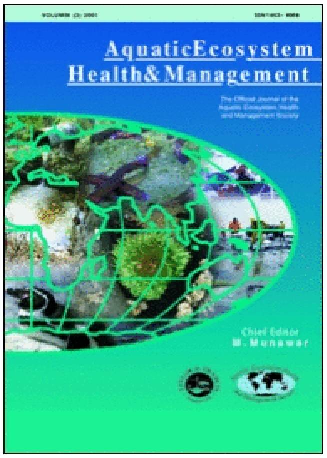

Aquatic Ecosystem Health & Management

Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change

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Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change

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We review the status of the freshwater fish fauna of Patagonia, an assemblage with 26 native species, comprising fishes of Gondwanan origin, marine dispersants, and oceanic elements of local origin. Several processes, old and new, have shaped the landscape of Patagonia and its fauna: a Gondwanan heritage, the Andes uplifting, Pleistocene ice, volcanic activity, introduction of exotic fishes, mostly Salmonids, and climate change. While there is a significant tradition of taxonomic work on native fish species, research on life history, trophic relationships, and community structure has started to emerge only in the last 15 years. Most studies were conducted in oligotrophic lakes of the Andes; while fauna of streams remains poorly observed. While documentation of impacts by salmonids is scarce, there is some compelling evidence indicating that freshwater communities have been significantly shaped by exotic fish. Impacts by exotic species appear to be dependent on temperature on the east side of the Andes, and land use and watershed perturbation on the west side.

In general, freshwater habitat conditions and how they affect fishes are poorly studied. In lakes, habitat complexity and its specialized use by native fishes may have ameliorated the impact by introduced salmonids. Although impacts on rivers abound, led by dam construction, the relationship between stream habitat integrity and native species health is still poorly understood. The future of freshwater resources will largely depend on how able we are to inform managers, the general public and colleagues about their value and the costs of not taking action. But current research capacity is insufficient to deal with most demands because of limitations in people, resources and baseline information. To support our claims, we need to promote regional assessments of freshwater resources and of major threats to their integrity, the building blocks of a regional agenda for their sustainable use.

Keywords: freshwater resources, impacts, research, management, legislation

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Introduction

In this paper we describe the freshwater fish fauna of Patagonia (Table 1), the southern tip of South America shared by Chile and Argentina (Figure 1). This fauna is made up by a small and unique group of indigenous species, and several exotic fishes, mostly salmonids (Dyer, 2000a; López et al., 2003; Menni, 2004).

We provide an overview of freshwater fish science in Patagonia, including a description of research and major gaps of knowledge for different taxonomic groups of fishes, as well as the development of freshwater fisheries and habitat studies. We then discuss the legislative framework and management problems surrounding freshwater fishes. We conclude with a critical view of freshwater fish science and management in the region.

An overview of freshwater resources, fish fauna, and fisheries of Patagonia

Patagonia is over 1.4 million km^2, or about one third of the area of Chile and Argentina combined, but only 5% of their populations (about 1.5 million people in Argentina and 1 million in Chile) inhabit the region. Ten of the freshwater ecoregions identified by Olson et al. (1998), grouped in the Southern Chile and Patagonia Complexes, comprise the freshwater resources of the region. Oligotrophic lakes and streams dominate the Andean and Pacific sectors (Modenutti et al., 1998a,b; Soto, 2002) and glacial fields occupy vast areas south of 47°S. A few major rivers flow east of the Andes, across the steppe, and into the Atlantic Ocean. The major Pacific drainages in the region are, from north to south, the Puelo (670m^{3}sec^{-1}, average flow), Yelcho (363), Palena (700), Cisnes (700), Aisén (628), Baker (875), and Pascua (574) rivers (Figure 1). The major Atlantic drainages in the region are, from north to south, the Colorado (148m^3 sec^{-1}), Negro (845), Chubut (48), Santa Cruz (698), Gallegos (35) and Grande (45) rivers (Figure 1). Six of these basins (Puelo, Yelcho, Palena, Baker, Gallegos and Grande) are shared by Chile and Argentina.

The native Patagonian freshwater fish fauna is small: 26 species, comprising fishes of Gondwanan origin (siluriforms and characids), marine dispersants (galaxiids), and oceanic elements (percichthyids, atherinopsids and mugilids) of local

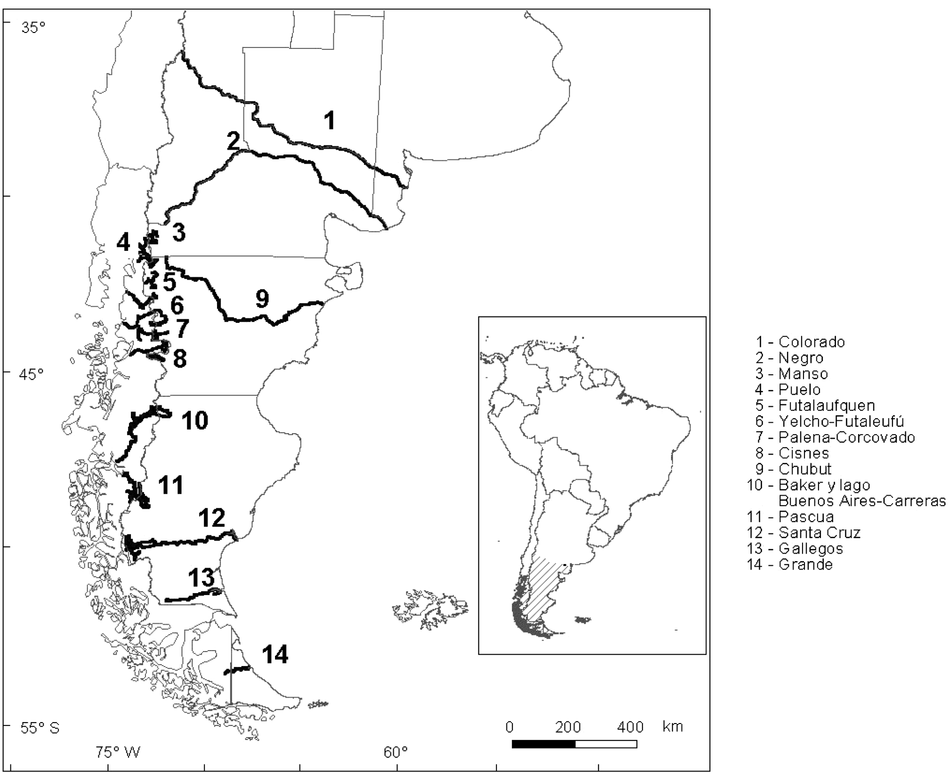

Figure 1. Patagonia and major river basins.

Table 1. Freshwater fish species of Patagonia. Austral (A), Brazilian (B), Andean-Cuyean (AN), Marine (M) and Exotic (E) origins were considered. *= species endemic to the Patagonian Province.

Order	Family	Species	Origin
Petromyzontiformes	Petromyzontidae	Geotria australis Gray 1851	M A
		*Mordacia lapicida Gray 1851	M A
Cypriniformes	Cyprinidae	Cyprinus carpio Linnaeus 1758	E
Characiformes	Characidae	Astyanax eigenmanniorum (Cope 1894)	B
		Cheirodon interruptus (Jenyns 1842)	B
		*Gymnocharacinus bergii Steindachner 1903	B
		Oligosarcus jenynsii (Günther 1864)	B
Siluriformes	Diplomystidae	*Diplomystes cuyanus Ringuelet 1965	A
		*D. mesembrinus Ringuelet 1982	A
		*D. viedmensis MacDonagh 1931	A
	Callichthyidae	Corydoras paleatus (Jenyns 1842)	B
	Trichomycteridae	Hatcheria macraei (Girard 1855)	A
		Trichomycterus areolatus (Valenciennes 1840)	A
Osmeriformes	Galaxiidae	Aplochiton marinus Eigenmann 1928	A
		A. taeniatus Jenyns 1842	A
		A. zebra Jenyns 1842	A
		Galaxias maculatus (Jenyns 1842)	A
		G. platei (Steindachner 1898)	A
Salmoniformes	Salmonidae	Salvelinus fontinalis (Mitchill 1814)	E
		S. namaycush (Walbaum 1792)	E
		Salmo salar (Linnaeus 1758)	E
		S. trutta Linnaeus 1758	E
		Oncorhynchus masou (Brevoort 1856)	E
		O. mykiss (Walbaum 1792)	E
		O. kisutch (Walbaum 1792)	E
		O. tshawytscha (Walbaum 1792)	E
Atheriniformes	Atherinopsidae	*Odontesthes hatcheri (Eigenmann 1909)	A
		O. bonariensis (Valenciennes 1835)	B
		O. argentinensis (Valenciennes 1835)	M
Cyprinodontiformes	Poeciliidae	Cnesterodon decemmaculatus (Jenyns 1842)	B E
	Anablepidae	Jenynsia multidentata (Jenyns 1842)	B E
Mugiliformes	Mugilidae	Mugil liza Valenciennes 1836	M
Pleuronectiformes	Paralichthydae	Paralichthys brasiliensis Ranzani 1842	M
Perciformes	Percichthyidae	*Percichthys altispinis Regan 1905	A
		*P. colhuapiensis MacDonagh 1955	A
		*P. trucha (Valenciennes 1833)	A
		*P. vinciguerrae Perugia 1891	A
	Cichlidae	Crenicichla scottii Eigenmann 1907	B E

origin (Table 1). Several processes, old and new, have shaped the landscape and fauna of Patagonia: a Gondwanan heritage, the Andes uplifting, Pleistocene ice, volcanic activity, introduction of exotic fishes, and climate change. For instance, diplomystid species and probably *Galaxias platei* have a Gondwanan origin (Barriga et al., 2002; Cussac et al., 2004), whereas the isolation of *Percilia*, *Basilichthys, Bullockia* and *Brachygalaxias* species in the Pacific slope and several species pairs on both sides of the mountains (Dyer, 2000a; Cussac et al., 2004) are the result of the Andes uplift. The effects of Pleistocene ice on species distribution and the colonisation process of post glacial lakes left their footprint on the contemporary distribution of some galaxiid species (Cussac et al., 2004). The introduction of salmonids and other species have been shaping fish communities throughout the last 100 years (Macchi et al., 1999, 2005; Soto and Stockner, 1996). The balance between the native and the exotic salmonid fauna appears to be strongly dependent on temperature on the east side of the Andes (Quirós, 1991) while on the west side other features such as land use and watershed perturbation appear to be most important. This leads us to believe that climate change and human perturbations will continue shaping the fish fauna of Patagonia, not only through its direct effects on species, but also by facilitating competition and predation between native and exotic species (Cussac et al., 2004).

Another major characteristic of the Patagonian fish fauna is the paucity of planktivorous fishes, probably as a consequence of the ultra-oligotrophic nature of many lakes in the region as mean annual chlorophyll values are rarely over 2 μg l^{-1} and secchi disks readings are often over 15 m; therefore productivity seems to be based on the benthos rather than on the plankton (Soto, 2002). Planktivory seems to be restricted to larval fishes in most lakes and only the Patagonian silverside (*Odontesthes hatcheri*) and *Galaxias maculatus* could be considered partially zooplanktivorous fishes. Most species feed in the littoral zone or on the bottom, mainly on benthos. Perhaps because of this lack of planktonic support, the phenomenon of species pairs involving planktivorous-benthivorous fishes, common in postglacial lakes of the Northern Hemisphere (Taylor, 1999), is biased in Patagonia towards benthic-benthic ecotypes (Ruzzante et al., 2003; Soto and Stockner, 1996). Ontogenetic shifts in diet, correlated with shifts in habitat, have been documented for *O. hatcheri* and *G. maculatus* (Cervellini et al., 1993). Sympatric radiation involving only benthic fishes has been documented for *Percichthys* and only partially for *G. platei,* but has not been observed in *Diplomystes, Odontesthes* or *G. maculatus* (Milano et al., 2002; Ruzzante at al., 1998; Cussac et al., 1998).

Although indigenous people of Patagonia included freshwater fishes in their diet, at present fishing is almost entirely practiced as a recreational activity and largely for exotic salmonids. Of native species, only the Patagonian silverside, the "peladilla" (*Aplochiton*), and the perches of the family Percichthyidae have some sport-fishing value.

Commercial exploitation of wild fish populations is limited to a few artisanal gillnet fisheries on lakes of the Argentinean plateau east of the Andes, targeting exotic rainbow trout, and native silversides and perches. Commercial exploitation of inland fishes is not allowed anywhere in Chile. On the other hand, freshwater aquaculture production, small in Argentina, constitutes a very important activity in Chile. This production not only includes rainbow trout for consumption, but also the production of smolts for marine aquaculture in Chile, the second largest salmon producer in the world with a production of over 350 thousand tonne in 2004 (www.salmonchile.cl).

A common practice both in Chile and Argentina is the supplementation of salmonid wild populations with hatchery fish with the expectation of maintaining or augmenting the production that sustains freshwater fisheries. In Argentina, every province has a hatchery destined to produce salmonids (mostly rainbow trout and some brown trout) for supplementation. In Chile, the seeding of lakes and rivers with hatchery individuals is also a common practise.

Freshwater fish science in Patagonia

State of knowledge of freshwater fishes of Patagonia

Albeit still small and somewhat restricted in geographic and thematic coverage, research on Patagonian freshwater communities has been growing. While there is a significant tradition of taxonomic work on native fish species, research about life history, community structure, distribution, and trophic relationships among species has started to emerge only in the last 15 years.

There is practically no information related to the composition of native fish communities before the introduction of salmonids or throughout the history of salmonid establishment, a process characterized by shifting patterns of species preferences and geographic location of plantings (Macchi et al., 2005). There is, however, some compelling evidence indicating that the structure and functioning of freshwater communities have been significantly shaped by exotic fish species. On top of predation effects, the introduced fishes brought over a heavy trophic competition (Macchi et al., 1999; Campos, 1970b; Soto and Stockner, 1996). Yet, the impact of introduced species is highly confounded by shifting stocking practices, habitat alterations, climate change and fishing pressure (Cussac et al., 2005).

In the following sections we provide a summary of research performed for different fish taxa (Table 1).

Native fishes

Biological data about fishes of Patagonia were summarised by Ringuelet et al. (1967), Campos et al. (1998), Férriz et al. (1998), Dyer (2000a), Bello (2002), Pascual et al. (2002), López et al. (2003), Baigún and Férriz (2003), Cussac et al. (2004), Menni (2004), and López & Miquelarena (2005). Most of the studies were conducted in the oligotrophic lakes of the Andes, while fauna of streams remains poorly observed (but see Soto et al., 2006).

Characidae

The naked characin (*Gymnocharacinus bergii*) deserves special consideration because it is the only threatened species in the region (Ortubay and Cussac, 2000) and has peculiar biological traits (Lozada et al., 2000; Cussac and Ortubay, 2002; Ortubay et al., 2002; Miquelarena et al., 2005). It is highly endemic, restricted only to Arroyo Valcheta, a spring creek in the Somuncura Plateau. Introduced rainbow trout prey heavily on the characin, confining it to the warm headwaters of this spring creek safeguarded from predation by its thermally-stable regime that is not suitable for trout (Menni and Gómez, 1995; Ortubay et al., 1997; Ortubay and Cussac, 2000).

Siluriformes

The most updated syntheses about the siluriforms of Patagonia, Diplomystidae and Trichomycteridae are included in the works of Dyer (2000a) and Menni (2004). It appears that both taxa had a wider distribution in the past, which could have been restricted by a variety of causes, including habitat loss, predation and competition from salmonids. These catfishes are poorly known, both because of their infrequent occurrence in surveys and because much more limited efforts have been applied to the study of streams in Patagonia than to lakes. Distribution patterns and abundance estimates are bound to be significantly revised as we learn where and how to capture them. Data on the thermal tolerance of *Hatcheria macraei* were obtained by Gómez (1990).

Phylogenetically, diplomystids are the most primitive and remarkable group of all catfish families (Arratia, 1987). They are restricted to the Patagonian and Chilean provinces and qualify as catfish "living fossils" (de Pinna, 1998). On the other hand, Trichomycterids are a species-rich and widely distributed group in the Neotropical Region, however trichomycterines and in particular *Trichomycterus* are questionably monophyletic (Arratia, 1990; de Pinna, 1998). *Trichomycterus areolatus* and *Hatcheria macraei* are present on both sides of the Andes and share a great amount of intra- and interspecific variation of internal and external features as well as a carnivorous diet (Arratia and Menu-Marque, 1981; Arratia et al., 1983).

Galaxiidae

Cussac et al. (2004) reviewed the biology and distribution of South American members of the family Galaxiidae. *Galaxias maculatus* is the most conspicuous fish prey item in fish communities of Andean lakes (Campos, 1970a; Ferriz, 1987, 1988, 1989; Arenas, 1978; Macchi et al., 1999). Practically all fish species, including adults of *G. maculatus*, feed on this species (Campos, 1970b; Macchi et al., 1999). *Salmo trutta* and *S. salar* prey on large specimens, probably from the littoral zone (Cussac et al., 1992; Macchi et al., 1999).

The long-term dispute on whether the disjoint distribution of *G. maculatus* between southern South America and Australia-New Zealand, the widest of any other freshwater fish, was due to dispersal (McDowall, 1978, 1980) or vicariance (Campos, 1984), now seems to be settled after allozyme electrophoresis and mitochondrial DNA studies show minor population differences between them (Berra et al., 1996; Waters and Burridge, 1999; Berra, 2003).

Galaxias platei, a specialised bottom dweller (Milano and Vigliano, 1997; Milano, 2003), has a wide latitudinal distribution as a result of general adaptations to benthic life, retina adaptation for vision in the dark (Schoebitz et al., 1973), the presence of a cephalic lateral line, gill protection against abrasion, strong endurance to low oxygen availability, and a physiological ability for aerobic metabolism (Milano, 2003). This species exhibits inter-lake morphological variability in the caudal region, largely influenced by differences in predation intensity, and within-lake variation at intermediate predation levels associated to trophic specialization (Milano et al., 2002). Limnetic larvae of *G. maculatus* and *G. platei* were studied by Cussac et al. (1992), Cervellini et al. (1993) and Barriga et al. (2002).

Percichthyidae

The specific status within *Percichthys* is partially controversial. Ringuelet et al. (1967) and Campos and Gavilán (1996) recognised five living species on the basis of their morphology. Arratia (1982) considered only the extant *P. altispinnis, P. trucha* and *P. melanops*; however, Arratia et al. (1983) also included *P. colhuapiensis* and*P. vinciguerrai*. López-Arbarello (2004) distinguishes three species in Argentina (*P. trucha* - including *P. vinciguerrai* and *P. altispinnis*, *P. colhuapiensis* and *P. laevis*) and two in Chile (*P. chilensis* and *P. melanops*). However, based on the analysis of mtDNA and nuclear GnRH3-2 intron allele sequences, Ruzzante et al. (2006) could recognise only two specific entities, one north of Puerto Mont in Chile and the other in Atlantic and Pacific basins south to 42°S in Argentina.

Early work on the species concentrated on breeding biology (González Regalado, 1945; Mastrarrigo, 1948; Fuster de Plaza & Plaza, 1955; Boschi & Fuster de Plaza, 1957) and distribution (Arratia, 1982; Arratia et al., 1983). Recently, a considerable amount of intra-specific polymorphism associated to trophic resource utilization has been found in this group (Cussac et al., 1998; Logan et al., 2000; Ruzzante et al., 1998, 2003).

Atherinopsidae

Published information about the Patagonian silverside is notoriously lacking. This euriphagous-zooplanktophagous fish is present in lakes and reservoirs of Atlantic and Pacific drainages of Patagonia (Ringuelet et al., 1967; Macchi et al., 1999; Cussac et al., 1998; Ruzzante et al., 1998, 2003; Dyer, 2000a,b; Bello, 2002). Early life history studies identified largely zooplanktivorous larva found in the littoral zone of lakes during the summer (Ferriz, 1987; Cussac et al., 1992; Cervellini et al., 1993; Battini et al., 1995). Ontogenetic shifts in diet have been documented for *O. hatcheri* in relation to habitat shifts from littoral to pelagic and from limnetic to benthic zones (Cervellini et al., 1993). Temperature-dependent sex determination was documented in this species (Strüssman and Patiño, 1985; Strüssman et al., 1996, 1997). *Odontesthes bonariensis* specimens have been captured on the lower reaches of the Río Negro River (Pablo Vigliano, Universidad Nacional del Comahue, Bariloche, Argentina, unpublished data). *Odontesthes hatcheri* and *O. bonariensis* have been hybridized in the laboratory (Strüssmann et al., 1997). Hybrids of *O. hatcheri* with the introduced *O. bonariensis* have been detected in the wild and in Japanese fish farms (Dyer, 2000b).

Basilichthys australis and *Odontesthes mauleanum* are very abundant in Chilean lakes and large rivers as far south as the Maullín River system. The riverine silverside *Basilichthys australis* and the estuarine silverside *Odontesthes brevianalis* have a range of distribution that extends south into rivers and lakes of Chiloé Island. However, no silversides have been recorded in rivers and lakes of continental Chiloé. Informal reports of silversides fished in the Puelo River need to be confirmed. Marine silversides, such as *O. argentinensis* and *O. nigricans*, regularly inhabit estuarine or brackish environments either for feeding or reproductive purposes (Dyer, 2000a,b).

Exotic fishes

Patagonian freshwater communities are today largely dominated by introduced fishes, mostly salmonids (Dyer 2000a, Pascual et al. 2002, Soto et al. 2006), which were first introduced in the early 1900's (Tulian, 1908; Marini, 1936; MacCrimmon, 1971; Basulto, 2003). Fifteen species have been introduced into Patagonia from North America and Europe or translocated from outside the region, of which at least 11 have established self-sustaining populations. Of those, salmonids are dominant, with three species widely distributed throughout the region: rainbow trout, brown trout, and brook trout (*Salvelinus fontinalis*). In addition, the recent significant introduction of northern species (*Astyanax eigenmanniorum, Cheirodon interruptus, Oligosarcus jenynsii, Corydoras paleatus, Cnesterodon decemmaculatus, Jenynsia multidentata,* and *Odontesthes bonariensis*) has been detected in the north of Patagonia (Cazzaniga, 1978; Ferriz & López, 1987; Almirón et al., 1997; Ortubay et al., 1997; Baigún et al., 2002). Also the common carp *Cyprinus carpio* has been recently found on northern Patagonia in the Río Negro (Pablo Vigliano, unpublished data) and down to Río Bueno in Chile.

A new wave of exotic salmonid imports for net pen aquaculture is now taking place. Beginning in the 1980s, salmon marine production in Chile grew dramatically, from 53 metric tonnes in 1981 to 300,000 metric tonnes in 2000 (SERNAP, 1996–1999; Anonymous, 2001). As salmon production increased, so did reports of fish escaping from net pens and straying into the rivers of southern Chile and Argentina (Vigliano and Darrigran, 2002; Ciancio et al., 2005).

Other exotic species that have been introduced for aquaculture purposes into Patagonian rivers of Aysén, Chile, are the white sturgeon (*Acipenser transmontanus*) and Siberian sturgeon (*Acipenser baeri*) for production of caviar.

Interaction between native and exotic fishes

Documentation of the impacts that salmonids had on native communities of Patagonia is scarce and largely inconclusive. Only a few non-experimental field studies looked specifically at the interaction between native and exotic fishes by examining the fish community and food web structure in northern Patagonia lakes and reservoirs (reviewed by Pascual et al., 2002). There are several sources of evidence of significant predation on native species by exotic fishes. Salmonids feed heavily on some native fishes, particularly on galaxiids (both *Aplochiton* and *Galaxias*) and silversides (Macchi, 2004), with large brown trout being the most piscivorous species. Yet, most native species show some degree of piscivory as well, particularly native perches, which are still very abundant and even dominant over trout in many lakes and rivers in the region. Shallow, vegetated lakes provide refuge to *Galaxias maculatus* from salmon predation (Macchi, 2004). In Chilean lakes, the most recently introduced salmonids, such as landlocked chinook and coho salmon, are primarily piscivorous with *Galaxias maculatus* as the most common prey (Leal, 2003). Meanwhile, recent studies in Chilean rivers failed to find piscivory in trout (Gonzalez, 2005).

Most studies found some degree of segregation between native and introduced species, either trophic (Vigliano et al., 2000), reproductive (Cussac et al., 1997), or in habitat use (Vigliano et al., 2000). A strong geographic segregation between native and exotic fishes was found in Chile (Soto and Arismendi, 2005), where native fish species are abundant in the central valley or central depression, while they are practically absent from Andean streams where trout are more abundant (Soto et al., 2006). Whether segregation provides a mechanism to alleviate competition and predation or is, itself, the result of species interactions remains a matter of speculation. Geographic studies of morphological traits of *Galaxias platei* (Milano et al., 2002, 2005), as well as size distribution for *G. maculatus* (Macchi, 2004), showed a correlation with abundance of exotic fishes and their predation rates, indicating the existence of significant population-level effects produced by salmonids.

Anadromous salmonids add a whole new dimension to the potential environmental impacts by exotic fishes. They not only can affect both freshwater and marine communities by the direct interaction with native communities but, by virtue of their unique life cycle, they constitute agents for the importation of marine-derived nutrients into fresh water. The fertilizing effects of semelparous salmon are well demonstrated in North America (Levy, 1997) and we are just starting to see such potential impacts on receiving rivers of Patagonia (Pascual and Ciancio, 2007). In River Petrohue in Chile, chinook salmon returns have taken place for the last 10 years, with evident fertilization pulses every fall (Doris Soto, FAO, Rome, Italy, unpublished data).

Freshwater fisheries in Patagonia

In continental Patagonia, the recreational use of freshwater fishes is prevalent over their commercial exploitation. In Argentina, there are only three artisanal gillnet fisheries with a relatively long history, while there are no inland fisheries in Chile, although some illegal gillneting for trout and salmon takes place on a regular basis in some of the large lakes. There are also some minor fisheries for *Galaxias maculatus* in brackish waters of fjords and estuaries of Chile.

On the other hand, recreational fisheries are quite developed throughout the region, both in Chile and Argentina, with a significant local and regional economic impact (Vigliano and Alonso, 2000). Freshwater fishing in Patagonia is associated to three types of recreational fisheries. The first type is related to freshwater habitats of the Andean reaches of Atlantic and Pacific drainage basins, targeting salmonid populations, including some of the best trout fisheries in the world (Leitch, 1991). The second is associated with the catch of native fishes on Atlantic river basins in their middle and lower reaches, sometimes coexisting with salmonid fisheries. These fisheries mostly congregate local fishermen. The third type of recreational fishery is that of anadromous species in lower reaches of some Pacific and Atlantic rivers or adjacent coastal areas, targeting runs of sea-run brown (Leitch, 1991) or rainbow (Pascual et al., 2001) trout and Pacific salmon of the genus *Oncorhynchus* (Soto et al., 2001). These highly prized fisheries are the target of mostly international, fly fishermen.

Fishing regulations exist for most rivers and lakes of Patagonia. Fishing takes place between late spring and mid or late fall, with a fishing ban imposed during winter. Catch rates are limited through the number of fish that may be sacrificed per fishermen per day and through size limits. However, freshwater stock assessment in Patagonia is rudimentary, in both Chile and Argentina, without the benefit of well-established information systems or analytical methods. Regulations are established through a somewhat informal process of trial and error or by the importation of general guidelines from other fisheries. Meanwhile, there are some consistent signs of declining quality in several trout recreational fisheries, both in catch rate and size of the fish caught, as indicated by our collective experience with fishes and fisheries in the region.

Freshwater trout production in Chile is small (probably less than 2,000 mt yr^{-1}), compared to trout production in fjords (about 80,000 mt in 2004) and compared to total salmonid production (350,000 mt exported in 2004 for a total value of over $1,400 million US). While most of the grow out is done in net pens in marine coastal areas, smolt production (30,000 mt in 2004) is undertaken in large Araucanian lakes (30-40%), small lakes in Chiloé Island (30%), and fully recycling hatcheries (30-40%). Although salmon production in Chile continues to increase, smolt production is slowly moving from lakes to high technology recycling hatcheries (D. Soto, Inland Water Resources and Aquaculture Service (FIRI), Fisheries Department, FAO of UN, pers. obs.). In Argentina, freshwater trout production is small (less than 2,000 mt yr^{-1}; Luchini, 1999) and it is unlikely to grow under current conditions, hindered by high production cost as compared to those of Chile.

Status of freshwater habitat

Lakes

Large glacial lakes are a conspicuous feature of Patagonian fresh water. They are found in Andean valleys between 39° S and 54° S, and receive precipitations as high as 3000 mm yr^{-1} (Paruelo et al., 1998). These lakes are temperate monomictic, with thermal stratification in summer, resulting in thermocline frequently found at depth of 30-40 m or greater (Quiros and Drago, 1985; Soto, 2002). Water clarity is high, with euphotic zone as deep as 50m (Morris et al., 1995). Some shallow mesotrophic, non-stratified lakes, with less clear water can be found in the Andean region of Patagonia (Diaz et al., 2000).

Fish communities in Patagonian glacial lakes appear to be sustained by energy funneled through benthic habitat. Fish biomass and diversity is largely associated to littoral areas and shallow lakes connected to deep lakes, indicating that this type of habitat is critical in ensuring the health of the fish community (Macchi, 2004; Soto and Campos, 1995; Soto and Stockner, 1996). Reproduction and larval development of native species is associated with littoral areas (Milano, 1996; Cussac et al., 1992; Cervellini et al., 1993; Barriga et al., 2002). Deep benthic waters are almost unpopulated, with the exception of *Galaxias platei* (Milano and Vigliano, 1997). While pelagic habitat represents a large proportion of these deep lakes, native species seldom use it, being the exclusive realm of salmonids, which nevertheless favor the use of littoral areas (Vigliano et al., 1999; Soto and Stockner, 1996). In general, habitat quality of glacial lakes both in Chile and Argentina is good (Dirección Nacional de Recursos Hídricos, 1995; Olson et al., 1998; Fundación Vida Silvestre Argentina, 2001), with potential risks resulting from growing human populations in lake-side cities, as well as agriculture, cattle ranching and salmon farming activities (Soto and Campos, 1995; Soto, 2002).

On the Argentinean side, the steppe is dotted by shallow lakes, most of them formed by tectonic depressions, and deepened by wind erosion (Modenutti et al., 1998). Many of them are temporary and eutrophic, with turbid water (Diaz et al., 2000).

Rivers

Patagonia has some large rivers, in both Atlantic and Pacific basins. Pacific rivers are relatively short, while Atlantic rivers flow across the steppe for hundreds of kilometers. Most rivers receive waters from fall precipitation and spring snowmelt. Habitat varies from those of typical mountain rivers, with riffles, pools and runs, to meandering slow rivers with secondary channels flowing across the steppeland into the Atlantic Ocean. Most of the Pacific rivers flow into the large fjords characteristic of the coast of southern Chile.

By far the largest threat for fish habitat in rivers is posed by hydroelectric projects. Four large rivers of Argentinean Patagonia (Colorado, Neuquén, Limay, Futaleufú) already have several impassable dams that have not only fragmented the river also but transformed hundreds of river kilometers in lake habitat. 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; Temporetti et al., 2001; Alonso, 2003). At present, the only confirmed effect is the disappearance of lamprey from the middle and upper reaches of the Limay River above dams. Both ammocoetes and adult lampreys are regularly found in the Rio Negro River, below dams.

While some large rivers in the region are still free of dams (all large rivers south from Puerto Montt in Chile and Santa Cruz River in Argentina,), this condition is unlikely to last. For instance, the Baker River is recognized as the Chilean river with greatest hydroelectric capability (Niemeyer and Cereceda, 1998) and the Puelo River, is being targeted by the largest Chilean electrical company for its next hydroelectric project. Plans by the Santa Cruz government in Argentina to build three dams in the Santa Cruz River are well advanced.

Freshwater fish management in Patagonia

Issues about the use and conservation of freshwater communities in Patagonia are strongly permeated by two types of conflicts: those between the development of hydroelectric projects and alternative uses of rivers described in the previous section, and, those between the promotion of freshwater fisheries and aquaculture based on exotic salmonids and the conservation of native species. Although scarce, some conservation-related legislation exists, both at the provincial and federal level in Argentina. But in reality, the protection of native species remains almost exclusively the mission of Park Services of Chile and Argentina, while provincial and regional governments direct nearly all efforts to promote sport fisheries and aquaculture, mostly through fishing regulations and supplementation of target species.

It is worth mentioning that in Chile, native fishes are doing better in central valley catchments with highest human perturbation (Soto et al., 2006). As most National Parks in the Lakes Region are connected to the Andes where native fishes are very scarce, Parks and Reserves are not protecting native fish but, paradoxically, protecting trout instead.

Legislative and regulatory treatment of fish, habitat, and fisheries

Argentina-legislation

Although comprehensive legislation concerning Patagonian freshwater fishes does not exist in Argentina, several pieces of relevant legislation exist, both federal and for each one of the five provinces in the region. This legislation pertains to activities that could potentially affect freshwater environmental health, such as fishing, aquaculture, mining, power production, dangerous wastes, and the use of flora and fauna.

The Constitution of Argentina guarantees the right to a balanced and healthy environment, appropriate for human development, and fosters productive sustainable activities. It also has provisions in relation to the civil, penal and administrative responsibilities regarding damage to the environment. The Argentine government also signed the Rio Convention on Biological Diversity in 1992.

The federal government has specific jurisdiction on environmental health through the Agency of Natural Resources and Sustainable Development pertaining to: 1) environmental matters related to inter-jurisdictional, internal and international transport of flora and fauna or related products, 2) the control and regulation of international agreements such as CITES, Convention on Biological Diversity, and Conservation of Migratory Species. This agency regulates the introduction of exotic species into the country, but the transplant of already introduced species into new areas and of native species outside of their original distribution is not explicitly considered.

Aquaculture is regulated by federal laws, including the importation and production of exotic aquatic species in the country. They include a list of exotic species for which importation is forbidden, and the requirement of production projects for other exotic species.

All Patagonian provinces have laws that regulate fishing within the jurisdiction of each province, aquaculture, and the protection of wildlife and vegetation. Sport fishing in is articulated among provinces and the National Parks Service by a consulting commission.

National parks

The first natural protected area of Argentina was created in 1903 in the Andean Patagonian region, where the Nahuel Huapi National Park was created later in 1934. The Administration of National Parks is the federal agency that creates and administrates the network of federal protected areas. Provinces also established protected areas. At present, continental protected areas of Patagonia cover approximately 37% of temperate rainforests and headwaters in the Andean region, but less than 5% of large rivers and shallow lakes in the steppe.

By nature of its mandate, the Administration of National Parks strives to protect native fishes. The introduction, transplant or re-introduction of species, its eggs, larvae or embryos are expressly prohibited within National Parks, except in those cases where the re-introduction of samples of native species has been programmed. Aquaculture is not authorized within National Parks. While sport fishing for salmonids is an important recreational activity within parks, fishing regulations typically have provisions to protect native species, such as mandatory release of native species.

Chile-legislation

Aquaculture in Chile has been regulated since 1991 by a General Fisheries and Aquaculture Law. Since 1997, all aquaculture projects should follow the mandate of the LBMA (Ley de Bases del Medio Ambiente) which includes an Environmental Impact Assessment procedure for all new aquaculture projects or any other activity that may affect or imperil the environment. This law affects only new projects; however, a new regulation of 2001 covers the potential environmental impacts of aquaculture activities, including the effects from excess nutrients on aquatic ecosystems and the escape of cultured fishes.

At present, a new legislation is being discussed to regulate recreational fisheries, which considers two objectives: the conservation of species important for recreational fisheries, and the enhancement of tourism and recreational fishery business. The new regulation includes the creation and management of preferential areas for recreational fisheries, based on approved management plans. One of the most discussed issues is the right of management, originally bestowed to counties, according to the new legislation could be sub-leased to private enterprises. The wellbeing and relevance of native fish fauna are not being properly recognized by any legal or administrative tool in Chile.

National parks

Chile has a national system of protected wild areas which includes 32 National Parks, 47 National Reserves and 15 Natural Monuments. All are administered by the National Forestry Corporation (CONAF) and its main objective is to "contribute to the conservation, increase, management and utilization of the forestry resources of the country". The first natural protected area was created in 1907 (Malleco Forestry Reserve) and the first National Park (Vicente Perez Rosales, in Llanquihue) was created in 1926. Within the Patagonia Area, there are 11 National Parks (7.557.442 ha or 10% of national territory) and 16 National Reserves. All protected areas have important aquatic ecosystems including rivers, lakes and ponds. National Parks have severe restrictions for economic activities within them. However, most of them do not protect native fishes or native aquatic organisms in general, but rather serve to protect exotic trout and sports fishing (Soto et al., 2006). Due to the presence of park rangers and vigilance, trout within National Parks are indeed more protected than outside, where overfishing is common.

Linkages with sustainable development and ecosystem health

Fish habitat has not been a key driver in biodiversity conservation of Patagonia. This is not surprising given that in general, Patagonian native fishes have been largely absent from conservation agendas of provincial, regional or federal governments, as well as of non governmental organizations (Pascual et al., 1998). While numerous initiatives exist for terrestrial or marine conservation both in Argentinean and Chilean Patagonia, there is no counterpart pertaining to freshwater conservation (but see Olson et al., 1998 for a general conservation assessment of freshwater biodiversity in Latin America). In fact, because salmonid introductions preceded the strongest influx of European immigration to the region, exotic fishes are not really regarded any differently from indigenous fishes by the general public and by most policymakers (Pascual et al., 2002). The result is that, besides the worries of a small academic community, no specific initiatives were ever proposed that contemplate the conservation of continental fish fauna of Patagonia as a central objective.

The paucity of habitat studies is nevertheless surprising. For instance, research on habitat as it affects the health of salmonid populations, a very well-developed research area in North America, has not yet been developed in Patagonia.

Conclusions

Overview of science and management

Until recently Patagonian continental fishes and their habitats were, on the whole, subjected to little pressure from human activities; therefore, management demands where minor. Population growth, development, and increasing awareness of the economic and social value of Patagonia as a pristine area led to a growing need for management actions. Current research capacity is insufficient to deal with most of these demands because of limitations in people, resources and baseline information. While research on the fish resources of Patagonia has increased sharply since the mid 1990s (Ferriz et al., 1998; Pascual et al., 2002; Menni, 2004; Soto et al., 2006), it amassed mostly background biological data, with relatively few studies providing the kind of information about the functioning of freshwater system that could guide management decisions.

The mismatch between management needs and research capacity stems in part from a societal failure to recognize the importance and fragility of freshwater resources. Some direct consequences of this are the overlooking of the importance of freshwater research, which conspires against its development and growth, a poor investment in highly qualified human resources made by management agencies, and the lack of regional views leading to working agendas for freshwater resources.

Therefore, research tends to concentrate on urgent or specific problems, many times responding to the requirements of particular interest groups (for example aquaculture), instead of serving a more strategic support function for comprehensive freshwater management. Meanwhile, we may be ill-prepared to anticipate the impacts of large-scale enterprises, such as hydroelectric projects, which would render all other management problems futile. As long as management measures are proposed from a sectarian rather than an integrative perspective, in which all stakeholders are involved in the different levels of decision-making, the ecosystem and its resources will continue to suffer the consequences of this imbalance.

Priority gaps and needs for fish research and management

Given the deficiencies in the current research and management system, building adequate scientific support for freshwater management in Patagonia emerges as a major undertaking. Rational research programs are not possible without a characterization and prioritization of environmental problems. Therefore, basic activities should include the elaboration of regional databases on the state of freshwater fishes and habitat. These catalogues should include primary drivers of the health of fish communities, and the identification of major threats to their integrity and functioning. Ideally, they should include estimates of economic and social costs of alternative courses of action -the kind of information that will draw the attention of public and politicians.

A critical issue for freshwater management, as well as for management-oriented research in Patagonia, is recognizing the inter-jurisdictional nature of most river basins. Practically all river basins in the region span across some kind of regional, provincial or international border, as well as across boundaries of protected areas. To produce sound and functional management advice, studies should adopt a whole system perspective. This process entails recognizing the existence of different, and potentially conflicting, objectives of different jurisdictions, such as improving recreational fishing, preserving native fishes, or producing electricity. Because of the lack of overall objectives for the management of multi-jurisdictional basins, scientists frequently find themselves operating as defenders of particular agendas, instead of as professionals in search of management schemes that could accommodate alternative agendas. A major challenge for fish management at the regional level is to find ways to protect native fishes, in a context of a growing human population and diversified activities impacting on freshwater resources. Such research and management approach should be done jointly by Chile and Argentina in trans-Andean watersheds.

Specific research areas that merit special attention are those related to understanding the way in which major factors that affect freshwater fishes operate, such as exotic species and habitat modification, including impoundment, urban encroachment, forestry and water appropriation.

Speculation on future trends and potential for fishes, fisheries and habitats

The future of the freshwater fishes of Patagonia will depend on the wisdom of the regional society to value them, on the ability of administrators to generate agendas for the integral management of freshwater resources, and on the capacity of scientists to build research capacity to provide sound advice.

A worst-case scenario can be conceived in which society and its representatives fail to perceive the risks faced by freshwater resources and the costs of not taking action. Population growth and development continues without making provisions for sustainability or environmental quality. Dams are built in all large and medium rivers; free-flowing water is as rare as native species, in communities dominated by exotic fishes. But these introduced fishes now fail to sustain the celebrated recreational fisheries of the past. Despite inordinate efforts to mitigate habitat destruction and the demise of forage fishes with hatcheries, spawning channels, introduction of new species, dam ladders, turbine bypass systems and all kinds of engineering tools, fish size and abundance decline. Water quality declines due to unregulated urban waste discharge and aquaculture. National parks located in headwaters, or in remote areas, have been able to preserve habitat, but fish communities are nonetheless impoverished and highly infested by exotic fishes because of mismanagement in neighbouring jurisdictions. Views are extremely polarized, with aquaculturists, recreational fishers, conservationists and managers declaring each other responsible for the calamitous state of fishes and the environment. Scientists cannot avoid being drawn into the fight, while trying to give answers to the problem of the day.

How well we can improve this grim picture will depend on how able we are to inform managers, the general public and colleagues about the value of freshwater resources and the costs of not taking action. To support our claims, we need to promote regional assessments of freshwater resources and of major threats to their integrity, the building blocks of a regional agenda for their sustainable use.

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