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Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects

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ABSTRACT

Aim Globally, one of the major threats to the integrity of native faunas is the loss of biodiversity that can result from the introduction of exotics. Here we document recent changes in the distribution of five common fish species that are linked to introductions in Chile.

Location Chile from 28° S to 54° S.

Methods We assess the extent of changes in distribution of galaxiid species by comparing their historical and current distributions based on the results of the most extensive survey of freshwater fishes in Chile to date, a range that encompasses the full latitudinal and elevational range of the Galaxiidae in Chile. We test for relationships of the distributions and abundances of native fishes with the incidence of introduced species.

Results The latitudinal range of *Galaxias maculatus* has declined by 26%, and most of this reduction has occurred in the northern part of its range. *Aplochiton taeniatus* and *Brachygalaxias bullocki* have experienced reductions (8–17% loss) in total drainage area occupied, and they have disappeared from, or are now extremely difficult to find, in latitudes 36° to 41° S, coincidently with areas of urban growth and intense economic activities. The distribution of *Galaxias platei* has, instead, increased considerably. In northern basins, *G. maculatus* has apparently been replaced by an introduced poeciliid *Gambusia* sp. High-elevation systems remain dominated by native *Galaxias platei*, whereas systems at intermediate elevations, especially rivers, are now dominated by introduced salmonids. Within drainages, native galaxiids remain abundant where exotic salmonid abundance is low.

Main conclusions We suggest that negative interactions between introduced and native fish are responsible for some of the range reductions among Galaxiidae in Chile. The severity of the impacts varies with latitude and altitude and is probably related to temperature. The effects of *Gambusia* are restricted to warmer systems. Native fish also appear to have found temperature refugia from salmonids; impacts are low in the warmer northern and coastal systems, as well as in high-altitude relatively cold systems. Native fish also appear less vulnerable to salmonids in lakes than in rivers. This study identifies watersheds critical for the conservation of biodiversity within the Galaxiidae.

Keywords

Anthropogenic impacts, conservation, Chile, distribution, Galaxiidae, introduced salmonids, Patagonia, temperature refugia.

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INTRODUCTION

Globally, one of the major threats to freshwater fish diversity is the homogenization that results from the introduction of non-native species into isolated, evolutionarily naive faunas (Rahel, 2002). Most successfully introduced species are top predators and/or strong competitors with broad environmental tolerances. In contrast, freshwater fishes from isolated faunas are often poor competitors and evolutionarily naïve prey (Mills *et al.*, 2004; Nannini & Belk, 2006). In the western United States, for example, the introduction of salmonids, carp and mosquitofish has caused declines in abundance or local extinctions of many native freshwater fishes via predation and competition (Rahel, 2000). Thus, homogenization results from the negative effects of introduced species on populations and distributions of native fishes and the eventual dominance of a relatively small number of introduced species over large areas (Rahel, 2002).

A large number of species were introduced to freshwater ecosystems world-wide in the first half of the 20th century, long before adequate census information on the native fauna was available. Many studies have now documented changes in abundance and range or distribution of native fauna due to introduced species, and there is good evidence of such effects in the temperate waters of North American, European and New Zealand/Australian systems. Much less is known about the effects of introduced species on the native fish of temperate South America, where almost all lakes and rivers now have one or more exotic species of fish.

The native fish fauna of temperate South America is relatively depauperate (approximately 40 species), with the highest biodiversity within the region found west of the Andes, in Chile. The Galaxiidae (Osmeriformes), the most species-rich family of freshwater fish in Chile, comprises over 50 species distributed throughout the Southern Hemisphere (South America, South Africa, Australia and New Zealand; McDowall, 1971, 2006). Eight species belonging to three genera (*Galaxias*, *Brachygalaxias* and *Aplochiton*) are found in Chile, five of which are endemic. Two of the endemics, *Brachygalaxias bullocki* and *Aplochiton taeniatus,* are widely distributed, but the other three (*Galaxias globiceps*, *Aplochiton marinus*, *Brachygalaxias gothei*) have very restricted distributions (McDowall, 1971; Campos, 1973; Berra *et al.*, 1995; Dyer, 2000). Three species (*Galaxias platei*, *Galaxias maculatus*, *Aplochiton zebra*) also occur east of the Andes (Cussac *et al.*, 2004; see, e.g. Ruzzante *et al.*, 2008; Zemlak *et al.*, 2008). Chilean freshwaters contain a historically isolated fauna, with the Atacama Desert forming a barrier in the north, the Andes to the east and the Pacific Ocean on the west and south. This system thus offers the opportunity to examine the response of species that evolved in species-poor environments to the introduction of broad generalist exotics such as salmonids. It also allows for a comparison of the response of the Chilean fauna with that of a similar fauna in New Zealand and that of the much less isolated systems of North America.

Freshwater ecosystems today face challenges world-wide, and in Chile the impact of humans currently extends to almost all aquatic systems. Many lakes and rivers are under continuing threat from pollutants and intensive forestry (Campos *et al.*, 1998; Goodwin *et al.*, 2006; Habit *et al.*, 2006b). Several major river systems have been dammed, and increasing demands for energy to sustain economic growth are fuelling plans for new dams, with some planned for the more pristine rivers in the south. Various exotic salmonids have been introduced into Chilean waters over the past century. The first recorded introduction of salmonids occurred in 1883, when *Oncorhynchus mykiss* (rainbow trout) were stocked in a small coastal basin at 37° S. After 1905, there were additional and frequent introductions of *O. mykiss*, from the Rapel River to the Valdivia River (34–39° S). The first recorded introductions of *Salmo trutta* (brown trout) were in 1910, when both brown and rainbow trout were introduced from the Aconcagua River to the Bueno River (32–40° S). Since that time both species have been introduced into nearly all basins, including those in the southern region (Magallanes, 53° S) beginning in 1927, and in northern basins such as the Loa River basin (21° S) beginning in 1949. Stocking has continued to the present in most systems (Basulto, 2003).

The history of fish introductions in Chile is not restricted to salmonids. *Gambusia* sp., a cyprinodontid, was introduced to the region from unknown sources for mosquito control in the early part of the 20th century, and current populations in Chile are known to have been present by 1937 (Welcomme, 1988). Along with *O. mykiss* and *S. trutta*, *Gambusia affinis* is included among the 100 ‘world's worst’ invaders (Lowe *et al.*, 2000).

Impacts of introduced salmonids are just starting to be evaluated, but several lines of evidence suggest they are likely to be substantial, particularly in Patagonia where other human activities are not yet significantly developed. Firstly, salmonid biomass in some systems exceeds that of native fish (Pascual *et al.*, 2002, 2007; Soto *et al.*, 2006), and secondly, trout have been documented to prey on galaxiids (Macchi *et al.*, 1999, 2007; Arismendi *et al.*, 2009). Local impacts of salmonids may vary among habitat types and fish communities. For example, the impact of introduced trout on native fish may be greater in streams than in lakes (Soto *et al.*, 2006) and greater in landlocked than in anadromous populations (Jowett *et al.*, 1998).

In this study we use newly acquired information on the distribution of the Chilean Galaxiidae to test for large-scale changes in this important component of the endemic fish fauna of central and southern Chile. We first assess the extent of changes in distribution (expansions or contractions) of the most abundant species by comparing their current and historical distributions. We then test for relationships of the distributions and abundances of native fishes with the incidence of introduced salmonids. We conduct this detailed analysis for two regions: the Aysén region (latitude 43°45′–49°15′ S) and the Valdivia River basin (*c.* latitude 39°50′ S), an important basin of the south-central region of Chile. Our goal is to provide the information necessary to understand how fish introductions have affected species distributions and to compare responses among species. Such knowledge should aid in delaying of the process of homogenization of this unique fauna, and help in the design of informed conservation plans and actions for native freshwater fishes both world-wide and in particular in central and southern Chile.

METHODS

Historical and current distribution of the Galaxiidae

We constructed historical distributions by assembling georeferenced data for all species of Galaxiidae in Chile, using data from: (1) the recent compilation by Cussac *et al.* (2004), (2) additional records cited by Arratia (1981) and Vila *et al.* (1999b), and (3) unpublished records (H. Campos *et al.* unpublished data) for Torres del Paine National Park (51° S). The time frame of the historical data was 1967–2002.

Current distributions were determined through extensive sampling (2003–09) from the Huasco River in the north (28° S) to Tierra del Fuego in the south (54° S). Sampling was stratified by microhabitats (e.g. zones of varying substrates, water depths and current velocities within the river channel, generally on a scale of tens of metres in extent; Maddock, 1999). We used multiple gear types to increase the capture efficiency in all microhabitats, counting individuals of all species (native and non-native) captured at each sample site. We used a backpack electroshocker and seine net (2-mm mesh) to sample rivers, streams and lake littoral zones, and gillnets (15, 20, 30, 50, 60, 70 and 120-mm mesh) placed on the bottom at different depths, to sample lakes. Differences in sampling efficiency of gears may arise in different habitats and could confound estimates of abundance, we thus only use presence and relative abundance data for these analyses. Our data set thus consisted of a total of 287 sampling localities: (1) 211 locations within 24 main Andean (Chilean) drainage systems, (2) 31 locations within 22 coastal basins, (3) 10 rivers and lakes from Chiloe Island, (4) 14 locations within 8 drainages in Tierra del Fuego, and 21 locations in islands of Magallanian Fjords (Appendix S1 in Supporting Information). In addition to our data, we used reports from Arismendi *et al.* (2006) for Tierra del Fuego (53–54° S). Despite the broad geographical coverage, we failed to collect individuals of the three rare species: *Galaxias globiceps, A. marinus* and *B. gothei*. Collection of these species will require additional, targeted sampling.

Data were incorporated using the GIS software ArcView 3.2. (ESRI), on digitized maps of river drainages at 1:50,000 scale. For each species, we plotted all historic and all current locations. We distinguish locations with historical records that have not been visited in our recent sampling from those that were visited with the focal species not being found. The distributional range of a species was measured in two ways. First, we measured the area of each drainage system where the species was recorded (historically and currently). Total area of occupancy was the sum of the occupied drainage areas. The difference between historic and current drainage area occupied was used to infer range expansion or contraction. Second, we looked for north–south shifts in distribution, measuring the distance from the northern-most occupied drainage to the southern-most occupied drainage.

Distribution of native fishes relative to that of introduced salmonids

We used three different data sets and analyses to examine the distribution of the native Galaxiidae in relation to that of the introduced salmonids. We first examined the latitudinal variation in dominance of native fish versus salmonids by plotting proportions of galaxiids and trout over latitudinal gradients for coastal systems (34–42° S) and Andean basins (36–47° S). We pooled data within 2° latitude. We also examined latitudinal variation in biomass of galaxiids versus salmonids in Andean basins from 39–47° S. For these analyses we included four galaxiid species (*G. maculatus*, *G. platei*, *A. taeniatus* and *A. zebra*) as they are widespread along Chile like salmonids (*S. trutta* and *O. mykiss*).

Secondly, we used data from the Aysén region (43°45′–49°15′ S, 109,025 km^2) to test for variation in salmonid dominance in lakes versus rivers and as a function of elevation. To standardize estimates of abundance and biomass we only use relative abundance to avoid differences in sampling gear efficiency and site effort (Clarke & Gorley, 2005). We compiled data for 23 lakes with 32 sampling locations and 19 river systems with 69 sampling locations from the Palena, Cisnes, Aysén, Baker and Pascua drainages (Appendix S2). Data were from our survey and from recent publications (CH$_2$MHILL 2000; Niklitschek & Aedo 2002; CEA, 2005). We classified lakes into four elevation categories (m a.s.l.): (1) 0–199, (2) 200–299, (3) 300–399, (4) > 400. Elevations were obtained directly in the field by an Etrex GPS or using the software Google Earth 4-beta (http://earth.google.es/).

Because of differences in effort among sampling sites, we analysed relative rather than absolute abundances. We used analysis of similarity (ANOSIM; Clarke *et al.*, 2005), a procedure that uses permutation and randomization methods based on similarity matrices, to test for differences in species composition between lakes and rivers and among elevation categories. Proportions were fourth-root-transformed, and similarity matrices were calculated using the Bray–Curtis measure. The similarity percentage procedure (SIMPER) (standardized, fourth-root-transformed data) was used to identify the species most important in generating differences among elevations (primer v.6, Clarke & Gorley, 2005).

Thirdly, we used samples from 35 locations along the San Pedro River (40-km length) from the Valdivia basin (39°52′–39°50′ S, 10,245 km^2) to examine the relationship between abundance of the native Galaxiidae and that of the two most common salmonids in Chile (*S. trutta* and *O. mykiss*) at a smaller spatial scale. This river contains all the galaxiid species present in Chile except the rare *G. globiceps, A. marinus* and *B. gothei*. All locations were sampled weekly between November 2005 and February 2008. Samples were collected by electrofishing, and abundance data are expressed as capture per unit effort (CPUE in $n \times 100\ \mathrm{h}^{-1}\ \mathrm{m}^2$).

RESULTS

Species distributions and habitat

Galaxias maculatus

A comparison of historical and current ranges indicates a reduction of 26% in the latitudinal range of *G. maculatus*, from a historical north–south distribution of 3118 km, to a current range of only 2319 km (Table 1). The loss occurred mainly in the north; *G. maculatus* was found in the Huasco and Elqui rivers 30 years ago, but we did not find it in any of six locations in the region (Fig. 1). Our sampling, however, did register several new locations for the species in Chile, mostly between the Maullín (41° S) and Serrano (51° S) river basins. The total drainage area currently occupied by *G. maculatus* is higher than that registered by historic records (Table 1) because of the more intensive sampling. We found potentially landlocked populations in the middle of the latitudinal range, mainly in lakes of the Valdivia River basin (Fig. 2).

In rivers, *G. maculatus* were found in shallow, slow current zones along river edges, on substrates ranging from mud to boulders, with or without aquatic vegetation. Larger individuals (> 12 cm standard length (SL)) tended to inhabit slightly deeper (> 50 cm) zones. During periods of high discharge, *G. maculatus* used river floodplains extensively. In lakes, *G. maculatus* inhabited littoral zones, sometimes forming large shoals, and was absent, or nearly so, from lake tributaries.

Galaxias platei

New records from Chiloé Island and from the Puelo, Palena, Cisnes, Cuervo, Baker, Serrano and Tierra del Fuego river basins increased the total drainage area known to be occupied by *G. platei* by 243% (Table 1, Fig. 1). We also increased its latitudinal range (Table 1) by 459 km due to new records in Chilean Tierra del Fuego. Arismendi *et al*. (2006) reported this species as absent in Tierra del Fuego, after sampling the littoral areas of lakes Lynch and Rasmussen by electrofishing. We suspected, however, that *G. platei* might be present at greater depths in lakes of this region, as it was found at 30–40 m depth in Pacific draining lakes on the Argentinean side of the island (Yehuín, Margarita and Escondido) (Milano *et al*., 2006; Ruzzante *et al*., 2008). We found *G. platei* in the benthic zone of lakes Blanco and Deseado at a depth of 50 m.

Galaxias platei inhabits rivers and lakes. In rivers, *G. platei* usually occupies shallow (< 50 cm depth), low-current habitats (< 0.3 m s^{-1}). Larger individuals tend to use deeper habitats, though the largest individual captured in the San Pedro River (16.8 cm SL) was in a shallow pool of depth 50 cm. *Galaxias platei* occurs on varied substrata, but appears to prefer habitats with refuges such as trunks and big boulders. During high flow, it moves to the floodplains. In the south (Aysén) *G. platei* is relatively uncommon in rivers but abundant in lakes, where it is commonly found in littoral zones with abundant large woody debris and coarse particulate organic matter from the native riparian forest. Only large adults (> 20 cm) were found on muddy bottoms at depths greater than 8 m. The largest individuals (35 cm total length) were caught in the Cochrane Lake (Aysén River basin) at 80 m depth.

Brachygalaxias bullocki

A comparison of historical and current ranges indicates a reduction of 17% in the latitudinal range of *B. bullocki* (Table 1), due to its current absence in the Biobío, Imperial, Toltén and Bueno river basins (Fig. 1). Locations in the Biobío River with historic records of *B. bullocki* are currently dominated by an introduced species, *Gambusia holbrooki* (Habit *et al*., 2006b). *Brachygalaxias bullocki* remains abundant in the Maullín River basin and in the rivers of Chiloe Island.

Brachygalaxias bullocki typically inhabits streams and rivers with high levels of humic acids, lowland rivers with native riparian forest and large floodplains. It is found in riverine habitats with little or no current, and is completely absent from rapids or riffles. We found only one specimen in all the lakes we sampled, in Riñihue Lake (Valdivia River basin).

Aplochiton taeniatus

We collected *A. taeniatus* from the Tirúa River (38°22′ S), extending the northern limit for this species from the historical

Table 1 Historic and current area (in 1000 km^2) and north–south linear extent (in 1000 km) of the distribution of galaxiids.

	Distribution range in historic records		Distribution range in current records	
Species	Area (1000 km^2)	North–south extent (1000 km)	Area (1000 km^2)	North–south extent (1000 km)
Galaxias maculatus	215.5	3.1	304.3	2.3
G. platei	82.6	1.4	200.5	1.9
Aplochiton taeniatus	122.7	1.4	112.6	1.5
A. zebra	120.5	1.9	160.5	1.5
Brachygalaxias bullocki	94.5	0.7	79.0	0.8

Increases in area and north–south linear extent reflect higher sampling effort in the current study; however, decreases occurred despite the increased sampling effort and reflect anthropogenic impact.

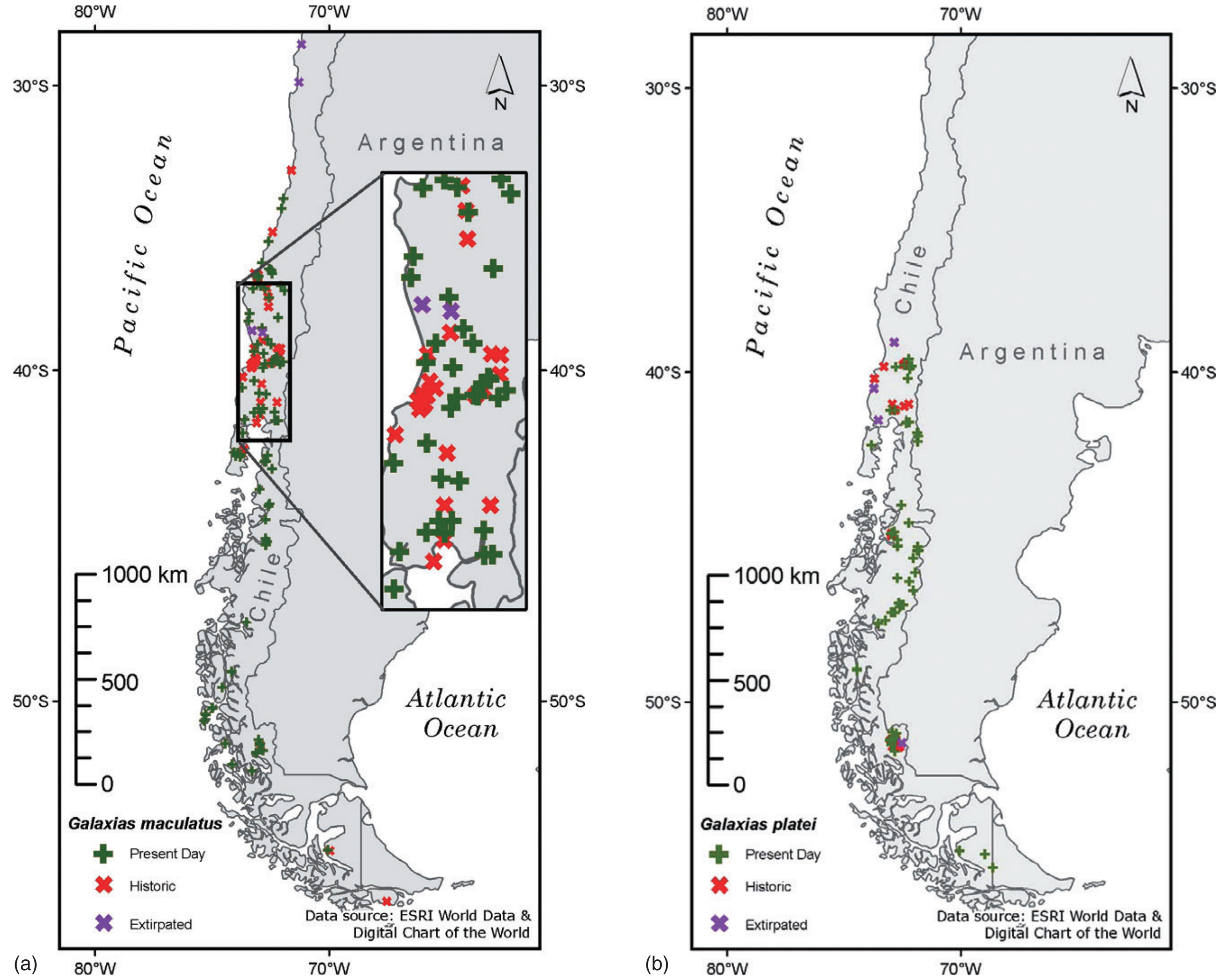


Figure 1 Distribution of (a) *Galaxias maculatus*, (b) *G. platei*, (c) *Brachygalaxias bullocki*, (d) *Aplochiton zebra* and (e) *A. taeniatus* in Chile. Green and red indicate 'presence' (green, no historical record for the species in location and species currently present; red, species historically and currently present). Purple indicates 'absence' (the species was historically present but is currently absent).

limit in the Toltén River (39°17′ S; McDowall, 1971). However, the drainage area occupied by *A. taeniatus* (Table 1) has declined by approximately 8%. Most of the loss is due to its absence (or extreme rarity) in the Bueno River basin (Fig. 1). *Aplochiton taeniatus* was not found in Chilean Tierra del Fuego. In south-central Chile, *A. taeniatus* is currently most abundant in the Valdivia and Maullín river basins and the northern rivers of Chiloé Island, but it is more frequent in the southernmost distribution range, including the Serrano River basin and islands of the Magallanic Fjords.

Aplochiton zebra

We increased the historically reported area occupied by *A. zebra* by approximately 33% (Fig. 1, Table 1), due mainly to new records in the Serrano River basin and islands of the Magallanic Fjords. It seems to be absent from the Biobío River basin, where it was reported in Galletué Lake by Campos *et al.* (1998) and where we did not sample. The abundance of *A. zebra* was also low in other central river basins (e.g. Valdivia River), but numbers remained high in the lakes of the Aysén region and Serrano River basin. *Aplochiton zebra* tended to be more abundant than *A. taeniatus* in the south, while the latter was more common in the north.

Both species of *Aplochiton* use shallow rapids or riffles in rivers as juveniles, and move to lakes or deep river pools as adults. Both species were rare in lake tributaries, but common in lake littoral zones close to tributaries. Neither species uses floodplain habitats. Specimens of *A. taeniatus* found in rivers were always close to lakes or estuaries, and those captured very close to the estuaries of the Maullín and Tirúa rivers were probably diadromous.

In sum, four of the five species of Galaxiidae that we surveyed in Chile show evidence of range contraction or reduction in abundance in some regions over the past few decades. *Galaxias maculatus* is no longer found in the northern part of its

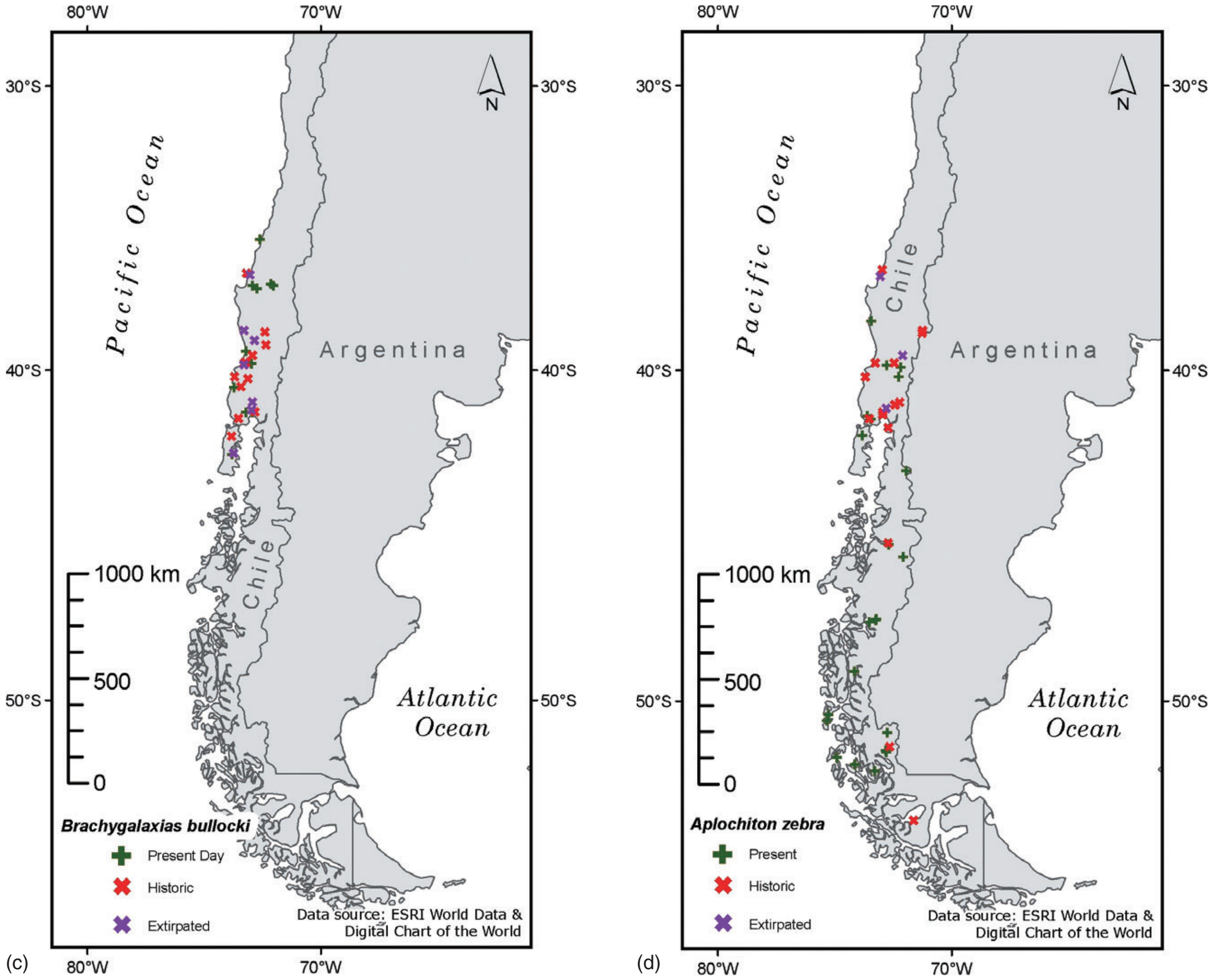


Figure 1 *Continued*

historical range, *A. zebra* and *A. taeniatus* appear to have reduced abundances and *B. bullocki*, the only galaxiid species restricted to the central area of Chile (north of Patagonia), showed a severe contraction in occupied range. The significant expansions that we document are almost certainly due to the high intensity of the recent sampling effort. The drainage area currently occupied by *G. maculatus* and *G. platei* is larger than that reported historically, and we report several new locations for *A. zebra* and *A. taeniatus*.

Latitudinal patterns

Species richness within the Galaxiidae varies with latitude, and the highest species richness occurs in the central part of the group's range, between 39 and 42° S (Fig. 3).

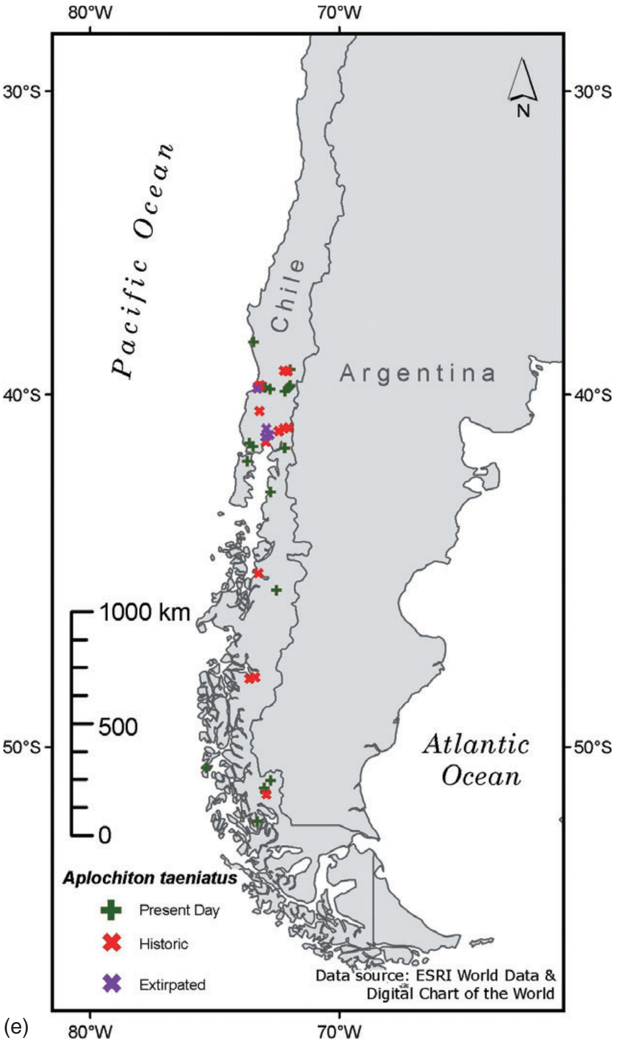
Coastal range (34–42° S)

Of the three native species present in the low-elevation coastal basins, *G. maculatus* was numerically dominant at all latitudes (Fig. 3), and more common than the introduced salmonids. Both species of *Aplochiton* were present, but only in the central coastal drainages (34–36° S). *Galaxias platei* was absent from the coastal rivers. Rainbow trout (*O. mykiss*) was more abundant than brown trout (*S. trutta*).

Andean basins (36–47° S)

Strong latitudinal patterns were found for the Andean basins (Fig. 3). The four most common species of Galaxiidae co-occur between 39 and 44° S. *Galaxias maculatus* was the only galaxiid found in northern drainages, and *G. platei* dominated the native fish assemblage in southern basins (Fig. 3). The two species of *Aplochiton* were most common in the centre of the range, with only *A. zebra* found south of 44° S.

Introduced salmonids were more abundant than galaxiids in both the most northern and southern basins, comprising up to 85% of the entire fish community south of 44° S. (Fig. 3). Within the salmonids, *O. mykiss* was relatively more abundant in the north, while *S. trutta* dominated southern basins. Salmonids



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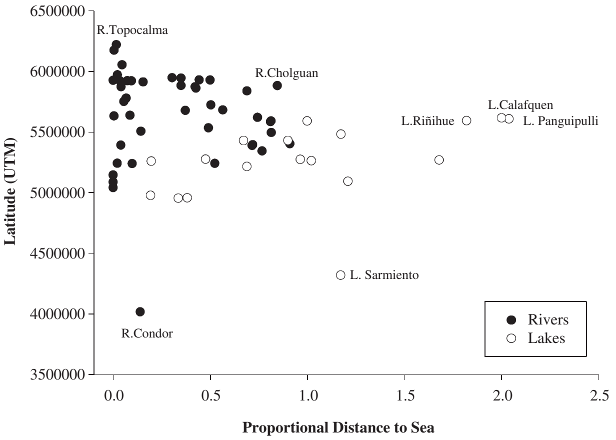

Figure 2 Distribution of *Galaxias maculatus* in relation to latitude (from north to south) and distance to sea (proportional to the country width). Black circles, rivers; white circles, lakes. Names of some systems are presented as references.

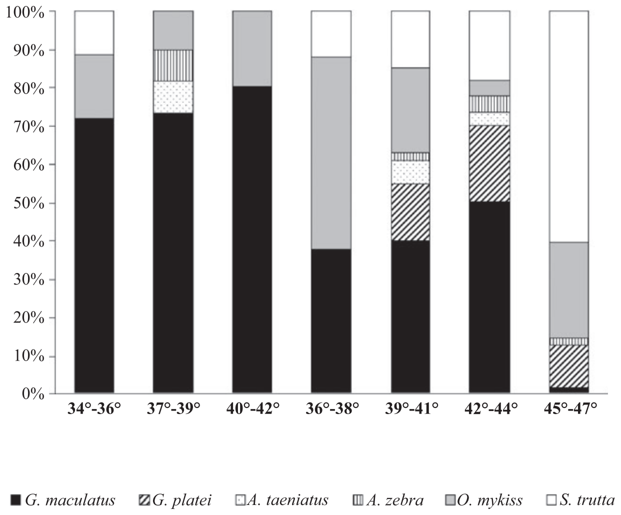

Figure 3 Proportion of four Galaxiidae species and the two dominant salmonids in the latitudinal gradient, for both coastal (34–42° S) and Andean basins (36–47° S).

also dominate in terms of biomass. In Andean basins, salmonids (rainbow and brown trout) make up 75% of the total fish biomass from 39–41° S, 89% from 42–44° S and 92% from 45–47° S. In the same latitudinal range, *G. maculatus, A. taeniatus* and *A. zebra* reduce their cumulative biomass from north to south, meanwhile *G. platei* increases its own biomass from 2–7% in the same gradient.

Relationships with introduced salmonids

Aysén region

A total of seven native and six introduced species were collected in the Aysén region (Table 2). The most widespread native species was *G. platei*, present in 41% of the sampled locations, and the most common introduced species, *S. trutta*, was found in 82% of the locations.

Individual lakes had between one and seven species, and higher-elevation lakes tended to have fewer species (Fig. 4). Species composition also varied significantly with elevation (ANOSIM, $R_{\text{global}} = 0.22$ $P = 0.001$), with native species, especially *G. maculatus* and *G. platei*, dominating at the lowest elevations, and *G. platei* dominating in high-elevation lakes (Table 3). Salmonids made up more than half of the total fish community at intermediate elevations (Table 3). Pairwise comparisons showed significant differences in species composition between the first two elevation categories (ANOSIM, $R = 0.26$; $P = 0.002$), and between categories 2 and 4 (ANOSIM, $R = 0.4$; $P = 0.007$).

Salmonids dominated rivers, while lakes had similar numbers of native and introduced species (Fig. 5). Rivers and lakes differed in species composition (ANOSIM, $R_{\text{global}} = 0.24$ $P = 0.001$), with higher abundances of *G. platei* in lakes and more *S. trutta* and *O. mykiss* in rivers.

Table 2 Species contributions to differences (dissimilarity) between lakes and rivers in the Aysén region, based on similarity percentage procedure (SIMPER) analyses for relative abundance.

Species	Average relative abundance in lakes	Average relative abundance in rivers	Mean dissimilarity and percentage of contribution (%) lake versus rivers
Galaxias platei	39.7	2.6	**19.5 (27.0)**
G. maculatus	9.5	2.9	4.8 (6.8)
Aplochiton zebra	3.4	3.7	5.0 (6.9)
Hatcheria macraei	3.0	1.6	2.0 (2.8)
Percichthys trucha	5.6	0.0	3.1 (4.3)
Geotria australis	0.5	0.1	0.98 (1.4)
Odontesthes hatcheri	0.02	0.0	0.4 (0.6)
Salmo trutta	28.1	54.9	**17.6 (24.4)**
S. salar	0.01	0.0	0.4 (0.5)
Oncorhynchus mykiss	9.5	28.9	**14.4 (20.1)**
O. kisutch	0.0	0.3	0.2 (0.3)
O. nerka	0.3	0.0	0.4 (0.5)
O. tshawytscha	0.0	1.1	1.0 (1.4)

Average dissimilarity between lakes and rivers considering all species is 72%. Bold text indicates species with higher contribution to dissimilarity.

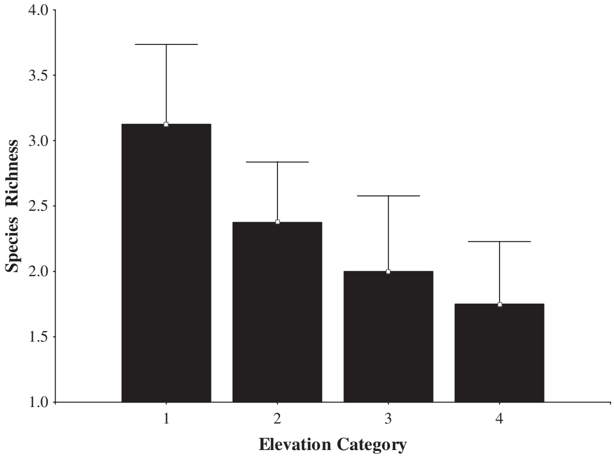

Figure 4 Mean lacustrine species richness in the elevation gradient the Aysén region (northern Chilean Patagonia), including native and non-native species. Error bars indicate SE.

San Pedro River

Four species of Galaxiidae (*G. platei*, *G. maculatus*, *A. taeniatus* and *B. bullocki*) were collected in sufficient numbers from the San Pedro River to examine their relationships with salmonids (Fig. 6). Locations with high abundances of salmonids (*S. trutta* or *O. mykiss*) had very few galaxiids, and high numbers of Galaxiidae were only found in locations with few salmonids (Fig. 6).

DISCUSSION

In this study we present evidence for important changes in the distributions of the five most abundant and widespread species within the Galaxiidae present in Chile. Distributions were mapped using historical records obtained from the literature (1960s and later) and current records obtained largely from our own sampling efforts (2003–09). The latitudinal range of *G. maculatus* has shrunk by approximately 26%, and this reduction has taken place in the northern part of its range. Two other species, *A. taeniatus*, and *B. bullocki,* have experienced reductions (8–17% loss) in total drainage area occupied, and they have disappeared from, or are now extremely difficult to find, in the Biobío, Imperial, Toltén, and Bueno river basins (latitudes 36–41° S). The distribution range for *G. platei* has instead, increased significantly, primarily as a result of our extensive sampling, mainly in the Patagonian region, where historical records are scarce.

Our results suggest that introduced species are generating local effects on galaxiids, but the relative role played by the presence and abundance of exotic species on the constriction of the distribution range of the native species is difficult to estimate. Locally, we found that the current patterns of native and exotic fish distributions support the hypothesis that introduced species are having a negative effect on native fish abundances, though effects vary spatially. Low-elevation coastal systems, common between latitudes 34 and 42°S, remain dominated by the native *G. maculatus*, though *O. mykiss* constitutes up to 20% of the current fish assemblage. However, in northern Andean basins *G. maculatus* has apparently been replaced by introduced mosquitofish, *Gambusia* spp. High-elevation (Andean) systems also remain dominated by native galaxiids (*Galaxias platei*), whereas systems at intermediate elevations, especially rivers, are now dominated by salmonids. Within drainages, galaxiids remain abundant where salmonid abundances are low. Below we examine the implications of these findings for the conservation and management of aquatic biodiversity in general and of southern Chile in particular.

Efforts to predict and document the consequences of human activity for native fish in Chilean watersheds have historically been hampered by a lack of data and inadequate geographical coverage (but see Habit *et al.*, 2006b; Soto *et al.*, 2006; Arismendi *et al.*, 2009). This study represents the most extensive survey of freshwater fishes in Chile to date, with samples from a total of 287 lakes and streams, from 56 drainages, a range that encompasses the full latitudinal and elevational range of the Galaxiidae west of the Andes. While some lines of evidence strongly suggest that the past introduction of exotic species has had local impacts on native fish communities in Chilean waters, introductions in most areas coincide with many other human activities (Campos *et al.*, 1998; Vila *et al.*, 1999a; Habit *et al.*, 2006a,b; Soto *et al.*, 2006, 2007), making it difficult to clearly delineate the relative importance of each factor (Leprieur *et al.*, 2008). Negative effects of multiple human activities within a region (e.g. pulp and mill industries, irrigation, replacement of native forest, hydropower) have been shown at individual (Orrego *et al.*, 2005) and community levels (Goodwin *et al.*, 2006; Habit *et al.*, 2007). These impacts are of special concern as the zone of highest native fish species richness (34–38° S) in Chile coincides with areas of urban

Table 3 Species contributions (cut-off low contributions equal 90%) to differences (dissimilarity) among elevation categories (1, 0–199; 2, 200–299; 3, 300–399; 4, > 400) based on similarity percentage procedure (SIMPER) analyses for relative abundance.

	Average relative abundance in each elevation category (m a.s.l)				Mean dissimilarity and percentage of contribution (%)	
Species	1	2	3	4	1 versus 2 avg. dissimilarity = 69.4	2 versus 4 avg. dissimilarity = 71.7
Salmo trutta	10.8	59.7	38.6	8.7	**16.6 (23.8)**	**26.6 (37.1)**
Galaxias platei	29.9	15.4	31.5	84.6	**13.5 (19.5)**	**24.1 (33.6)**
G. maculatus	30.6	0.0	0.0	0.0	**11.2 (16.1)**	–
Oncorhynchus mykiss	14.9	4.2	13.0	6.24	9.2 (13.2)	**8.0 (11.2)**
Percichthys trucha	10.3	2.5	0.0	0.0	7.4 (10.7)	4.1 (5.7)
Aplochiton zebra	0.9	0.0	17.1	0.0	5.0 (7.1)	4.1 (5.7)
Hatcheria macraei	0.0	9.8	0.0	0.0	–	3.9 (5.4)

Bold text indicates species with higher contribution to dissimilarity.

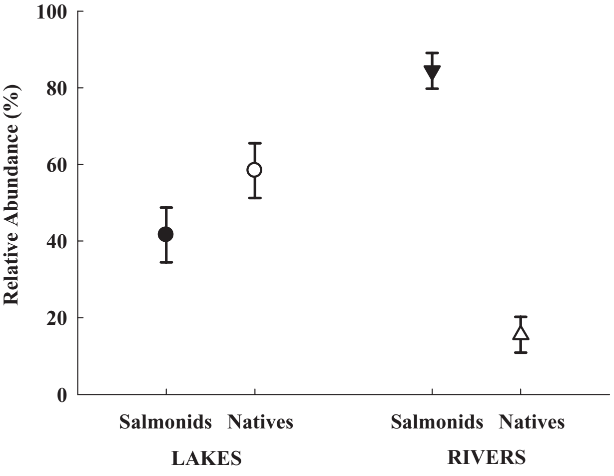

Figure 5 Mean relative abundance of native and non-native species (salmonids) in rivers and lakes of the Aysén region (northern Chilean Patagonia). Error bars indicate SE.

growth and intense economic activities related to resource extraction.

Two regions of decreased species richness

Our study identified two regions of particular concern. One significant distributional change was the shift in the northern limit of the range of *G. maculatus*. Historic records for this species in northern areas come from Arratia (1981), who cited a personal communication of Cabrera in 1975 for populations inhabiting the estuaries of the Huasco and Elqui rivers (28 and 29° S, respectively). Although we sampled both estuaries and also areas upstream in both rivers, we did not find *G. maculatus*. The cause of this disappearance is not known, but we suggest three non-exclusive hypotheses. First, *G. maculatus* is a temperate species, and the northern limit for coastal, diadromous populations may fluctuate, depending on seawater temperature. The Chilean coast north of latitude 43° S is dominated by the cold north-flowing Humboldt Current (Acha *et al.*, 2004), the strength of which is affected by El Niño–Southern Oscillation (ENSO) fluctuations. Strong positive phases can result in the displacement of tropical water southward (McPhaden, 2001), and the four ENSO events between 1980 and 2000, which included two very intense events (1982–83 and 1997–98; Bello *et al.*, 2004), could have raised estuary temperatures in northern rivers. A second contributing factor could be changes in flow, sediment and temperature regimes following the construction of dams for irrigation purposes in both rivers. The dams have significantly altered the aquatic environment, causing changes in river temperature and decreased macroinvertebrate abundances (Habit, personal observations). The third factor may be the presence of exotic species. Almost all the northern rivers we sampled were dominated by the exotic *Gambusia* spp., which occupy the same habitat types as *Galaxias maculatus*. In New Zealand, *Gambusia affinis* was shown to cause high mortality of *Galaxias maculatus* in experimental trials (Rowe *et al.*, 2007). These hypotheses are clearly non-exclusive and the factors may have acted synergistically to produce dramatic reductions in the abundance of *G. maculatus* in the northern part of its range.

The second region of concern lies between 36 and 41° S, where several major watersheds (Biobío to Bueno) appear to have lost at least two species of Galaxiidae over the past few decades (*A. taeniatus* and *B. bullocki*). This region, which includes the cities of Concepción and Temuco, has experienced multiple pressures from rapidly expanding economic activity, much of which occurs in or near rivers: (1) conversion of native forest to plantations with exotic species, (2) increasing pulp and mill production, and (3) hydropower generation (Parra *et al.*, 2004). Introduced species probably also contribute to species reductions and losses. High numbers of salmonids now occupy headwaters. The disappearance of *B. bullocki* from several drainages near Concepción (36–38° S) is most easily explained by the presence of *Gambusia* spp. Within the Biobío River basin *Gambusia* appears to have completely replaced *B. bullocki* in its

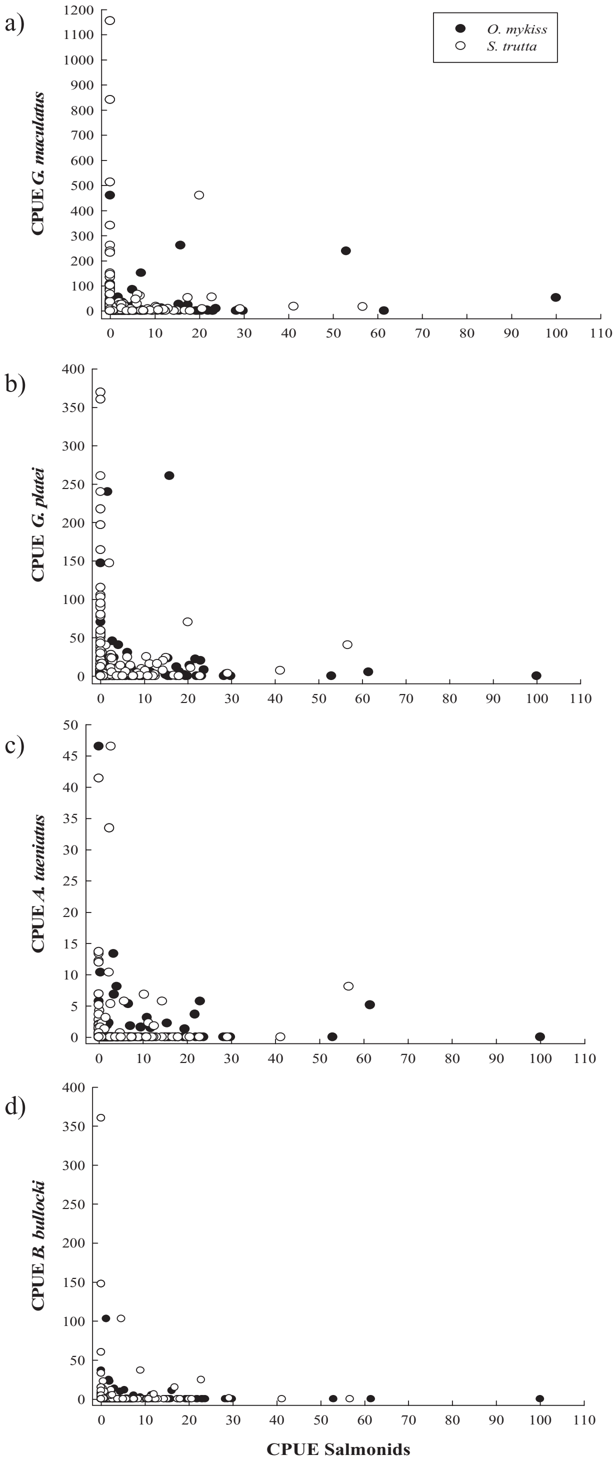

Figure 6 Abundance relationship among galaxiids and salmonids in the San Pedro River. Abundance is expressed as capture per unit effort (in number of individuals × 100/sampling time × area in m^2): (a) *Galaxias maculatus*, (b) *G. platei*, (c) *Aplochiton taeniatus*, (d) *Brachygalaxias bullocki*.

favoured habitats (Habit *et al*., 2006b); similar patterns were seen in New Zealand and Australia after the introduction of *Gambusia* (Rowe *et al*., 2007).

Introductions and their effect on the native fish fauna

Non-native fish species have been introduced into Chilean freshwaters since the early 20th century, doubling the total number of freshwater fish species in the country. Most were introduced for recreational purposes or as an accidental side-effect of aquaculture activity (Welcomme, 1988), and are now established as self-sustaining populations. *Gambusia* was introduced for mosquito control in central Chile (Campos, 1973; Welcomme, 1988). Our analysis suggests significant effects of two groups of exotic fish on galaxiids in Chile, the poecilid *Gambusia* spp. and salmonids. *Gambusia* is restricted to warmer waters, but its effects on *Galaxias maculatus* and *B. bullocki* appear dramatic. The watersheds formerly occupied by these species are subject to the effects of other human activities, however, and whether extirpation from affected drainages would have occurred in the absence of these other impacts is uncertain.

Salmonids are a much more widely distributed exotic group, and the most abundant species in Chile are rainbow trout (*O. mykiss*) and brown trout (*S. trutta*), both of which sustain recreational fisheries. Salmonids have been introduced into cool temperate waters world-wide, and negative effects on native fish, especially on galaxiids, have been reported or inferred in virtually all locations (McDowall, 2006), but especially in New Zealand (Townsend & Crowl, 1991; Flecker & Townsend, 1994; McIntosh, 2000; Simon & Townsend, 2003) and Tasmania (Hardie *et al*., 2006). One of the most important effects on river *Galaxias* in New Zealand was population fragmentation, with local extirpation in larger rivers and viable populations remaining only in isolated headwaters inaccessible to salmonids (Townsend, 1996). Various mechanisms contribute to the dominance of salmonids in Southern Hemisphere fish communities, including competition, predation and indirect effects (Simon & Townsend, 2003). There is good evidence for predation by introduced trout on native galaxiids from both sides of the Andes (Ruiz & Berra, 1994; Macchi *et al*., 1999, 2007). In our surveys we found *Galaxias maculatus* and *G. platei* in the stomachs of *O. mykiss* and *S. trutta* as small as 12 cm and in the stomachs of juvenile *Oncorhynchus tshawytscha* no larger than 9 cm long.

We suggest that negative interactions between introduced and native fish are probably responsible in part for the range reductions of Galaxiidae in Chile, but these effects are difficult to separate from those of other human activities. For example, we found *A. zebra* in lower abundance in lakes with salmonids in the Serrano River drainage in the Torres del Paine region (J. Gonzalez *et al*. unpublished observations). This region has experienced very little direct human impact; it is a remote region in the extreme south of the country, with limited road access, sparse human settlement and little economic activity. The only major environmental change over the past 100 years in rivers and lakes of this region has been the introduction and establishment of salmonids, especially *S. trutta*. Galaxiids, where they are still present in other southern watersheds, are already far less abundant than salmonids. Future development in the region, such as expansion of salmonid aquaculture and plans to build five hydroelectric dams in the Baker and Pascua rivers (see http://www.hidroaysen.cl), is likely to push abundances of remaining populations even lower.

Distributional patterns within watersheds suggest that there is considerable spatial variation in vulnerability to salmonid impacts. The disproportionate dominance of salmonids in streams and rivers compared with lakes is similar to that reported in another Chilean study (Soto *et al.*, 2006), and coincides with evidence from New Zealand and Australia where the strongest negative effects of salmonids on Galaxiidae also occur in streams (McDowall, 2003). Trout, especially *S. trutta*, preferentially lay their eggs in the riffles of small to medium-sized streams (Raleigh *et al.*, 1986), and exclusion of galaxiids from stream habitats may be due to interactions early in the life cycle. Galaxiids that spawn in the littoral zones of lakes probably experience lower predation rates, and the shallow littoral areas and deep benthic zones of lakes probably provide refugia from trout predation at other life stages. Rivers with large floodplains, like the San Pedro River, probably also provide refugia for galaxiids. The variation in the degree of salmonid dominance among lakes at different elevations indicates that galaxiids may have a temperature refuge; summer temperatures reached in many low-elevation lakes may be suboptimal for salmonids, and low visibility and extreme cold may reduce the impacts of salmonids in high-elevation glacial-fed lakes. A temperature refuge probably also explains lower abundances of salmonids in central and northern watersheds (Soto *et al.*, 2006) and coastal basins (Fig. 3). *Galaxias maculatus* dominates in coastal rivers despite the presence of trout, and *G. platei* is abundant in both rivers and lakes in central and northern watersheds. In the cooler south, however, *G. platei* has become predominantly a lake species, as is currently also seen east of the Andes in southern Argentina (Milano *et al.*, 2006; Ruzzante *et al.*, 2008; Zemlak *et al.*, 2008). Thus salmonids greatly reduce the abundance of galaxiids in certain habitats – especially cool running water. Galaxiid species persist by occupying less favoured habitats; *G. maculatus* remains abundant in coastal systems, *G. platei* in warmer central rivers or in southern lakes. It is important to note, however, that if these habitats are to maintain healthy galaxiid populations, they must be protected from the effects of other types of human activity. The cause of the range reductions in *A. taeniatus* is not clear, especially as little is known about its ecology. Microhabitat use overlaps greatly with that of *S. trutta* and *O. mykiss*; all inhabit shallow rapids or riffles in rivers as juveniles and move to lakes or deep river pools as adults. None use floodplain habitats. The near absence of *Aplochiton* from the small tributaries of rivers and lakes suggests interference from trout, especially as it remains common in habitats not used by trout, i.e. the littoral zones of lakes.

The evidence above collectively suggests that galaxiids have temperature refugia from salmonids in both the northern portion of their range, where summer water temperatures are relatively warm, and in the southern portion of their range at high altitude, where winter water temperatures may be too low for salmonids. Galaxiids also appear to have found refugia from salmonids in lakes, as has been found by others in northern and Argentinean Patagonia (Soto *et al.*, 2006; Pascual & Ciancio, 2007; Arismendi *et al.*, 2009). In general, however, the various freshwater fish species introductions in Chile (salmonids, poeciliids) seem to have caused declines in the abundance and distribution of native galaxiids, partially restricting their presence to more marginal habitats and potentially leading to increases in population fragmentation but not to total extinctions. World-wide evidence of the primary role for invasive aliens in total extinctions remains limited (Gurevitch & Padilla, 2004), but synergistic effects of introduced species and other human actions could increase the likelihood of extinction.

Four areas of special conservation concern

Our study also identified four geographical areas of special conservation interest, where the effects of salmonids and human activity have been low enough that abundant galaxiid populations remain. These include: (1) the coastal areas of the Maullín River basin and the Maullín River itself, which still hosts abundant populations of *G. maculatus, B. bullocki*, *A. zebra* and *A. taeniatus*, and probably *G. globiceps*; (2) the Valdivia River basin, which contains all the Chilean Galaxiidae, except the rare *B. gothei* and *G. globiceps*; (3) the northern rivers of Chiloé Island; and (4) several lakes in the Aysén region, including lakes Yulton and Meullín, which are still salmonid free (Soto *et al.*, 2006), Lake Thompson, where *G. platei* remains dominant to salmonids (Habit *et al.*, 2006a), and Riesco Lake, which has a high species richness for its latitude (45° S). None of these areas are currently protected and only one (the coastal area of Maullín) has been proposed as an important area for vertebrate conservation (Tognelli *et al.*, 2008).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Coordinates of the sampling locations in Chile ordered from north to south.

Appendix S2 Coordinates of lakes and rivers with sampling locations in the Aysén region.

BIOSKETCH

This paper is a result of an ongoing collaboration between E.H. of Universidad de Concepción (Chile), with D.E.R. and S.J.W. of Dalhousie University (Canada), M.C.B. of Brigham Young University (USA) and V.E.C. of Universidad del Comahue (Argentina) to study the biodiversity and conservation status of freshwater native fish fauna of Patagonia. E.H. conducts research on the native and introduced fishes of Chile, D.E.R. is interested in conservation genetics and phylogeography, S.J.W. and V.E.C. work in freshwater ecology. M.C.B. works on evolution, ecology and conservation of native fishes in North and South America. P.P., J.G. and N.C. are graduate students of Universidad de Concepción, working with E.H. in freshwater ecology of native fish.

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