (2006, 2011), this species occurs in west Patagonia only in catchments that currently, or in the past, have their origin in east Patagonia. Juvenile *P. trucha* is associated with low-water velocity habitats, depositional zones with silt, and submerged macrophytes that provided them with shelter (Barriga *et al.*, 2013*a*).

The presence of *O. hatcheri* and Diplomystidae individuals exclusively in the Baker River basin in Chilean Patagonia supports the evidence for river capture (Turner *et al.*, 2005; Muñoz-Ramírez *et al.*, 2010, 2014).

The distribution of *H. macraei* was recently extended by Unmack *et al.* (2009*a*, *b*), from the Baker and Aysén catchments to the Baker in the south, and to the Imperial River in the North. Larval *H. macraei* prefer shallow marginal pools and feed mainly on small Chironomidae larvae. Juveniles and adults, on the other hand, prefer zones with high water velocity, such as riffles or runs, with large interstitial space, and prey on Ephemeroptera nymphs and chironomid larvae. Small individuals preferr gravel-pebbles and cobbles while larger fish choose cobbles and boulders (Barriga & Battini, 2009; Barriga *et al.*, 2013*a*). Studies based on individual identification may provide data about the population dynamic of this species (Barriga *et al.*, 2015).

Two relic groups of neotropical fishes are present in the streams of Patagonia. Among characids, the presence of *Cheirodon australe* Eigenmann 1928 in Lake Tarahuin (42°40′S; 73°56′W, Campos *et al.*, 1996) and the particular endemism of the scale-less characin *Gymnocharacinus bergii* Steindachner 1903 in the Valcheta stream (40°51′S, 66°34′W) have been comprehensively studied (Ortubay *et al.*, 1997; Ortubay, 1998; Ortubay & Cussac, 2000; Lozada *et al.*, 2000; Cussac & Ortubay, 2002; Körber & Ortubay, 2004). The recently noted presence of *Cheirodon interruptus* (Jenyns 1842) in the Valcheta Stream (López *et al.* 2013) is probably due to southward human transport of live bait. Both east and west of the Andes, new localities for Diplomystidae (Gosztonyi, 1988) have been recorded. *Olivaichthys viedmensis* (MacDonagh 1931) juveniles have been caught in the River Caleufú (Barriga *et al.*, 2007) and other rivers the of Negro basin (Table I), and new records of *Diplomystes* spp., previously found from the Aconcagua River to the Valdivia River, are from the Mataquito and Baker River basins (Muñoz-Ramírez *et al.*, 2010). In particular, existing records of Diplomystidae individuals in the Baker River basin in Chilean Patagonia represent the southernmost locality for the family (Muñoz-Ramírez *et al.*, 2010, 2014).

Galaxias platei is the most widespread species in west Patagonia. New records from Chiloé Island and from the Puelo, Palena, Cisnes, Cuervo, Baker, Serrano and Tierra del Fuego river basins have increased the total drainage area known to be occupied by this species by 243% (Habit *et al.*, 2010). A recent phylogenetic study by Burridge *et al.* (2012) recovered *G. platei* as a sister group of the genus *Neochanna*, shedding new light on the significance of the adaptations that allowed the species to endure glacial periods (Shuter & Post, 1990; Ruzzante *et al.*, 2008; Zemlak *et al.*, 2008; Barriga *et al.*, 2013*b*).

The north to south decline of diversity does not occur among diadromous species, represented mainly by galaxiids. The species *Aplochiton zebra* Jenyns 1842, *Aplochiton taeniatus* Jenyns 1842, *Aplochiton marinus* Eigenmann 1928 and *Galaxias maculatus* (Jenyns 1842) occur in the majority of the lower zones of rivers in west Patagonia (Puelo to Serrano river basins). *Galaxias maculatus* occurs in east Patagonia, and also in small streams of the Magellan Islands or fjord zone (Gosztonyi & McDowall, 1974; Alò *et al.*, 2013; Carrea *et al.*, 2013). These four species are, however, less abundant in Tierra del Fuego, probably due to synergetic negative effects of salmonid and beaver *Castor canadensis* invasion (Boy *et al.*, 2007, 2009). Another two diadromous species that have been described for Chilean Patagonia are the anadromous lampreys *Geotria australis* Gray 1851 and *Mordacia lapicida* (Gray 1851). Both species are rare in west Patagonia and are only present in the lower areas of rivers and in lakes very close to the sea. In the east, only *G. australis* is present in the Negro (Alvear *et al.*, 2007), Chubut (Azpelicueta *et al.*, 2001) and Santa Cruz basins (C. M. Riva Rossi & M. A. Battini, pers. obs.).

Salmonid predation and competition has severely impacted galaxiids in streams (Aigo *et al.*, 2008; Habit *et al.*, 2010). All South American Galaxiidae have been recorded both in rivers and lakes, but *G. maculatus* is the best represented in lotic systems (Cussac *et al.*, 2004), with landlocked riverine (Ferriz *et al.*, 2001; Barriga *et al.*, 2007) and diadromous populations (Boy *et al.*, 2007, 2009). Recently, Carrea *et al.* (2013) obtained the first results regarding the degree of isolation of populations in the Negro and Santa Cruz Rivers, the largest Patagonian rivers east of the Andes. Another galaxiid that splits its life between lakes and rivers is *A. zebra*. Adult *A. zebra* were captured starting their reproductive migration up the Pocahullo Stream at Lake Lácar, and eggs have been found adhering to the substratum in this inlet river (Lattuca *et al.*, 2008*a*). Probably, the newly hatched free embryos drift into the lake and grow, as larvae, in the limnetic zone. Juveniles and adults are usually found in lake littoral zones (Lattuca *et al.*, 2007, 2008*a*, *b*).

THE LIMNETIC ZONES OF THE LAKES

Another conspicuous gap in information about Patagonian fishes was the lack of knowledge of the use of the limnetic zone of lakes. The only early works considering the limnetic zone were those of Cussac *et al.* (1992), Barriga *et al.* (2002) and Buria *et al.* (2007) about intra-lacustrine movements of larval *G. maculatus*, larval *G. platei* and adult *P. trucha*.

Vigliano *et al.* (2008*a*, *b*) generated the first absolute estimates of fish abundance in Andean lakes, and Rechencq *et al.* (2011) found sound scattering layers (SSLs) both in the nearshore and pelagic habitats at different times of the day. These SSLs, formed by galaxiid larvae and adults, underwent displacement at dawn and dusk, displaying different behaviours depending on moon phases and showing, in agreement with Barriga *et al.* (2002), that the deep pelagic habitats provide diurnal refugia for native galaxiids. Rechencq *et al.* (2014) observed that fish >12 cm total length (L_T)

showed preference for the nearshore habitat during lake stratification and always appeared as individual targets. As previously described by Carrea *et al.* (2012), fish larvae and small fishes <12 cm L_T mainly used the pelagic habitat during mixis, where they formed dense SSLs. During lake stratification however, many individual targets from this group were found both in pelagic and nearshore habitats. Lindegren *et al.* (2012) demonstrated, by means of hydro-acoustics and advanced spatial modelling, how native fish species, as a result of previous exposure to native predators, may successfully respond to invasive novel predators through a complicated game of hide and seek, minimizing spatio-temporal overlap with predators, and potentially facilitating coexistence between native prey species (galaxiids) and introduced novel predators (salmonids).

Recent results regarding the predation activity of *O. mykiss* on *G. maculatus* larvae and juveniles, along with simulations of stocking strategies normally proposed for this region, showed that consumption demands on prey would increase to unsustainable levels for native fish populations (Vigliano *et al.*, 2009). In particular, Juncos *et al.* (2011) provided evidence for the plasticity of *O. mykiss*, regarding different growth strategies, facilitating the successful colonization of environments with different food availability. Juncos *et al.* (2013, 2015) highlighted the importance of keystone prey for the coexistence of native species with non-native top predators, providing new quantitative and qualitative evidence of the high predation pressure exerted on *G. maculatus*, the keystone prey species, during the larval to juvenile transition from pelagic to littoral-benthic habitat in Patagonian lakes.

ANADROMOUS SALMONIDS

Feral freshwater salmonid populations have been introduced in several river basins around the world, but most worldwide attempts to establish anadromous populations have failed (Pascual & Ciancio, 2007). Anadromous *O. mykiss* and anadromous *Salmo trutta* L. 1758, however, successfully established in Atlantic Patagonian basins and ***O. tshawytscha***, introduced in Chilean Patagonia only 30 years ago, are establishing populations in virtually all the main Pacific river basins and in some of the southernmost Atlantic river basins (Ciancio *et al.*, 2005; Correa & Gross, 2007; Fernandez *et al.*, 2010; Riva Rossi *et al.*, 2012) (Fig. 2).

Anadromous salmonids grow larger than resident fishes, and are considered the top sport salmonid fisheries. In the last 20 years, fishing for anadromous salmonids in Patagonia has become a high-revenue economic industry (Pascual *et al.*, 2009). The main income of some traditional sheep farms in Tierra del Fuego has turned almost completely to sport fishing. These anadromous populations raise concerns about potential effects on resident native fish communities, either in marine or freshwater environments. For example, blooms of the invasive algae *Didymosphenia geminate* that were recently found in many Patagonian rivers, were probably introduced by contaminated anglers' waders (Segura, 2011) and have spread quickly (Beamud *et al.*, 2013).

Feral anadromous salmonids are top predators that can affect host communities. Salmonid smolts are prey of other fishes and sea birds during their initial entry to the ocean, but rapidly grow to become top predators. Salmonids have high feeding rates (Quinn, 2005) and they can exert considerable predation pressure on localized food resources at sea, particularly in confined areas such as fjords or estuaries (Ciancio *et al.*, 2010). Anadromous salmonids can compete for food with other upper trophic level predators on the Atlantic Patagonian Shelf. Stable isotope analysis revealed that anadromous *O. mykiss* showed the same trophic level as other macro zooplankton feeders, including the rockhopper penguin *Eudyptes chrysocome*. Anadromous *S. trutta* and *O. tshawytscha* fed at the same trophic level as the piscivorous Magellanic penguin *Spheniscus magellanicus*, feeding mainly on schooling fishes, such as sprat *Sprattus fuegensis* (Jenyns 1842) and silversides *Odontesthes* sp. (Ciancio *et al.*, 2008*a*).

In Chile, recent studies have explored the effect of anadromous salmonids from two different perspectives. The first relates to their effect as temporary residents during their juvenile period in lakes and rivers, and the second to their role as carriers of persistent organic compounds. Ibarra *et al.* (2011) studied the diet and age of *O. tshawytscha* juveniles in rivers and lakes of four catchments in Chilean Patagonia (Puelo, Blanco, Aysen and Futaleufu River basins). They concluded that age 1 year (or having reached $L_T > 8{\cdot}5$ cm before completion of the first year) juvenile *O. tshawytscha* enter Patagonian systems as piscivorous predators. In all cases, prey fishes were composed of native fishes, both *G. maculatus* and *G. platei*. This implies a new negative interaction for the native fish fauna of Patagonia; predation and possibly also competition for allochthonous organisms. Montory *et al.* (2010) analysed the role of *O. tshawytscha* in the transport of pollutants from the sea to these pristine rivers. They accumulate 95% of their biomass in the sea (Naiman *et al.*, 2002) and transport marine nutrients and pollutants accumulated during their life to the headwaters where they die after spawning. This situation could cause ecosystem disruptions due to perturbation in the natural biogeochemical cycles of ultra-oligotrophic systems such as those of Patagonian systems (Soto *et al.*, 2006, 2007). Persistent organic pollutants (POPs) are among the compounds that andromous salmonids could transport and, in agreement with this, Montory *et al.* (2010) found that *O. tshawytscha* act as bio-vectors of POPs in Patagonia, with similar levels to those reported for the same species in the northern hemisphere. Furthermore, Montory *et al.* (2011) showed that concentration of POPs varies among farmed, escaped and wild *O. kisutch* and *O. mykiss*. Considering that Chile has at the moment the second highest production of salmonids in the world, this situation is not only of ecological concern, but also an important concern for human health.

Andean headwaters of Patagonian rivers are oligotrophic or ultra-oligotrophic (Depetris *et al.*, 2005) and anadromous salmonids are sources of marine-derived energy and nutrients for rivers and riparian ecosystems (Naiman *et al.*, 2002; Schindler *et al.*, 2003). Terrestrial ecosystems close to spawning anadromous salmonid rivers may benefit too (Hilderbrand *et al.*, 1999; Helfield & Naiman, 2001). Responses of rivers to artificially added salmonid carcasses include greater production of macrophytes, periphyton (Wipfli *et al.*, 1999), invertebrates (Chaloner & Wipfli, 2002) and fishes (Bilby *et al.*, 1998). Direct consumption of salmonids and recycling of the products of decomposition, leaching and excretion allow marine derived nutrients to be incorporated into terrestrial and freshwater ecosystems (Gende *et al.*, 2002). In the Caterina River (Santa Cruz River basin), the trophic web in areas with high salmonid nest densities showed enriched C and N stable isotopes values when compared with a control site upriver from spawning grounds and a neighbouring river free of salmonids (Ciancio *et al.*, 2008*b*). Similar results were found by Arismendi & Soto (2012) in rivers draining to the Pacific Ocean.

The literature on exotic salmonids has greatly emphasized their negative effects on native fishes and ecosystems (Simon & Townsend, 2003), but they have also provided unique opportunities for studying adaptation and ongoing evolution into novel environments (Hendry & Kinnison, 1999; Quinn *et al.*, 2001; Huey *et al.*, 2005; Crozier *et al.*, 2008).

In Patagonia, a number of life-history traits linked to migration are different from those of the original populations, indicating that adaptive capabilities to the new environment have been displayed soon after introduction (Pascual *et al.*, 2001; Riva Rossi *et al.*, 2004). *Oncorhynchus mykiss* were first introduced in Patagonia between 1904 and 1938 from the west coast of North America, and between 1950 and 1970 from Denmark (U.S. Fish Commission Reports, 1904–1938; Marini, 1936; Mac Crimmon, 1971; Baigún & Quirós, 1985). Mitochondrial DNA analysis revealed a mixed ancestry for *O. mykiss* in Patagonia, with major contributions of coastal anadromous stocks from northern California, Oregon and Washington to northern Patagonian basins, and inland anadromous (redband steelhead) and resident stocks from the McCloud River, in the upper Sacramento basin (California), and from the middle Columbia Basin (Washington) to the Santa Cruz River (50° S), in southern Patagonia (Riva Rossi *et al.*, 2004; C. M. Riva Rossi, unpubl. data) (Fig. 3). An anadromous life-history pattern failed in northern Patagonia, as the new populations only developed freshwater-resident life histories. A partially migratory population was established only in the Santa Cruz River (Pascual *et al.*, 2001). Environmental characteristics differ among these basins, such as relative food availability in fresh water and in the ocean, flow regimes, and ocean water temperatures, giving support to the idea that the environmental differences among these systems may have promoted between-population variation in the frequency of anadromous behaviour of *O. mykiss* in Patagonia (Riva Rossi 2004).

In the Santa Cruz River, the steelhead *O. mykiss* undergoes smoltification after 2 or 3 years in fresh water and migrates to the ocean to grow and mature before returning to fresh water to spawn, spending less than a year at sea (Riva Rossi *et al.*, 2003, 2007). Steelhead and resident *O. mykiss* are genetically indistinguishable (Pascual *et al.*, 2001) and can interbreed (Riva Rossi *et al.*, 2007), suggesting that the life history an individual fish adopts is the consequence of the environmental conditions it was subjected to (Riva Rossi, 2004). Several phenotypic traits differ drastically between the two forms, with anadromous fish displaying much faster growth, increased body size and fecundity, longevity and increased iteroparity, relative to resident fish (Pascual *et al.*, 2001; Riva Rossi *et al.*, 2007).

The frequency of iteroparity in Santa Cruz River steelhead *O. mykiss*, with rates estimated to be as high as 84 %, is higher than in northern hemisphere populations, where ocean migration is more often associated with reduced iteroparity (Pascual *et al.*, 2001). In the northern hemisphere, historical rates of repeat spawning were quite high, averaging 58%, but current rates are much lower, ranging from 2 to 63% (Busby *et al.*, 1996; Hopelain, 1998; Quinn, 2005; Narum *et al.*, 2008), due largely to high mortality of downstream migrating post-spawned adults (kelts) at hydropower dams (Busby *et al.*, 1996; Hatch *et al.*, 2004; Narum *et al.*, 2008). In pristine populations, such as those of the Kamchatka Peninsula of Russia, iteroparity is still predominant among individuals, with rates as high as 79% (Withler, 1966; Lohr & Bryant, 1999; Savvaitova *et al.*, 1999; McMillan, 2008). In native steelhead *O. mykiss*, reduced iteroparity and concomitant low post-spawning survival, are the result of a higher allocation of energy to longer, arduous migrations between feeding and spawning grounds, coupled with increased body size and reproductive investment (Crespi & Teo, 2002; Gayeski *et al.*,

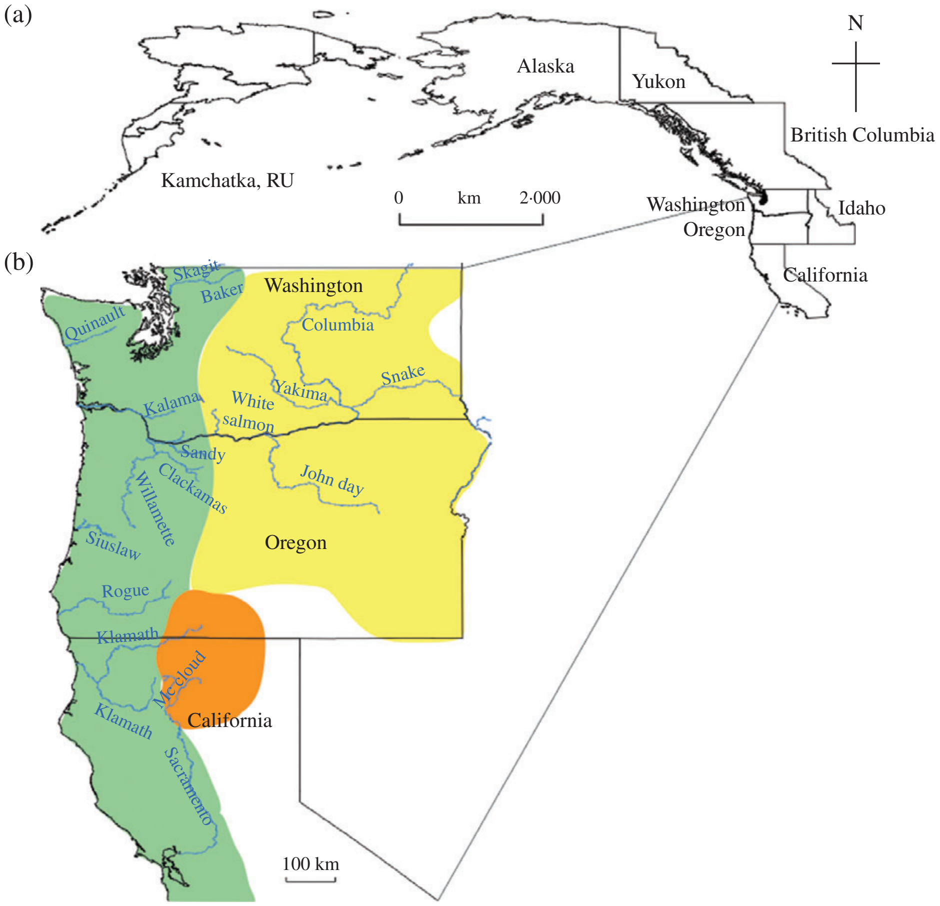

FIG. 3. Ancestry of *Oncorhynchus mykiss* introduced into Argentina. (a) Native range distribution of *O. mykiss* and (b) main rivers used for egg collection at the time of *O. mykiss* (varities: 🟩, coastal steelhead and rainbow trout; 🟨, Columbia River steelhead and redband trout; 🟧, McCloud River steelhead and redband trout) introduction in Argentina. Geographic range of coastal and inland lineages is based on Behnke (1992).

2011; Quinn *et al.*, 2011). By contrast, in the Santa Cruz River, steelhead *O. mykiss* high iteroparity appears to be accompanied by high reproductive investment and does not come at the expense of post-reproductive growth and survival (Pascual *et al.*, 2001; Riva Rossi *et al.*, 2007). The phenotypic variation of *O. mykiss* in the Santa Cruz River provides a remarkable natural experiment regarding how life-history trade-offs interplay in the displaying of anadromy and iteroparity within salmonid populations (Pascual *et al.*, 2001; Riva Rossi *et al.*, 2007).

Although the negative effects of anadromous salmonids are pervasive, their scientific value as a model system to understand fundamental ecological and evolutionary processes raises the controversial issue of whether a conservation value should be ascribed to the Santa Cruz River anadromous *O. mykiss* population, which is now at high risk of extirpation from their novel environment. If such a value is accepted, then elucidating the linkages between the expression and maintenance of the anadromous life history and ecosystem attributes could be an important first step towards developing conservation goals for salmonids in Patagonia.

RECENT KNOWLEDGE ABOUT OLD FISHES

An understanding of the biogeographic history of Patagonian fishes is one of the fields where major improvement has taken place. Cione & Báez (2007) reviewed fossil evidence of the presence of Percichthyidae and Siluriformes in the Eocene (58·8 and 33·9 million years ago) and of *Percichthys* and *Odontesthes* in the Miocene records (23·0 and 5·3 million years ago) of Patagonia. Thus, the presence of *Percichthys* prior to the formation of the Andes emphasizes vicariance hypotheses and agrees with the results of Ruzzante *et al.* (2006, 2011) about genetic differences between *P. trucha* populations east and west of the Andes. Similarly, Zemlak *et al.* (2008) observed two main genetic clades within *G. platei* also east and west of the Andes. Molecular-clock estimates, however, suggested that the splitting between eastern and western lineages occurred at *c.* 1·5 million years ago. As the southern Andes began their uplift much earlier, the data imply gene flow across the divide. In a different way, genetic studies (Zemlak *et al.*, 2010) indicate that *G. maculatus* began to diversify in systems of northern Chilean Patagonia and subsequently spread south along the Pacific coast, colonizing adjacent coastal systems and eventually reaching Atlantic systems *via* the southern tip of South America. On the Atlantic side, range expansion and diversification probably continued northward and westward. These different patterns (vicariance *v.* marine dispersal) between congeneric species agree with the alternative life-history patterns of *G. maculatus* (Chapman *et al.*, 2006; Barriga *et al.*, 2007) and the lack of strong evidence supporting a diadromous life-history pattern for *G. platei* (McDowall, 1971; Cussac *et al.*, 2004, Belk *et al.*, 2014).

Cione *et al.* (2005) showed the presence of loricariids in the Miocene site of Punta Delgada, Península Valdés and suggested that the climate was much warmer than today, perhaps at least as warm as that of the central part of Buenos Aires province. In effect, cooling of Patagonia during the Oligocene (Cione *et al.*, 2007) would explain the isolation of *G. bergii* in a thermal stream (Menni & Gómez, 1995; Ortubay *et al.*, 1997; Körber & Ortubay, 2004), the unexpectedly high thermal tolerance of *H. macraei* (Gómez, 1990) at Lake Buenos Aires (46°32′S), and the positive relationship between thermal tolerance and acclimation temperature of *P. trucha* (Aigo *et al.*, 2014).

A substantial improvement has occurred in knowledge about two trichomycterids, *Trichomycterus areolatus* Valenciennes, 1846 and *H. macraei*. Unmack *et al.* (2009*b*) updated *H. macraei* distribution data and improved morphological criteria for their identification. Unmack *et al.* (2009*a*), however, also found that *H. macraei* individuals are within *T. areolatus* genetic dendrograms. This could be caused by introgressive hybridization of the mitochondrial genome of *T. areolatus* into *H. macraei*, or simply by an incorrect current taxonomy, with *H. macraei* actually representing an individual lineage within *T. areolatus*. It must be noted that glaciations have had a major effect on the southern distributional limit of *T. areolatus*, as it is not found anywhere on the mainland of Chile south of Maullín River (41°23′8″S). On the other hand, *H. macraei* reaches 47°34′27″S (Blanco River) emphasizing the view of *H. macraei* as being morphologically diverged and specialized from ancestral *T. areolatus* lineages (Baigún & Ferriz, 2003; Aigo *et al.*, 2008; Unmack *et al.*, 2009*a*). Preliminary phylogeographic analysis based on mtDNA shows three main clades within *H. macraei*. The first one corresponds with Colorado basin populations, the second includes Baker basin and Lake Cholila (both Pacific), and the third and largest clade incorporates a mix of populations from both Pacific (Valdivia, Bueno, Puelo, Yelcho, Palena and Aysén) and Atlantic (Negro, Chubut and Deseado) basins (Unmack *et al.*, 2012). Morphology was strongly related to this phylogeographic pattern, showing the main variation on locomotion structures, such as caudal peduncle and both dorsal and anal fins (Battini *et al.*, 2008).

Both the native *O. hatcheri* and the translocated *Odontesthes bonariensis* (Valenciennes 1835) occur in east Patagonia (Dyer 2006). Both species have disjunct original distributions; *O. hatcheri* in the south-west (the Andean Cuyan and Patagonian Provinces of López *et al.*, 2008) and *O. bonariensis* in the north-east (the Pampean Province of López *et al.*, 2008). Stocking practices of *O. bonariensis* in the original distribution area of *O. hatcheri*, and their ability for hybridization (Crichigno *et al.*, 2014*a*), however, led to the establishment of a hybrid zone in northern Patagonia (Crichigno *et al.*, 2013).

EXPECTATIONS ABOUT SILVERSIDES

As the first detected effects of global warming on Patagonian freshwater fishes, Aigo *et al.* (2008) obtained correlative results showing a numeric decline of introduced salmonid populations from littoral zones of east Patagonian lakes as a consequence of global warming. These results have been validated by causal evidence of thermal preferences of *O. mykiss* and *P. trucha* (Aigo *et al.*, 2014), and thermal-dependent reproductive disturbances observed in salmonids (Pankhurst & King, 2010). This fact leaves an unanswered question about the future of salmonid culture in northern Patagonia (Báez *et al.*, 2011) and about the alternative culture of *O. hatcheri* (Hualde *et al.*, 2011). Expectations about the economic activity generated by the *O. bonariensis* sport fishery and its potential for aquaculture (Somoza *et al.*, 2008) led to the translocation of *O. bonariensis* into the original distribution of *O. hatcheri* during the 20th century, generating new possibilities (Crichigno *et al.*, 2014*a*). The fact that both species hybridize and that reciprocal hybrids mature with a viable F2 suggest that complex degrees of hybridization in natural habitats (Strüssmann *et al.*, 1997), leads to a possible hybrid zone. In effect, a hybrid zone between both species has been recently documented, with lakes and reservoirs where both species, as well as individuals with intermediate morphology, are present; reservoirs where morphological *O. hatcheri* individuals show a *O. bonariensis* mtDNA signature, and lakes and reservoirs where, only *O. hatcheri* is caught, a high percentage of which show body and head shape resembling *O. bonariensis* (Conte-Grand 2012; Crichigno *et al.*, 2013). Based on previous studies about growth and body shape of *O. hatcheri* (Ruiz, 2002), Conte-Grand (2012) indicates that growth parameters of *O. hatcheri* in this hybrid zone do not differ from those of *O. bonariensis*. Hybrid and introgressed individuals, however, seem to be shorter and deeper-bodied than pure breeds (Crichigno *et al.*, 2014*a*). One lake in this hybrid area, Lake Pellegrini, at present supports a small artisanal fishery, based on gillnet capture and with small freezer facilities. Although Argentine statistics did not regard any Patagonian river or lake (www.minagri.gob.ar/SAGPyA/pesca/pesca_continental/04-estad%C3%ADsticas/index.php), they did *O. bonariensis* coming from the Pampean Region.

LAKE COMMUNITIES AND FISHERIES MANAGEMENT: AN ENVIRONMENTAL APPROACH

Patagonian recreational fisheries are based mostly on exotic species, introduced at the beginning of the 20th century, representing the basis for a successful recreational activity (Baigún & Quirós, 1985; Pascual *et al.*, 2002, 2007; Macchi *et al.*, 2008). Not surprisingly after more than 100 years of intensive stocking, landlocked salmonids, mainly *O. mykiss* (and *S. trutta* on a minor basis), have become widely distributed, inhabiting most basins in Argentina (Baigún, 2001). This situation created a contrast with the artisanal/commercial fishery, which historically was restricted to a few large lakes located in the dry Patagonian plateau (Cardiel, Musters and Colhue Huapi Lakes) and mostly focused on *P. trucha* (Baigún & De Nichilo, 1985). In Chile, although the National Fisheries Agency (www.sernapesca.cl) recognizes eight sport fish species in Patagonia, the most widespread (and the one on which sport fisheries are mostly based on) is *S. trutta* (Habit *et al.*, 2010).

Surprisingly, and despite the importance of the recreational fishery, almost no fish yield data and no catch and effort data have been gathered, as well as data from the main recreational fisheries being also unavailable, precluding managers from estimating long-term fish yields and detecting fishery trends. Abundance or biomass data are still sparse and have generally been collected using different gear and capture methods (Quirós & Baigún, 1984; Quirós *et al.*, 1986; Vigliano *et al.*, 1999, 2008*a*, *b*; Baigún *et al.*, 2007).

Alternative approaches have been considered in order to assess fishery resources, attempting to link relative fish abundance and species composition to environmental characteristics. Such approaches were supported by the fact that Patagonian lakes include a wide array of limnological characteristics defining a complex mosaic of water bodies (Baigún & Marinone, 1995; Baigún *et al.*, 2006). For example, Quirós & Baigún (1984) used relative fish abundance as surrogate for potential fish yield for large lakes and reservoirs whereas Baigún *et al.* (2007) related CPUE data and hydro-acoustic fish biomass assessment in small-sized lakes to environmental variables. In this context, the central tenet adopted in assessing Patagonian lakes is that fish communities and potential yield could be related and therefore become predictable from lake environmental conditions as well as surrounding landscape characteristics.

Successful adaptation of salmonid species has been observed for more than one century, strongly modifying original native communities (Pascual *et al.*, 2007; Aigo *et al.*, 2008; Macchi *et al.*, 2008). As noted by Aigo *et al.* (2008), lakes without salmonids exhibit higher diversity, which can be related to observed salmonid impact on native species in lakes and rivers (Macchi *et al.* 1999, 2007; Milano *et al.* 2002; Buria *et al.* 2007; Vigliano *et al.*, 2009). Such premises are also useful when testing if successful adaptation exhibited by salmonids has promoted fish assemblages that can be forecasted based on climatic, edaphic and morphometric lake characteristics. This approach is in fact not new, and has been widely applied for other cold temperate areas by developing univariate or multivariate empirical models (Ryder, 1965, 1978; Matuszek, 1978; Schlesinger & Regier, 1982; Young & Heimbuch, 1982). Baigún *et al.* (2007), however, demonstrated that, since Patagonian lakes exhibit important limnological differences from their northern hemisphere counterparts, no direct extrapolations were feasible or if applicable, they tended to overestimate potential fish yield. For example, unlike most dimictic cold temperate northern hemisphere lakes, the majority of Patagonian

TABLE II. Patagonian lake categories and main productive driving variables (modified from Baigún & Marinone, 1995). Group A represents Andean oligothrophic lakes (A1 includes large lakes; A2 and A3 comprise typical Andean lakes ranging from medium to small, from deep to shallower, from oligo to mesotrophic, with low conductivities and high transparencies. All group A lakes were thermally stratified, except for A3, which includes small and shallow foothill lakes). Group B includes ecotone lakes in the Andean foothills, typically shallow, unstratified, meso to eutrophic, with moderate to high levels of nutrients and conductivity. Group C comprises lakes and reservoirs in the plateau (C1 includes reservoirs of the north-western boundary of the plateau region, that are distinctively large, deep, oligotrophic and thermally stratified during summer. C2 includes some very large lakes and reservoirs of moderate depth, which do not stratify). Values are means with ranges in parentheses

Lake Category	Type	Area (km^2)	Depth (m)	TP (μg l^{-1})	ZTH (m)	TDS (mg l^{-1})
A	A1	868 (580–1466)	129 (80·7–157)	2·9 (2–3·8)	74 (64–88)	34 (25–52)
	A2	33 (5·4–86·7)	73 (22·4–166)	5·2 (1–20·2)	35 (0–85)	45 (19–124)
	A3	2·2 (0·6–6·3)	12·6 (4·3–19·5)	6·7 (4–9)	4·2 (0–21)	44 (36–58)
B		2·4 (0·3–4·6)	4·4 (2·1–6·1)	82·8 (29–294)	0	136 (40–260)
C	C1	350 (174–816)	43·1 (24·7–79·4)	5·3 (3·5–9)	19·5 (0–39)	83·8 (64–140)
	C2	260 (65–460)	25·8 (9·4–49·1)	93·2 (23·5–276)	0	884 (159–2837)

TP, total phosphorous; ZTH, thermocline depth; TDS, total of dissolved solids.

lakes are either warm monomictic or cold polymictic and do not stratify if water depth is <20 m mean depth or 50 m maximum depth (Baigún & Marinone, 1995). Based on contrasting different climatic, edaphic, morphometric and limnological variables these authors were able to recognize up to three well defined main lake groups composed of secondary categories (Table II).

Such classification improved and refined pioneer results observed by Quirós *et al.* (1986) and properly reflects lake environmental complexity in Patagonia. Nevertheless, some similar general ecological principles observed for other worldwide temperate lakes also apply to Patagonian lakes. For example mean depth and total dissolved solids (TDS), as encapsulated by the morphoedaphic index (MEI) (Ryder, 1965, 1978; Ryder *et al.*, 1974), appear to reflect the potential fish production, which allows relating lake fish assemblages to fish yield in Patagonian lakes (Fig. 4). Adams & Olver (1977), *e.g.* based on the assessment of 70 Ontario lakes suggested that a MEI from 0·8 to 5·9 represents oligotrophic conditions, a MEI from 6 to 7·3 indicates meso-eutrophic characteristics and a MEI from 7·3 to 50 eutrophic conditions. Ultra-oligotrophic to oligotrophic Patagonian lakes, with MEI ranging between 0 and 1 and mostly found in the mountain areas, are dominated by salmonids. On the other side of the trophic spectrum, *P. trucha* and *O. hatcheri* are more abundant in lakes with $\text{MEI} > 10$ reflecting eutrophic and even distrophic scenarios, mostly found in plateau areas. Finally, mixed communities are expected in lakes with MEI between 3 and 11, showing mesotrophic characteristics. Thus, communities dominated by *Percichthys* are almost absent in lakes showing $\text{MEI} < 3$ and conversely salmonid dominance is almost absent in lakes with $\text{MEI} > 60$. The above analysis also displays a natural species replacement driven by trophic lake status as has been also noted by Hartmann (1977), Ryder & Kerr (1978) and Oglesby *et al.* (1987) for European and North American lakes.

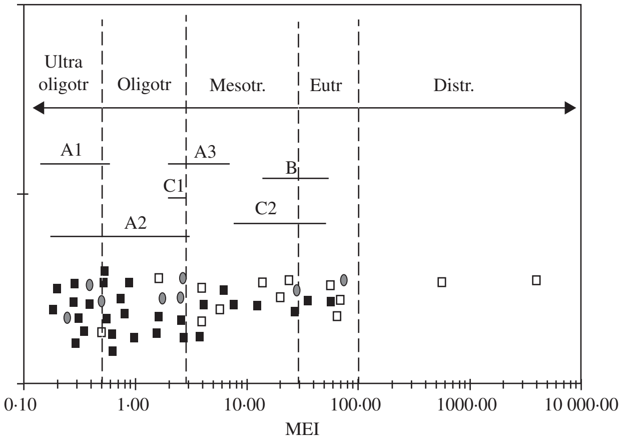

Fig. 4. Trophic categorization of Patagonian lakes according to their typology (Baigún & Marinone, 1995). Group A represents Andean oligothrophic lakes (A1 includes large lakes. A2 and A3 comprise typical Andean lakes ranging from medium to small, from deep to shallower, from oligo to mesotrophic, with low conductivities and high transparencies. All group A lakes were thermally stratified, except for A3 which includes small and shallow foothill lakes). Group B includes ecotone lakes in the Andean foothill, typically shallow, unstratified, meso to eutrophic, with moderate to high levels of nutrients and conductivity. Group C comprises lakes and reservoirs in the plateau (C1 includes reservoirs of the north-western boundary of the plateau region, that are distinctively large, deep, oligotrophic and thermally stratified during summer. C2 includes some very large lakes and reservoirs of moderate depth, that do not stratify). Fish community categories [MIX, communities where salmonids, *Percichthys* or atherinids represent 30 to 70% of relative abundance (⬮); PER communities where *Percichthys* and/or atherinids represent 70% of relative abundance (□); SAL, communities where salmonids represent 70% of relative abundance (■)] along the morhoedaphic index (MEI) gradient (ULTRAOLIG, ultraoligotrophic; OLIGOTR, oligotrophic; MESOTR, mesotrophic; EUTR, eutrophic; DISTR, distrophic).

This scenario is the same in west Patagonia, where small mesotrophic lakes are dominated by native species, *P. trucha* and *O. hatcheri* in the Baker River basin (*e.g.* Lake Maldonado), or are single species systems, inhabited only by *P. trucha* (*e.g.* Silvia Lake) or *G. platei* (*e.g.* Lake Thompson in the Aysén basin, Habit *et al.* 2012; Belk *et al.*, 2014). Large oligotrophic lakes are highly dominated by salmonids, in Chile predominantly by *S. trutta*. The only oligotrophic lakes which remain salmonid free are the Yulton and Meullin, located in the Cuervo River basin in the Aysén Region (Habit *et al.*, 2010) and these lakes are severely threatened by hydropower development (Vince, 2010*a*, *b*).

LAKE CHARACTERISTICS AND BIONOMIC FEATURES

The potential effects of lake characteristics on population bionomic characteristics should be considered. Recently, Crichigno *et al.* (2012, 2014*b*) showed the great magnitude of the effects of phenotypic plasticity on the morphology of *O. hatcheri* and *P. trucha*. Latitude, longitude and area of lakes were significant in the explanation of the gradient of relative abundances, the high abundances of salmonids being related to high latitudes and longitudes, and lakes smaller than those where the abundances of *Odontesthes* sp. and *P. trucha* were higher. *Odontesthes* sp. had its higher abundance at lower longitudes and *P. trucha* at lower latitudes (Aigo *et al.*, 2008). Growth parameters and mortality for instance, may strongly differ among lakes (Barriga *et al.*, 2012) and therefore strongly influence a population's response to exploitation. Unfortunately, information on Patagonian fish population parameters and biological attributes is still scarce (Guerrero, 1984, 1991; Lafarga & Guerrero, 1991; Ruiz, 2002; Lopez Cazorla & Sidorkewicj, 2008, 2011).

At a broad regional scale, it is of major interest to explore how such parameters could be related to environmental conditions in order to use this information for fishery management. Lafarga & Guerrero (1991) noted that *O. mykiss* growth was positively related to total phosphorous and total organic nitrogen. For 23 North American lakes, Donald & Anderson (1982) noted that *O. mykiss* growth was related to area, TDS and mean depth, with the lake area being the main factor governing growth of lake trout *Salvelinus namaycush* (Walbaun 1792) in Canada. Recently, Arismendi *et al.* (2011) proposed a model based on condition indices of *O. mykiss* to estimate salmonid abundance in Chilean lakes that can be used to improve lake and fishery management decisions for introduced salmonids in southern South America. This is an interesting approach considering the lack of information regarding most of the Patagonian systems.

APPLICATIONS FOR FISHERIES MANAGEMENT

Management policies can be defined and considered by applying an ecological framework and could even be related to expected climatic changes to which salmonids appear to be highly vulnerable (Cussac *et al.*, 2009; Báez *et al.*, 2011; Aigo *et al.*, 2014). Predicted climate change in Patagonia may modify trophic conditions indirectly by increasing TDS concentration or water conductivity as well as nutrient inputs related to surrounding modifications (Jönsson *et al.*, 2011). Such patterns would promote lakes with higher MEI and thus greater fish yields, whereas balance between salmonids and *Percichthys* dominated communities would be a direct consequence of lake thermal shifts according to basin characteristics and lake morphometry.

A remarkable feature of most of Patagonian lakes is that the main fisheries have been developed in oligotrophic lakes which are dominant at a large geographical scale (Pedrozo *et al.*, 1993; Baigún & Marinone, 1995). Thus, general guidelines can be developed to optimize fishery management based on an ecological approach, taking into account lake natural productivity. In this context, small or large oligotrophic lakes should be allocated only to recreational fisheries or to a very controlled artisanal fishery based on poor potential productivity. Lakes located in the ecotone and the plateau are suitable for practicing both artisanal and commercial fisheries mostly based on percychthids and atherinopsids, with salmonids as a secondary target. These lakes exhibit the largest yield per unit area but, due to their small size, they should be managed differently using alternative exploitation under appropriate fishing effort regulations. Is interesting to note that ecotone lakes are usually avoided by recreational anglers due to poor infrastructure, unfavourable climatic conditions or because they are located on private properties.

On the other hand, differences in bionomic response to environmental conditions suggest that fishing regulations should be adapted to local or regional lake characteristics avoiding the application of regulations that consider similar legal sizes for most of the lakes. Since growth is directly related to reproductive patterns, it is apparent that fishing regulations should adapt to local population characteristics. Such patterns could be even exacerbated by the influence of temperature. As noted by Baigún & Marinone (1995) water temperature decreases with latitude, thus influencing growth performance (Conover, 1990).

THE FISHES IN FUTURE PATAGONIA

One of the major threats that the fish fauna in Patagonia faces is the high economic pressure for hydropower development. During the last two decades in Chile there has been a boom in constructing hydropower plants, damming and diverting a wide range of rivers, in order to meet energy demands. Hydroelectricity is particularly attractive in Chile, since rivers are short and torrential due to the high east to west gradient produced in the Andes Mountain range. Patagonia contains 25–30% of Chile's hydroelectric potential, is barely inhabited (0·84 inhabitants km^{-2}, source: census 2002 INE; www.ine.cl) and its rivers have a high flow in summer, when the northern rivers have their low flow season.

Five large rivers of Argentinean Patagonia (Colorado, Neuquén, Limay, Futaleufú and Chubut) already have several impassable dams. While the effect of dams on fish habitat is obviously large, the distinct effects on particular species or community characteristics are poorly known (Cussac *et al.*, 1998; Macchi *et al.*, 1999). At present, the only confirmed effect is the disappearance of lamprey *Geotria australis* Gray 1851 from the middle and upper reaches of the Limay River above dams. Both ammocoetes and adult *G. australis* are regularly found in the Negro River, below dams (Pascual *et al.*, 2007).

While all large rivers south from Puerto Montt in Chile and Santa Cruz River in Argentina are still free of dams, this condition is unlikely to last. Recently, five major dams have been approved in the Baker and Pascua catchments (Vince, 2010*a*, *b*; Nature News 17 May 2011), despite the fact that the changes that they would bring upon these little studied ecosystems are not well understood. The knowledge gap in the species inventory, biodiversity, eco-structure, physico-chemical and biological dynamics, ecological integrity and loading capacity of most ecosystems (Goodwin *et al.*, 2006) is not sufficient to support management strategies in damming projects. Knowledge regarding the habitat requirements, reproduction and ecology of species is limited to a small number of fish species. This makes the assessment of the impact of anthropogenic activities, like the construction and operation of dams, a difficult task.

Dam effects are not only restricted to the impounded area (reservoir), but they encompass the entire river downstream of the dam, due to the change in the flow regime caused by its operation. This flow regime modification has severe effects on physical habitat availability. García *et al.* (2011) reported the effect of dam operation with hydro-peaking on the habitat availability of native fishes of the Biobío River in central Chile, showing major changes in habitat availability at a daytime scale. These changes affect mainly the riparian zones, which are rearing, feeding and refuge habitats for the majority of the native fish species. Furthermore, catchments like the Baker or Pascua, with complex hydrographic networks enclose complex fish metapopulation dynamics.

Dams are frequently accompanied by fish culture cages and fish culture usually involves fish escapes. Escaped fishes not only affect fish population in the same reservoir, but also their consequences may be observed at headwater lakes and rivers (Cussac *et al.*, 2014).

The need to understand the environmental factors driving life-history variations in anadromous and resident *O. mykiss* is particularly relevant in the Santa Cruz River, where two large hydropower dams will be built blocking the migratory corridor, altering the flow, sediments and temperature regimes downstream (M.A. Pascual, C.M. Riva Rossi & M. García Asorey, unpubl. data). Flow and temperature influences the spawning of adults, the emergence of fry and the migration of smolts (Anguilleta Jr *et al.*, 2008). Changes in these variables can lead to mismatches between the environmental cues and the anadromy triggers and could threaten the persistence of this life history in the population.

Other threats that have not been properly quantified, but could modify the fish community structure should be also taken into account (Miserendino *et al.*, 2008, 2011). For example, change in land use, riparian deforestation and cattle practices could alter dramatically main fish habitats and deteriorate water quality as reviewed by Salo & Cundy (1987) and Mehan (1991).Baigún *et al.* (2006), for example, noted that lake nitrogen input correlated inversely with *Notophagus* spp. forest density, pointing out the relevance of considering surrounding land practices mostly ignored by previous studies.

Conservation of native Patagonian fishes should be envisioned as a priority in view of their low richness and the potential impacts of habitat deterioration and salmonid introduction. A sound debate is still merited on how exotic salmonids need to be managed according to their socioeconomic importance under an ecosystem approach. Salmonids have been introduced everywhere in Patagonia, but their impact on native species has not been similar in all environments. Of particular concerns are low order streams and isolated or poorly connected small lakes where recreational fisheries are negligible. In such lakes and streams, predation or competition with native species could be exacerbated due to absence of fishing and low habitat complexity, which increases species vulnerability. It is important to note that few lakes and streams are still salmonid free, thus such basins or areas should be not stocked without proper justification.

Fishing regulations can be used to protect native fishes. Since humans represent the exclusive predator for salmonids, capable of controlling their population abundance and size composition, catch-and-release strategies could be inappropriate in Patagonia and therefore their application waived in those basins where conservation priorities require recovering or preserving native fishes (www.reglamentodepesca.org.ar). Such an approach reinforces the concept that inland Patagonian fisheries can be managed by considering regional or catchment templates based on a community perspective, instead of on a single target species, integrating river and lake ecological complexity and surrounding landscapes with bionomic population features and socioeconomic factors.

Knowledge about fishes of Patagonia has grown at the same time as human efforts, actions and presence. Like Tantalus, as soon as being within grasp of an appreciable comprehension of the ecological status of its populations, the climate changes, the rivers are dammed, and new exotics are dispersing.

We thank the editors for providing us with a vehicle to promote some of our views. We would like to acknowledge the following institutions for granting previous and present projects that have enabled the elaboration of these ideas: Universidad Nacional del Comahue, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Agencia Nacional de Promoción Científica y Tecnológica (ANPCYT), Argentina, FONDECYT (Proyecto 1080082 to E.H.), Chile and the NSF-PIRE award (OISE 0530267, U.S.A.) for supporting collaborative research on Patagonian Biodiversity, throughout the following institutions (listed alphabetically): Brigham Young University, Centro Nacional Patagónico, Dalhousie University, Darwinion Botanical Institute, Universidad Austral de Chile, Universidad Nacional del Comahue, Universidad de Concepción and University of Nebraska.

References

Adams, G. G. & Olver, C. R. (1977). Yield properties and structure of boreal Percid communities in Ontario. *Journal of Fisheries Research Board of Canada* **34,** 1613–1625.

Aigo, J., Cussac, V., Peris, S., Ortubay, S., Gómez, S., López, H., Gross, M., Barriga, J. & Battini, M. (2008). Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages. *Reviews in Fish Biology and Fisheries* **18,** 387–408. doi: 10.1007/s11160-007-9080-8

Aigo, J., Lattuca, M. E. & Cussac, V. (2014). Susceptibility of native perca (*Percichthys trucha)* and exotic rainbow trout *(Oncorhynchus mykiss*) to high temperature in Patagonia: different physiological traits and distinctive responses. *Hydrobiologia* **736,** 73–82. doi: 10.1007/s10750-014-1888-3

Alò, D., Correa, C., Arias, C. & Cárdenas, L. (2013). Diversity of *Aplochiton* fishes (Galaxiidea) and the taxonomic resurrection of *A. marinus*. *PLoS ONE* **8,** e71577. doi: 10.1371/journal.pone.0071577

Alvear, P. A., Rechencq, M., Macchi, P. E., Alonso, M. F., Lippolt, G. E., Denegri, M. A., Navone, G., Zattara, E. E., García Asorey, M. I. & Vigliano, P. H. (2007). Composición, distribución y relaciones tróficas de la ictiofauna del río Negro, Patagonia Argentina. *Ecología Austral* **17,** 231–246.

Angilletta, M. J. Jr., Steel, E. A., Bartz, K. K., Kingsolver, J. G., Scheuerell, M. D., Beckman, B. R. & Crozier, L. G. (2008). Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications* **1,** 286–299.

Arismendi, I. & Soto, D. (2012). Are salmon-derived nutrients being incorporated in food webs of invaded streams? Evidence from southern Chile. *Knowledge Management of Aquatic Ecosystems* **405**. doi: 10.1051/kmae/201200901

Arismendi, I., Penaluna, B. & Soto, D. (2011). Body condition indices as a rapid assessment of the abundance of introduced salmonids in oligotrophic lakes of southern Chile. *Lake and Reservoir Management* **27,** 61–69.

Arismendi, I., Penaluna, B., Dunham, J., García de Leaniz, C., Soto, D., Fleming, I., Gomez-Uchida, D., Gajardo, G., Vargas, P. & León-Muñoz, J. (2014). Differential invasion success of salmonids in southern Chile: patterns and hypotheses. *Reviews in Fish Biology and Fisheries* **24,** 919–994.

Arismendi, I., Soto, D., Penaluna, B., Jara, C., Leal, C. & León-Muñoz, J. (2009). Aquaculture, non-native salmonid invasions, and associated declines of native fishes in lakes of the northern Chilean Patagonia. *Freshwater Biology* **54,** 1135–1147.

Arratia, G. (1982). A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae, and Percillidae). *Senckenberg Naturforsch Gesellsch* **540,** 1–52.

Arratia, G., Rojas, G. & Chang, A. (1981). Géneros de peces de aguas continentales de Chile. *Publicaciones ocasionales Museo Nacional de Historia Natural, Santiago de Chile* **34,** 3–108.

Azpelicueta, M. M., Figueroa, D. E., Herrera, R. & Gosztonyi, A. E. (2001). The macrophthalmia stage of *Geotria australis* Gray, 1851 [Petromyzontiformes: Geotridae] in Argentina. *Neotropica* **47,** 81–84.

Báez, V. H., Aigo, J. C. & Cussac, V. E. (2011). Climate change and fish culture in Patagonia: present situation and perspectives. *Aquaculture Research* **42,** 787–796. doi: 10.1111/j.1365-2109.2011.02804.x

Baigún, C. R. (2001). Ecología pesquera de lagos y embalses patagónicos (Argentina). Doctoral thesis. Universidad de Buenos Aires, Argentina.

Baigún, C. & De Nichilo, A. (1985). Pesca experimental. III Parte. Páginas 66–130. In *Evaluación del potencial pesquero en seis lagos de la Provincia del Chubut* (Quirós, R., ed.), pp. 66–130. *Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Dirección de Recursos Marítimos y Pesca Continental, Provincia de ChubutInforme de Avance No 1.*

Baigún, C. & Ferriz, R. (2003). Distribution patterns of native freshwater fishes in Patagonia, Argentina. *Organisms, Diversity and Evolution* **3,** 151–159.

Baigún, C. & Marinone, M. C. (1995). Cold-temperate lakes of South America: do they fit northern hemisphere models? *Archiv für Hydrobiologie* **135,** 23–51.

Baigún, C. & Quirós, R. (1985). *Introducción de peces exóticos en la República Argentina*. INIDEP, Departamento de Aguas Continentales: Mar del Plata.

Baigún, C., Mugni, H. & Bonetto, C. (2006). Nutrient concentration and trophic state of small Patagonian Andean lakes. *Journal of Freshwater Ecology* **21,** 449–456.

Baigún, C., Oldani, N., Madirolas, A. & Álvarez Colombo, G. (2007). Assessment of fish yield in Patagonian lakes (Argentina): development and application of empirical models. *Transactions of the American Fisheries Society* **136,** 846–857.

Barletta, M., Jaureguizar, A. J., Baigún, C., Fontoura, N. F., Agostinho, A. A., Almeida-Val, V. M. F., Val, A. L., Torres, R. A., Jimenes-Segura, L. F., Giarrizzo, T., Fabré, N. N., Batista, V. S., Lasso, C., Taphorn, D. C., Costa, M. F., Chaves, P. T., Vieira, J. P. & Corrêa, M. F. M. (2010). Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. *Journal of Fish Biology* **76,** 2118–2176. doi: 10.1111/j.1095-8649.2010.02684.x

Barriga, J. P., Battini, M. A., Macchi, P. J., Milano, D. & Cussac, V. E. (2002). Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South American Andes. *New Zealand Journal of Marine and Freshwater Research* **36**, 349–363.

Barriga, J. P. & Battini, M. A. (2009). Ecological significances of ontogenetic shifts in the stream-dwelling catfish, *Hatcheria macraei* (Siluriformes, Trichomycteridae), in a Patagonian river. *Ecology of Freshwater Fish* **18,** 395–405.

Barriga, J. P., Battini, M. A., García-Asorey, M., Carrea, C., Macchi, P. J. & Cussac, V. E. (2012). Intraspecific variation in growth and morphology of landlocked *Galaxias maculatus* during the limnetic period of its life history. *Hydrobiologia* **679,** 27–41.

Barriga, J. P., Espinós, N. A., Chiarello-Sosa, J. M. & Battini, M. A. (2013*a*). The importance of substrate size and interstitial spacein the microhabitat selection by the stream-dwelling catfish *Hatcheria macraei* (Actinopterygii, Trichomycteridae). *Hydrobiologia* **705,** 191–206. doi: 10.1007/s10750-012-1398-0

Barriga, J., Chiarello-Sosa, M., Juncos, R. & Battini, M. (2015). Photo-identification and the effects of tagging on the Patagonian catfish *Hatcheria macraei*. *Environmental Biology of Fishes* **98,** 1163–1171. doi: 10.1007/s10641-014-0349-1

Barriga, J., Milano, D. & Cussac, V. (2013*b*). Variation in vertebral number and its morphological implication in the South American galaxiid, *Galaxias platei*. *Journal of Fish Biology* **83,** 1321–1333.

Barriga, J. P., Battini, M. A. & Cussac, V. E. (2007). Annual dynamics variation of landlocked *Galaxias maculatus* (Jenyns 1842) population in a northern Patagonia river: occurrence of juvenile upstream migration. *Journal of Applied Ichthyology* **23,** 128–135.

Battini, M. A., Unmack, P., Barriga, J. P., Johnson, J., Azpelicueta, M. & Cussac, V. (2008). *Morfometría geométrica y relaciones filogenéticas en Trichomycteridae (Pisces) de Cuyo y Patagonia*. Esquel: Primeras Jornadas de Ciencias Naturales en la Patagonia.

Beamud, G., Baffico, G., Pedrozo, F. & Díaz, M. (2013). First record of the invasive algae *Didymosphenia geminata* in the Lake Nahuel Huapi: Argentina, Patagonia. *Revista Chilena de Historia Natural* **86,** 493–496.

Behnke, R. J. (1992). *Native Trout of Western North America*. Bethesda, MD: American Fisheries Society.

Belk, M., Habit, E., Ortiz-Sandoval, J. J., Sobenes, C. & Combs, E. (2014). Ecology of *Galaxias platei* in a depauperate lake. *Ecology of Freshwater Fish* **23,** 615–621.

Bilby, R. E., Fransen, B. R., Bisson, P. A. & Walter, J. K. (1998). Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1909–1918.

Boy, C. C., Morriconi, E. & Calvo, J. (2007). Reproduction in puyen, *Galaxias maculatus* (Pisces: Galaxiidae), in the southernmost extreme of distribution. *Journal of Applied Ichthyology* **23,** 547–554.

Boy, C. C., Pérez, A. F., Lattuca, M. E., Calvo, J. & Morriconi, E. (2009). Reproductive biology of *Galaxias maculatus* (Jenyns 1842) in the Río Ovando, a high-latitude environment in southernmost Patagonia, Argentina. *Journal of Applied Ichthyology* **25,** 661–668.

Buria, L., Walde, S. J., Battini, M., Macchi, P. J., Alonso, M., Ruzzante, D. E. & Cussac, V. E. (2007). Movement of a South American perch *Percichthys trucha* in a mountain Patagonian lake during spawning and prespawning periods. *Journal of Fish Biology* **70,** 215–230.

Burridge, C. P., McDowall, R. M., Craw, D., Wilson, M. V. H. & Waters, J. M. (2012). Marine dispersal as a pre-requisite for Gondwanan vicariance among elements of the galaxiid fish fauna. *Journal of Biogeography* **39,** 306–321.

Busby, P. J., Wainwright, T. C., Bryant, G. J., Lierheimer, L., Waples, R. S., Waknitz, F. W. & Lagomarsino, I. V. (1996). Status review of west coast steelhead from Washington, Idaho, Oregon and California. *NOAA Technical Memorandum* **NMFS-NWFSC-27**.

Campos, H. & Gavilán, J. (1996). Diferenciación morfológica entre *Percichthys trucha* y *Percichthys melanops* (Perciformes: Percichthyiidae) entre 36° y 41° L.S. (Chile y Argentina) a través de análisis multivariado. *Gayana Zoología* **60,** 99–120.

Campos, H., Gavilán, J. F., Murillo, V. & Alarcón, P. (1996). Presencia de *Cheirodon australe* (Pisces: Characidae) en Lago Tarahuín (Isla Grande de Chiloé, 42–40_S, Chile) y su significado zoogeográfico. *Medio Ambiente* **13,** 69–79.

Carrea, C., Barriga, J. P., Cussac, V. E. & Ruzzante, D. E. (2012). Genetic and phenotypic differentiation among *Galaxias maculatus* populations in a Patagonian postglacial lake system. *Biological Journal of the Linnean Society* **107,** 368–382.

Carrea, C., Cussac, V. E. & Ruzzante, D. E. (2013). Genetic and phenotypic variation among *Galaxias maculatus* populations reflects contrasting landscape effects between northern and southern Patagonia. *Freshwater Biology* **58,** 36–49.

Chaloner, D. T. & Wipfli, M. S. (2002). Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. *Journal of the North American Benthological Society* **21,** 430–442.

Chapman, A., Morgan, D. L., Beatty, S. J. & Gillet, H. S. (2006). Variation in life history of land-locked lacustrine and riverine populations of *Galaxias maculatus* (Jenyns 1842) in Western Australia. *Environmental Biology of Fishes* **77,** 21–37.

Ciancio, J. E., Pascual, M. A., Lancelotti, J., Riva Rossi, C. M. & Botto, F. (2005). Natural colonization and establishment of a Chinook salmon (*Oncorhynchus tshawytscha*) population in the Santa Cruz River, an Atlantic basin of Patagonia. *Environmental Biology of Fishes* **74,** 217–225.

Ciancio, J. E., Pascual, M. A., Botto, F., Frere, E. & Iribarne, O. (2008*a*). Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. *Limnology and Oceanography* **53,** 788–798.

Ciancio, J. E., Pascual, M. A., Botto, F., Amaya-Santi, M., O'Neal, S., Riva Rossi, C. M. & Iribarne, O. O. (2008*b*). Stable isotope profiles of partially migratory salmonid populations in Atlantic rivers of Patagonia. *Journal of Fish Biology* **72,** 1708–1719.

Ciancio, J. E., Beauchamp, D. A. & Pascual, M. A. (2010). Marine effect of introduced salmonids: Prey consumption by exotic steelhead and anadromous brown trout in the Patagonian Continental Shelf. *Limnology and Oceanography* **55,** 2181–2192.

Cione, A. L. & Báez, A. M. (2007). Peces continentales y anfibios cenozoicos de Argentina: los últimos cincuenta años. *Ameghiniana* **11,** 195–220.

Cione, A. L., Azpelicueta, M. M., Casciotta, J. R. & Dozo, M. T. (2005). Tropical freshwater teleosts from Miocene beds of eastern Patagonia, southern Argentina. *Geobios* **38,** 29–42.

Cione, A. L., Reguero, M. A. & Acosta Hospitaleche, C. (2007). Did the continent and sea have different temperatures in the northern Antarctic peninsula during the middle Eocene? *Revista de la Asociación Geológica Argentina* **62,** 586–596.

Conover, D. O. (1990). The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Transactions of the American Fisheries Society* **119,** 416–430.

Consuegra, S., Phillips, N., Gajardo, G. & Garcia de Leaniz, C. (2011). Winning the invasion roulette: escapes from fish farms increase admixture and facilitate establishment of non-native rainbow trout. *Evolutionary Applications* **4,** 660–671.

Conte-Grand, C. (2012). El pejerrey patagónico, *Odontesthes hatcheri*: biología y potencialidades para su cultivo. Doctoral Thesis. Universidad Nacional del Sur. Bahía Blanca, Argentina.

Correa, C. & Gross, M. R. (2007). Chinook salmon invade southern South America. *Biological Invasions* **10,** 615–639.

Correa, C. & Hendry, A. P. (2012). Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. *Ecological Applications* **22,** 828–842.

Correa, C., Bravo, A. P. & Hendry, A. P. (2012). Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes. *Freshwater Biology* **57,** 1769–1781. doi: 10.1111/j.1365-2427.2012.02837.x

Crespi, B. J. & Teo, R. (2002). Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution* **56,** 1008–1020.

Crichigno, S. A., Battini, M. A. & Cussac, V. E. (2012). Early morphological variation and induction of phenotypic plasticity in Patagonian pejerrey. *Neotropical Ichthyology* **10,** 341–348.

Crichigno, S., Conte-Grand, C., Battini, M. & Cussac, V. (2013). Cephalic morphological variation in freshwater silversides, *Odontesthes hatcheri* and *Odontesthes bonariensis* in Patagonia: introgression and ecological relationships. *Journal of Fish Biology* **83,** 542–559.

Crichigno, S. A., Hattori, R. S., Strüssmann, C. A. & Cussac, V. (2014*a*). Morphological comparison of wild, farmed and hybrids of two South American silversides, *Odontesthes bonariensis* and *Odontesthes hatcheri*. *Aquaculture Research* **47**, 1797–1808. doi: 10.1111/are.12638

Crichigno, S. A., Battini, M. Á. & Cussac, V. E. (2014*b*). Diet induces phenotypic plasticity of *Percichthys trucha* (Valenciennes, 1833) (Perciformes, Percichthyidae) in Patagonia. *Zoologischer Anzeiger* **253,** 192–202.

Crozier, L. G., Hendry, A. P., Lawson, W., Quinn, T. P., Mantua, N. J., Battin, J., Shaw, R. G. & Huey, R. B. (2008). Potential responses to climate change in organisms withcomplex life histories: evolution and plasticity in Pacific salmon. *Evolutionary Applications* **1,** 252–270.

Cussac, V. & Ortubay, S. (2002). Gametogenesis and development of *Gymnocharacinus bergi* (Pisces, Characidae): reproductive mode relative to environmental stability. *Environmental Biology of Fishes* **63,** 289–297.

Cussac, V., Ortubay, S., Iglesias, G., Milano, D., Lattuca, M. E., Barriga, J. P., Battini, M. & Gross, M. (2004). The distribution of South American galaxiid fishes: the role of biological traits and post glacial history. *Journal of Biogeography* **31,** 103–122.

Cussac, V. E., Cervellini, P. M. & Battini, M. A. (1992). Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. *Environmental Biology of Fishes* **35,** 141–148.

Cussac, V. E., Ruzzante, D., Walde, S., Macchi, P. J., Ojeda, V., Alonso, M. F. & Denegri, M. A. (1998). Body shape variation of three species of *Percichthys* in relation to their coexistence in the Limay river basin, in Northern Patagonia. *Environmental Biology of Fishes* **53,** 143–153.

Cussac, V., Becker, L., Aigo, J., Conte-Grand, C., Blasetti, G., Cordero, P., Crichigno, S. & Nabaes, D. (2014). Abundance of native fishes, wild-introduced salmonids and escaped farmed rainbow trout in a Patagonian reservoir. *Lakes and Reservoirs: Research and Management* **19,** 1–12. doi: 10.1111/lre.12063

Cussac, V. E., Fernández, D. A., Gómez, S. E. & López, H. L. (2009). Fishes of southern South America: a story driven by temperature. *Fish Physiology and Biochemistry* **35,** 29–42. doi: 10.1007/s10695-008-9217-2

Depetris, P. J., Gaiero, D. M., Probst, J. L., Hartmann, J. & Kempe, S. (2005). Biogeochemical output and typology of rivers draining Patagonia's Atlantic seaboard. *Journal of Coastal Research* **21,** 835–844.

Deutsch, C., Sarmiento, J., Sigman, D. M., Gruber, N. & Dunne, J. (2007). Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* **445,** 163–167.

Donald, D. B. & Anderson, R. S. (1982). Importance of environment and stocking density for growth of rainbow trout in mountain lakes. *Transactions of the American Fisheries Society* **111,** 675–680.

Dyer, B. (2000). Systematic review and biogeography of the freshwater fishes of Chile. *Estudios Oceanológicos* **19,** 77–98.

Dyer, B. (2006). Symposium: biology and culture of silversides (pejerreyes). Systematic revision of the South American silversides (Teleostei, Atheriniformes). *Biocell* **30,** 69–88.

Elgueta, A., Gonzalez, J., Ruzzante, D. E., Walde, S. J. & Habit, E. (2013). Trophic interference by *Salmotrutta* on *Aplochiton zebra* and *Aplochiton taeniatus* in southern Patagonian lakes. *Journal of Fish Biology* **82,** 430–443.

Fernandez, D. A., Ciancio, J. E., Ceballos, S., Riva Rossi, C. & Pascual, M. A. (2010). Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum 1792) in the Beagle Channel, Tierra del Fuego: the onset of an invasion. *Biological Invasions* **12,** 2191–2197. doi: 10.1007/s10530-010-9731-x

Ferriz, R. A., Aramburu, W. S., Gómez, S. E. & Menni, R. C. (2001). Morphological difference in the *Galaxias maculatus* (Jenyns, 1842) population, an Osmeriform fish from Southern Argentina. *Bioikos* **15,** 83–89.

García de Leaniz, C., Gajardo, G. & Consuegra, S. (2010). From best to pest: changing perspectives on the impact of exotic salmonids in the southern hemisphere. *Systematics and Biodiversity* **8,** 447–459.

García, A., Jorde, K., Habit, E., Caamaño, D. & Parra, O. (2011). Downstream environmental effects of dam operations: changes in habitat quality for native fish species. *River Research and Application* **27,** 312–327.

Gayeski, N., McMillan, B. & Trotter, P. (2011). Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 498–510.

Gende, S. M., Edwards, R. T., Willson, M. F. & Wipfli, M. S. (2002). Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* **52,** 917–928.

Gómez, S. E. (1990). Some thermal ecophysiological observations on the catfish *Hatcheria macraei* (Girard 1855) (Siluriformes, Trichomycteridae). *Biota* **6,** 89–95.

Gonçalves, R. J., Souza, M. S., Aigo, J., Modenutti, B., Balseiro, E., Villafañe, V. E., Cussac, V. & Helbling, E. W. (2010). Responses of plankton and fish from temperate zones to UVR and temperature in a context of global change. *Ecología Austral* **20,** 129–153.

González, J. (2012). Distribución, estructura comunitaria y poblacional de Galáxidos en Patagonia: aspectos determinantes históricos y actuales amenazas para su conservación. Doctoral Thesis, Universidad de Concepción, Chile.

Goodwin, P., Jorde, K., Meier, C. & Parra, O. (2006). Minimizing environmental impacts of hydropower development: transferring lessons from past projects to a proposed strategy for Chile. *Journal of Hydroinformatics* **8,** 253–270.

Gosztonyi, A. E. (1988). Peces del río Chubut inferior, Argentina. *Physis* **B46,** 41–50.

Gosztonyi, A. E. & McDowall, R. M. (1974). Zoogeography of *Galaxias maculatus* in South America. *Copeia* **1974,** 978–979.

Guerrero, C. A. (1984). Edad y crecimiento en la perca criolla bocona "*Percichthys colhuapiensis*" Mac Donagh, 1955 (Osteichthyes, Percichthydae). *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Zoología* **4,** 95–108.

Guerrero, C. A. (1991). Crecimiento de la perca boca chica (*Percichthys trucha*) en cuatro ambientes leníticos patagónicos. In *Trabajos presentados al segundo taller internacional sobre ecología y manejo de peces en lagos y embalses* (Vila, I., ed.), pp. 47–71. *COPESCAL Documento Técnico* **9.**

Habit, E., Gonzalez, J., Ruzzante, D. E. & Walde, S. J. (2012). Native and introduced fish species richness in lacustrine Chilean Patagonia: inferences on species invasion from salmonid free lakes. *Diversity and Distributions* **18,** 1153–1165.

Habit, E., Piedra, P., Ruzzante, D., Walde, S., Belk, M., Cussac, V., Gonzalez, J. & Colin, N. (2010). Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecology and Biogeography* **19,** 697–710. doi: 10.1111/j.1466-8238.2010.00541.x

Habit, E., Belk, M., Victoriano, P. & Jaque, E. (2007). Spatio-temporal distribution patterns and conservation of fish assemblages in a Chilean coastal river. *Biodiversity and Conservation* **16,** 3179–3191.

Habit, E., Dyer, B. & Vila, I. (2006). Estado de conocimiento de los peces dulceacuícolas de Chile. *Gayana* **70,** 100–112.

Hartmann, J. (1977). Changes in fishes with cultural lake eutrophication. *Schweizerische Zeitschrift für Hydrologie* **39,** 243–254.

Helfield, J. M. & Naiman, R. J. (2001). Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* **82,** 2403–2409.

Hendry, A. P. & Kinnison, M. T. (1999). The pace of modern life: measuring rates of contemporary evolution. *Evolution* **53,** 1637–1653.

Hilderbrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M. & Servheen, C. (1999). The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* **77,** 132–138.

Hopelain, J. S. (1998). Age, Growth, and Life History of Klamath River Basin Steelhead Trout *(Oncorhynchus mykiss irideus*) as Determined from Scale Analysis. Sacramento, CA: The Resources Agency, Department of Fish and Game, Inland Fisheries Division.

Hualde, J. P., Torres, W. D. C., Moreno, P., Ferrada, M., Demicheli, M. A., Molinari, L. J. & Luquet, C. M. (2011). Growth and feeding of Patagonian pejerrey *Odontesthes hatcheri* reared in net cages. *Aquaculture Research* **42,** 754–763.

Hubert, N. & Renno, J. F. (2006). Historical biogeography of South American freshwater fishes. *Journal of Biogeography* **33,** 1414–1436.

Huey, R. B., Gilchrist, G. W. & Hendry, A. P. (2005). Using invasive species to study evolution: case studies with *Drosophila* and salmon. In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (Sax, D. F., Stachowicz, J. J. & Gaines, S. D., eds), pp. 139–164. Sunderland, MA: Sinauer Associates Inc.

Hulme, P. E. (2005). Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology* **42,** 784–794.

Ibarra, J., Habit, E., Solis, K. & Barra, R. (2011). Juveniles de Salmón Chinook (*Oncorhynchus tshawytscha*) en Ríos y Lagos de la Patagonia Chilena. *Gayana* **75,** 90–99.

Jönsson, M., Ranåker, L., Nicolle, A., Ljungberg, P., Fagerberg, T., Hylander, S., Jephson, T., Lebret, K., von Einem, J., Hansson, L., Nilsson, P. A., Balseiro, E. & Modenutti, B. (2011). Glacial clay affects foraging performance in a Patagonianfish and cladoceran. *Hydrobiologia* **663,** 101–108. doi: 10.1007/s10750-010-0557-4

Juncos, R., Milano, D., Macchi, P. J., Alonso, M. F. & Vigliano, P. H. (2011). Response of rainbow trout to different food web structures in Northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* **140,** 415–428.

Juncos, R., Beauchamp, D. A. & Vigliano, P. H. (2013). Modelling prey consumption by native and non-native piscivorous fishes: implications for competition and impacts on shared prey in an ultraoligotrophic lake in Patagonia. *Transactions of the American Fisheries Society* **142,** 268–281.

Juncos, R., Milano, D., Macchi, P. J. & Vigliano, P. H. (2015). Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake. *Hydrobiologia* **747,** 53–67. doi: 10.1007/s10750-014-2122-z

Körber, S. & Ortubay, S. (2004). Literature published on the naked tetra *Gymnocharacinus bergii* (Characiformes: Characidae: Gymnocharacinae) from Patagonia, Argentina. *Zeitschrift für Fischkunde* **7,** 5–8.

Lafarga, A. M. & Guerrero, C. A. (1991). Crecimiento de la trucha arco iris (*Oncorhynchus mykiss*) en ambientes patagónicos. In *Trabajos presentados al segundo taller internacional sobre ecología y manejo de peces en lagos y embalses* (Vila, I., ed.), pp. 72–90. *COPESCAL Documento Técnico* **9**.

Lattuca, M. E., Battini, M. A. & Macchi, P. J. (2008*a*). Trophic interactions among native and introduced fishes in a northern Patagonian oligotrophic lake. *Journal of Fish Biology* **72,** 1306–1320.

Lattuca, M. E., Brown, D., Castiñeira, L., Renzi, M., Luizon, C., Urbanski, J. & Cussac, V. (2008*b*). Reproduction of landlocked *Aplochiton zebra* Jenyns (Pisces, Galaxiidae). *Ecology of Freshwater Fish* **17,** 394–405. doi: 10.1111/j.1600-0633.2008.00292.x

Lattuca, M. E., Ortubay, S., Battini, M. A., Barriga, J. P. & Cussac, V. E. (2007). Presumptive environmental effects on body shape of *Aplochiton zebra* (Pisces, Galaxiidae) in Northern Patagonian lakes. *Journal of Applied Ichthyology* **23,** 25–33.

Lindegren, M., Vigliano, P. & Nilsson, P. A. (2012). alien invasions and the game of hide and seek in Patagonia. *PLoS ONE* **7,** e44350. doi: 10.1371

Liotta, J. (2006). Distribución geográfica de los peces continentales de la República Argentina. *Serie Documentos N3, ProBiota*. La Plata: Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Lohr, S. C., & Bryant, M. D. (1999). Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. *General Technical Report PNW-GTR-407*. Portland, OR: U.S. Forest Service, Pacific Northwest Research Station.

Lopez Cazorla, A. & Sidorkewicj, N. (2008). Age and growth of the largemouth perch *Percichthys colhuapiensis* in the Negro river, Argentine Patagonia. *Fishery Research* **92,** 169–179.

Lopez Cazorla, A. & Sidorkewicj, N. (2011). Age, growth and reproduction in creole perch (*Percichthys trucha*) in the Negro River, Argentinean Patagonia. *Journal of Applied Ichthyology* **27,** 30–38.

López, H. L., Menni, R. C., Donato, M. & Miquelarena, A. M. (2008). Biogeographical revision of Argentina (Andean and Neotropical Regions): an analysis using freshwater fishes. *Journal of Biogeography* **35,** 1564–1579.

Lozada, M., Ortubay, S. & Cussac, V. (2000). Fright reaction in *Gymnocharacinus bergi* (Pisces, Characidae), a relict fish from Patagonia. *Environmental Biology of Fishes* **58,** 227–232.

Mac Crimmon, H. R. (1971). World distribution of rainbow trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada* **26,** 1699–1725.

Macchi, P. J., Cussac, V. E., Alonso, M. F. & Denegri, M. A. (1999). Predation relationships between introduced salmonids and the native fish fauna in lakes and reservoirs in Northern Patagonia. *Ecology of Freshwater Fish* **8,** 227–236.

Macchi, P. J., Pascual, M. A. & Vigliano, P. H. (2007). Differential piscivory of the native *Percichthys trucha* and exotic salmonids upon the native forage fish *Galaxias maculatus* in Patagonian Andean lakes. *Limnologica* **37,** 76–87.

Macchi, P. J., Vigliano, P. H., Pascual, M. A., Alonso, M., Denegri, M. A., Milano, D., García Asorey, M. & Lippolt, G. (2008). Historical policy goals for fish management in northern continental Patagonia Argentina: a structuring force of actual fish assemblages? *American Fisheries Society Symposium* **49,** 331–348.

Marini, T. L. (1936). Los salmónidos en nuestro Parque Nacional Nahuel Huapi. *Sociedad Científica Argentina* **121,** 1–24.

Matuszek, J. E. (1978). Empirical predictions of fish yields of large North American lakes. *Transactions of the American Fisheries Society* **107,** 385–396.

McDowall, R. M. (1971). The galaxiid fishes of South America. *Zoological Journal of the Linnean Society* **50,** 33–73.

McDowall, R. M. (2006). Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries* **16,** 233–422.

McMillan, J. (2008). What is the importance of repeat spawners, including return timing, spawn timing, differential sex ratio, and fecundity? What is a good level of repeat spawners in a population? How do you manage to protect kelts? Summary of the Eleventh Pacific Coast Steelhead Management Meeting. Boise, Idaho, pp 35.

Mehan, W. R. (1991). Influences of forest and rangeland management on salmonid fishes and their habitats. *American Fisheries Society Special Publication* **19**, Bethesda, Maryland.

Menni, R. C. (2004). Peces y ambientes en la Argentina continental. *Monografías del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* **5,** 1–316.

Menni, R. C. & Gómez, S. E. (1995). On the habitat and isolation of *Gymnocharacinus bergi* (Osteichthyes: Characidae). *Environmental Biology of Fishes* **42,** 15–23.

Milano, D., Cussac, V. E., Macchi, P. J., Ruzzante, D. E., Alonso, M. F., Vigliano, P. H. & Denegri, M. A. (2002). Predator associated morphology in *Galaxias platei* in Patagonian lakes. *Journal of Fish Biology* **61,** 138–156.

Miserendino, M. L., Brand, C. & Di Prinzio, C. Y. (2008). Assessing urban impacts on water quality, benthic communities and fish in streams of the Andes Mountains, Patagonia (Argentina). *Water, Air, and Soil Pollution* **194,** 91–110.

Miserendino, M. L., Casaux, R., Archangelsky, M., Di Prinzio, C. Y., Brand, C. & Kutschker, A. M. (2011). Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. *Science of the Total Environment* **409,** 612–624.

Montory, M., Habit, E., Bahamonde, P., Grimalt, J. O., Saez, K., Rudoph, I. & Barra, R. (2011). Polychlorinated biphenyls in farmed and wild *Onchorhynchus kisutch* and *Onchorhynchus mykiss* from the Chilean Patagonia. *Environmental Science Pollution Research* **18,** 629–637.

Montory, M., Habit, E., Fernández, P., Grimalt, J. O. & Barra, R. (2010). PCBs and PBDEs in Wild Chinook Salmon (*Oncorhynchus tshawytscha*) in the Northern Patagonia, Chile. *Chemosphere* **78,** 1193–1199.

Muñoz-Ramírez, C. P., Unmack, P. J., Habit, E., Johnson, J. B., Cussac, V. E. & Victoriano, P. (2014). Phylogeography of the ancient catfish family Diplomystidae: biogeographic, systematic, and conservation implications. *Molecular Phylogenetics and Evolution* **73,** 146–160.

Muñoz-Ramírez, C., Jara, A., Beltrán-Concha, M., Zúñiga-Reinoso, A., Victoriano, P. & Habit, E. (2010). Distribución de la familia Diplomystidae (Pisces: Siluriformes) en Chile: nuevos registros. *Boletín de Biodiversidad de Chile* **4,** 6–17.

Naiman, R. J., Bilby, R. E., Schindler, D. E. & Helfield, J. M. (2002). Pacific Salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5,** 399–417.

Narum, S. R., Hatch, D., Talbot, A. J., Moran, P. & Powell, M. S. (2008). Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Biology* **72,** 45–60.

Oglesby, T. T., Leach, J. H. & Forney, J. (1987). Potential *Stizostedion* yield as a function of chlorophyll concentration with special reference to Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* **44,** 166–170.

Ortubay, S. G. (1998). Biología de *Gymnocharacinus bergi* Steindachner, 1903 (Pisces, Characidae). Doctoral Thesis, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina.

Ortubay, S. G., Gómez, S. E. & Cussac, V. E. (1997). Lethal temperatures of a Neotropical fish relic in Patagonia, the scale-less characinid *Gymnocharacinus bergi*. *Environmental Biology of Fishes* **49,** 341–350.

Ortubay, S. & Cussac, V. (2000). Threatened fishes of the world: *Gymnocharacinus bergi* Steindachner, 1903 (Characidae). *Environmental Biology of Fishes* **58,** 144.

Pankhurst, N. W. & King, H. R. (2010). Temperature and salmonid reproduction: implications for aquaculture. *Journal of Fish Biology* **76,** 69–85.

Pascual, M. A. & Ciancio, J. E. (2007). Introduced anadromous salmonids in Patagonia: risk, uses, and a conservation paradox. In *Ecological and Genetic Implications of Aquaculture Activities* (Bert, T. M., ed). New York, NY: Springer.

Pascual, M. A., Bentzen, P., Riva Rossi, C. M., Mackey, G., Kinnison, M. & Walker, R. (2001). First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. *Transactions of the American Fisheries Society* **130,** 53–67.

Pascual, M., Macchi, P., Urbanski, J., Marcos, F., Riva Rossi, C., Novara, M. & Dell´Archiprete, P. (2002). Evaluating potential effects of exotic freshwater fish from incomplete species presence–absence data. *Biological Invasions* **4,** 101–113.

Pascual, M. A., Cussac, V., Dyer, B., Soto, D., Vigliano, P., Ortubay, S. & Macchi, P. (2007). Freshwater fishes of Patagonia in the 21st century after a hundred years of human settlement, species introductions, and environmental change. *Aquatic Ecosystem Health & Management* **10,** 212–227.

Pascual, M. A., Lancelotti, J., Ernst-Elizalde, B., Ciancio, J. E., Aedo-Marchant, E. & Garcia-Asorey, M. (2009). Scale, connectivity, and incentives in the introduction and management of non-native species: the case of exotic salmonids of Patagonia. *Frontiers in Ecology and Environment* **7,** 533–540.

Pedrozo, F., Chilrud, S., Temporetti, P. & Diaz, M. (1993). Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39·5°-42°S, 71°W)(Rep. Argentina). *International Association of Theoretical and Applied Limnologie* **25,** 207–214.

Quinn, T. P., Seamons, T. R., Vøllestad, L. A. & Duffy, E. (2011). Effects of growth and reproductive history on the egg size-fecundity trade-off in steelhead. *Transactions of the American Fisheries Society* **140,** 45–51.

Quinn, T. P. (2005). *The Behaviour and Ecology of Pacific Salmon and Trout*. Seattle, WA: University Press.

Quinn, T. P., Kinnison, M. T. & Unwin, M. J. (2001). Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: Pattern, Rate and Process. *Genetica* **112/113,** 493–513.

Quirós, R. (1991). Factores que afectan la distribución de salmónidos en Argentina. *COPESCAL, FAO, Documento Técnico* **9,** 163–173.

Quirós, R. & Baigún, C. (1984). Prospección pesquera en 33 lagos y embalses patagónicos. Taller internacional sobre ecología y manejo de peces patagónicos. *COPESCAL, FAO, Documento Técnico* **4,** 159–179.

Quirós, R., Cuch, S. & Baigún, C. (1986). Relación entre abundancia de peces y ciertas propiedades físicas, químicas y biológicas, en lagos y embalses patagónicos (Argentina). *COPESCAL, FAO, Documento Técnico* **4,** 180–186.

Rechencq, M., Sosnovsky, A., Macchi, P. J., Alvear, P. A. & Vigliano, P. H. (2011). Extensive diel fish migrations in a deep ultraoligotrophic lake of Patagonia Argentina. *Hydrobiologia* **658,** 147–161. doi: 10.1007/s10750-010-0458-6

Rechencq, M., Vigliano, P. H., Macchi, P. J. & Lippolt, G. E. (2014). Fish distribution patterns and habitat availability in lakes Moreno Este and Moreno Oeste, Patagonia, Argentina. *Limnologica* **49,** 73–83.

Ringuelet, R. A., Arámburu, R. H. & Alonso de Arámburu, A. (1967). *Los peces argentinos de agua dulce*. La Plata: Comisión de Investigaciones Científicas de la Provincia de Buenos Aires.

Riva Rossi, C. M. (2004). *Origen y desarrollo de historias de vida alternativas en poblaciones introducidas de trucha arco iris (Oncorhynchus mykiss) en Patagonia.* Doctoral thesis. Universidad Nacional del Comahue, Bariloche Argentina.

Riva Rossi, C. M., Pascual, M. A., Aedo Marchant, E., Basso, N., Ciancio, J. E., Mezga, B., Fernández, D. A. & Ernst-Elizalde, B. (2012). The invasion of Patagonia by Chinook salmon (*Oncorhynchustshawytscha*): inferences from mitochondrial DNA patterns. *Genetica* **140,** 439–453. doi: 10.1007/s10709-012-9692-3

Riva Rossi, C., Pascual, M. A., Babaluk, J. A., García-Asorey, M. & Halden, N. M. (2007). Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. *Journal of Fish Biology* **70,** 1780–1797.

Riva Rossi, C. M., Arguimbau, M. & Pascual, M. A. (2003). The spawning migration of anadromous rainbow trout in the Santa Cruz River, Patagonia (Argentina) through radio - tracking. *Ecología Austral* **13,** 151–159.

Riva Rossi, C. M., Lessa, E. P. & Pascual, M. A. (2004). Origins of introduced rainbow trout in the Santa Cruz River as inferred by mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1095–1101.

Ruiz, A. E. (2002). Biología del pejerrey patagónico, *Odontesthes hatcheri* (Eigenmann, 1909), Dyer, 1993, en el embalse Florentino Ameghino, Chubut, Argentina. PhD thesis, Facultad de Ciencias Exactas, Fiscias y Naturales Universidad Nacional de Cordoba, Argentina.

Ruzzante, D. E., Walde, S. J., Cussac, V. E., Dalebout, M. L., Seibert, J., Ortubay, S. & Habit, E. (2006). Phylogeography of the Percichthyidae (Pisces) in Patagonia: roles of orogeny, glaciation, and volcanism. *Molecular Ecology* **15,** 2949–2968. doi: 10.1111/j.1365-294X.2006.03010.x

Ruzzante, D. E., Walde, S. J., Macchi, P. J., Alonso, M. & Barriga, J. P. (2011). Phylogeography and phenotypic diversification in the Patagonian fish *Percichthys trucha*: the roles of Quaternary glacial cycles and natural selection. *Biological Journal of the Linnean Society* **103,** 514–529.

Ruzzante, D. E., Walde, S. J., Gosse, J. C., Cussac, V. E., Habit, E., Zemlak, T. S. & Adams, E. D. M. (2008). Climate control on ancestral population dynamics: insight from Patagonian fish phylogeography. *Molecular Ecology* **17,** 2234–2244.

Ryder, R. A. (1965). A method for estimating the potential fish production of north-temperate lakes. *Transactions of the American Fisheries Society* **94,** 214–218.

Ryder, R. A. (1978). Fish yield assessment of large lakes and reservoirs. A prelude to management. In *Ecology of Freshwater Fish Production* (Gerking, S. D., ed), pp. 403–423. Oxford: Blackwell Scientific Publications.

Ryder, R. A. & Kerr, S. R. (1978). The adult walleye (*Stizostedion v. vitreum*) in the percid community: a niche definition based on feeding behaviour and food specificity. *American Fisheries Society Special Publication* **11,** 39–51.

Ryder, R. A., Kerr, S. K., Loftus, K. H. & Regier, H. A. (1974). The morphoedaphic index, a fish yield estimator-review and evaluation. *Journal of the Fisheries Research Board of Canada* **31,** 663–688.

Salo, E. O. & Cundy, T. W. (eds) (1987). Streamside management: forestry and fishery interactions. *University of Washington, Contribution* **57**.

Savvaitova, K. A., Kuzishchin, K. V. & Maximov, S. V. (1999). Kamchatka steelhead: population trends and life history variations. In *Sustainable Fisheries Management: Pacific Salmon* (Knudsen, E. E., ed), pp. 195–206. New York, NY: Lewis Publishers.

Schindler, D. E., Scheuerell, M. D., Moore, J. W., Gende, S. M., Francis, T. B. & Palen, W. J. (2003). Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and Environment* **1,** 31–37.

Schlesinger, D. & Regier, H. A. (1982). Climatic and morphoedaphic indices of fish yields from natural lakes. *Transactions of the American Fisheries Society* **111,** 141–150.

Segura, P. (2011). A slimy invader blooms in the rivers of Patagonia. *Science* **331,** 18. doi: 10.1126/science.331.6013.18

Shuter, B. J. & Post, J. R. (1990). Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* **119,** 314–336.

Simon, K. S. & Townsend, C. R. (2003). Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology* **48,** 982–994.

Somoza, G. M., Miranda, L. A., Berasain, G. E., Colautti, D., Remes, L. M. & Strüssmann, C. A. (2008). Historical aspects, current status and prospects of pejerrey aquaculture in South America. *Aquaculture Research* **39,** 784–793.

Soto, D., Arismendi, I., Di Prinzio, C. & Jara, F. (2007). Establishment of Chinook salmon (*Oncorhynchus tshawytscha*) in Pacific basins of southern South America and its potential ecosystem implications. *Revista Chilena de Historia Natural* **80,** 81–98.

Soto, D., Arismendi, I., González, J., Sanzana, J., Jara, F., Jara, C., Guzman, E. & Lara, A. (2006). Sur de Chile, país de truchas y salmones: patrones de invasión y amenazas para las especies nativas. *Revista Chilena de Historia Natural* **79,** 97–117.

Strüssmann, C. A., Saito, T., Usui, M., Yamada, H. & Takashima, F. (1997). Thermal thresholds and critical period of thermolabile sex determination in two atherinid fishes, *Odontesthes bonariensis* and *Patagonina hatcheri*. *The Journal of Experimental Zoology* **278,** 167–177.

Turner, K. J., Fogwill, C. J., McCulloch, R. D. & Sugden, D. E. (2005). Deglaciation of the eastern flank of the North Patagonian Icefield and associated continental-scale lake diversions. *Geografiska Annaler* **87A**, 363–374.

U.S. Fish Commission (1904–1938). *Report of the Commissioner. Volumes 1904 through1938*. Washington, DC: US Government Printing Office.

Unmack, P. J., Bennin, A. P., Habit, E. M., Victoriano, P. F. & Johnson, J. B. (2009*a*). Impact of ocean barriers, topography, and glaciation on the phylogeography of the catfish *Trichomycterus areolatus* (Teleostei: Trichomycteridae) in Chile. *Biological Journal of the Linnean Society* **97,** 876–892.

Unmack, P. J., Habit, E. M. & Johnson, J. B. (2009*b*). New records of *Hatcheria macraei* (Siluriformes, Trichomycteridae) from Chilean Province. *Gayana* **73,** 102–110.

Unmack, P. J., Barriga, J. P., Battini, M. A., Habit, E. M. & Johnson, J. B. (2012). Phylogeography of the catfish *Hatcheria macraei* revealsa negligible role of drainage divides in structuringpopulations. *Molecular Ecology* **21,** 942–959.

Vigliano, P. H., Macchi, P. J., Denegri, M. A., Alonso, M. F., Milano, D., Lippolt, G. & Padilla, G. (1999). Un diseño modificado de calado de redes agalleras para estudios cuali-cuantitativos de peces por estratos de profundidad en lagos araucanos. *Natura Neotropicalis* **30,** 1–12.

Vigliano, P. H., Macchi, P. J., Alonso, M., Denegri, M. A., García Asorey, M. I. & Lippolt, G. (2008*a*). Gill net and hydroacoustic fish resource evaluation of an ultraoligotrophic lake of Northern Patagonia Argentina. *American Fisheries Society Symposium* **49,** 1765–1768.

Vigliano, P. H., Beauchamp, D. A., Milano, D., Macchi, P. J., Alonso, M. F., García Asorey, M. I., Denegri, M. A., Ciancio, J. E., Lippolt, G., Rechencq, M. & Barriga, J. P. (2009). Quantifying predation on galaxiids and other native organisms by introduced rainbow trout in an ultraoligotrophic lake in Northern Patagonia, Argentina: a bioenergetics modelling approach. *Transactions of the American Fisheries Society* **138,** 1405–1419.

Vigliano, P. H., Macchi, P. J., Alonso, M., Denegri, M. A., Asorey, M. G. & Lippolt, G. (2008*b*). Gill net and hydroacoustic fish resource evaluation of an ultraoligotrophic lake of Northern Patagonia Argentina. *American Fisheries Society Symposium* **49,** 1725–1747.

Vince, G. (2010*a*). Dams for Patagonia. *Science* **23,** 382–385.

Vince, G. (2010*b*). A craving for hydropower. *Science* **23,** 384.

Wegrzyn, D. & Ortubay, S. (2009*a*). *Salmónidos en Patagonia*, Vol. I. Bariloche: Mar del Plata.

Wegrzyn, D. & Ortubay, S. (2009*b*). *Salmónidos en Patagonia*, Vol. II. Bariloche: Mar del Plata.

Wipfli, M. S., Hudson, J. P., Chaloner, D. T. & Caouette, J. P. (1999). Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 1600–1611.

Withler, R. E. (1966). Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific coast of North America. *Journal of the Fisheries Research Board of Canada* **23,** 365–393.

Young, K. A., Dunham, J. B., Stephenson, J. F., Terreau, A., Thailly, A. F., Gajardo, G. & Garcia de Leaniz, C. (2010). A trial of two trouts: comparing the impacts of rainbow and brown trout on a native galaxiid. *Animal Conservation* **13,** 399–410.

Young, W. D. & Heimbuch, D. G. (1982). Another consideration of the morphoedaphic index. *Transactions of the American Fisheries Society* **111,** 151–153.

Zemlak, T. S., Habit, E. M., Walde, S. J., Battini, M. A., Adams, E. D. M. & Ruzzante, D. E. (2008). Across the southern Andes on fin: glacial refugia, drainage reversals and a secondary contact zone revealed by the phylogeographical signal of *Galaxias platei* in Patagonia. *Molecular Ecology* **17,** 5049–5061. doi: 10.1111/j.1365-294X.2008.03987.x

Zemlak, T. S., Habit, E. M., Walde, S. J., Carrea, C. & Ruzzante, D. E. (2010). Surviving historical Patagonian landscapes and climate: molecular insights from *Galaxias maculatus*. *BMC Evolutionary Biology* **10,** 67.

Zemlak, T. S., Walde, S. J., Habit, E. M. & Ruzzante, D. E. (2011). Climate-induced changes to the ancestral population size of two Patagonian galaxiids: the influence of glacial cycling. *Molecular Ecology* **20,** 5280–5294. doi: 10.1111/j.1365-294X.2011.05352.x

Electronic Reference

Hatch, D. R., Branstetter, R. D., Whiteaker, J., Blodgett, J., Bosch, B., Fast, D., & Newsome, T. (2004). Kelt reconditioning: a research project to enhance iteroparity in Columbia Basin steelhead (*Oncorhynchus mykiss*). *Annual Report to U.S. Department of Energy, Bonneville Power Administration, Project No. 2000–017.* Portland, OR: Bonneville Power Administration. Available at http://www.critfc.org/wp-content/uploads/2015/06/04_08.pdf (last accessed 29 March, 2016).

López, H., Pérez, C., Kacoliris, F., Petracci, P., Gosztonyi, A., Povedano, H. & Miquelarena, A. (2013). *¿Qué implicancias tiene la presencia de* Cheirodon interruptus *en la Meseta de Somuncurá? 3° Simposio Argentino de Ictiología. Santa Fé. Argentina.* Available at http://www.conicet.gov.ar/new_scp/detalle.php?keywords=&id=05424&inst=yes&congresos=yes&detalles=yes&congr_id=2067167 (last accessed 29 March, 2016).