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Original article

Evaluating potential effects of exotic freshwater fish from incomplete species presence–absence data

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Abstract

Many freshwater ecosystems and biotas around the world are threatened with extinction. Freshwater fishes, for example, are the most endangered vertebrates after amphibians. Exotic fish are widely recognized as a major disturbance agent for native fish. Evaluating the ecological effects of invaders presents many challenges and the problem is greatly augmented in parts of the world where the native fauna is poorly known and where exotic species are commonplace. We use the fish community of Patagonia, a small and distinct native biota dominated by exotic salmonids, as a case study to ask: what can we learn about the effects of exotic fish species from fragmentary or partial data and how do such data point the way to what needs to be learned? We review the available data and literature on the distribution and status of native and introduced fish. We compile a novel regional presence/absence species database, build fish distribution maps, describe distribution patterns of native and exotic species, and identify critical information voids. A comparative review of literature from Patagonia and Australasia, where a similar native and exotic fish fauna is found, helps us to identify research priorities and promising management strategies for the conservation of native fish fauna. We conclude that the main challenge for fish conservation in Patagonia is to identify management strategies that could preserve native species while maintaining the quality of salmonid fisheries.

Introduction

Throughout the world, whole freshwater ecosystems and biotas are threatened with extinction on a grand scale (Olson et al. 1998; Ricciardi et al. 1999). By and large, however, freshwater biodiversity has been seriously neglected (Allan and Flecker 1993; Leidy and Moyle 1998; Saunders et al. 2002). Conservation biology has chiefly concentrated on terrestrial biodiversity, which is readily observed and with which humans are more familiar (Olson et al. 1998). The lesser attention paid to freshwater ecosystems has also been attributed to the fact that freshwater conservation requires greater attention to complex processes, such as large scale dynamics, complex interactions and linkages with terrestrial systems, which are poorly understood, difficult to study and politically challenging (Olson et al. 1998).

The problem of freshwater conservation is well illustrated by the case of fish species. More than one-half of all vertebrates, about 24,600 species, are fish, 41% of which are exclusively freshwater (Leidy and Moyle 1998). Freshwater fishes are thought to be the most endangered vertebrates after amphibians (Saunders et al. 2002). The fish fauna of North America, arguably one of the best known in the world, presents a compelling example of the vulnerability of freshwater fish. Miller et al. (1989) identify 27 species that became extinct during the last century. About one-third of the existing 1174 freshwater fish species are threatened (Leidy and Moyle 1998). The chief factors affecting fish in watersheds around the world are habitat loss and species introductions, followed by chemical pollution, hybridization, and overharvesting (Allan and Flecker 1993; Saunders et al. 2002).

The issue of introduced fish species deserves a special treatment. Freshwater fish species have been purposely and extensively transferred around the world. Only 10% of successful fish introductions have been unintended transfers (Welcomme 1984). The main motivations for introductions have been esthetical, recreational and, more recently, to promote aquaculture (Allan and Flecker 1993); in fact, many successful transfers gave rise to well-established recreational fisheries and aquaculture activities. The transfer of exotic fish is an ongoing and very active process worldwide, as intensive aquaculture based on non-native species is promoted in many parts of the world as an instrument of economic development (Anonymous 1990). Accidental introductions due to the escape/release of aquarium fish are likely to increase; as many as 6000 species may ultimately be of interest to the pet trade (Allan and Flecker 1993).

Evaluating the ecological effects of invaders presents many challenges and there is a lack of generalizations regarding the development of measures of impact from empirical examples or from theoretical reasoning (Parker et al. 1999). The problem is greatly augmented in parts of the world where the native fauna is poorly known and where exotic species are commonplace. Given these circumstances, what can we nevertheless learn from fragmentary or partial data – and, in particular, how do such partial data point the way to what needs to be learned?

This paper deals with the native fish fauna of lakes and rivers in Patagonia, the southernmost region of South America, which is poorly known and is presently dominated by several species of salmonids, the exclusive focus of significant recreational fisheries (Leitch 1991). Patagonian fish have been largely absent from conservation agendas of provincial and federal governments, as well as of NGOs [Pascual et al. (1998), but see Olson et al. (1998) for a general conservation assessment of freshwater biodiversity in Latin America].

A review of the status of native and introduced fish on a regional scale appears to be a fitting initial step. We start by compiling presence/absence data on both native and introduced fish in the Argentinean portion of Patagonia, building what we believe is the most updated species distribution database for the region. We then analyze available evidence of impacts by introduced fish, including information from New Zealand and Australia where fish assemblages share some similarities with those of Patagonia. Finally, we critically examine all the information presented to identify approaches that appear to be more promising in focusing future research on the effects of exotic species, and to identify species and conditions that appear to demand particular attention within future conservation plans for Patagonian fish.

Materials and methods

River basins of Patagonia

Argentinean Patagonia is an area of over 800,000 km^2, comprised of 5 of the 23 provinces of Argentina. It extends from latitude 37°–55° S, comprising 28% of the national territory. The hydrographic network of Patagonia consists of 32 major river basins (Figure 1). Fifteen watersheds drain from the Andes across the Patagonian steppe into the Atlantic Ocean, 9 are shared with Chile, draining across the Andes into the Pacific Ocean, 1 basin has mixed Pacific and Atlantic drainage, and 7 are endorheic.

Our examination of the fish fauna of Patagonia is intended as groundwork, large-scale analysis and does not consider the heterogeneity within and among river basins of the region. It must be recognized, however, that Patagonia is environmentally and ecologically diverse. Olson et al. (1998) recognized three major habitat types for the region (Wet Region Rivers and Streams, Xeric Region Rivers and Streams, and Xeric Region Endorheic Basins), dividing it into two distinct ecoregion complexes (Southern Chile Complex and Patagonia Complex).

The fish fauna of Patagonia

Indigenous fauna

While South America as a whole has the highest freshwater fish species diversity in the World, with 40% of all known continental fish species (Lagler et al.

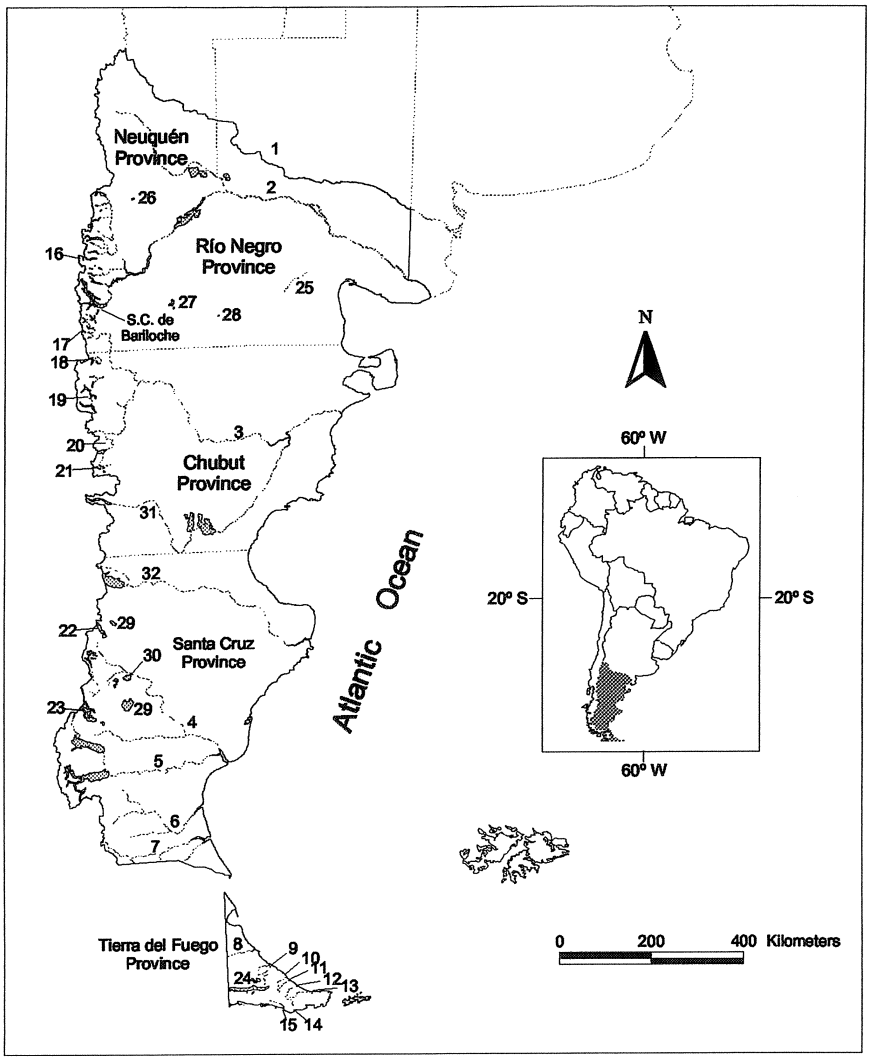

Figure 1. Patagonia, its provinces, and major river basins. Atlantic river basins: 1 Colorado, 2 Negro, 3 Chubut, 4 Chico, 5 Santa Cruz, 6 Coyle, 7 Gallegos, 8 Grande, 9 Ewan, 10 San Pablo, 11 Lainez, 12 Irigoyen, 13 Bueno, 14 López, 15 Moat. Pacific river basins: 16 Lácar, 17 Manso, 18 Puelo, 19 Futaleufu, 20 Corcovado, 21 Pico, 22 Pueyrredón, 23 San Martín, 24 Fagnano. Endorheic basins: 25 Arroyo Valcheta, 26 Laguna Blanca, 27 Laguna Carrilaufquen, 28 Laguna Ñe Luan, 29 Lago Cardiel, 30 Lago Strobel, 31 Senguerr. Mixed Pacific–Atlantic basins: 32 Buenos Aires Lake.

1962), the indigenous fauna of Patagonia is composed of only 20 species (Table 1). Albeit species poor, this fish fauna is distinct, including species of assorted origins: neotropical, circumpolar, and a significant number of endemisms (Arratia et al. 1983).

Only four of the 20 known species are widely distributed throughout South America, with the remainder being restricted to the northern fringe in Patagonia: two Characidae (*Astianax eigenmaniorum* and *Cheirodon interruptus*), one Anablepidae (*Jenynsia lineata*), and one Poeciliidae (*Cnesterodon decenmaculatus*). Two species are widely distributed throughout circumpolar regions: *Galaxias maculatus*, the most widely distributed Galaxiidae (McDowall 1971), and the Petromyzontidae *Geotria australis* (Nelson 1994), found also in Australia, New Zealand, Tasmania and Chile.

The remaining 14 species are restricted to southern South America. Three species of Galaxiids, *Aplochiton teniatus*, *A. zebra* and *Galaxias platei*, are found on both sides of the Andes, from Central Chile to Patagonia, all the way south to Tierra del Fuego

Table 1. Freshwater fishes of Argentinean Patagonia. Indigenous species are shown in the left column (present distribution for families and species indicated with letters: P – Patagonia, CH – Chile, CW – central-western Argentina, C – circumpolar, S – South America, A – Americas). The right column shows introduced species (origin and year of first introduction into Patagonia).

Indigenous species	Exotic species
Order Siluriformes	*Established*
Family Diplomystidae (A)	Order Salmoniformes
Diplomystes viedmensis (P), otuno	Family Salmonidae
D. mesembrinus (P), otuno	*Salmo trutta* (Europe, 1909), brown trout
D. cuyanus (P + CW), otuno	*S. salar* (USA, Canada, 1904), Atlantic salmon
	Oncorhynchus mykiss (USA, 1904), rainbow trout
Family Trichomycteridae (A)	*O. tshawytscha* (USA, 1904; Chile, 1984), chinook salmon
Hatcheria macraei (P + CW), bagre del torrente	*O. masou* (Japan, 1987), cherry salmon
Trichomycterus areolatus (S + CW), bagre pintado	*Salvelinus fontinalis* (USA, 1904), brook trout
	S. namaycush (USA, 1904), lake trout
Order Osmeriformes	
Family Galaxiidae (C)	Order Atheriniformes
Galaxias maculatus (C), small puyen	Family Atherinopsidae
G. platei (P + CH), large puyen	*Odontesthes bonariensis* (Arg, 1939), silverside
Aplochiton taeniatus (P + CH), peladilla	
A. zebra (P + CH), peladilla listada	Order Cypriniformes
	Family Cyprinidae
Order Perciformes	*Cyprinus carpio* (Brazil,?), common carp
Family Percichthydae (G)	
Percichthys colhuapensis (P), largemouth perch	Order Siluriformes
P. trucha (P + CH), smallmouth perch	Family Callichthydae
P. altispinnis (P), largespine perch	*Corydoras* sp. (?), armored catfish
P. vinciguerrai (P), perch	
	Non-established
Order Petromyzontiformes	Order Salmoniformes
Family Petromyzontidae (C)	Family Salmonidae
Geotria australis (C), pouched lamprey	*O. kisutch* (USA, 1904), coho salmon
	O. nerka (USA, 1904), sockeye salmon
Order Characiformes	*Coregonus clupeaformis* (USA, 1904), lake whitefish
Family Characidae (A)	
Astyanax eigenmanniorum (S)	
Cheirodon interruptus (S), Uruguay tetra	
Gymnocharacinus bergi (P), naked characin	
Order Atheriniformes	
Family Atherinopsidae (A)	
Odontesthes hatcheri (P + CH), patagonian silverside	
Order Cyprinodontiformes	
Family Anablepidae (W)	
Jenynsia lineata (S), one-sided livebearer	
Family Poeciliidae (W)	
Cnesterodon decenmaculatus (S), ten-spotted livebearer	

(McDowall and Nakaya 1987; McDowall 1988). One species of Atherinopsidae, *Odontesthes hatcheri*, is found in Patagonian lakes and rivers of Argentina and Chile, and north throughout the central Andean region of Argentina (Dyer 1998). Two species of Siluriforms of the family Trichomycteridae (*Trichomycterus areolatus* and *Hatcheria macraei*) are found in Patagonia and north throughout the central Andean region of Argentina (Arratia 1983, 1987; Arratia and Menú Marqué 1981).

Three species of Siluriforms of the family Diplomystidae are found exclusively in Argentina, two of which (*Diplomystes mesembrinus* and *D. viedmensis*) are found exclusively in Patagonia (Azpelicueta 1994a, b). There are four species of the family Percichthydae in Patagonia. One of them, *Percichhtys trucha*, is found in Argentinean Patagonia and Chile and the other three species (*P. colhuapensis*, *P. altispinnis* and *P. vinciguerrai*) are found exclusively in Argentinean Patagonia.

Finally, the most restricted distribution of all fish taxa in the region is that of the naked characin, *Gymnocharacinus bergi*, limited to the thermal headwaters of a 100-km long endorheic stream, the Arroyo Valcheta (Figure 1), in the Río Negro Province (Ortubay and Cussac 2000). This is the only fish in Argentina that is listed in the red book of species, classified as endangered (Baillie and Groombridge 1996).

In summary, lakes and rivers of Patagonia are inhabited by 20 native species of fish, 4 of which have wide South American distribution, 2 have a circumpolar distribution, 8 are found in Patagonia, with distribution extending northwest towards central Chile, and 6 are found exclusively in Patagonia. Of all these species, only the patagonian silverside, *Odonthestes hatcheri*, and the perches of the family Percichthydae have some value for sport fishing.

Introduced fish

Thirteen species have been introduced into Patagonia, 10 of which have established self-sustaining populations (Table 1). Of those, 7 are salmonids, 3 of them being widely distributed: rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and brook trout (*Salvelinus fontinalis*) and the remaining 4 are only locally abundant. The 3 non-salmonid species (Table 1) have restricted distributions.

Salmonid introductions started early in the twentieth century, when the Federal Government initiated an aggressive importation program from the US and England to populate basins throughout the region with ‘valuable’ sport fish (Marini 1936; Tulian 1908; MacCrimmon 1971). By the 1930s, salmonid production had been centered at the Bariloche Hatchery in Northern Patagonia, which became the main focus of salmonid propagation in Argentina. By that time, salmonids were already well established throughout the region, except in Tierra del Fuego, where official attempts to introduce them took place later, throughout the 1930s and 1940s. By the 1980s, all five provinces of Patagonia had their own hatcheries, continuing the spread of salmonids up to the present.

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 tons in 1981 to 300,000 metric tons 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. In recent years, we have been detecting anadromous chinook salmon spawning in headwaters of Pacific basins in Argentina (M. Pascual, unpub. data).

Present-day distribution of native and exotic fish species

We created distribution maps for all native and exotic fish species in each of the 32 major river basins of Argentinean Patagonia. For practicality, we did not consider small streams or lakes, limiting our focus on medium to large-size water bodies. The database encompasses a total of 8810 km of rivers and a total of 10,656 km^2 of lakes. We started by dividing river basins into strata. Each stratum consists of a single lake or reservoir (average area 120 km^2), or a physically distinct section of a river (average length 113.3 km), defined as a free-flowing portion of a river limited upriver and downriver by either a lake, a reservoir, a dam, or a major tributary. This partitioning scheme resulted in 148 strata (Table 2).

We then built a database of presence/absence data for all strata and all species in Table 1. A code was assigned to each species at each stratum to represent confirmed presence (1), confirmed absence (0), or unknown status (−99). In order to do this, we circulated the database among the authors repeatedly and completed as much of it as possible. Because the available literature in refered journals is scarce, we rely heavily on gray literature, unpublished reports, personal communications and, in many cases, our own fieldwork experience. We also consulted several colleagues with recognized

Table 2. Distribution of 148 freshwater strata defined in our database of Patagonia by type and province (see Figure 1).

Province	Rivers	Lakes	Reservoirs
Neuquén	14	20	1
Shared Neuquén/Rio Negro	4		5
Río Negro	6	15	
Chubut	18	19	2
Santa Cruz	17	14	
Tierra del Fuego	8	5	

field experience at particular sites. Confirmed absences were assigned only to those strata where multi-year monitoring surveys based on the use of multiple sampling techniques had failed to record the presence of a species. The database was built in Access (Microsoft Corp., US), and queries were used to extract general distribution patterns of native and exotic species.

To visualize distribution patterns from the database, we built a geographic information system (GIS) using ArcView GIS 3.2 (ESRI Inc., US). Presence/absence values were assigned to strata in the maps with either polygons to represent lakes or arcs to represent sections of rivers. In order to characterize gradients in species distributions, each stratum was assigned a central location, given by its mean latitude and longitude.

In order to show comprehensive distribution maps on a regional scale for this paper, we defined larger scale strata, consisting of groups of strata sub-basins. To each of these larger strata, 70 in total, we assigned a presence if the species was present in at least one of the original composing strata, an absence if the species was absent from all original strata, or an unknown status if the original strata contained all unknowns.

Literature review

We reviewed 298 published papers about Patagonian continental fish (Ferriz et al. 1998). We characterized the focus of the papers, looked into the type of research approach selected, determined the type of interaction between exotic and native species reported, and looked at evidence for impacts on the receiving community.

We also reviewed 36 papers dealing with the interaction between exotic salmonids and native freshwater fish in Australia and New Zealand. We looked, in particular, for the research approaches used and whether they were successful at characterizing the type of interaction taking place between native and exotics, and at gauging the ensuing impact on indigenous fish.

Results

Species distribution

A most disturbing feature readily emerges from our species-distribution database, which is the large proportion of strata for which we could not assign a presence/absence value (Table 3). The uncertainty is particularly abundant for native fish, where for most species there are more information voids than confirmed status. Information for all Galaxiids and for Siluriforms of the genus *Diplomystes* and *Hatcheria* are particularly deficient, with over 30% and as much as 60% of strata for which a presence/absence status could not be assigned. Albeit substantial, uncertainties about the distribution of exotic fish are significantly smaller (Table 3).

Table 3. Presence/absence data of native and exotic species in our database. For each species, the number of strata (out of a total of 148) where the species is present, absent, and where the status of the species is still unknown are shown

	Number of strata		
	Present	Absent	Unknown
Native species			
Percichthys sp.	76	28	44
Galaxias maculatus	59	25	64
Galaxias platei	50	16	82
Odontesthes hatcheri	45	43	60
Diplomystes sp.	39	52	57
Hatcheria macraei	24	46	78
Jenynsia lineata	9	138	1
Aplochiton sp.	3	58	87
Astianax eigenmanniorum	2	146	
Cheirodon interruptus	2	146	
Cnesterodon decenmaculatus	2	135	11
Gymnocharacinus bergi	1	147	
Exotic species			
Oncorhynchus mykiss	121	7	20
Salmo trutta	100	21	27
Salvelinus fontinalis	75	46	27
Salmo salar	17	94	37
Oncorhynchus tshawytscha	6	129	13
Salvelinus namaycush	5	134	9
Odontesthes bonariensis	4	140	4
Oncorhynchus masou	3	139	6
Cyprinus carpio	2	146	
Corydoras sp.	2	146	

Uncertainty about species status varies regionally and with habitat type (Figure 2). In general, very few strata have low uncertainty levels (i.e. less than 5 out of 38 species with unknown status) and for only a handful there is no uncertainty (i.e. zero species with unknown status). This corresponds to the few locations where long-term surveys have been conducted. On average, uncertainties are greater for rivers than for lakes and reservoirs. The best information corresponds to lakes and reservoirs in the Río Negro Province, while the greatest uncertainties correspond to lakes and reservoirs in the Santa Cruz Province, as well as to rivers in northern Santa Cruz. Some of these strata present as

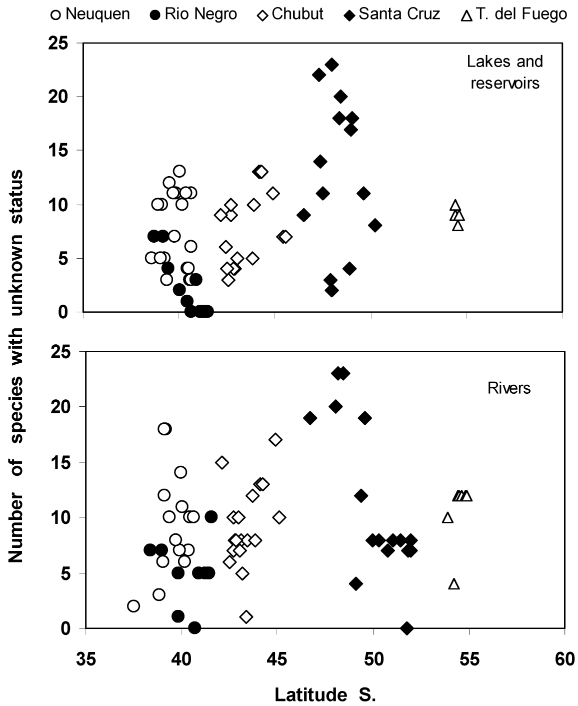

Figure 2. The number of species (of a total of 38) with unknown status along the latitudinal gradient of Patagonia. Symbols indicate the province where a stratum is located. The upper panel shows the data corresponding to the 81 lake and reservoir strata and the lower panel shows those corresponding to the 67 river strata.

many as 23 species (61%) for which status could not be established.

The confirmed presence of native and exotic species allows us to build distribution maps (Figures 3 and 4). Because of the significant uncertainties in species status, these maps are likely to change considerably as more information is gathered and should be regarded only as preliminary. Nevertheless, they provide a general portrait of the distribution of some species. The most widely distributed native fish are Percichthyds, Galaxiids and the Patagonian silverside, *Odontesthes hatcheri* (Figure 3). On the other side, the naked characin, *Gymnocharacinus bergi*, is restricted to a single endorheic stream (Figure 3D). The most widely distributed exotic fishes are rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), with confirmed presences in 82% and 68% of all investigated strata, respectively (Figure 4 and Table 3), and both with pan Patagonian distributions. Brook trout (*Salvelinus fontinalis*) are also widespread (51% of all strata investigated, Figure 4C), while the remaining salmonids have restricted distributions (Figure 4D).

Because of the large information gaps in our database, apparent simpatry between native and exotic fish will underestimate true simpatry. Yet, we found widely overlapping distributions at the spatial scale of our analysis. Most indigenous fish are found to coexist in most strata with at least two, and most commonly with three, exotic species (Table 4). In only 6 strata, indigenous fish were reported with no co-occurring exotic fish. These strata, however, correspond to areas which are so poorly surveyed and contain so many unknowns for introduced fish that we believe there is a low probability that they constitute true 'sanctuaries' for indigenous fish. In general, the four most conspicuous native species are found in simpatry with virtually all exotic species, while the three most conspicuous exotic fish have a large overlap at the geographic scale with all native species.

The interaction between native and exotic fish in Patagonia and Australasia

After analyzing how deficient the available information on species presence/absence is, it should come as no surprise that documentation on the impacts that salmonids have on native communities of Patagonia is scarce and largely inconclusive. The few reports available from those who witnessed the initial stages of salmonid introductions are based on largely circumstantial evidence and present contrasting views on how abundant native fish were prior to the introductions (Marini 1936; González Regalado 1945).

Modern literature on Patagonian fish is relatively little, largely concentrated on systematics and biology of native fish (some 175 references) and on the biology and demography of salmonids (about 105 references). Only 15 papers, all non-experimental field studies published after 1985, looked specifically at the interaction between native and exotic fish. Most of them examined fish communities in individual lakes and reservoirs of northern Patagonia. A handful of papers attempted to identify community structuring processes by looking for contrasts in species composition, microhabitat use and trophic relationships in collections of lakes.

The main results of these papers can be summarized as follows. Salmonids feed heavily on some native fish, particularly on *Galaxiids* (both gen *Aplochiton* and *Galaxias*) and silversides (Macchi et al. 1999), with large brown trout being the most piscivorous

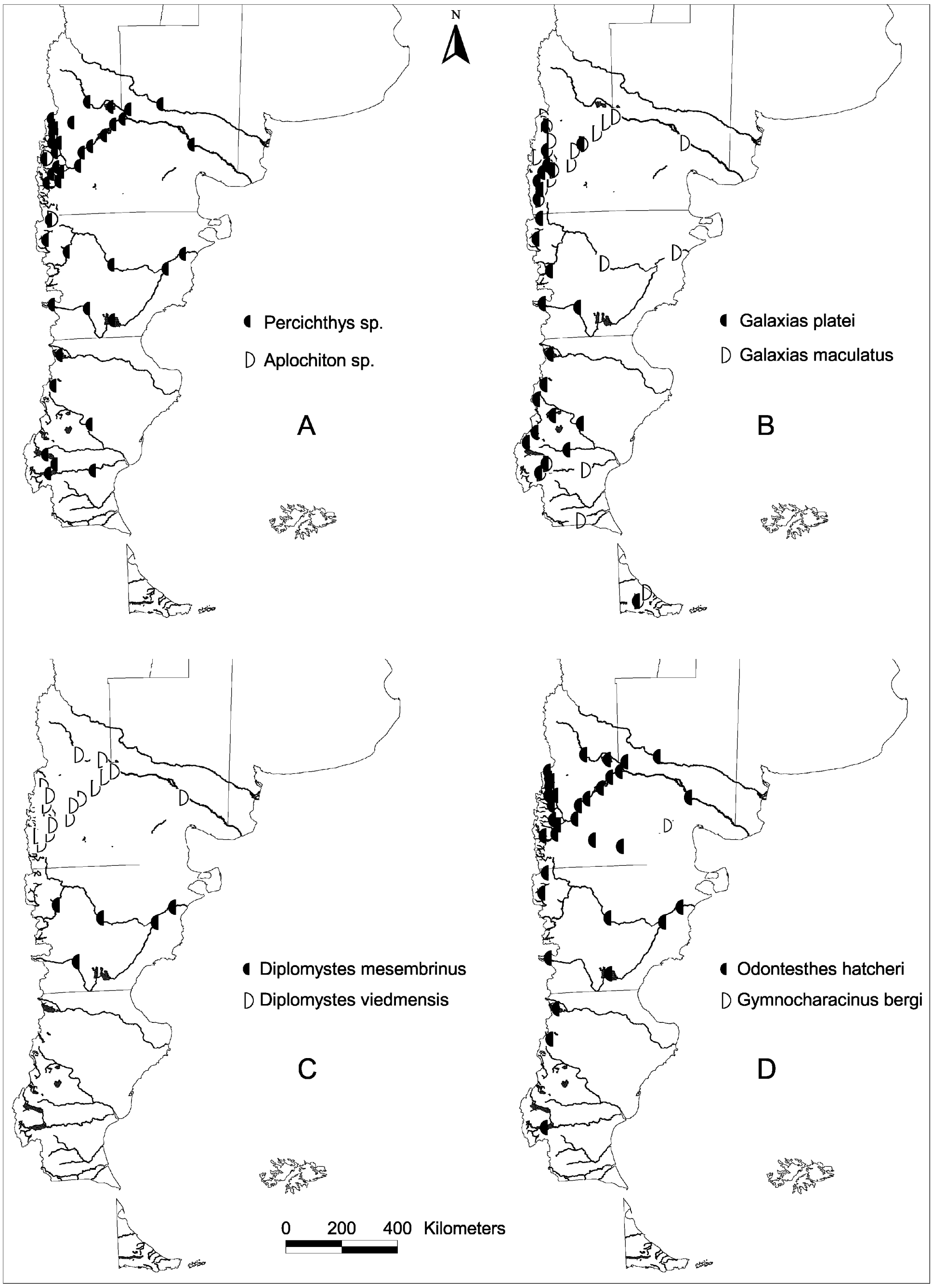

Figure 3. Distribution of the most endemic indigenous fish species. A: *Percichthys* sp. and *Aplochiton* sp.; B: *Galaxias platei* and *G. maculatus*; C: *Diplomistes mesembrinus* and *D. viedmensis*; D: *Odonthestes hatchery* and *Gymnocharacinus bergi*.

species. Yet, most native species show some degree of piscivory (Ferriz 1993–1994; Bello et al. 1991; Macchi et al. 1999), particularly native perches, which are still very abundant and even dominant over trout in many lakes and rivers in the region.

Most studies found some degree of segregation between native and introduced species, either trophic (Ferriz 1993–1994; Ferriz and Salas Aramburu 1994; Grosman 1993–1994; Macchi et al. 1999; Vigliano et al. 2000), reproductive (Cussac et al. 1997), or in

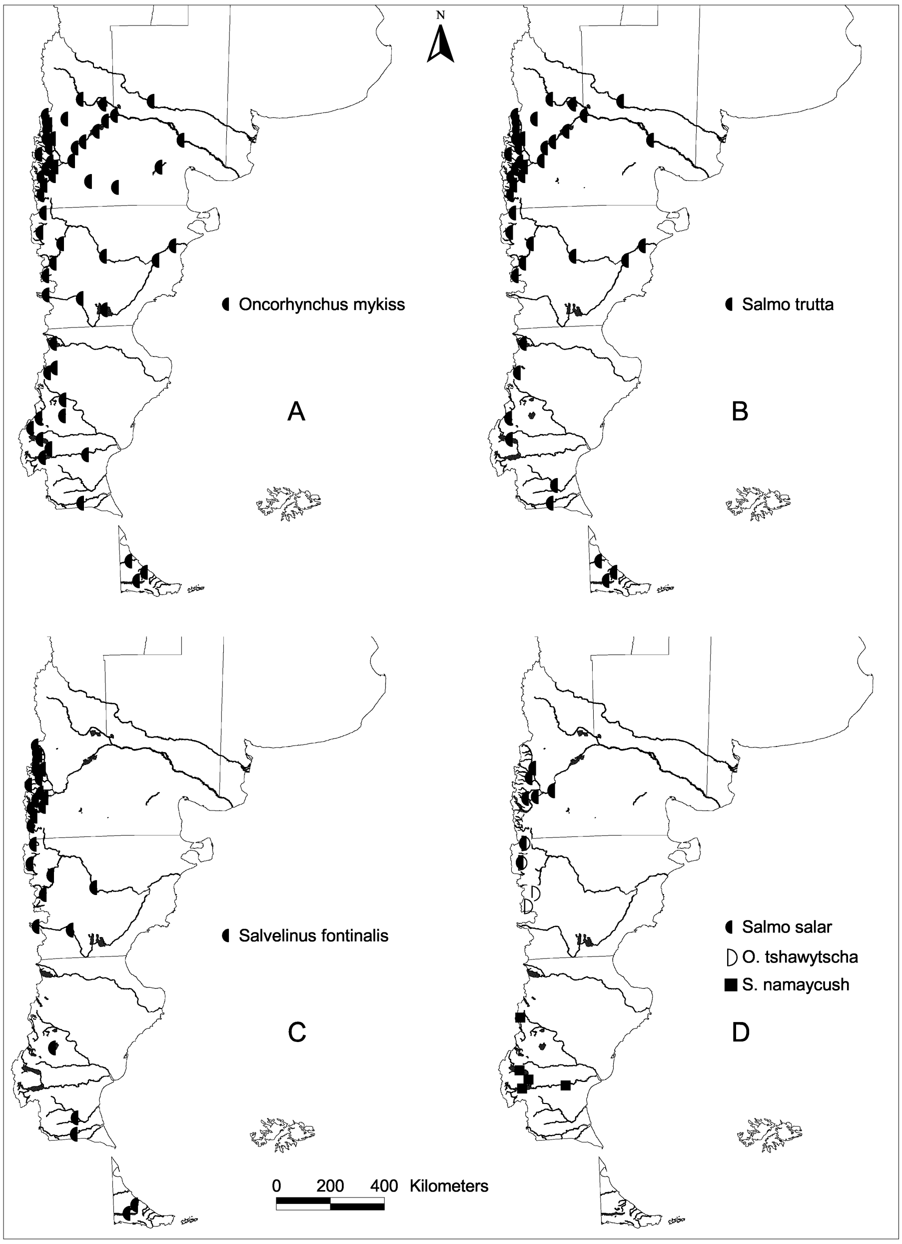

Figure 4. Distribution of major groups of exotic fish. A: rainbow trout, *Oncorhynchus mykiss*; B: brown trout, *Salmo trutta*; C: brook trout, *Salvelinus fontinalis*; D: Atlantic salmon, *Salmo salar*, chinook salmon, *Oncorhynchus tshawytscha*, and lake trout, *Salvelinus namaycush*.

habitat use (Vigliano et al. 2000). Whether segregation provides a mechanism to alleviate competition and predation or is itself the result of species interactions remains a matter of speculation.

Only one study provides conclusive evidence of an ecological disruption resulting from exotic species. In Arroyo Valcheta, a spring creek, rainbow trout prey heavily on the listed and strictly endemic naked characin, confining it to warm headwaters (Ortubay et al. 1997; Ortubay and Cussac 2000).

The same species of salmonids found in Patagonia were introduced into Australia and New Zealand at about the same time. Brown and rainbow trout are the most widespread exotic salmonids in Australasia (McDowall 1990). In contrast, brook trout, which is widespread in Patagonia, is restricted to a few

Table 4. Number of strata where indigenous species are known to co-occur with a different number of exotic species.

Species	Number of strata where it coexists with *N* exotic species					
	0	1	2	3	4	5
Percichthys sp.	1	7	16	35	16	1
Galaxias maculatus		1	11	38	9	
Galaxias platei	5	4	9	24	8	
Odontesthes hatcheri		9	11	16	8	1
Diplomystes sp.		3	8	22	6	
Hatcheria macraei		1	5	10	8	
Jenynsia lineata		2	3	2	2	
Aplochiton sp.				1	1	1
Astianax eigenmannioruum		1			1	
Cheirodon interruptus		1			1	
Cnesterodon decenmaculatus		1		1		
Gymnocharacinus bergi		1				

localities in New Zealand (McDowall 1968) and Australia (McKay 1984). Unlike Patagonia, studies in Australasia were largely conducted in rivers, many of them small streams; as in Patagonia, opinions about the extent of the effects that trout have on native fish in New Zealand are contradictory (McIntosh 2000).

Significant diet overlap exists between native and introduced species, and spatial-distribution patterns consistent with strong interaction have been documented (reviewed in Crowl and Townsend 1992). Native fish in Australasian rivers have fragmented distributions, highly segregated from those of brown and rainbow trout (McDowall 1968; Cadwallader 1978; Fulton 1978; Main et al. 1985), with an almost complete lack of co-occurrence at the level of individual sample sites (Minns 1990; Townsend and Crowl 1991). Available information suggests that once salmonids are introduced, their impacts may be severe and rapid (Crowl et al. 1992). A manipulative field experiment, where brown trout were introduced into a section of a New Zealand stream, resulted in a dramatic decline in abundance and condition of *G. olidus* within a four month period (Fletcher 1979).

As far as we can tell, in no instance was competition demonstrated as a critically important mechanism for the interaction between native and exotic fish, but there are multiple evidences of significant predation on native species by exotic fish (reviewed in Crowl et al. 1992). Field studies and a few laboratory experiments showed that, as in Patagonia, large brown trout are the most conspicuous piscivores in New Zealand. Studies based on historical data suggest that rainbow trout can also have a strong predatory effect, being apparently responsible for the demise of *Galaxias maculatus* in Lake Purrumbete, Australia (Cadwallader and Eden 1982).

Discussion

A logical first step for research on Patagonian freshwater fish is to build up the information available on distribution of native and exotic species. This kind of data will facilitate producing workable hypotheses about the interaction between native and exotic species and may also help to identify conservation-oriented actions, even before underlying mechanisms are understood. The database we present in this paper is intended as the foundation for such inventory work.

Our analysis revealed what some of the most notorious deficiencies in our current knowledge are. It shows, for example, that data on some of the most conspicuous preys of trout (Galaxiids and Siluriforms) are particularly incomplete. It also indicates that uncertainties are greater for rivers than for lakes, and that some areas of Patagonia are particularly data-deficient, such as the north of Santa Cruz Province. Meanwhile, data for northern Patagonia, particularly for lakes of the Río Negro Province, are significantly better.

The literature about New Zealand rivers indicates that segregation between native and exotic species occurs on a much smaller scale than that of our database. More specific analyses on the interaction between trout and natives will require looking at a smaller scale, a type of research virtually nonexistent for Patagonian rivers. Also, while we found no 'sanctuaries' for native species at the scale of our database, smaller rivers are more likely to provide trout-free sites and should be considered as part of future research. For example, small and unstable streams, which are unsuitable for brown and rainbow trout, have been found to provide refuge to some native species in New Zealand (McIntosh 2000).

To understand attitudes towards exotic and native fish in Patagonia, it is necessary to bear in mind that salmonid introductions preceded the strongest influx of European immigration to the region. Exotic fish are not really regarded any differently from indigenous fish by the general public and by most policymakers. Therefore, although management goals for Patagonian fish communities have not been established explicitly, they effectively encompass: (a) preserving world-renowned trout sport fisheries, the dominating and exclusive focus of provincial fisheries administrations, and (b) preserving native biodiversity, the guiding principle of the National Parks Administration and a much relegated objective in practice. Even when there are good reasons to believe that salmonids have had significant effects on the native freshwater biota, the lack of an articulate vision of how virgin communities might have looked before introductions seriously compromises the proposal of coherent conservation goals and actions.

There are, nevertheless, some opportunities for direct conservation actions in Patagonia at the local level, such as protecting critically endemic species through protected areas and active exclusion of non-native species (Saunders et al. 2002). The Arroyo Valcheta, a small and manageable stream, provides an excellent opportunity to protect the highly endemic and endangered naked characin through habitat preservation and exclusion of rainbow trout.

At the regional level, however, protecting native fish requires a more pragmatic approach for the preservation of native species. The true challenge for fish conservation at the regional level, we believe, is to find ways to protect native fish, compatible with maintaining highly priced sport fisheries. Is this at all possible? Are there management strategies that could balance fishing quality and conservation of native species? Such an approach may not appear completely satisfactory from a conservation viewpoint, but the current management scheme simply leaves native species out of the picture.

Trout management plans typically include establishing catch and size limits, as well as stocking fish from hatcheries, actions that ultimately affect the composition of exotic species, as well as their population age and size structure. For instance, the stocking of rainbow and brown trout is regularly conducted throughout lakes and rivers of Patagonia. How would such regulations and actions ultimately affect native species? Setting up a research program to deal with this question would require two things. First, the conservation of native fish should be evaluated in concert with fishery management of exotic species as an integrated 'cost–benefit' analysis, something rarely done in typical invasion ecology studies. Second, research should be directed at understanding whether and how particular exotic species affect native species. For example, is the most piscivorous brown trout more detrimental to native species than rainbow trout? Are the predatory impacts of a small population of large fish greater than the competition impacts of a large population of small fish? Also, do these effects vary across habitat types? Are native species more vulnerable to exotics in lakes than in rivers (Crowl et al. 1992)?

Answering these complex questions will no doubt demand going beyond inventory work and simplistic analyses of fish distribution. Exposing the nature and extent of interactions between native and exotic fish will require implementing lab experiments, field experiments based on species removal or addition, and even adaptive-management frameworks based on experimental fishing programs (Parma et al. 1998). Opportunities for such research and actions abound in Patagonia.

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