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RESEARCH PAPER

Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages

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Abstract The interaction between native fishes and salmonids introduced in Patagonia at the beginning of the 20th Century, developed at the same time as the environmental change. The phenomenon of global warming has led to the formulation of predictions in relation to changes in the distribution of species, in the latitudinal dimension, both at intralacustrine, or small streams levels. The aim of the present work includes three main objectives: a) to compose a general and updated picture of the latitudinal distribution range of native and alien fishes, b) to analyze the historical changes in the relative abundance of *Percichthys trucha*, *Odontesthes* sp., and salmonids in lakes and reservoirs, and c) to relate the diversity and relative abundance of native and salmonid fishes to the environmental variables of lakes and reservoirs. We analysed previous records and an ensemble of data about new locations along the northern border of the Patagonian Province. We compared current data about the relative abundance of native fishes and salmonids in lakes and reservoirs, with previous databases (1984–1987). All samplings considered were performed during spring-summer surveys and include relative abundance, as proportions of salmonids, *P. trucha*, and *Odontesthes* sp. For the first time, we found changes in fish assemblages from twenty years back up to the present: a significant decline in the relative abundances of salmonids and an increase of *P. trucha*. We studied the association between the diversity and relative abundance of native and salmonid fishes and the environmental variables of lakes and reservoirs using Canonical Correspondence Analysis. Relative abundance showed mainly geographical cues and the diversity relied largely on morphometric characteristics. Relative abundance and diversity seem to have a common point in the lake area, included into the PAR concept. Native abundance and alien diversity were negatively related with latitude. Greater native diversity was observed in lakes with high PAR compared with salmonids.

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Historical changes such as southward dispersion, relative abundance changes, and geographical patterns for relative abundance and diversity are basic concepts needed not only in future research but also in management design for Patagonian fish populations.

Keywords Fishes · Abundance · Diversity · Alien · Lake and river assemblages

Introduction

The biogeography of Patagonian fishes has been marked by the Andes uplift, marine incursions, and glaciations (Moyle and Cech 1982; Nelson 1994; Menni 2004; Hubert and Renno 2006). After the glacial retreat during the Pleistocene, Patagonian fishes' ability to colonise postglacial water bodies determined their present distribution (Cussac et al. 2004; Ruzzante et al. 2006), clearly constrained by climate and, in particular, by temperature. Temperature has been recognised as one of the cues for the understanding of the biogeography of fish in Southern South America (Ringuelet 1975; Gómez 1988; 1996; Menni and Gómez 1995; Menni et al. 1996; 1998). Simultaneously and consistent with historical changes occurring in the South American transition zone (Lopretto and Menni 2003; Morrone 2004), the northern border of the Patagonian Province (Ringuelet 1975) was shifted southward by Arratia et al. (1983) and Almirón et al. (1997, Fig. 1).

In a comprehensive survey, Quirós et al. (1986) and Quirós (1991) related the abundances of fish species to annual mean air temperatures. Shuter and Post (1990) discussed the potential effects of climate warming on the zoogeography of temperate freshwater fishes, assuming that the limit of distribution towards high latitudes depends on the size of the young-of-the-year necessary to minimize specific metabolic rates and maximize stored energy for the fish to endure periods of resource scarcity.

The localities for native fishes in Patagonia show a clear pattern (for example in Baigún and Ferriz (2003) and Liotta (2006)), where diversity exhibits a similar declining trend toward high latitudes, already reported for the Brazilic Subregion (Lopretto and Menni 2003). From north to south, it is possible to note the progressive disappearance of *Diplomystes*

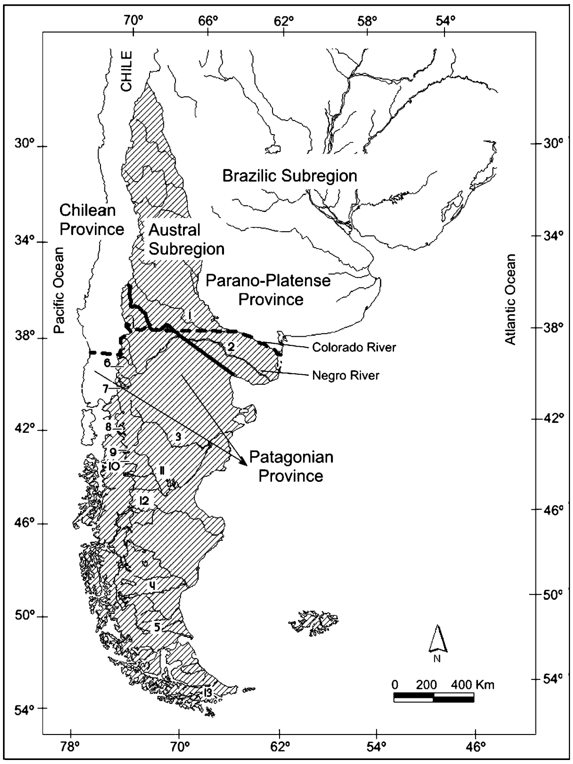

Fig. 1 Austral Subregion (shaded area) and northern limit of the Patagonian Province. This limit is indicated according to Ringuelet (1975, dotted line), Arratia et al. (1983, dashed line) and the southern limit of the transition zone of Almirón et al. (1997, solid line). Numbers indicate the main basins, Atlantic (1: Colorado, 2: Negro, 3: Chubut, 4: Santa Cruz, 5: Gallegos) Pacific (6: Hua Hum, 7: Manso, 8: Futaleufu, 9: Corcovado, 10: Engaño), Intermitent (11: Senguerr, 12: Deseado) and Beagle channel (13: Pipo)

cuyanus Ringuelet 1965, *Diplomystes viedmensis* MacDonagh, 1931, *Trichomycterus areolatus* Valenciennes, 1846, *D. mesembrinus*, *H. macraei, O. hatcheri* and finally *P. trucha*. Only species of the family Galaxiidae are found in Tierra del Fuego (Cussac et al. 2004).

The invasive capacity of introduced fish is well documented (Marchetti et al. 2004a; b). Fish introductions (Welcomme 1988; Cambray 2003) are frequent and usually elicit changes in the trophic web (McDowall 2003; Reissig et al. 2006), predation on amphibians (Fox et al. 2005; Ortubay et al. 2006), and negative interactions with other fishes (Macchi et al. 1999; McDowall et al. 2001; Milano et al. 2002; McDowall 2006). The interaction between native fishes and the salmonids introduced into Patagonia (Table 1) at the beginning of the Twentieth

Table 1 Salmonid and native fish species present in Patagonia

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

Century as environmental (Pascual et al. 2002; Macchi et al. 1999; Milano et al. 2002; 2006) developed at the same time as environmental change (Raven 1987; Gille 2002; Munn 1996; Jansen and Hesslein 2004; Rahel 2002).

The widely introduced salmonids show a complex pattern. In northern Patagonia, a loss of diversity can be seen eastward (Pascual et al. 2007). Macchi et al. (2007) point out that stocking policies, dispersal capabilities of each salmonid species and interactions among them produced changes in local and regional abundance and distribution throughout the last 100 years. Whereas *S. fontinalis* was dominant until the mid-1940s (Bruno Videla 1944; Gonzáles Regalado 1945), *O. mykiss* became the most important salmonid species in the 1950s (Fuster de Plaza 1950). Today *O. mykiss, S. trutta* and *S. fontinalis* are the most commonly found salmonid species (Pascual et al. 2002). Another source of salmonid diversity is the recent immigration of *O. kisutch* and

O. tshawystcha through Pacific drainages. Today, *S. namaycush* is exclusively located at high latitude and longitude, *S. fontinalis* is restricted to the Andes (higher longitude) and *O. mykiss* and in less extent *S. trutta*, are scattered throughout the Patagonian Province.

The aim of the present work includes three main objectives: (a) to compose a general and updated picture of the latitudinal distribution range of native and alien fish species, (b) to analyze the historical changes in the relative abundance of *Percichthys trucha* (sensu Ruzzante et al. 2006), *Odontesthes* sp., and salmonids in lakes and reservoirs, and (c) to relate the diversity and relative abundance of native and salmonid fishes to the environmental variables of lakes and reservoirs, in order to improve our knowledge of habitat use and our criteria for management and conservation.

Materials and methods

To characterize the fish assemblages in streams and lakes, we took information about presence/absence of species. Information for streams was limited to recent presence/absence data recorded in our own samplings and data obtained from the literature. In the same way, information about lakes came from data obtained recently, some by us. For both streams and lakes, we calculated the "zoogeographic integrity coefficient" (ZIC, Elvira 1995), which refers to the number of native species $\times$ (total number currently recorded)$^{-1}$, as an index of the degree to which fish populations have been invaded by introduced species. This index ranges from "1", which is equivalent to pristine conditions, to "0", showing the highest degree of alteration. Differences of integrity (ZIC) between rivers and lakes were analysed through the Mann–Whitney test. The different distributions of ZIC values were analysed with the Kolmogorov–Smirnov test. All statistical analyses were conducted with Statistical Package for Social Sciences (SPSS; Norusis 1986). Presence of native and alien species in Patagonian basins was visualised using the frequency of occurrence FO (%) $= 100 \cdot$ number of streams with presence $\cdot$ (number of streams sampled within the basin)$^{-1}$.

The changes in the northern border of the Patagonian Province (*sensu* Ringuelet 1975) mainly involved lotic systems of the basins of the rivers Colorado and Negro. A set of isolated references of new localities for Brazilian fish species was considered in the Patagonian Province (Cazzaniga 1978; Ferriz and López 1987; Almirón et al. 1997; Ortubay et al. 1997; Baigún et al. 2002).

To analyze the historical changes in the relative abundance of native fishes and salmonids in lakes and reservoirs we used Quirós' (1991) database, which included relative abundances, as proportions of salmonids, *P. trucha*, and *Odontesthes sp.* in captures for lakes sampled between 1984 and 1987. Quirós (1991) treated salmonids (including *O. mykiss, S. trutta, S. fontinalis* and *S. salar*), *Percichthys* (including all the nominal species of the genus) and *Odontesthes* (including *O. bonariensis* and *O. hatcheri*) together as single categories. Considering the results of Ruzzante et al. (2006), we considered all the nominal species of *Percichthys* as *P. trucha*. Regarding *Odontesthes*, the only reference to *O. bonariensis* southward the river Negro is that of the Ramos Mexia reservoir. In consequence, we considered that all the *Odontesthes* were *O. hatcheri* for the subsequent analysis.

We compared Quirós' findings with data obtained recently (Table 2), some of them by us. All past and present samplings considered were performed during spring-summer surveys and include data on relative abundance (Table 2) from littoral gillnet captures using low selective mesh arrangements. Initially, we only considered lakes of Quirós' (1991) database included within the geographic range of the most recent studies (38 to 54°S). We visualised past and present values of relative abundance by constructing bubble plots (Sigmaplot (R)). In a second step we kept only the lakes that coincided in both databases, constructed the bubble plots for relative abundances, and tested the median differences between them (Wilcoxon test on two related samples).

In order to relate the zoological integrity, diversity and relative abundance of native and salmonid fishes with the environmental variables of lakes and reservoirs, we considered the ZIC, the number of native and alien species, and the relative abundance of *P. trucha*, *Odontesthes sp.* and salmonids. The altitude, geographic position, area and perimeter were obtained from Google Earth images (http://www.earth.google.com/) processed with an image analyzer (Image Pro Plus). Areas and perimeters were also considered as line coast development (DL = perimeter $\cdot$ [2 $\cdot$ (π area)$^{1/2}$]$^{-1}$, Wetzel 1981) and as perimeter $\cdot$ area^{-1}

Table 2 Latitude, longitude, altitude and morphometry-area, perimeter, perimeter area^{-1} ratio (PAR) and line coast development (DL)- of Patagonian lakes ($N = 99$). Zoogeographic Integrity Coefficient (ZIC), presence (number of species) of natives[a], aliens[b] and relative abundance of *P.trucha* (P), salmonids (S), and *Odontesthes* (O) are indicated. Comparisons with abundance data of Quirós (1991)[c] are indicated in partitioned cases

Lake	South	West	Altitude (m.a.s.l.)	Area (km^2)	Perimeter (km)	PAR (km/km^2)	DL (km)	Native fishes	Alien fishes	ZIC (%)	Abundance P:S:O (%)
Alicura1[1, 5, 6, 9, 10, 12, 13]	40°40′	71°00′	705	67.50	215.60	3.19	7.40	*Hm, Dv, Gm, Oh, Pt*	*Om, Sf, Ss, St*	56	21:59:20
Aluminé[10, 16, 18]	38°55′	71°10′	1125	60.58	56.83	0.94	2.06	*Pt, Gp*	*Om, Sf*	50	
Amutui Quimei[9, 10, 18]	43°03′	71°45′	485	93.89	123.02	1.31	3.58	*Az, Oh, Pt*	*Om, Sf, St, Ss*	43	
Argentino[6, 10, 16, 18, 24]	50°20′	72°45′	187	1554.21	509	0.33	3.64	*Gm, Pt*	*Om, Sn*	50	82:18:0
											3:97:0[c]
Arroyito[1, 10]	39°14′	68°40′	315	41.46	61.37	1.48	2.69	*Oh, Pt*	*Om, St*	50	66:2:32
Azul[2, 27]	44°25′	71°19′	1150	1.24	5.37	4.33	1.36	*Gp*		100	
Baguillt[7, 18]	43°15′	71°10′	1050	0.98	8.27	8.40	2.35	*Gp*	*Om*	50	
Belgrano[6, 15]	47°55′	72°09′	780	46.90	116	2.47	4.78	*Gp*		100	0:0:0
Buenos Aires[18]	46°30′	71°35′	214	1870.33	504.29	0.27	3.29	*Om*	*Hm*	50	
Caradogh[18, 27]	42°54′	71°23′	746	1.42	5.65	3.98	1.34	*Gp*	*Om*	50	
Carrilafquen Chica[27]	41°12′	69°25′	825	5.78	10.69	1.85	1.25	*Oh*	*Om*	50	
Casa de Piedra[10, 18]	38°10′	67°30′	285	272.30	140.93	0.52	2.41	*Oh*	*Om*	50	
Cholila[10, 18]	42°27′	71°40′	547	17.18	30.85	1.80	2.10	*Pt, Gp, Az*	*Om, St, Sf, Ss*	43	
Constancio[2, 17, 27]	44°12′	71°22′	554	0.46	4.53	9.85	1.88	*Gp*		100	
Correntoso[6, 22, 26]	40°40′	71°40′	800	19.78	43.76	2.21	2.78	*Gm, Pt*	*Om, Sf, St*	40	53:47:0
Coyte[6, 14, 15]	45°25′	71°22′	795	6.53	12.24	1.87	1.35	*Gp*		100	0:0:0
Currue Chico[26, 27]	39°54′	71°20′	1106	0.51	4.42	8.63	1.74	*Gp, Pt*	*Om, Ss*	50	39:61:0
Currue Gde[27]	39°51′	71°27′	987	10.24	25.02	2.44	2.21	*Gp, Pt*	*Om, Ss*	50	0:100:0
De las Cármenes[27]	40°20′	71°29′	1063	1.94	12.34	6.37	2.50	*Gm, Gp*	*Om, St*	50	
De las Taguas[27]	40°18′	71°24′	1038	0.41	3.27	7.88	1.43	*Gp*	*Om, St*	33	
Del Mie[15]	47°54′	71°59′	800	0.07	1.04	15.96	1.15	*Gp*		100	0:0:0
El Casco[27]	40°29′	71°20′	904	0.02	0.61	28.16	1.17	*Gp, Pt*	*Om, St*	50	
Del Engaño[2, 27]	43°51′	71°31′	935	3.55	8.45	2.38	1.27	*Gp*	*Sf*	50	
Epulafquen[27]	39°51′	71°27′	987	8.25	18.30	2.22	1.80	*Gp, Oh, Pt*	*Om, St*	60	
Epuyén[10, 18]	42°11′	71°30′	250	17.40	33	1.90	2.23	*Az, Gp, Pt*	*Om, Sf, St*	50	
Escondido[27]	40°14′	71°33′	1046	3.15	12.09	3.84	1.92		*Om, St*	0	
Escondido[7, 15, 27]	54°38′	67°48′	140	6.06	18.73	3.09	2.15	*Gp*	*Sf, Om, St*	25	0:100:0
											0:100:0[c]
Espejo[6, 14, 15, 23, 26]	40°38′	71°45′	772	38.83	72.62	1.87	3.29	*Dv, Gm, Gp, Pt*	*Om, Sf, St*	57	45:55:0
Espejo Chico[8, 26, 29]	40°36′	71°42′	800	0.45	4.90	10.79	2.05	*Gm*		100	

Table 2 continued

Lake	South	West	Altitude (m.a.s.l.)	Area (km^2)	Perimeter (km)	PAR (km/km^2)	DL (km)	Native fishes	Alien fishes	ZIC (%)	Abundance P:S:O (%)
Esperanza[18]	42°13′	71°50′	500	4.03	13.38	3.32	1.88	*Gp*	*Om*	50	
Esquel[18]	42°51′	71°05′	650	1.38	6.45	4.67	1.55	*Gp, Pt*	*Om*	67	
Ezequiel Ramos Mexía[1, 10, 18]	39°30′	69°00′	381	816	565.30	0.69	5.58	*Gm, Gp, Oh, Pt, Ob, Jl*	*Om, St*	75	85:4:11 40:48:12[c]
Ezquerra[4, 18]	41°03′	71°33′	764	0.11	2.14	20.11	1.85	*Gm, Gp, Oh, Pt*	*Om*	80	
Falkner Villarino[6, 14, 15, 22]	40°27′	71°32′	950	15.98	38.13	2.39	2.69	*Gm, Gp, Pt*	*Om, Sf, St*	50	39:61:0
Filo Hua Hum[18]	40°28′	71°15′	850	4.12	13.96	3.39	1.94	*Dv, Gm, Gp, Pt*	*Om, St*	67	
Fonk[6, 14, 15, 26]	41°19′	71°45′	775	4.07	14.54	3.57	2.03	*Gm, Gp*	*Om, Sf, St*	40	0:100:0
Foye[l6, 18, 27]	41°55′	71°18′	824	0.06	1.65	29.40	1.97	*Az, Oh*	*Sf, Om, St*	40	
Futalaufquen[6, 10, 18]	42°49′	71°43′	518	44.28	64.30	1.45	2.73	*Az, Gp, Oh, Pt*	*St, Om*	67	31:69:0 8:92:0[c]
Guacho[2, 28, 28]	43°48′	71°28′	1168	4.18	14.34	3.43	1.98	*Oh*	*Sf, Om*	33	
Guillelmo[7, 13, 29]	41°22′	71°29′	826	6.50	19.65	3.02	2.17	*Gm*	*Sf, Om*	33	
Gutierrez[3, 6, 10, 13, 14, 15, 18]	41°05′	71°25′	750	16.40	25	1.52	1.74	*Dv, Gm, Gp*	*Sf, St, Om*	50	0:100:0 0:100:0[c]
Hermoso[27]	40°21′	71°31′	975	8.57	23.99	2.80	2.31	*Gm, Gp*	*Om, Sf*	50	0:100:0
Hess[7, 18]	41°22′	71°43′	750	1.34	8.78	6.54	2.14	*Dv, Gp, Pt*	*Om, St*	60	
Huechulaufquen[10, 18, 26]	39°46′	71°20′	875	78.20	68	0.87	2.17	*Dv, Hm, Gm, Gp, Oh, Pt*	*Om, Sf, Ss, St*	60	39:61:0 0:100:0[c]
Hui Hui[27]	39°21′	71°19′	1043	3.18	10.76	3.38	1.70	*Gp*	*Om, St*	33	
La Balsa[18, 27]	43°10′	71°43′	343	0.08	1.98	25.96	2.02	*Oh, Pt*		100	
La Pava[2, 15, 18, 27]	44°10′	71°30′	873	0.19	2.23	11.71	1.44	*Gp*		100	0:0:0
La Plata[10, 21, 25]	44°52′	71°49′	940	76	97	1.28	3.14	*Oh, Pt, Gp*	*Sf*	75	3:96:1 0:100:0[c]
Lacar[6, 10, 18, 29]	40°09′	71°37′	625	49	58	1.18	2.34	*Az, Dv, Gm, Gp, Pt*	*Om, St*	71	51:49:0 5:95:0[c]
Laguna Blanca[10, 20]	39°03′	70°22′	1230	17	30	1.76	2.05	*Pt*	*Om*	50	100:0:0 57:43:0[c]
Larga[18]	42°53′	71°35′	800	2.20	10.36	4.70	1.97	*Gp*	*St*	50	
Lezama[2, 18]	42°26′	71°28′	750	7.97	20.65	2.59	2.06	*Oh, Gp, Pt*	*Om*	75	
Los Barreales[1, 10]	38°35′	68°50′	421	413.10	214.50	0.52	2.98	*Oh, Pt*	*Om*	67	60:10:30 59:36:4[c]
Los Césares[18, 26]	41°18′	71°42′	1150	1.39	7.06	5.08	1.69	*Gp*	*Om*	50	

Table 2 continued

Lake	South	West	Altitude (m.a.s.l.)	Area (km^2)	Perimeter (km)	PAR (km/km^2)	DL (km)	Native fishes	Alien fishes	ZIC (%)	Abundance P:S:O (%)
Los Moscos[6, 14, 15, 26]	41°21′	71°36′	800	2.30	5.78	2.51	1.08	*Gm, Gp*	*Om, Sf, St*	40	0:100:0
Los Mosquitos[2, 18]	42°28	71°21′	500	5.08	12.26	2.41	1.53	*Oh*		100	
Machonico[27]	40°20′	71°29′	975	1.45	8.70	6.00	2.04	*Pt*	*Om, St*	33	86:14:0
Margarita[6, 15, 27]	54°40′	67°50′	86	0.87	7.71	8.86	2.33	*Gp*		100	0:100:0
Mari Menuco[1, 10, 18]	38°36′	68°37′	414	173.90	77.50	0.45	1.66	*Oh, Pt*	*Om*	67	74:7:19
											50:7:43[c]
Martin[6, 14, 15]	41°30′	71°40′	510	7.56	24.48	3.24	2.51	*Gp, Gm*	*St, Om, Sf*	40	0:100:0
Mascardi[6, 10, 14, 15, 29]	41°17′	71°38′	750	39.20	56	1.43	2.52	*Gm, Gp*	*Om, Sf, St*	50	0:100:0
											0:100:0[c]
Meliquina[18]	40°23′	71°17′	925	13.93	24.61	1.77	1.86	*Gm, Gp*	*Om, Sf, Ss, St*	33	
Mercedes (Ivic)[18, 27]	40°10′	71°22′	583	0.72	4.71	6.55	1.57	*Gm*	*Sf*	50	
Morenito[6, 13, 22, 26]	41°02′	71°32′	760	0.26	2.49	9.58	1.38	*Gm, Gp, Oh, Pt*	*Sf, Om*	67	74:3:23
Moreno[6, 13, 14, 15, 18, 26]	41°05′	71°32′	764	11.38	33.40	2.93	2.79	*Dv, Gm, Gp, Oh, Pt*	*Sf, Ss, Om*	62	54:45:1
Musters[6, 10, 18, 21, 24, 27]	45°27′	69°10′	260	414	150	0.36	2.08	*Gp, Oh, Pt*	*Om*	75	69:8:23
											86:8:6[c]
Nahuel Huapi[10, 18]	41°03′	71°25′	764	557	357	0.64	4.27	*Dv, Gm, Gp, Oh, Pt*	*St, Om, Sf, Ss*	56	
Nonthue[27]	40°09′	71°38′	640	4.20	11.68	2.78	1.61	*Az, Gm, Gp, Pt*	*Om*	80	0:100:0
Ñorquinco[18, 21]	39°09	71°17′	1025	7.09	18.13	2.56	1.92	*Gm, Pt*	*Om, Sf, St*	40	
Paimun[27]	39°43′	71°35′	926	15.77	34.75	2.20	2.47	*Oh, Pt*	*Om, St*	50	39:59:2
Pellegrini[10, 18]	38°40′	68°00′	270	112	69	0.62	1.84	*Oh, Pt, Jm*	*Om*	75	
Pico 2[2, 6, 15, 21]	44°18′	71°30′	950	6.65	21.38	3.22	2.34	*Gp*	*Om*	50	0:100:0
Piedra del Aguila[1, 5, 6, 10, 12, 13]	40°20′	70°10′	590	305	783.60	2.57	12.66	*Hm, Dv, Gm, Oh, Pt*	*Om, Ss, St, Sf*	56	37:29:34
Pilhué[27]	39°07′	71°23′	1131	1.48	8.25	5.56	1.91		*Om, St*	0	
Polco[18, 27]	42°27′	71°20′	575	0.29	2.46	8.37	1.28	*Oh*		100	
Pudu[27]	40°21′	71°28′	975	0.09	1.33	15.47	1.28	*Gm*	*Om, Sf*	33	0:100:0
Puelo[6, 10, 11, 18]	42°10′	71°40′	150	44	57	1.30	2.42	*Az, Gp, Oh, Pt*	*Om, Ot, Sf, St, Ss*	44	82:18:0
											45:50:5[c]
Pueyrredon[6, 15, 18]	47°18′	71°55′	155	325.83	211.06	0.65	3.30	*Gp, Oh, Pt*	*Om*	75	58:22:20
Pulmarí[2, 27]	39°06′	71°06′	1059	2.24	15.66	6.98	2.95	*Gm, Oh, Pt*	*Om*	75	
Queñi[27]	40°08′	71°42′	932	3.34	12.37	3.70	1.91	*Az*	*Om*	50	0:100:0
Quillen[10, 18, 23, 27]	39°25′	71°17′	975	23.91	50.52	2.11	2.92	*Dv, Gm, Gp, Oh, Pt*	*Om, Sf, St*	62	72:27:1
											23:45:32[c]

Table 2 continued

Lake	South	West	Altitude (m.a.s.l.)	Area (km^2)	Perimeter (km)	PAR (km/km^2)	DL (km)	Native fishes	Alien fishes	ZIC (%)	Abundance P:S:O (%)
Rivadavia[6, 10, 11, 15, 23, 27]	42°36′	71°39′	527	22.55	30.79	1.37	1.83	*Az, Gp, Oh, Pt*	*Om, Sf, St*	57	65:35:0
											6:94:0[c]
Rosales[19, 27]	40°06′	71°20′	982	0.30	3.78	12.55	1.94	*Gm, Pt*	*Om*	67	
Rosario[10, 18]	43°15′	71°20′	650	14.50	21	1.45	1.56	*Gp, Oh, Hm*	*Om*	75	
Ruca Choroi[18, 22, 27]	39°14′	71°11′	1254	3.10	10.35	3.34	1.66	*Gm, Gp, Oh, Pt*	*Om, Sf*	67	36:64:0
Steffen[6, 15]	41°31′	71°33′	525	5.39	17.47	3.24	2.12	*Gm, Gp*	*Om, Sf, St*	40	0:100:0
											0:100:0[c]
Terraplén[2, 18]	42°59′	71°32′	750	2.70	7.33	2.72	1.26	*Oh*	*Sf*	50	
Torres[2, 6, 15, 27]	44°07′	71°06′	847	1.06	4.59	4.32	1.26	*Gp*	*Om*	50	0:100:0
Traful[18, 26]	40°37′	71°25′	800	78.80	91.60	1.16	2.91	*Gp, Gm, Oh, Pt, Dv*	*Om, St, Sf, Ss*	56	
Trebol[18, 26]	41°04′	71°30′	764	0.30	2.20	7.33	1.13	*Gm*		100	
Tres[18, 27]	44°15′	71°35′	503	2.53	7.30	2.89	1.30	*Gp*	*Om, St*	33	
Tromen[21, 27]	39°31′	71°26′	1000	28.99	44.99	1.55	2.36	*Dv, Gm, Gp, Oh, Pt*	*Om, Ss, St*	62	
Venados[27]	40°12′	71°41′	876	0.68	4.41	6.49	1.51		*Om*	0	0:100:0
Verde[26, 27, 29]	40°46′	71°43′	790	0.21	4.14	19.37	2.53	*Gm*		100	
Vilches[2, 6, 15, 27]	44°07′	71°34′	723	1.98	6.33	3.19	1.27	*Gp*	*Om*	50	0:100:0
Vintter[18, 21, 27]	43°56′	71°35′	920	140.16	110.92	0.79	2.64		*Sf*	0	
Willimanco[18]	42°52	71°17′	700	0.60	3.69	6.15	1.34	*Gp*	*Om*	50	
Yehuin[6, 10, 15, 18]	54°24′	67°44′	241	43.50	51	1.17	2.18	*Gp*	*St*	50	0:100:0
											0:100:0[c]
Zeta[18]	42°53′	71°20′	850	0.65	4.21	6.49	1.48	*Gp, Pt*	*Om*	67	

[a] *Dv*: *Diplomystes viedmensis*, *Hm*: *Hatcheria macraei*, *Gm*: *Galaxias maculatus*, *Gp*: *G. platei*, *Oh*: *Odontesthes hatcheri*, *Ob*: *O. bonaerensis*, *Az*: *Aplochiton zebra*, *Pt*: *Percichthys trucha*, *Jl*: *Jenynsia lineata*, *Jm*: *J. multidentata*

[b] *Om*: *Oncorhynchus mykiss*, *Ot*: *O. tshawystcha*, *St*: *Salmo trutta*, *Ss*: *S. salar*, *Sf*: *Salvelinus fontinalis*, *Sn*: *S. namaycush*

[c] Years 1984–1987 (Quirós 1991)

References: 1: Alonso (2003). 2: Baigún and Férriz (2003). 3: Barriga et al. (2002). 4: Cussac et al. (1992). 5: Cussac et al. (1998). 6: Cussac et al. (2004). 7: De Negri pers. com. 8: Díaz et al. (2000). 9: Hidroeléctrica Futaleufú pers. com. 10: IARH-INCYTH. (1995). 11: Lattuca et al. (2007). 12: Macchi et al. (1999). 13: Macchi (2004). 14: Milano et al. (2002). 15: Milano et al. (2006). 16: Oliveros and Cordiviola (1974). 17: Ortubay and Wegrzyn (1991). 18: Ortubay et al. (1994). 19: Ortubay et al. (2002). 20: Ortubay et al. (2006). 21: Quirós (1991). 22: Ruzzante et al. (1998). 23: Ruzzante et al. (2003). 24: Ruzzante et al. (2006). 25: Ruzzante pers. com. 26: Semenas pers. com. 27: This paper. 28: Wegrzyn pers. com. 29: Zattara and Prémoli (2004) ratio (PAR). PAR and DL reflect the development of the littoral zone, nutrient input, macrophyte abundance and shelter availability. The association between fish assemblage characteristics (ZIC, diversity, and abundance) and geographic and environmental variables was treated using Canonical Correspondence Analysis (CANOCO 4.5, ter Braak and Smilauer 1998).

Results

River and lake assemblages

The ZIC data (Tables 2 and 3) revealed that many more lakes than streams were sampled. In addition, there are basins whose streams have been better sampled than others due to geographic or human constraints.

Rivers showed lower integrity than lakes (Mann–Whitney test, $n = 154$, $P < 0.002$) and a different distribution of ZIC values (Kolmogorov–Smirnov test, $n = 154$, $P < 0.004$), unimodal in lakes and with three modes in rivers. Salmonids were always strongly present both in lakes and streams. Rainbow trout was the most frequent among salmonids. *Galaxias platei* and *P. trucha* were the most widespread native species (Fig. 2).

We observed a conspicuous overlap of specific localities for Austral, Brazilic and Marine species (Table 4) along the basins of the rivers Colorado and Negro. Before Ringuelet (1975), the following species composition existed (excluding the exotic species of Salmonidae introduced since 1904, see Pascual et al. 2002) 2 Brazilic (*Gymnocharacinus bergii* Steindachner, 1903, *Jenynsia multidentata* Jenyns, 1842), 3 Austral (*D. viedmensis, P. trucha* and *Galaxias maculatus* (Jenyns, 1842)), and 1 Andean (*D. cuyanus*). Since the general scheme of Ringuelet (1975), new localities for Brazilic, marine and non-salmonid exotic species in the Austral Subregion have been noted. The new records were: 7 Brazilic (*Astyanax eigenmanniorum* Cope, 1894, *Cheirodon interruptus* Jenyns, 1842, *Oligosarcus jenynsii* Günther, 1864, *Corydoras paleatus* Jenyns, 1842, *Cnesterodon decemmaculatus* (Jenyns, 1842), *J. multidentata*-a new southern record, and *O. bonariensis*); 4 Austral (*Hatcheria macraei* (Girard, 1855), *T. areolatus, Galaxias platei* Steindachner, 1898, *O. hatcheri*); 3 marine (*Odontesthes argentinensis* (Valenciennes, 1835), *Mugil liza* Valenciennes, 1836, *Paralichthys brasiliensis* (Ranzani, 1842)), and 1 exotic species (*Cyprinus carpio* Linnaeus, 1758), introduced into the south of the Brazilic Subregion and arriving at the Austral Subregion with no known means of dispersal. Thus, we considered a total of 8 Brazilic, 7 Austral, 1 Andean, 3 marine, and 1 exotic species, summing a total of 20 species (Table 4).

Some of the new records reveal established populations with a high number of individuals captured, such is the case of *J. multidentata*, *A. eigenmanniorum*, *O. jenynsii*, *C. carpio*, and *M. liza* (Almirón et al. 1997). The "new record" condition of *J. multidentata* deserves additional explanation. This species was already recorded in the rivers Colorado (in 1916) and Negro (in 1967). However, new records (1987 and 1997) confirm a southward displacement (from 40 to 41°S).

In addition to the new localities for Brazilic and marine species at the northern border of the Austral Subregion, new localities for Austral species already cited in the northwest of the Austral Subregion were also found southward of their known distribution range: *H. macraei* (at Jeinimeni and Ecker rivers) and *T. areolatus* (in the Negro, Tecka and Lepa rivers) (Almirón et al. 1997; Baigún and Ferriz 2003).

Historical changes in fish abundances

In lakes, the graphs for the relative abundances of salmonids in the area common (38 to 55°S) to the databases of Quirós (1991, $n = 42$) and our own present databases ($n = 44$) showed, at first view, a similar situation regarding distribution and relative abundance (Fig. 3). However, comparing these databases restricted to common lakes ($n = 18$, Table 2), we observed that the relative abundance of salmonids decreased (Wilcoxon signed-ranks test, $n = 18$, $P < 0.001$, Fig. 4) and *P. trucha* increased (Wilcoxon signed ranks test, $n = 18$, $P < 0.001$, Fig. 5). It must be noted that although the relative abundance values are linked, there is variation within native fishes since changes in silverside abundances were not significant (Wilcoxon signed ranks test, $n = 18$, $P > 0.68$). Among these 18 lakes and reservoirs, five lakes (Gutiérrez, Mascardi, Steffen, Yehuin, and Escondido) showed no changes for 100% of salmonids. However, we must note that only salmonid populations in littoral gillnet captures were considered (the small *G. maculatus* is not captured by gillnets and *G. platei* dwells in the deep bottom, Table 2).

Table 3 Patagonian streams ($N = 56$). Basin, Zoogeographic Integrity Coefficient (ZIC) and presence of natives[a] and aliens[b] fishes

Stream	Native fishes	Alien fishes	ZIC (%)	Basin	References
Calafate	*Gm*		100	Santa Cruz	14
Caleufú	*Gm, Hm, Oh, Pt*	*Om, St*	67	Negro	16, 13
Calfiquitra		*Om*	0	Negro	65
Cangrejo	*Gm, Gp*	*Om*	67	Santa Cruz	14
Carrileufu	*Az, Gp, Hm, Pt*	*Om, Sf, Ss, St*	50	Futaleufú	1, 65, 63, 93
Caterina		*Om, Ot, Sn*	0	Santa Cruz	72
Chenqueniyen	*Hm*		100	Chubut	12
Chico	*Hm, Oh, Pt*	*Om, Sf*	60	Senguerr	61
Chico	*Gm, Pt*	*Ot*	67	Santa Cruz	12, 16, 56
Chimehuin	*Dv, Oh, Pt*	*Om, St*	60	Negro	1, 16, 23, 91
Chubut	*Dm, Gp, Hm, Oh, Pt*	*Om, Sf, St,*	63	Chubut	8, 10, 11, 17, 22, 25, 36, 77, 82, 93
Colorado	*Ae, Ci, Dc, Dv, Hm, Jm, Ml, Oa, Ob, Oh, Oj, Pb, Pt*	*Cc*	93	Colorado	3, 4, 18, 25, 28, 38, 49, 79, 82
Commonpulli		*Om*	0	Negro	65
Corcovado	*Gp*	*Om, Ot, Sf*	25	Corcovado	88, 63, 24
Córdoba		*Om*	0	Negro	65
Córdoba Grande		*Om*	0	Negro	65
Coronado	*Az*	*Om, St*	33	Futaleufú	22
Culebra		*Om, Sf*	0	Negro	91
Currhue Chico	*Pt*	*Om, St*	33	Negro	91
De los Raulíes		*Om*	0	Negro	62
Ecker	*Hm, Oh*		100	Deseado	12
Engaño		*Sf*	0	Engaño	62
Filuco		*Om, Sf*	0	Negro	91
Gallegos	*Gm, Pt*	*Om, Ot, St*	40	Gallegos	16, 56, 58, 71
Gualjaina	*Oh, Pt*	*Om, Sf, St*	40	Chubut	93
Hermoso	*Gp*	*Om, Sf, St*	25	Negro	91
Huaca Mamuil		*Om*	0	Negro	65
Hui Hui		*Om*	0	Negro	65
Jeinimeni	*Hm*		100	Deseado	12
La Leona	*Gm, Gp, Pt*	*Om, Ot, Sn, St*	43	Santa Cruz	19
Lepa	*Hm, Ta*	*Om, St*	50	Chubut	12, 93
Limay	*Cp, Dv, Gm, Gp, Hm, Oh, Pt*	*Cc, Om, Sf, Ss, St*	58	Negro	8, 17, 25, 29, 30, 31, 32, 33, 34, 35, 40, 41, 43, 46, 52, 53, 54, 55, 56, 47, 64, 77, 82, 78, 89, 90, 87
Malalco		*Om*	0	Negro	65
Malleo	*Dv, Oh*	*Om, St*	50	Negro	16, 91
Manso	*Gm, Gp*	*Om, Sf, St*	40	Manso	48
Meliquina		*Om*	0	Negro	91
Negro	*Ci, Cp, Dv, Ga, Gm, Gp, Hm, Jm, Ob, Oh, Pt, Ta*	*Cc, Om*	86	Negro	10, 8, 2, 3, 5, 25, 37, 45, 44, 52, 53, 57, 49, 50, 51, 64, 77, 80, 82, 81
Neuquén	*Dv, Hm, Oh, Pt*	*Om, St*	67	Negro	8, 17, 25, 34, 57, 77, 82, 88
Nonthué		*Om*	0	Hua Hum	91
Ñireco	*Hm*	*Om*	50	Negro	16, 62
Ñirihuau	*Hm, Oh*	*Om, St*	50	Negro	16, 35, 47, 60, 66
Pescado	*Oh, Pt*	*Om*	67	Chubut	93

Table 3 continued

Stream	Native fishes	Alien fishes	ZIC (%)	Basin	References
Pichi Hua Hum		*Om*	0	Hua Hum	91
Pichi Leufu	*Gm, Hm, Pt*	*Om, St, Sf*	50	Negro	59
Pichi Traful		*Om, Sf*	0	Negro	91
Pinturas	*Pt*		100	Deseado	12
Pipo	*At, Gm*	*Om, Ot, St*	40	Pipo	65, 21
Pocahullo	*Az*	*Om, St*	33	Hua Hum	61
Pucará		*Om*	0	Hua Hum	65
Quillén	*Dv*	*Om, St*	33	Negro	91
Roble	*Gp*	*Sn*	50	Santa Cruz	61, 86
Santa Cruz	*Ga, Gm, Gp, Pt*	*Om, Ot, Sn, St*	50	Santa Cruz	3, 8, 14, 15, 16, 19, 20, 26, 27, 39, 56, 58, 63, 64, 76, 70, 73, 71, 68, 69, 75, 74, 77, 82, 84, 83, 85
Senguerr	*Dm, Gp, Oh, Pt*	*Om, Sf*	67	Senguerr	8, 7, 10, 11, 9, 12, 25, 63, 93
Tecka	*Hm, Ta*	*Om, Sf*	50	Chubut	12, 22, 71
Traful	*Dv, Gp, Oh*	*Om, Sf, Ss, St*	43	Negro	8, 29, 82, 92,
Vaca Laufquen	*Pt*		100	Negro	12

[a] (*Az: A. zebra, Ci: C. interruptus, Cp: Corydoras paleatus, Dv: D. viedmensis, Ga: G. australis, Gm: G. maculatus, Gp: G. platei, Hm: H. macraei, Jm: J. multidentata, Ob: O. bonaeriensis, Oh: O. hatcheri, Oj: O. jenynsi, Ta: T. areolatus*)

[b] (*Cc: Cyprinus carpio, Om: O. mykiss, Ot: O. tshawystcha, Sf: S. fontinalis, Sn: S. namaycush, Ss: S. salar, St: S. trutta*)

References: 1: Aigo pers. obs., 2: Almirón et al. (1983), 3: Almirón et al. (1997), 4: Alonso pers. com., 5: Alvear et al. in press, 6: Amaya and Pascual (2006), 7: Arratia (1987). 8: Arratia et al. (1983), 9: Azpelicueta and Gosztonyi (1998), 10: Azpelicueta (1994a), 11: Azpelicueta (1994b), 12: Baigún and Férriz (2003), 13: Barriga et al. (2007), 14: Battini pers. obs., 15: Becker (2004), 16: Bello (2002), 17: Bruzone (1986), 18: Cazzaniga (1978), 19: Ciancio (2000), 20: Ciancio et al. (2005), 21: Cussac et al. (2004), 22: Cussac pers. obs., 23: Del Valle et al. (1996), 24: Di Prinzio (2001), 25: Dyer (1993), 26: Eigenmann (1909), 27: Eigenmann (1910), 28: Eigenmann (1911), 29: Evermann and Kendall (1906), 30: Férriz (1984), 31: Férriz (1993), 32: Férriz (1994), 33: Fuster de Plaza and Plaza (1955), 34: Gneri and Nani (1960), 35: Gonzáles Regalado (1945), 36: Gosztonyi (1988), 37: Hasemann (1911), 38: Henn (1916), 39: Hidalgo (2003), 40: Lippolt (2004), 41: López (1981), 42: López and Ferriz (1981), 43: López et al. (1978), 44: López Cazorla and Miganne (1996), 45: López Cazorla and Tejera (1996), 46: Luchini (1981), 47: Macchi pers. com., 48: Macchi (2004), 49: Mac Donagh (1936), 50: Mac Donagh (1937), 51: Mac Donagh (1938), 52: Mac Donagh (1950), 53: Mac Donagh (1953), 54: Mac Donagh (1955), 55: Mac Donagh and Thormählen (1945), 56: McDowall (1969), 57: McDowall (1970), 58: McDowall (1971), 59: Navone (2006), 60: Noguera pers. com., 61: Ortubay pers. com., 62: Ortubay pers. obs., 63: Ortubay and Wegrzyn (1991), 64: Ortubay et al. (1994), 65: Ortubay et al. (2003), 66: Ostrowsky de Núñez pers. com., 67: Pascual and Hidalgo (2004), 68: Pascual and Riva Rossi (1999), 69: Pascual and Soverel (1997), 70: Pascual et al (2001), 71: Pascual et al. (2002), 72: Pascual et al. (2003), 73: Pascual et al (2005), 74: Pellanda and Fernández (1997), 75: Pellanda et al. (2006),. 76: Perugia (1891), 77: Pozzi (1945), 78: Rechencq (2003), 79: Regan (1905), 80: Ringuelet (1965), 81: Ringuelet and Aramburu (1957), 82: Ringuelet et al. (1967), 83: Riva Rossi (2004), 84: Riva Rossi et al. (2003), 85: Riva Rossi et al. (2004), 86: Ruzzante pers. com., 87: Semenas et al. (1987), 88: Semenas et al. (1989), 89: Szidat (1956), 90: Szidat and Nani (1951), 91: This paper, 92: Vigliano pers. com., 93: Wegrzyn pers. obs.

Spatial distribution patterns in abundances and diversity

The relationship between relative abundances of species and environmental variables was significant (Monte Carlo test, $n = 44$, $F = 20.9$, $P < 0.001$) and explained (the first two axes) the 100 % of the variance. The CCA revealed an appreciable separation among the relative abundances of *P. trucha, Odontesthes sp*. and salmonids in relation to the environmental variables, along the two canonical axes ($\lambda 1 = 0.193$, $\lambda 2 = 0.033$). Latitude, longitude and area of lakes were significant in the explanation of the gradient of relative abundances (Table 5). In Fig. 6, we could see that the high abundances of salmonids were 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.

The relationship between diversity variables (number of native and alien species and ZIC) and

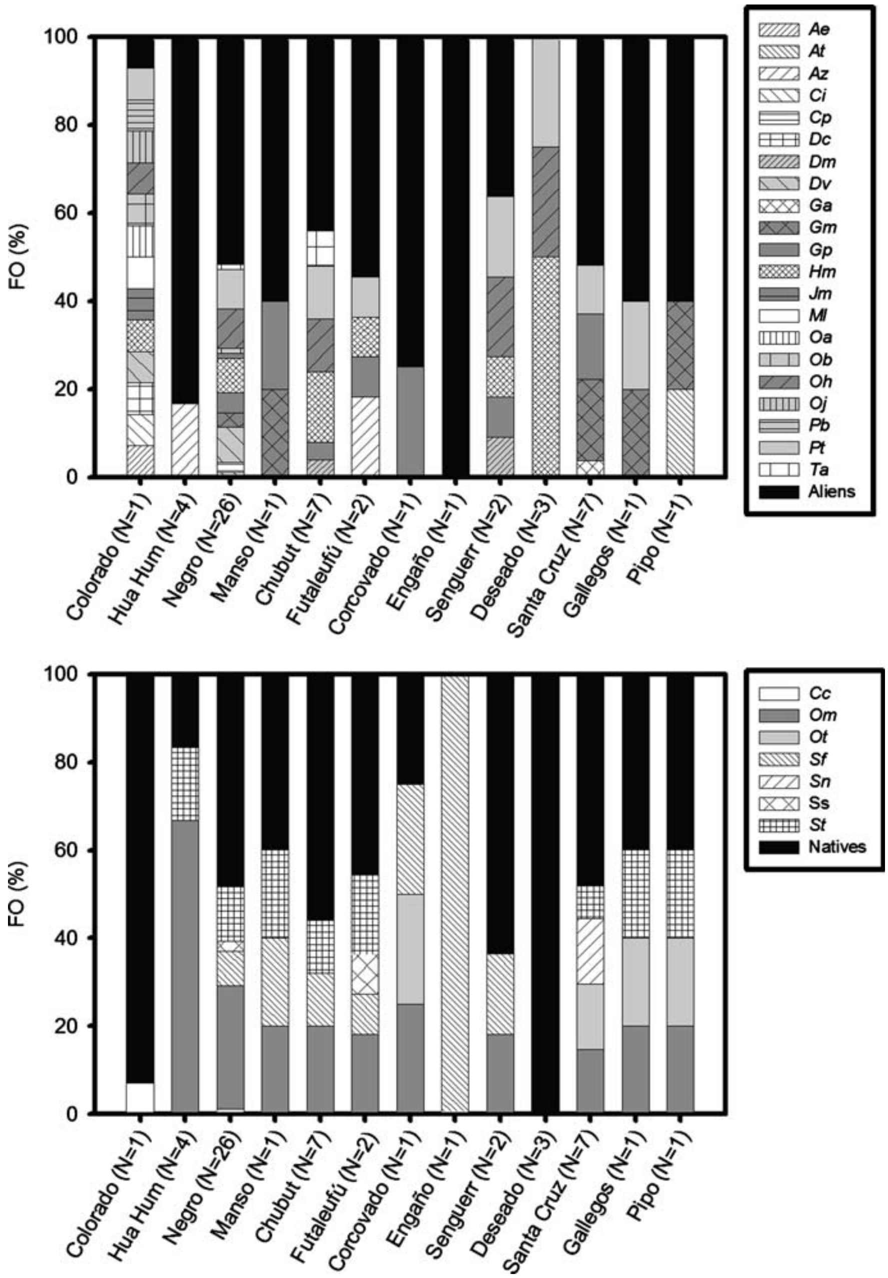

Fig. 2 Frequency of occurrence (percentual, FO (%)) of native (top panel, *At: A. taeniatus, Az: A. zebra, Ci: Cheirodon interruptus, Cp: Corydoras paleatus, Dm: D. mesembrinus, Dv: D. viedmensis, Ga: G. australis, Gm: G. maculatus, Gp: G. platei, Hm: H. macraei, Jm: J. multidentata, Ob: O. bonariensis, Oh: O. hatcheri, Oj: O. jenynsi, Pt: P. trucha, Ta: T. areolatus*) and alien species (bottom panel, *Cc: C. carpio, Om: O. mykiss, Ot: O. tshawystcha, Sf: S. fontinalis, Sn: S. namaycush, Ss: S. salar, St: S. trutta*) in the Patagonian basins (ordered by increasing latitude, N = number of streams sampled within the basin)

environmental variables was significant (Monte Carlo test, $n = 99$, $F = 3.38$, $P < 0.007$) and explained (the first two axes) the 100% of the variance. The CCA revealed an appreciable separation among diversity variables in relation to the environmental ones, along the two canonical axes ($\lambda1 = 0.013$, $\lambda2 = 0.001$). Only latitude and PAR were significant in the explanation of the gradient of diversity variables (Table 5). In Fig. 7, we could see that the higher number of alien species was more related to lower latitudes and lower PAR than the high number of native species. The ZIC was mostly associated with high latitudes. However, the meaning of ZIC was constrained by the simultaneous change of alien and native diversity. Although not significant ($P > 0.06$), high DL resulted strongly associated with high number of native species and greater longitude with a high number of alien species.

Table 4 Specific localities (first records) for Austral (A), Brazilic (B), Andean (AN), and Marine (M) species at the northern border of the Austral Subregion. Over 20 species, 40% are Brazilic and 37% Austral. Localities considered new records after the general scheme of Ringuelet (1975) for Brazilic (B), Andean (AN) and Marine (M) species are indicated with capture date (CD), latitude and longitude. The exotic species *Cyprinus carpio* (E) was also considered

Species	Origin	CD	Authors	Locality	South	West
Astyanax eigenmanniorum	B	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
Cheirodon interruptus	B	1978	Cazzaniga (1978)	lower Colorado river	39°40′	62°28′
		2003	Alvear et al. (2007)	Negro river	39°01′	67°52′
Gymnocharacinus bergi	B		Steindachner (1903)	Valcheta stream		
Oligosarcus jenynsii	B	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
Corydoras paleatus	B	2000	Baigún et al. (2002)	Limay river	41°02′	71°07′
		2003	Alvear et al. (2007)	Negro river, Allen	39°01′	67°52′
Diplomystes cuyanus	AN		Eigenmann (1911)	Colorado river		
Diplomystes viedmensis	A		MacDonagh (1936)	lower Colorado river, Negro river, Viedma		
Hatcheria macraei	A		Almirón et al. (1997)	lower Colorado river		
Trichomycterus areolatus	A		Almirón et al. (1997)	Negro river		
Cyprinus carpio	E	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
			Alvear et al. (2007)	Negro river	39°01′	67°52′
Galaxias maculatus	A		López and De Carlo (1959)	Negro river		
Galaxias platei	A		Almirón et al. (1997)	Negro river		
Cnesterodon decemmaculatus	B	1994	Ortubay et al. (1997)	Curicó lake	40°29′	65°40′
		1994	Ortubay et al. (1997)	Valcheta stream	40°36′	65°50′
Jenynsia multidentata	B		Henn (1916)	Colorado river		
			Ringuelet et al. (1967)	Colorado river, Pedro Luro, Negro river, San Blas		
		1987	Ferriz and López (1987)	Limay river	41°02′	71°07′
		1994	Ortubay et al. (1997)	Valcheta stream, Curicó lake	40°36′	65°50′
Odontesthes bonariensis	B	1978	Cazzaniga (1978)	lower Colorado river	39°40′	62°28′
		2003	Alvear et al. (2007)	Negro river	39°01′	67°52′
Odontesthes hatcheri	A		Dyer (1993)	Colorado river		
			Ortubay et al. (1994)	Negro river		
Odontesthes argentinensis	M	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
Mugil liza	M	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
		2003	Alvear et al. (2007)	Negro river	39°01′	67°52′
Paralichthys brasiliensis	M	1994	Almirón et al. (1997)	lower Colorado river	39°40′	62°28′
Percichthys trucha	A		Regan (1905), MacDonagh (1936), Ringuelet et al. (1967)	Limay River, Pelegrini lake, Negro river, Viedma, Fortín Uno, Colorado river		

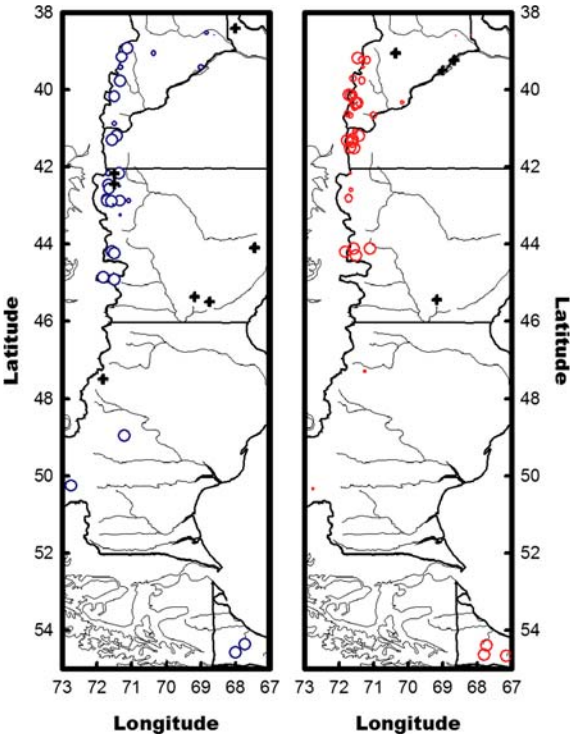

Fig. 3 Relative abundance (bubble size indicates the % of total capture) for salmonid populations of lakes and reservoirs (from 38 to 54° S), according to the database of Quirós (1991) for years 1984–1987 (left, blue circles, $n = 42$) and recent samplings (right, red circles $n = 44$). Crosses indicate absences

Discussion

Salmonid and native assemblages

The data about the ZIC in lakes and streams are limited due to the varying sources of information. In this sense, data have been reported by sport anglers and divers; dead fish have been observed by rangers, and information has been gathered in scientific studies. While there have been multiple efforts to survey fish in lakes, river surveys have been rare and sketchy. However, the resulting ZIC has a clear consistency. The analysis points to a variable impact of salmonids on lakes, ameliorated by the availability of littoral refuges (Cussac et al. 1992; Barriga et al. 2002, Buria et al. 2007), and a major impact on streams, where salmonids (in particular *O. mykiss*) seem to have displaced the native fishes almost completely. Stream records with significant captures

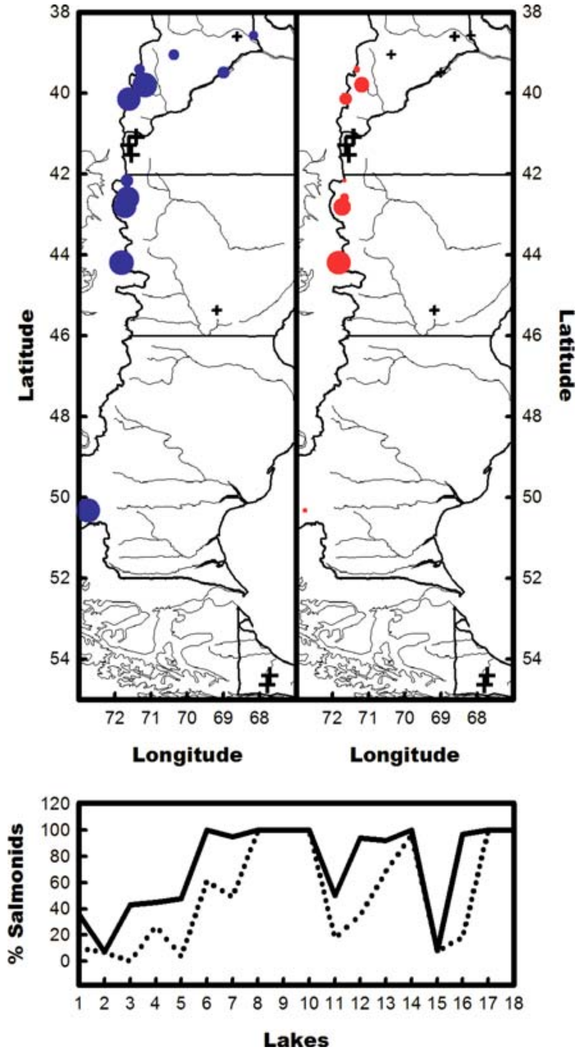

Fig. 4 Bubble plot (size indicates the % of total capture, top panel) and line plot (bottom panel) for relative abundance of salmonid populations of lakes and reservoirs ($n = 18$, ordered by latitude from 38 to 54° S) common to the database of Quirós (1991) (left, blue circles) and recent samplings (right, red circles). Big crosses indicate unchanged values. Small crosses indicate absence or values lower than 10% (see Table 2 for details)

of *H. macraei, D. viedmensis, G. maculatus* or *P. trucha* nowadays seldom occur (Barriga et al. 2007). The causes involved in the generation of a salmonid-rich or -poor stream (Allouche 2002), together with the role of rising temperature (Dunham et al. 2003; Wehrly et al. 2003), have just begun to be studied in Patagonia (Habit et al. 2007). In all cases, the impact is notorious when comparing the situation in Patagonia with that of heavily populated areas such

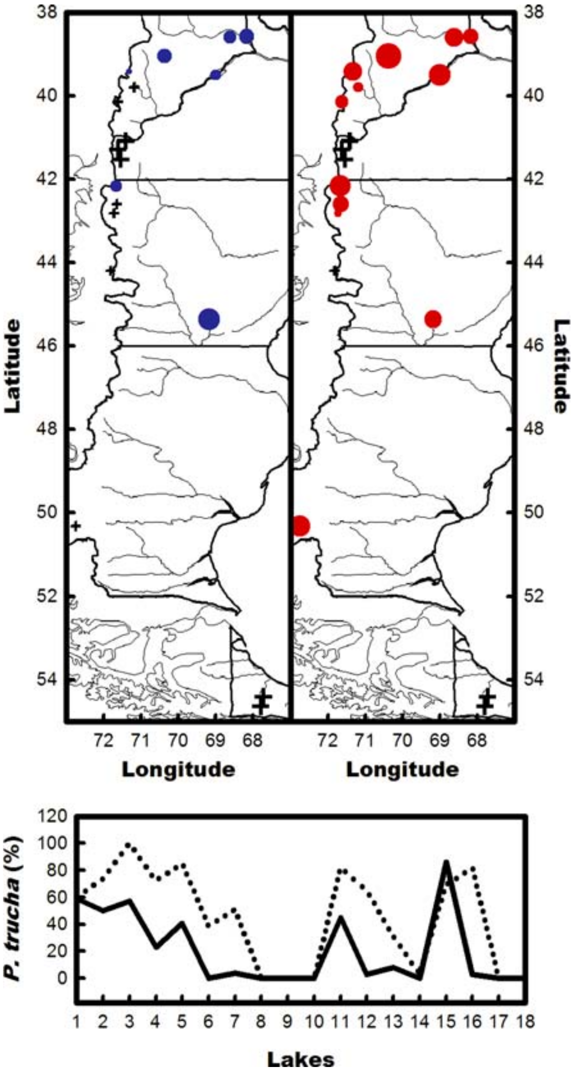

Fig. 5 Bubble plot (size indicates the % of total capture, top panel) and line plot (bottom panel) for relative abundance of *P. trucha* populations of lakes and reservoirs ($n = 18$, ordered by latitude from 38 to 54° S) common to the database of Quirós (1991) (left, blue circles) and recent samplings (right, red circles). Big crosses indicate unchanged values. Small crosses indicate absence or values lower than 10% (see Table 2 for details)

as Greece (ZIC = 88), Italy (ZIC = 56), Portugal (ZIC = 65), and Spain (ZIC = 63, Elvira 1995).

Changes in fish distribution

A dispersion of Brazilic, Andean and marine populations into the Austral Subregion was observed, as well as a southward movement of northernmost Austral species. While the movement of northern species into Patagonia appears as a likely scenario, the comparison of historical and modern records has the weakness of comparing poor historical records and more intensive recent sampling. However, it should be noted that no new record for Austral species within the Brazilic Subregion was found in

Table 5 Forward selection of geographic and environmental variables to determine their importance (Lambda-A) in explaining the abundance (relative abundance of salmonids, *P. trucha* and *O. hatcheri*) and diversity (number of native and alien species, and ZIC) variables

Variable	Abundance			Diversity		
	Lambda-A	*F*-value	*P*-value	Lambda-A	*F*-value	*P*-value
Longitude	0.07	5.88	0.003	0.00		
Latitude	0.05	5.00	0.012	0.00	6.27	0.006
Area	0.07	8.22	0.001			
Altitude	0.02			0.00		
DL	0.01			0.01	3.28	0.064
PAR	0.01				4.86	0.021

Only significant values ($P < 0.05$) are indicated

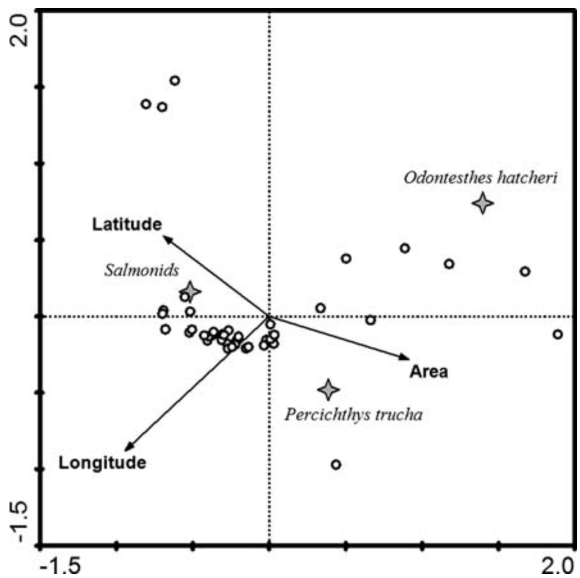

Fig. 6 First two axes of the canonical correspondence analysis for abundances of *P. trucha, Odontesthes* and salmonids populations, geographical (latitude and longitude) and morphometric (area) variables in lakes and reservoirs (circles) of Patagonia. Only significant variables are indicated

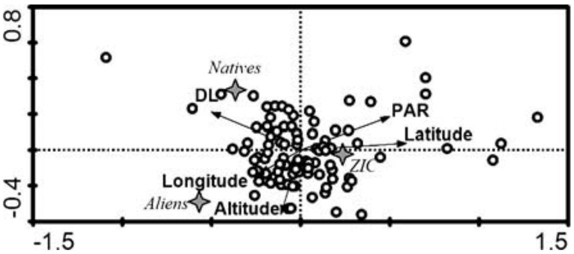

Fig. 7 First two axes of the canonical correspondence analysis for number of native (*Natives*) and alien species (*Aliens*), *ZIC*, geographical (Latitude, Longitude and Altitude), and morphometric variables (DL and PAR) in lakes and reservoirs (circles) of Patagonia

the literature and data reviewed. In addition, the observed increase (300%, from 2 to 8 species, excluding *J. multidentata*) in the number of Brazilic species is far greater than the increase in Austral species (133%, from 3 to 7 species) which is an expected increase from better sampling.

In addition to the introduction of salmonids, the last century witnessed major artificial changes involving damming, canal construction, water extraction (Almirón et al. 1997; Gómez et al. 2004b), deforestation, and the consequently increased rainfall (Hoffmann 1989; Dyer 2000). Currently, we have the first evidence of a complex environmental change, with multiple causes, contemporary with native-exotic interactions. Artificial changes to the landscape (canal construction and weirs) obviously facilitate the movement of biota out of their natural range. In addition, an obvious man made fish transport could be observed in the sale of bite fish (Alvear et al. 2007). However, the potential for such landscape changes and transport to cause range expansion in the absence of climatic change is not clear. For example, Dyer (2000) noted that the Atacama Desert area of northern Chile and southern Perú between the rivers Loa and Rimac, previously considered "empty" (Ringuelet 1975; Arratia et al. 1983; Arratia 1997), is at present inhabited by the Atherinopsidae *Basilichthys semotilus* (Cope, 1874) and the Trichomycteridae *Trichomycterus punctulatus* Valenciennes, 1846. Similarly, Hoffmann (1989) reported an important change in the position of the 800 mm isohyets before and after 1959 in the south of the Brazilian Subregion. During 2000, new wetlands with nine species of Brazilian fishes were recorded there, in the formerly called "pampeana" dry zone (*sensu* Canevari et al. 1998). These new locations were the consequence of an increase in average annual rainfall and the construction of new artificial drainage channels, allowing the rapid dispersion of fish into an ecophysiologically suitable range (Gómez et al. 2004a, 2004b). The southern limits of the distribution of two Brazilian species—*O. bonariensis* and the Pimelodidae *Rhamdia quelen* (Quoy and Gaimard, 1824)—are clearly related to their tolerance to low temperature (Gómez 1988, 1990, 1996). In addition, Gómez et al. (2004b) observed new southernmost localities for these Brazilian fishes. New records of the Serrasalmidae *Serrasalmus spilopleura* Kner, 1858, found southwards of its known distribution range, have been published by Gómez et al. (2004a), and new records of two Brazilic species (from a total of 12) in the southern Brazilic Subregion (38°S) have been reported by Casciotta et al. (1999).

Regarding abundance of native fishes and salmonids in lakes and reservoirs, the link established by the relative abundance data between the different species cannot be eliminated, however some punctual data could improve our comprehension. For example, in the Lake Laguna Blanca the records of Quiros (1991) showed near 50% of salmonids and 50% of *P. trucha* in 1984–1987 samplings. After 20 years, capture of *P. trucha* was the highest recorded in all Patagonian lakes and reservoirs, and salmonids were nearly undetectable (Ortubay et al. 2006). In the same way, the results of Alonso (2003) and Vigliano and Alonso (2007), expressed as caught per unit effort, signaled a significant decrease in the abundance of wild salmonid populations in three reservoirs in the Limay river basin.

The decrease of salmonid abundance in lakes and reservoirs could have different causes. One is a pioneer effect and its consequent stabilization (Macchi et al. 2007). Another possibility is that, considering we are working with littoral captures, the decrease of relative abundance of salmonids could be another example of the exclusion of salmonids from the littoral zone observed by Jansen and Hesslein (2004) in relation to an increase in water temperature at lake shores.

The knowledge about the responses of fish species to habitat heterogeneity in multiple scales can be used for management purposes, conservation and restoration (Ferreira et al. 2007). We can expect that the intralacustrine and between-lakes distributions of fish populations change even at spatial and geographical scales. Our results agree with the pattern found by Quirós (1991) regarding the relationship between abundance, latitude and temperature. Most of the geographic and morphometric variables explained fish abundance and diversity. Particularly, abundance showed mainly geographical cues and the diversity relied largely on morphometric characteristics. The cues of abundance and diversity seem to have a common point in the lake area, included into the PAR concept. Following Quirós (1991), the coexistence of salmonids and native populations mainly depends on the existence of multiple habitats, allowing negative interactions to be minimised. Native abundance and alien diversity were negatively related with latitude. The PAR, and to a less extent the DL, showed greater native diversity in lakes with high PAR.

Diversity seems to have a strong relationship with the morphometry of the lake. Pascual et al. (2007) found that abundance, diversity and even the existence of fish populations are related with the lake and shallow water bodies connected to deeper lakes. Most of the literature concerning Patagonian fishes suggests that the interaction between salmonids and native species mostly takes place in the littoral zone (Macchi et al. 1999; Quirós 1991; Ruzzante et al. 1998, 2003; Milano et al. 2002, 2006). The coexistence between salmonids and native fishes has mainly benefited from the spatial and temporal segregation of breeding habitats; streams during autumn-winter for salmonids, and lake's littoral zone during spring-summer for native fishes (Cussac et al. 1992; Cervellini et al. 1993; Barriga et al. 2002, 2007; Buria et al. 2007). Macchi et al. (1999) showed that salmonids and *P. trucha* share benthic food resources and also predation on Galaxiidae species. These shared roles have been confirmed in several studies addressing fish diets in Patagonia (Cussac et al. 1998; Ruzzante et al. 1998, 2003; Logan et al. 2000; Milano et al. 2002, 2006; Ferriz 1984, 1987, 1988, 1989, 1993/94, 1994).

Climatic relationships

The climate trends regarding southern South America provide some relevant data. One is the two-degree (Celsius) increase in the mean annual air temperature over the last century in the South Orcadas Islands (60°45′ S, 44°43′ W, Servicio Meteorológico Nacional 2007). In the last decade, the increase has been 0.2°C (Servicio Meteorológico Nacional 2007). The exclusion of salmonids from the littoral zone due to an increase in water temperature at lake shores (Jansen and Hesslein 2004) could benefit *P. trucha* and could adversely affect salmonids (Elliot 1981), at least according to preliminary data on thermal tolerances and preferences (Ortubay et al. 2004, Cussac et al. 2005, Aigo et al. 2006) and the data of Quirós (1991) and Quirós et al. (1986).

The present situation features an Austral fish fauna (Ringuelet 1975; Arratia et al. 1983; Almirón et al. 1997) interacting with salmonids from the beginning of the 20th Century, and suggests that major artificial changes plus a detectable climate change, are probably at the root of a change in the composition and relative abundances of fishes in the assemblages. The result of the new interactions is a highly dynamic situation, hardly predictable and one that should be carefully observed in the future. Particularly, the importance of the heterogeneity of the littoral zone (Wei et al. 2004; Lewin et al. 2004) is awaiting further studies in Patagonia in relation to the relative abundance of Salmonidae and native fishes.

Conclusion

Although other factors like geological history, population dynamics, and interspecific interactions could affect native and alien fish distribution (Ferreira et al. 2007), we could find patterns for abundance and diversity clearly related with the development of the littoral zone. Our results agreed with previous literature regarding the geographical pattern of native and alien fish abundances and with the importance of the lake littoral zone for the conservation of native diversity. Description of geographical patterns for abundance and diversity and historical changes, like southward dispersion and abundance changes, is a useful tool not only for research but also for future management design of Patagonian fish populations.

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References

Aigo J, Conte Grand C, Ortubay S, Battini M, Cussac V (2006) El cambio de las distribuciones de salmónidos y peces nativos en patagonia en las últimas dos décadas. XXII Reunión Argentina De Ecología. Córdoba.

Allouche S (2002) Nature and functions of cover for riverine fish. Bull Francais Peche et Piscicul 365/6:297–324

Almirón A, Azpelicueta M, Casciotta J, López Cazorla A (1997) Ichthyogeographic boundary between the Brazilian and Austral Subregions in South America, Argentina. Biogeographica 73:23–30

Alonso MF (2003) Variación temporal en la estructura de los ensambles de peces de los embalses de la cuenca de los ríos Limay y Neuquén: diagnóstico y efectos de los escapes de peces de cultivo. Magister Thesis. Universidad de Buenos Aires, 131 p

Alvear P, Rechencq M, Macchi PJ, Alonso MF, Lippolt GE, Denegri MA, Navone G, Zattara E, Garcia Asorey MI, Vigliano PH (2007) Composición, distribución y relaciones tróficas de la ictiofauna del río Negro, Patagonia Argentina. Ecol Aust 17:231–246

Amaya Santi MM, Pascual MA (2006) Censos de captura y esfuerzo en la pesquería deportiva de trucha marrón (*Salmo trutta*) del río Gallegos: Temporada 2004–2005. http://www.gesa.com.ar. Cited 22 Jun 2007

Arratia G (1987) Description of the primitive family Diplomystidae, Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. Bonn Zool Monogr 24:1–44

Arratia G (1997) Brazilian and Austral freshwater fish faunas of South America. A contrast. In: Ulrich H (ed) Tropical biodiversity and systematics. Bonn, Museum Alexander Koenig, pp 179–187

Arratia G, Peñafort B, Menú-Marque S (1983) Peces de la región sureste de los Andes y sus probables relaciones biogeográficas actuales. Deserta 7:48–108

Azpelicueta MM (1994a) Los diplomístidos en Argentina (Siluriformes, Diplomystidae). In: Castellanos Z (ed) Pises. Fauna de agua dulce de la República Argentina, vol 40. PROFADU-CONICET, La Plata, pp 1–27

Azpelicueta MM (1994b) Three East-Andean species of Diplomystes (Siluriformes: Diplomystidae): Ichthyol Explor Fresh-waters 5(3):223–240

Azpelicueta MM, Gosztonyi A (1998) Redescription of *Diplomystes mesembrinus* (Siluriformes, Diplomystidae). Rev Suisse Zool 105:901–910

Baigún C, Ferriz R (2003) Distribution patterns of native freshwater fishes in Patagonia, Argentina. Org Divers Evol 3:151–159

Baigún C, López G, Dománico A, Ferriz R, Sverlij S, Delfino Schenke R (2002) Presencia de *Corydoras paleatus* (Jenyns, 1842), una nueva especie brasílica en el norte de la Patagonia (río Limay) y consideraciones ecológicas relacionadas con su distribución. Ecol Aust 12:41–48

Barriga JP, Battini MA, Macchi PJ, Milano D, Cussac VE (2002) Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South American Andes. New Zeal J Mar Fresh Res 36:349–363

Barriga JP, Battini MA, Cussac VE (2007) Annual dynamics variation of landlocked Galaxias maculatus (Jenyns 1842) population in a northern Patagonia river: occurrence of juvenile upstream migration. J Appl Ichthyol 23:128–135

Becker L (2004) Determinación del origen del salmón chinook (Oncorhynchus tshawytscha) del río Santa Cruz aplicando técnicas de ADN mitocondrial. Tesis de Licenciatura. Universidad Nacional de la Patagonia SJB, Sede Puerto Madryn, Argentina

Bello MT (2002) Los peces autóctonos de la Patagonia Argentina. Distribución natural. Cuadernos Universitarios no 43. CRUB-UNCo. SIN-0325–6308/43, 56 p

Bruno Videla PH (1944) Algunos controles efectuados sobre peces existentes en la región de los lagos. Rev Fac Agron Vet 11:1–33

Bruzone JH (1986) Relevamiento de la fauna ictícola de los parques nacionales Lanín, Nahuel Huapi, Puelo y loa Alerces. APN-INVAP, Inf. Int (Ed mimeografiada), 18 p

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

Cambray JA (2003) Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500:217–230

Canevari P, Blanco DE, Bucher E, Castro G, Davidson I (1998) Los humedales de la Argentina. Clasificación, situación actual, conservación y legislación. Buenos Aires, Wetlands International Publication 46:66

Casciotta J, Almirón A, Cione A, Azpelicueta M (1999) Brazilian freshwater fish assemblages from Southern Pampean area, Argentina. Biogeographica 75:67–78

Cazzaniga NJ (1978) Presencia de *Cheirodon interruptus* en el valle bonaerense del Río Colorado (Pisces, Tetragonopteridae). Neotrópica 24:25–46

Cervellini PM, Battini MA, Cussac VE (1993) Ontogenetic shifts in the feeding of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae). Environ Biol Fish 36:283–290

Ciancio J (2000) Evaluación del rol de los crustáceos anomuros del género *Aegla* en la dieta y crecimiento de los salmónidos introducidos en la Patagonia Argentina. Tesis de Licenciatura, Universidad Nacional de la Patagonia San Juan Bosco, 66 p

Ciancio JE, Pascual MA, Lancelotti J, Riva Rossi CM, Botto F (2005) Chinook Salmon (*Oncorhynchus tshawytscha*) in the Santa Cruz River, an Atlantic Basin of Patagonia. Environ Biol Fish 74:219–227

Cussac VE, Cervellini PM, Battini MA (1992) Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. Environ Biol Fish 35:141–148

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

Cussac V, Ortubay S, Gómez S, Aigo J, Lattuca ME, Battini M (2005) La importancia de la temperatura para los peces de Patagonia. III Congreso Argentino de Limnología.

Cussac VE, Ruzzante D, Walde S, Macchi PJ, Ojeda V, Alonso MF, Denegri MA (1998) Body shape variation of three species of *Percichthys* in relation to their coexistence in the Limay river basin, in Northern Patagonia. Environ Biol Fish 53:143–153

Del Valle AE, Espinos AC, Urbansky J, Roa R (1996) Evaluación de la pesca deportiva de truchas marrones (*Salmo trutta*) de tipo migratorio en el río Chimehuín, Neuquén. Etapa I. Boletín del C.E.A.M. 3:22–26

Díaz M, Pedrozo F, Baccalá N (2000) Summer classification of Southern Hemisphere temperate lakes (Patagonia, Argentina). Lakes and Reservoirs: Research and Management 5:213–229

Di Prinzio C (2001) Estudio de la remonta del salmón chinook (Oncorhynchus tschawtscha) en las cuencas de los ríos Corcovado, Futaleufú y Pico, Chubut, Argentina. Tesis de Licenciatura. Universidad Nacional de la Patagonia SJB, Sede Esquel, Argentina

Dunham J, Schroeter R, Rieman B (2003) Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. NA J Fish Manage 23: 1042–1049

Dyer BS (1993) A phylogenetic study of atheriniform fishes with a systematic revision of the South American silversides (Atherinomorpha, Atherinopsinae, Sorgentinini). Ph.D. Thesis dissertation. University of Michigan, 596 p

Dyer B (2000) Systematic review and biogeography of the freshwater fishes of Chile. Estud Oceanol 19:77–98

Eigenmann CH (1909) The fresh-water fishes of Patagonia and an examination of the Archiplata–Archhelenis theory. Rep Princeton Univ Exped Patagonia 1896–1899, 3 (3): 227–374

Eigenmann CA (1910) Catalogue of the fresh water fishes of tropical and south temperate America. Rep Princeton Univ Exped Patagonia Zool 3(2):375–511

Eigenmann CH (1911) The localities at which Mr. John D. Haseman made colections. Annals Carnegie Mus 7: 299–314

Elliot JM (1981) Some aspects of thermal stress on freshwater teleosts. In: Pickering AD (ed) Stress and fish. Academic Press, London, pp. 209–246

Elvira B (1995) Native and exotic freshwater fishes in Spanish river basins. Freshwater Biol 33:103–108

Evermann BW, Kendall WC (1906) Notes on a collection of fishes from Argentina. South America, with descriptions of three new species. Proc US Nat Mus 31:67–108

Ferreira MT, Sousa L, Santos JM, Reino L, Oliveira J, Almeida PR, Cortes RV (2007) Regional and local environmental correlates of native Iberian fish fauna. Ecol Freshwater Fish 1–11

Ferriz RA (1984) Alimentación del puyen *Galaxias maculatus* (Jenyns) en el río Limay, Provincia de Neuquén. Physis 42:29–32

Ferriz RA (1987) Alimentación del pejerrey patagónico *Patagonina hatcheri* (Eigenmann, 1909) en el embalse Ramos Mexia, Neuquén, Argentina. Hidrobiología 6:61–66

Ferriz RA (1988) Relaciones tróficas de trucha marrón, *Salmo fario* Linné, y trucha arco iris, *Salmo gairdneri* Richardson (Osteichthyes, Salmoniformes) en un embalse norpatagónico. Stud Neotrop Fauna Environ 23:123–131

Ferriz RA (1989) Alimentación de *Percichthys colhuapiensis* (Mac Donagh, 1955) y *P. trucha* (Girard, 1854) (Osteichthys, Percichthyidae), en el embalse Ramos Mexía, Provincia del Neuquén, Argentina. Iheringia 69:109–116

Ferriz RA (1993/94) Algunos aspectos de la dieta de cuatro especies ícticas del río Limay (Argentina). Rev Ictiol 2/3:1–7

Ferriz RA (1994) Alimentación de *Olivaichthys viedmensis* (Mac Donagh, 1931) y *Hatcheria macraei* (Girard, 1855) (Teleostei, Siluriformes) en el río Limay, Argentina. Naturalia Patag 2:83–88

Ferriz RA, López GR (1987) *Jenynsia lineata lineata* (Teleostei, Cyprinodontiformes, Jenynsiidae) nueva cita para el norte de patagonia. Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia Servicio de Hidrobiología 4:23–27

Ferriz RA, López HL, Gómez SE (1998) Bibliografía de los peces continentales patagónicos. Aquatec 6:1–12

Fox SF, Yoshioka JH, Cuello ME, Úbeda C (2005) Status, distribution and ecology of an endangered semi-aquatic frog (*Atelognathus patagonicus*) of Northwestern Patagonia, Argentina Copeia 2005:921–929

Fuster de Plaza M (1950) Reconocimiento y determinación de las especies de salmones introducidos en el Parque Nahuel Huapi. Publicaciones Misceláneas Ministerio de Agricultura y Ganadería de la República Argentina 336:1–55

Fuster de Plaza ML, Plaza JC (1955) Nuevos ensayos para obtener la reproducción artificial de las percas o truchas criollas (*Percichthys* sp). Pub Misc Min Agric Ganad Arg 407:5–48

Gille ST (2002) Warming of the Southern Ocean since 1950s. Science 295:1275–1277

Gneri FS, Nani A (1960) El dominio acuático, los peces y las actividades económicas derivadas. Suma de Geografía, Peuser 5 (2):177–272

Gómez SE (1988) Susceptibilidad a diversos factores ecológicos extremos, en peces de la Pampasia bonaerense, en condiciones de laboratorio. PhD Thesis 502, La Plata, Argentina, Facultad de Ciencias Naturales y Museo, Universidad Nacional del La Plata, 308 p

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

Gómez SE (1996) Resistance to temperature and salinity in fishes of the province of Buenos Aires (Argentina), with zoogeographical implications. In: 4° Convegno Nazionale A.I.I.A.D. 1991 ATTI Congressuali, Trento, Italy, pp 171–192

Gómez SE, Bentos CA, Ramírez JL (2004a) Humans attacked by piranhas (Pisces: Serrasalmidae) in Buenos Aires Province, Argentina. Aqua 9:24–28

Gómez SE, Trenti PS, Menni RC (2004b) New fish populations as evidence of climate change in former dry areas of the

pampa region (southern South America). Physis (Buenos Aires) Section B 59:43–44
González Regalado T (1945) Peces de los Parques Nacionales Nahuel Huapi, Lanín y Los Alerces. Anales del Museo de la Patagonia 1:121–138
Gosztonyi AE (1988) Peces del río Chubut inferior, Argentina. Physis, Secc B 46(110):41–50
Habit E, Belk M, Victoriano P, Jaque E (2007) Spatio-temporal distribution patterns and conservation of fish assemblages in a Chilean coastal river. Biodivers Conserv 16: 3179–3191
Haseman JD (1911) A brief report upon the expedition of the Carnegie Museum to Central South America. Ann Carnegie Mus 7(2):287–314
Henn AW (1916) On various South American poeciliid fishes. Annals of the Carnegie Museum 10:93–142
Hidalgo F (2003) Comparación de patrones de crecimiento en truchas arco iris (Oncorhynchus mykiss) residentes y anádromas del río Santa Cruz, Argentina. Licenciate Thesis. Universidad Nacional de la Patagonia San Juan Bosco
Hoffmann JA (1989) Las variaciones climáticas ocurridas en la Argentina desde fines del siglo pasado hasta el presente. Servicio Meteorológico Nacional (FAA). Serie Divulgación 15:1–19
Hubert N, Renno J-F (2006) Historical biogeography of South American freshwater fishes. J Biogeogr 33:1414–1436
IARH-INCYTH (1995) Catálogo de los lagos y embalses de la Argentina. Proyecto Catálogo Nacional de Lagos y Lagunas Argentinas y su Medio Ambiente. Ministerio de Economía y Obras Servicios Públicos Secretaría de Obras y Servicios Públicos.
Jansen W, Hesslein RH (2004) Potential effects of climate warming on fish habitats in temperate zone lakes with special reference to Lake 239 of the experimental lakes area, north western Ontario. Environ Biol Fish 70:1–22
Lattuca ME, Ortubay S, Battini MA, Barriga JP, Cussac VE (2007) Presumptive environmental effects on body shape of *Aplochiton zebra* (Pisces, Galaxiidae) in northern Patagonian lakes. J Appl Ichthyol 23:25–33
Lewin WC, Okun N, Mehner T (2004) Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. Freshwater Biol 49:410–424
Liotta J (2006) Distribución geográfica de los peces de aguas continentales de la República Argentina. ProBiota. Serie Documentos 3. Universidad Nacional de La Plata, p 701
Lippolt GE (2004) Dinámica de las poblaciones de salmónidos en arroyos tributarios del río Limay. Magister Thesis. Universidad de Buenos Aires, 111 p
Logan MS, Iverson SJ, Ruzzante DE, Walde SJ, Macchi PJ, Alonso MF, Cussac VE (2000) Long term diet differences between morphs in trophically polymorphic *Percichthys trucha* (Pisces: Percichthyidae) populations from the southern Andes. Biol J Linnean Soc 69:599–616
López RB (1981) Introducción a los aspectos ecológicos de las represas de los ríos Limay y Neuquén. Res IX Reu Arg Ecol S C de Bariloche: 81
López Cazorla A, Miganne V (1996) Edad y crecimiento de la perca bocona *Percichthys colhuapiensis* (Mac Donagh, 1955) que habita el Río Negro, Argentina. Res III Jorn Patag Medio Amb Esquel: 66
López Cazorla A, Tejera L (1996) Alimentación de dos especies de peces frecuentes en el río Negro, Argentina. *Percichthys trucha* (Valenciennes, 1859) y *Percichthys colhuapiensis* (Mac Donagh, 1955). Res III Jor Patag Medio Amb, Esquel: 64
López RB, Torno A, Guerrero C, Lopez GR, Ferriz RA (1978) Plan de estudios ecológicos de la cuenca del río Negro. Conv. HIDRONOR SA-MACN. Inf final 1ra etapa 3: 228–353
López RB, Ferriz RA (1981) Adaptaciones de las truchas criollas y pejerrey patagónico a los embalses. Res IX Reu Arg Ecol SC de Bariloche: 84
López HL, Menni RC, Ferriz RA, Ponte Gómez J, Cuello MV (2006) Bibliografía de los peces continentales de la Argentina. ProBiota, FCNyM, UNLP. Serie Técnica-Didáctica no. 9
Lopretto EC, Menni RC (2003) Raúl Ringuelet: la zoogeografía como síntesis. In: Morrone JJ, Llorente J Bousquets (eds), Una perspectiva latinoamericana de la biogeografía, Las Prensas de Ciencias, Facultad de Ciencias, UNAM, México, DF, pp 75–85
Luchini L (1981) Estudios ecológicos en la cuenca del río Limay (Argentina). Rev Asoc Cienc Nat Lit 12:44–58
Macchi PJ (2004) Respuestas poblacionales de *Galaxias maculatus* a la depredación por parte de *Percichthys trucha* y los salmónidos introducidos en la Patagonia. PhD Thesis, Universidad Nacional del Comahue, San Carlos de Bariloche, Argentina, 172 p
Macchi PJ, Cussac VE, Alonso MF, Denegri MA (1999) Predation relationships between introduced salmonids and the native fish fauna in lakes and reservoirs in Northern Patagonia. Ecol Fresh Fish 8:227–236
Macchi PJ, Pascual MA, Vigliano PH (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
Mac Donagh E (1936) Sobre los peces del territorio de Río Negro. Instituto y Museo de la Universidad La Plata; Notas Museológicas 1:409–422
Mac Donagh E (1937) Estudios zoológicos en el río Negro inferior. Rev Mus La Plata (NS), Secc of 1936: 166–174
Mac Donagh E (1938) Contribución a la Sistemática y Etología de los peces fluviales argentinos. Rev Mus La Plata I (NS), Secc Zool 5:119–208
Mac Donagh EJ (1950) Las razas de percas o truchas criollas (*Percichthys*) y su valor para la repoblación pesquera. Rev Mus La Plata (NS), Secc Zool 6(39):71–170
Mac Donagh EJ (1953) Las truchas criollas. An Mus Nahuel Huapi 3:89–104
Mac Donagh EJ (1955) Las truchas criollas (*Percichthys*) del lago Colgué Huapi (Comodoro Rivadavia) y el problema de la especie. Descripción de *Percichthys colhuapiensis* n sp. Rev Mus La Plata (NS), Secc Zool 6(45):297–329
Marchetti MP, Moyle PB, Levine R (2004a) Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecol Applic 14:587–596
Marchetti MP, Moyle PB, Levine R (2004b) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshwater Biol 49:646–661

McDowall RM (1969) The relationships of the galaxioid fishes, with a further discussion of the classification of salmoniform fishes. Copeia 4:796–824

McDowall RM (1970) Fishes of the family Aplochitonidae. J Roy Soc New Zealand 1:31–52

McDowall RM (1971) The galaxiid fishes of South America. Zool J Linnean Soc 50:33–73

McDowall RM (2003) Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. Trans Am Fish Soc 132:229–238

McDowall RM (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? Rev Fish Biol Fisheries 16:233–422

McDowall RM, Allibone RM, Chadderton WL (2001) Issues for the conservation and management of Falkland Islands freshwater fishes. Aquatic Conserv Mar Freshw Ecosyst 11:473–486

Menni RC (2004) Peces y ambientes en la Argentina continental. Buenos Aires, Monografías del Museo Argentino de Ciencias Naturales, 316 p

Menni RC, Gómez SE (1995) On the habitat and isolation of *Gymnocharacinus bergi* (Osteichthyes: Characidae). Environ Biol Fish 42:15–23

Menni RC, Gómez SE, López Armengol F (1996) Subtle relationships: freshwater fishes and water chemistry in southern South America. Hydrobiologia 328:173–197

Menni RC, Miquelarena AM, Gómez SE (1998) Fish and limnology of a thermal water environment in subtropical South America. Environ Biol Fish 51:165–283

Milano D, Cussac VE, Macchi PJ, Ruzzante DE, Alonso MF, Vigliano PH, Denegri MA (2002) Predator associated morphology in *Galaxias platei* in Patagonian lakes. J Fish Biol 61:138–156

Milano D, Ruzzante DE, Cussac VE, Macchi PJ, Ferriz RA, Barriga JP, Aigo JC, Lattuca ME, Walde SJ (2006) Latitudinal and ecological correlates of morphological variation in *Galaxias platei* (Pisces, Galaxiidae) in Patagonia. Biol J Linnean Soc 87:69–82

Morrone JJ (2004) La zona de transición sudamericana: caracterización y relevancia evolutiva. Acta Ent Chilena 28:41–50

Moyle PB, Cech Jr JJ (1982) Fishes: an introduction to ichthyology. New Jersey, Prentice Hall, 593 p

Munn RE (1996) Atmospheric change and biodiversity: formulating a Canadian science agenda. Toronto, Institute of Environmental Studies, University of Toronto, 80 p

Navone G (2006) Distribución y uso del hábitat de la ictiofauna en el río Pichi Leufu. Licentiate Thesis. Universidad Nacional del Comahue. 116 p

Nelson JS (1994) Fishes of the world, 3rd ed. New York, John Wiley and Sons, 614 p

Norusis MJ (1986) SPSS/PC+ Advanced Statistics. Chicago, Illinois, SPSS Inc., 481 p

Oliveros OB, Cordiviola de Yuan E (1974) Contribución al conocimiento de la biología del "puyen" *Galaxias variegatus* (Lesson) del lago Argentino, provincia de Santa Cruz (Pisces, Galaxiidae). Physis, Secc B 33:227–231

Ortubay S, Cussac V, Battini M, Barriga J, Aigo J, Alonso M, Macchi P, Reissig M, Yoshioka J, Fox S (2006) Is the decline of birds and amphibians in a steppe lake of northern Patagonia a consequence of limnological changes following fish introduction? Aquatic Conserv: Mar Freshw Ecosyst 16:93–105

Ortubay SG, Gómez SE, Cussac VE (1997) Lethal temperatures of a Neotropical fish relic in Patagonia, the scale-less characinid *Gymnocharacinus bergi* Steindachner 1903. Environ Biol Fish 49:341–350

Ortubay S, Lozada M, Cussac V (2002) Aggressive behaviour between *Gymnocharacinus bergi* (Pisces, Characidae) and other Neotropical fishes from a thermal stream in Patagonia. Environ Biol Fish 63:341–346

Ortubay S, Manzur C, Iglesias G (2003) Pesca deportiva y turismo asociado en los parques nacionales del sur. In: Wegrzyn D, Rey G (eds) Pesca Deportiva en Argentina. Buenos Aires, Secretaría de Turismo de la Nación, pp 45–71

Ortubay S, Semenas L, Úbeda C, Quaggiotto A, Viozzi G (1994) Catálogo de peces dulceacuícolas de la Patagonia argentina y sus parásitos metazoos, Río Negro, Argentina, Subsecretaría de Recursos Naturales, 110 p

Ortubay S, Wegrzyn D (1991) Fecundación artificial y desarrollo embrionario de *Galaxias platei* Steindachner (Salmoniformes, Galaxiidae). Medio Ambiente 11: 84–89

Pascual MA, Hidalgo F (2004) Análisis Preliminar de la Fauna Íctica del Río La Leona. http://www.gesa.com.ar. Accessed 22 Jun 2007

Pascual MA, Riva Rossi CM (1999) Diferenciación poblacional, dinámica y manejo de la trucha arco iris (*Oncorhynchus mykiss*) introducida en el río Santa Cruz. http://www.gesa.com.ar. Accessed 22 Jun 2007

Pascual MA, Soverel P (1997) Evaluación de las poblaciones de trucha arco iris anádroma del río Santa Cruz, provincia de Santa Cruz, Argentina. http://www.gesa.com.ar. Accessed 22 Jun 2007

Pascual M, Bentzen P, Riva Rossi C, Mackey G, Kinnison M, Walker R (2001) First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Trans Am Fish Soc 130:53–67

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

Pascual MA, Ciancio JE, Lancelotti JL (2003) Presencia de salmón chinook (*Oncorhynchus tshawytscha*) en el Río Caterina, Estancia la Cristina, Parque Nacional los Glaciares. http://www.gesa.com.ar. Accessed 22 Jun 2007

Pascual MA, Riva Rossi CM, García Asorey M (2005) Un análisis preliminar de la fauna de peces del Río Santa Cruz y de los potenciales impactos de la construcción de las represas "Cóndor Cliff" y "La Barrancosa". http://www.gesa.com.ar. Accessed 22 Jun 2007

Pascual MA, 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. Aquat Ecosyst Health Manage 10:212–227

Pellanda L, Fernández P (1997) Evaluación de la población de trucha de lago americana (*Salvelinus namaycush*) de la cuenca del río Santa Cruz. Provincia de Santa Cruz. Argentina. http://www.gesa.com.ar. Cited 22 Jun 2007

Pellanda L, García Asorey MI, Pascual MA (2006) Censos de captura y esfuerzo en la pesquería deportiva de trucha arco iris (*Oncorhynchus mykiss*) variedad steelhead del río Santa Cruz: Temporada 2000–2001. http://www.gesa.com.ar. Accessed 22 Jun 2007
Perugia A (1891) Appunti sopra alcuni peci Sud-americani conservati nel Museo Civico di Storia Naturale di Genova. Ann Mus Civ Stor Nat Genova (Ser 2) 10:605–657
Pozzi A (1945) Sistemática y distribución de los peces de agua dulce de la República Argentina. GAEA 7:239–292
Quirós R (1991) Factores que afectan la distribución de salmónidos en Argentina. COPESCAL, FAO, Documento Técnico 9:163–173
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
Rahel FJ (2002) Using current biogeographic limits to predict fish distributions following climate change. Am Fisher Soc Symp 32:99–109
Raven PH (1987) Biological resources and global stability. In: Kawano S, Connell JH, Hideaka T (eds) Evolution and coadaptation in biotic communities. Tokyo, University of Tokyo Press, pp 3–27
Rechencq M (2003) Uso de registros de pescadores voluntarios para el estudio de la pesqueria recreacional del río Limay: Evaluación de metodología, calidad de datos y capturas. Licentiate Thesis. Universidad Nacional del Comahue, 157 p
Regan CT (1905) Description of a new percichthyd fish from Argentina. Rev Suisse Zool 13:1–390
Reissig M, Trochine C, Queimaliños C, Balseiro E, Modenutti B (2006) Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. Cons Biol 132:437–447
Ringuelet RA (1965) Diferenciación geográfica del "Otuno" *Diplomystes viedmensis* Mac Donagh, 1931 (Pisces, Siluriformes). Physis 25:89–92
Ringuelet RA (1975) Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. Ecosur Argentina 2:1–122
Ringuelet RA, Arámburu RH (1957) Enumeración sistemática de los vertebrados de la Provincia de Buenos Aires. Min Asuntos Agrarios Publ 119:1–94
Ringuelet RA, Arámburu RH, Alonso de Arámburu A (1967) Los peces argentinos de agua dulce. La Plata, Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, 602 p
Riva Rossi CM, Arguimbau M, Pascual MA (2003) The range and timing of the spawning migration of anadromous rainbow trout in the Santa Cruz River, Patagonia (Argentina) through radio – tracking. Ecol Aust 13:151–159
Riva Rossi C, Lessa E, Pascual M (2004) Origins of introduced rainbow trout in the Santa Cruz River as inferred by mitochondrial DNA. Can J Fisher and Aqua Sci 61:1095–1101
Riva Rossi CM (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, 198 p
Ruzzante DE, Walde SJ, Cussac VE, Macchi PJ, Alonso MF (1998) Trophic polymorphism, habitat and diet segregation in *Percichthys trucha* (Pisces: Percichthyidae) in the Andes. Biol J Linnean Soc 65:191–214
Ruzzante DE, Walde SJ, Cussac VE, Macchi PJ, Alonso MF, Battini M (2003) Resource polymorphism in a Patagonian fish *Percichthys trucha* (Percichthyidae): phenotypic evidence for interlake pattern variation. Biol J Linnean Soc 78:497–515
Ruzzante DE, Walde SJ, Cussac VE, Dalebout ML, Seibert J, Ortubay S, Habit E (2006) Phylogeography of the Percichthyidae (Pisces) in Patagonia: roles of orogeny, glaciation, and volcanism. Mol Ecol 15:2949–2968
Semenas L, Ubeda C, Cassola I (1987) Campaña de recolección de datos con pescadores deportivos. Encuesta piloto sobre parasitismo en peces. In: Memorias I Jor. Arg. Salmonicultura, Bariloche 1986
Semenas L, Ubeda C, Ortubay S, Noguera P, Revenga J, Viozzi G (1989) Estado sanitario de las poblaciones de peces de cuerpos de agua Andino Patagónicos. In: Actas I Jorn. Nat. Fauna Silvestre, Santa Rosa, 1987
Servicio Meteorológico Nacional (2007). Climatología. http://www.meteonet.com.ar. Accessed 22 Jun 2007
Shuter BJ, Post JR (1990) Climate, population viability, and the zoogeography of temperate fishes. Trans Am Fish Soc 119:314–336
Szidat L (1956) Über die Parasitenfauna von *Percichthys trucha* (Cuv & Val) Girard der patagonischen Gewässer und die Beziehungen des Wirtsfisches und seiner Parasiten zur paläarktischen Region. Arch F Hydrobiol 51:542–577
Szidat L, Nani A (1951) Diplostomiasis cerebralis del pejerrey. Una grave epizootia que afecta a la economía nacional producida por larvas de trematodes que destruyen el cerebro de los pejerreyes. Rev Inst Nac Inv Cienc Nat anexo al M.A.C.N.B.R. Secc Zool 1(8):324–383
ter Braak CJF, Smilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY, USA, 352 p
Vigliano PH, Alonso MF (2007) Salmonid introductions in Patagonia: a mixed blessing. In: Bert TM (ed) Ecological and Genetic Implications of Aquaculture Activities. Methods and technologies in fish biology and fisheries, vol 6. Springer, Berlin, pp 315–331
Wehrly KE, Wiley MJ, Seelbach PW (2003) Classifying regional variation in thermal regime based on stream fish community patterns. Trans Am Fish Soc 132:18–38
Wei A, Chow-Fraser P, Albert D (2004) Influence of shoreline features on fish distribution in the Laurentian Great Lakes. Can J Fisher and Aqua Sci 61:1113–1123
Welcomme Rl (1988) International introduction of Inland Aauatic species. Rome, Fao Fisheries Technical Papers No 294, 318 p
Wetzel R (1981) Limnología. Barcelona, Omega, 679 p
Zattara EE, Premolí AC (2004) Genetic structuring in Andean landlocked populations of *Galaxias maculatus*: effects of biogeographic history. J Biogeogr 31:1–10