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APPLIED ISSUES

Aquaculture, non-native salmonid invasions and associated declines of native fishes in Northern Patagonian lakes

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SUMMARY

1. Even though intensive aquaculture production of salmonids in lakes occurs in many locations around the world published studies on the survival and reproductive success of escaped cultured salmonids in freshwater ecosystems are not common. A recent expansion of aquaculture in Chile has led it to become the world's second largest producer of cultured salmonids.

2. We document the recent history of escaped and self-sustaining salmonid populations over a wide spatial scale and a long temporal scale in Chilean Patagonian lakes. Our hypotheses are that salmonid density in lakes will be higher where there is intensive aquaculture, due to greater numbers of potential escapees. Secondly, if non-native salmonids have adverse impacts on native fishes, increases in the abundance of non-native species should be associated with decreases in relative abundance of native species. Finally, if the first two hypotheses are correct we anticipate that diets of salmonids may show evidence of predation on native fishes, diet overlap with native species, and evidence of the influence of feed from aquaculture operations in the diets of salmonids and native fishes.

3. We sampled six lakes with gill nets from 1992 to 2001. Our results show that the relative abundance of free-living salmonids is closely related to the level of fish farming production. Salmonids are the top predators and in lakes with fish farming the main prey item is native fishes. The relative abundance of native fishes has decreased, most likely due to predation by salmonids.

4. Our study contributes to the understanding of the effects of non-native salmonids in oligotrophic lakes, and it provides a starting point to judge the establishment of new fish farming sites in lakes around the world.

Keywords: gillnet, oligotrophic lakes, predation, salmon farming, stomach analysis

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Introduction

Non-native fish introductions in freshwater may threaten the structure and functioning of receiving ecosystems (Vitousek *et al.*, 1996; Simon & Townsend, 2003; Carpenter *et al.*, 2007), leading to declines of native fish populations due to predation (e.g. Kaufman, 1992) and competition for food and habitat (e.g. Vander Zanden, Casselman & Rasmussen, 1999). The result may often be the extinction of native fish species (Clavero & García-Berthou, 2005). Aquaculture, which has increased rapidly worldwide, especially for salmon and trout (salmonids; FAO 2007), provides an important pathway for non-native fish establishment (Cook *et al.*, 2008). The escape of cultured salmonids can occur during routine operations (e.g. accidental losses associated with fish handling) or result from more extreme events such as storm or predator damage to containment structures (Esmark, Stensland & Synnove Lilleeng, 2005; Podemski & Blanchfield, 2006). As a consequence, increasing numbers of cultured fishes may enter freshwater ecosystems every year (Soto, Arismendi & Sanzana, 2001b; Naylor *et al.*, 2005; Carr & Whoriskey, 2006). Although intensive aquaculture production of salmonids in lakes occurs in many locations around the world (Eloranta & Palomaki, 1986; Karaca & Pulats, 2003; Costello *et al.*, 2004; Podemski & Blanchfield, 2006; Soto *et al.*, 2006) published studies on the survival and reproductive success of escaped cultured salmonids in freshwater ecosystems are relatively scarce (Podemski & Blanchfield, 2006). Even if escaped fish do not establish naturally reproducing populations, they may produce persistent impacts due to the repeated supply of propagules (escaped individuals; Weber & Fausch, 2003).

Salmonid escapees in freshwater systems have been tied to the decline of many native salmon populations in the northern hemisphere (Fleming *et al.*, 2000; Volpe, Anholt & Glickman, 2001), and salmonid invaders have also caused negative effects on native fishes in the southern hemisphere (McIntosh, Townsend & Crowl, 1992; Ault & White, 1994; McDowall, 2003). Given the recent expansion of its aquaculture, Chile has become the world's second largest producer of cultured salmonids (FAO 2007). In many cases, juveniles are grown in net-pens in lakes for subsequent transfer to marine environments to produce larger juveniles and adults for market. In light of these increasing aquaculture activities, the potential impacts of juvenile fish-farming escapees needs to be better understood (Soto *et al.*, 2006). Also, these escapees may continue to feed on feed pellets near the net-pens, as seen in inner seas and fjords in southern Chile (Soto, Jara & Moreno, 2001a; Soto *et al.*, 2001b), and ultimately be artificially maintained above the carrying capacity of the lake.

Aquaculture operations in Chile are concentrated in larger oligotrophic lakes in the southern regions (Patagonia) where ecosystems were historically devoid of large piscine predators, such as salmonids (Campos, 1970, 1984; Soto & Campos, 1996). Such environments may be particularly susceptible to invasion by salmonids (Moyle & Light, 1996). Currently, salmonid escapees in Chile include rainbow trout (*Oncorhynchus mykiss* Walbaum), Atlantic salmon (*Salmo salar* L.), coho salmon (*O. kisutch* Walbaum) and Chinook salmon (*O. tshawytscha* Walbaum) (Soto *et al.*, 2006). In addition to impacts from each individual species, synergistic interactions among these invaders might magnify impacts of non-native salmonids on native fishes and ecosystem processes in Patagonian lakes (Simberloff & Von Holle, 1999; Simberloff, 2006).

The main goal of our study was to document the recent history of escaped and self-sustaining populations of non-native salmonids among lakes and over time in Patagonian lakes. Our first hypothesis is that the density of trout and salmon in lakes will be higher in lakes with intensive aquaculture, due to increased numbers of potential escapees supplementing abundance, especially for species with little or no natural reproduction. Secondly, if non-native salmon and trout have direct or indirect adverse effects on native fishes, increases in the abundance of non-native species should be related to decreases in relative abundance of native species. Finally, if the first two hypotheses are correct we anticipate that diets of non-native salmonids may show evidence of predation on native fishes, diet overlap with native species, and evidence of the influence of feed (e.g. feed pellets) from aquaculture operations in the diets of both native and non-native fishes. We conclude by suggesting management strategies to benefit native fishes in the face of potential threats posed by aquaculture of non-native salmonids.

Methods

Study area

We selected six lakes in the Lakes District of northern Patagonia (Chile) in South America (40–43°S, Fig. 1). The Lakes District is part of the Valdivian Rainforest Ecoregion (Dinerstein *et al.*, 1995) and is characterised by a temperate climate (Amigo & Ramírez, 1998). The selected lakes are located at an altitude of 44–189 m with surface areas ranging from 119 to 870 km^2 and mean depths between 76 and 191 m (Table 1). All lakes are of glacial origin with volcanic influence in the soils (Campos, 1984). Typical of the region, these lakes are monomictic with thermal stratification in the summer (Campos, 1984; Soto & Campos, 1996) and relatively oligotrophic as evidenced by high transparency, low nutrient concentration and low algal production (Table 1).

According to several authors (Campos, 1970; Soto & Stockner, 1996), the most common native fishes found in these lakes are: (i) species endemic to southern South America – *Galaxias platei* Steindachner, *Percichthys trucha* Valenciennes, *Basilichthys australis* Eigenmann and *Odontesthes mauleanum* Steindachner and (ii) species endemic to the Southern Hemisphere – *Aplochiton taeniatus* Jenyns, *A. zebra* Jenyns and *Galaxias maculatus* (Jenyns). In the late 1890s, rainbow trout and brown trout (*Salmo trutta fario* L.) were introduced to Chilean Patagonia (Basulto, 2003) for recreational fishing and aquaculture (Campos, 1970). Since their introduction, trout have spread to almost all lakes, and were present in every lake selected for this study (Soto *et al.*, 2006).

Fig. 1 Location of sampled lakes in the northern Chilean Patagonia.

Aquaculture

Modern salmon aquaculture began around 1980 and is responsible for further introductions of rainbow trout and other salmonid species, including Atlantic salmon, coho salmon and Chinook salmon (for stocking history in Chile see Basulto, 2003). At present, the largest salmon and trout farms in Chile are concentrated in the southern portion of the country, near and below 40°S.

The first commercial salmonid fish farming site in Chile was established in 1975 in Pescado River, a tributary of Lake Llanquihue (Basulto, 2003). Since that time commercial juvenile salmonid production has increased and currently there are net-pens in five of the lakes considered in this study (Table 2). However, Lake Todos Los Santos, located in Vicente Pérez Rosales National Park, does not have aquaculture and, thus, we use it as a reference lake. Lake Llanquihue sustains the highest production of smolts among all freshwater salmonid aquaculture sites in Chile, accounting for over 36% of the total smolt production in lakes; between them, the remaining four lakes in this study with fish farming sites make up an additional 29% of the total (León-Muñoz *et al.*, 2007). In Chile, there is a lack of consistent information about salmonid fish farming smolt production before 1998. However, we compiled information on the number of smolts produced by all commercial salmonid farming sites in each lake for 1995 and for all years from 1998 to 2005, using data from León-Muñoz *et al.* (2007) and unpublished information from Subsecretaría de Pesca of Chile (Table 2).

Fish sampling

Fish sampling was conducted from 1992 to 2001 during different seasons and years (Table 3). Each

Table 1 Characteristics of the six study lakes in the northern Chilean Patagonia

Lake name	Lat S	Long W	Altitude (m)	Catchment area (km^2)	Lake surface (km^2)	Mean depth (m)	Temperature (°C)	O_2 (mg L^{-1})	Transparency (m)	NO_3–N (µg L^{-1})*	PO_4–P (µg L^{-1})	P total (µg L^{-1})	Chl-*a* (mg m^{-3})
Llanquihue[†]	41° 08′	72° 47′	51	1605	870.5	182.0	10.4–18.5	10.0–10.9	14.0–21.0	0.1–1.1	0.0–1.3	1.1–5.6	0.043–1.15
Puyehue[‡]	40° 40′	72° 28′	184	1510	165.4	76.3	9.5–19.0	6.7–12.8	6.5–13.0	0.1–1.0	0.2–7.9	0.4–12.1	0.06–0.31
Ranco[§]	40° 13′	72° 23′	69	3997	442.6	122.1	9.9–21.0	9.5–11.1	5.0–16.0	0.1–0.7	0.4–2.7	2.3–16.1	0.22–1.67
Rupanco[¶]	40° 50′	72° 26′	118	909	233.4	163.0	10.1–19.7	6.5–13.0	11.5–20.5	0.3–1.6	0.1–2.7	0.07–13.3	0.06–0.16
Yelcho[**,††]	43° 18′	72° 19′	44	2101	119.8	110.0	8.5–12.0	8.6–9.6	4.0–13.0	0.0–34.6	4.0–6.0	2.5–55.4	0.07–1.04
Todos Los Santos[‡‡]	41° 08′	72° 12′	189	3036	178.5	191.0	8.1–19.4	7.7–10.9	4.0–13.0	1.0–27.0	0.0–1.5	1.0–5.5	0.19–0.79

[*] Data corrected according to Woelfl *et al.* (2003).
[†] Campos *et al.* (1988).
[‡] Campos *et al.* (1989).
[§] Campos *et al.* (1992a)
[¶] Campos *et al.* (1992b).
[**] Prado (1999).
[††] Soto (2002).
[‡‡] Campos *et al.* (1990).

sample in each lake consisted of two experimental gill net sets of varying mesh size (3.81, 7.62, 12.06 and 15.24 cm) that were 280 m long and 3.5 m deep. Each net was checked every 8 h and left for, on average, 48 h. Captured fishes were identified to the lowest possible taxon, weighed (g) and length measured (cm; total length). For each species population, we used catch per unit effort (CPUE; individuals per fishing hour) as an indirect measure of population standing stock. Additionally, the stomachs of a sub-sample of 828 salmonids were preserved in 70% ethanol for later identification of prey to the lowest possible taxon.

Data analysis

We divided salmonid species into two groups: 'trout' representing only rainbow trout and 'salmon' representing coho salmon, Atlantic salmon and Chinook salmon. We grouped native fishes as follows: *B. australis* and *O. mauleanum* as Atherinidae; *A. taeniatus* and *A. zebra* as *Aplochiton*; *G. maculatus* and *G. platei* as *Galaxias*; and *P. trucha* as *Percichthys*. Additionally, we considered both spatial (including all six lakes) and temporal scales. Spatially, we showed trends for the Northern Patagonia Lakes region and temporally we captured the time-period that included the rapid increase in salmonids aquaculture production. However, for our temporal analysis related to mean CPUE of fish species we only analysed Lake Llanquihue because we had data spanning the most years (see Table 3).

To determine the relationship between salmon abundance and salmon aquaculture, we used all six lakes across years in a negative exponential regression model where the mean CPUE of salmon represented the dependent variable and the total salmon farming smolt production (1995–2001) represented the explanatory variable. We did not consider trout in this analysis because the trout have self-sustaining populations that were established previous to aquaculture activities.

To describe the relationship between the abundance of native fishes and salmonids, we used all six lakes across years in a linear regression model where the mean CPUE of native fishes represented the dependent variable and the mean CPUE of salmonids represented the explanatory variable. Also, to identify time trends in the abundance of fish assemblages, we used Pearson's product-moment analysis for only

Table 2 Total accumulated smolt production (millions of fishes) over time (information only available for 1995 and from 1998 to 2005) for each salmonid species and lake

		Lake					
Species	Salmon farming activities	Llanquihue	Puyehue	Ranco	Rupanco	Yelcho	Todos Los Santos
Oncorhynchus mykiss	Years of operation	All	1998–2005	2004–05	All		
	Total accumulated smolt production	41.27	2.77	0.68	31.01		
	Stocked after 1980*			X		X	X
Salmo salar	Years of operation	All	1998–2005	1998–2005	All	1998–2004	
	Total accumulated smolt production	168.33	29.96	16.97	87.54	7.33	
Oncorhynchus kisutch	Years of operation	All	1998–2004	1998–2002	All		
	Total accumulated smolt production	54.85	5.76	3.68	2.77		
Oncorhynchus tshawytscha	Years of operation		1998–2001				
	Total accumulated smolt production		1.52				

Source: Subsecretaría de Pesca, Chile (unpubl. data). 'All' includes data for 1995 and from 1998 to 2005.
*For recreational fishing purposes. Numbers released are unknown.

Table 3 Number of gill net samples each year

Year	1992	1993	1995	1996	1997	1998	1999	2000	2001
Llanquihue	5	1	3	9	1	1	1	1	7
Puyehue						1	3	4	7
Ranco							2	4	7
Rupanco							2		3
Yelcho									5
Todos Los Santos						2	1		

Lake Llanquihue because it had the greatest production of salmonid smolts and the most thorough historical data (Tables 2 & 3).

To understand the possible mechanisms of interference between native fishes and salmonids, we determined the composition of trout and salmon diets. Dietary composition was expressed as frequency of occurrence, defined as the number of stomachs containing one or more individual items divided by the total number of stomachs analysed (Hyslop, 1980). We used chi-square goodness of fit analyses under the null hypothesis that the diet of salmonids in lakes with aquaculture activities has the same frequency of occurrence of diet categories as the reference lake. We were able to compare the lakes to one another because they have similar geological, physical, chemical and biological conditions (Campos, 1984; Soto & Campos, 1996; Soto & Stockner, 1996; Soto, 2002). We considered the diet of salmonids in the reference lake as expected frequencies and the diet of salmonids in the other lakes as observed frequencies.

Results

We captured a total of 6121 fishes of which 38% were salmonids and 62% were native fishes (Table 4). In the case of salmonids, brown trout and rainbow trout were present in all six lakes, whereas coho and Atlantic salmon were only present in lakes which farmed those species (Tables 2 & 4). Chinook salmon were captured in all lakes, except in Lake Todos Los Santos where aquaculture was not present. Salmonids had a range of sizes from 15 to 90 cm (mean 46.7 cm) and a range of weights from 25 to 8250 g (mean 1800 g). Native species were captured in all six lakes with all four native fish groups in both Lake Todos Los Santos (reference lake) and Lake Llanquihue (Table 4). *Percichthy*s and *Galaxias* groups were in all lakes, Atherinidae were in four of the lakes, and *Aplochiton* were captured in three lakes. Length of native species ranged from 11 to 60 cm (mean 26.6 cm) and weight from 14 to 2600 g (mean 320 g).

Table 4 Salmonid and native fishes captured in each lake with total length and weight information

	Llanquihue		Puyehue		Ranco		Rupanco		Yelcho		Todos Los Santos	
Fishes	Salmonids (*n* = 758)	Natives (*n* = 2317)	Salmonids (*n* = 622)	Natives (*n* = 221)	Salmonids (*n* = 506)	Natives (*n* = 1073)	Salmonids (*n* = 140)	Natives (*n* = 154)	Salmonids (*n* = 202)	Natives (*n* = 2)	Salmonids (*n* = 96)	Natives (*n* = 32)
Rainbow trout	X		X		X		X		X		X	
Brown trout	X		X		X		X		X		X	
Coho salmon	X		X		X		X					
Chinook salmon	X		X		X		X					
Atlantic salmon	X		X		X		X		X			
Aplochiton		X		X								X
Percichthys		X		X		X		X		X		X
Galaxias		X		X		X		X		X		X
Atherinidae		X				X		X				X
Mean length (cm)	43.9	21.8	52.2	34.5	44.4	36.6	45.7	32.2	47.7		42	28.2
Range of lengths	15–85	11–45	16–90	15–58	18–77	15–50	16–78	19–45	28–98		31–63	15–47
Mean weight (g)	1127	120	2091	659	1021	455	1544	342	1237		877	371
Range of weights	25–7450	14–1125	45–11 250	40–2600	56–5858	38–1650	42–6500	52–1215	125–8250		325–3200	50–1450

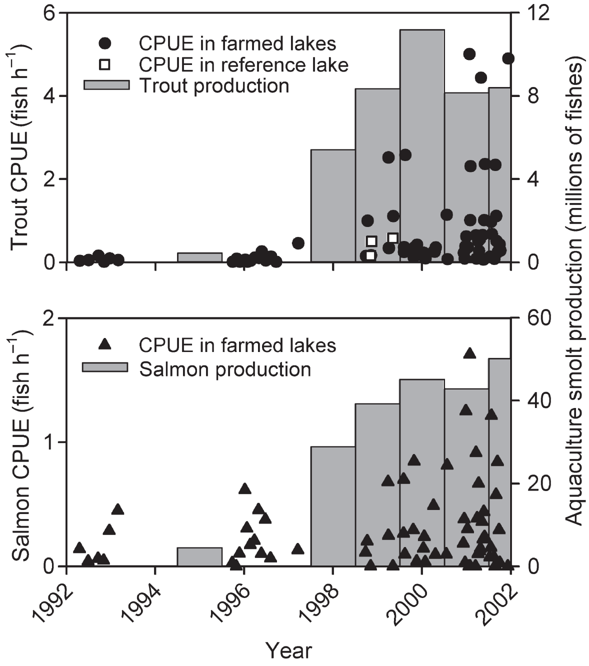

Fig. 2 Trout CPUE and trout smolt production by year in lakes with aquaculture activities and CPUE of reference lake without aquaculture (Lake Todos Los Santos). Salmon CPUE and salmon smolt production by year in lakes with aquaculture activities.

We found a substantial increase in salmon and trout relative abundance associated with production of smolts from aquaculture (Fig. 2). Salmonid aquaculture production increased from 4.9 million fish in 1995 to 58.4 million fish in 2002. Trout CPUE ranged from 0–0.14 ind. h^{-1} in 1992–93 to 0.6–4.8 ind. h^{-1} in 2000–01 and salmon CPUE ranged from 0.04–0.44 ind. h^{-1} in 1992–93 to 0.12–1.70 ind. h^{-1} in 2000–01. In the reference lake, Todos Los Santos, CPUE of rainbow and brown trout was between 0.2 and 0.7 ind. h^{-1}.

Among lakes, we found a positive relationship between salmon aquaculture production and salmon CPUE (Fig. 3). The relationship is nonlinear with an apparent plateau. Lake Llanquihue had the highest salmon aquaculture production (mean 18.4 ± 4.4 million fish per year) and Lake Yelcho had the lowest production (mean 0.82 ± 0.5 million per year).

We found that among lakes, salmonid CPUE was negatively related to the CPUE of native species (Fig. 4). Lakes Llanquihue, Todos Los Santos and Ranco had the highest CPUE of native fishes across years and Lakes Yelcho and Puyehue had the lowest. Also, on a temporal scale, for Lake Llanquihue, the

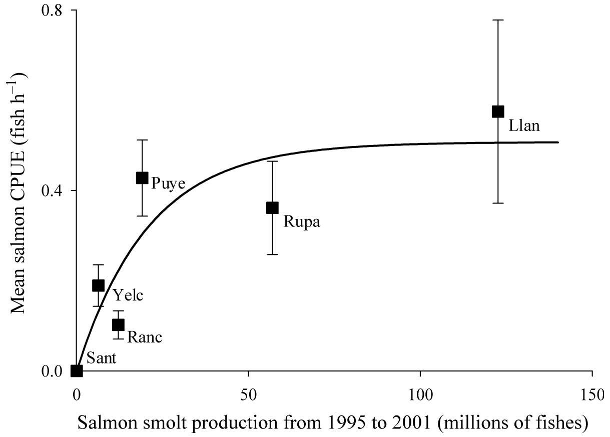

Fig. 3 Negative exponential regression model of mean salmon CPUE (±SE) across sampled years and total salmon smolt production for each lake from 1995 to 2001 for all six lakes ('salmon CPUE' = $0.5072 \times [1-e^{-0.0477 \times \text{'salmon smolt production'}}]$; $r^2 = 0.78$, $r^2_{\text{adj}} = 0.72$, SE = 0.11, $P < 0.01$). Sant, Todos Los Santos; Ranc, Ranco; Yelc, Yelcho; Puye, Puyehue; Rupa, Rupanco; Llan, Llanquihue.

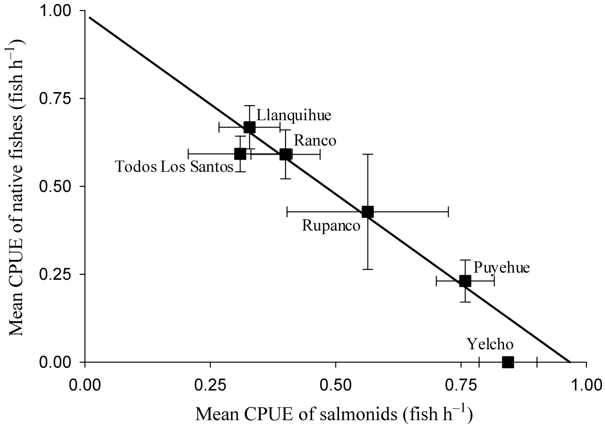

Fig. 4 Linear regression model of CPUE of salmonids (±SE) and native fishes (±SE) for all six lakes across years ('CPUE of native fishes' = 1.008–1.105 × 'CPUE of salmonids'; $r^2 = 0.947$, $r^2_{\text{adj}} = 0.93$, SE = 0.067, $P < 0.001$).

CPUE of trout ($r = 0.70$; $P < 0.001$) and salmon ($r = 0.36$; $P < 0.05$) increased over time, but the native species *Aplochiton* ($r = -0.58$; $P < 0.001$), *Atherinidae* ($r = -0.37$; $P < 0.05$), and *Percichthys* ($r = -0.44$; $P < 0.01$) showed a tendency to decrease, with the greatest reduction for *Aplochiton*. The native *Galaxias* showed the most variability between years ($r = -0.23$; $P = 0.23$), and they were not captured since 1998 (Fig. 5).

More than 92% of the trout and salmon stomachs were from fishes over 30 cm in length. Stomach contents included molluscs (*Chilina* spp.), crustaceans (amphipods, *Samastacus spinifrons* Philippi and *Aegla* spp.), feed pellets (from fish farming sites), insects (Coleoptera, Hemiptera and Diptera), fishes and other items (aquatic plants, other invertebrates and sediments). We were able to properly identify the taxon of 15% of the total fish stomach contents and of these all identified fishes were natives (*Galaxias*, *Aplochiton* and Atherinidae) with the rest of the fish remains being digested beyond recognition (e.g. spines) and thus unidentifiable. Only 14% of stomachs were empty. In the reference lake without aquaculture, Lake Todos Los Santos, insects (81%) dominated and fishes had a low frequency of occurrence in trout diet (9%) (Fig. 6). All lakes with aquaculture contrasted with this pattern (χ^2, $P < 0.001$ in each case), with fishes being the most frequently preyed upon item by salmonids in lakes with aquaculture, except in Lake Llanquihue where feed pellets were most frequent followed by fishes, other items and insects (Fig. 6).

Discussion

Aquaculture and non-native salmonid assemblages in Northern Patagonian lakes

Our results show that lakes with intensive aquaculture in the northern Patagonia are strongly correlated with the relative abundance of free living trout and salmon (individuals from stocking, aquaculture escapees and self-sustaining). The reference lake without fish farming sites, Todos Los Santos, did not contain species used for aquaculture purposes (except rainbow trout stocked both before and after salmon farming was established elsewhere). In general, lakes with intensive fish farming had free living salmonids of the same species as those farmed. We suggest that the increase in relative abundance of free living salmonids is due to an increase in the number of potential escapees associated with the substantial increase in juvenile aquaculture production. This idea is supported by studies in rivers in the Northern Hemisphere where high percentages of escaped farmed fish have been reported near areas of intense fish farming (Esmark *et al.*, 2005) and high fidelity of juvenile salmonids has been noted next to hatchery sites (Carr & Whoriskey, 2006).

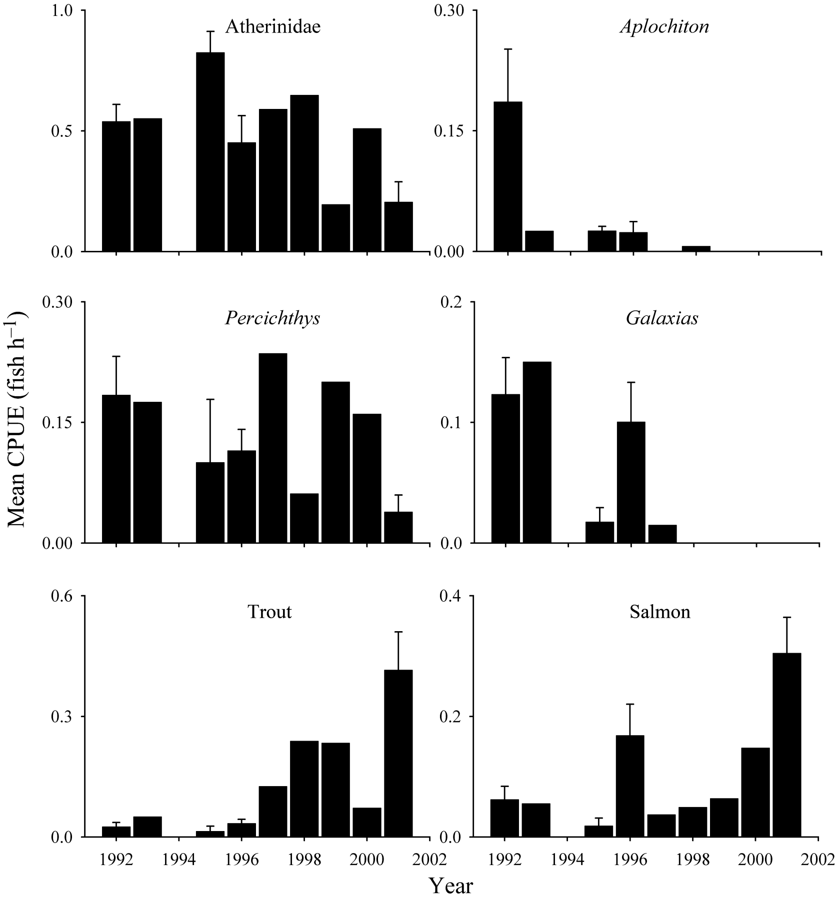

Fig. 5 Distribution of mean CPUE of native and salmonid species in Lake Llanquihue across years.

Currently, major salmonid farmers in Chile, Norway, Scotland, New Brunswick, Tasmania and the Faroe Islands are not obliged to systematically monitor or report fish escapees from fish farming sites (Soto *et al.*, 2001a; Naylor *et al.*, 2005; Skilbrei & Wennevik, 2006). Studies in Scotland and Norway have estimated that escaped fishes in freshwater systems represent 3–5% of the total net-pen production (Phillips, Beveridge & Ross, 1985; Hindar & Diserud, 2007). Assuming the same escapement in Chilean lakes, and based on smolt production in 2005 (Subsecretaría de Pesca, Economy Department, Government of Chile; unpubl. data), between 4.0 and 5.8 million fish per year may be escaping. Specifically, Lake Llanquihue would account for 1.3–2.3 millions of escaped fishes alone. Our data led us to expect that the relative abundance of cultivated free living salmon among lakes will continue to increase as fish farming production continues to increase; however, this relationship is nonlinear. The apparent plateau in our results, from the relationship between salmon CPUE and aquaculture production, may be explained by the dependence of salmon survival on the carrying capacity of each lake and thus overall salmon abundance may level off.

Each salmon species has a different level of establishment success in lakes of the Chilean Patagonia. Chinook salmon seem to be the most successful because they are only cultivated in Lake Puyehue at a very low production level, but they are present in every lake except Lake Todos Los Santos (natural waterfall barrier in its only effluent river). In addition, in other basins in the Patagonia, Chinook salmon have established self-sustaining populations (Ciancio *et al.*, 2005; Soto *et al.*, 2007) and are currently expanding their range (Soto *et al.*, 2007). On the other hand, Atlantic and coho salmon have failed to successfully reproduce or form self-sustaining populations in the Chilean Patagonia and there is no evidence of juveniles in affluent streams (Soto *et al.*, 2001b; Soto, Arismendi & Solar, 2002) despite high levels of smolt production. Coho salmon are only present in lakes

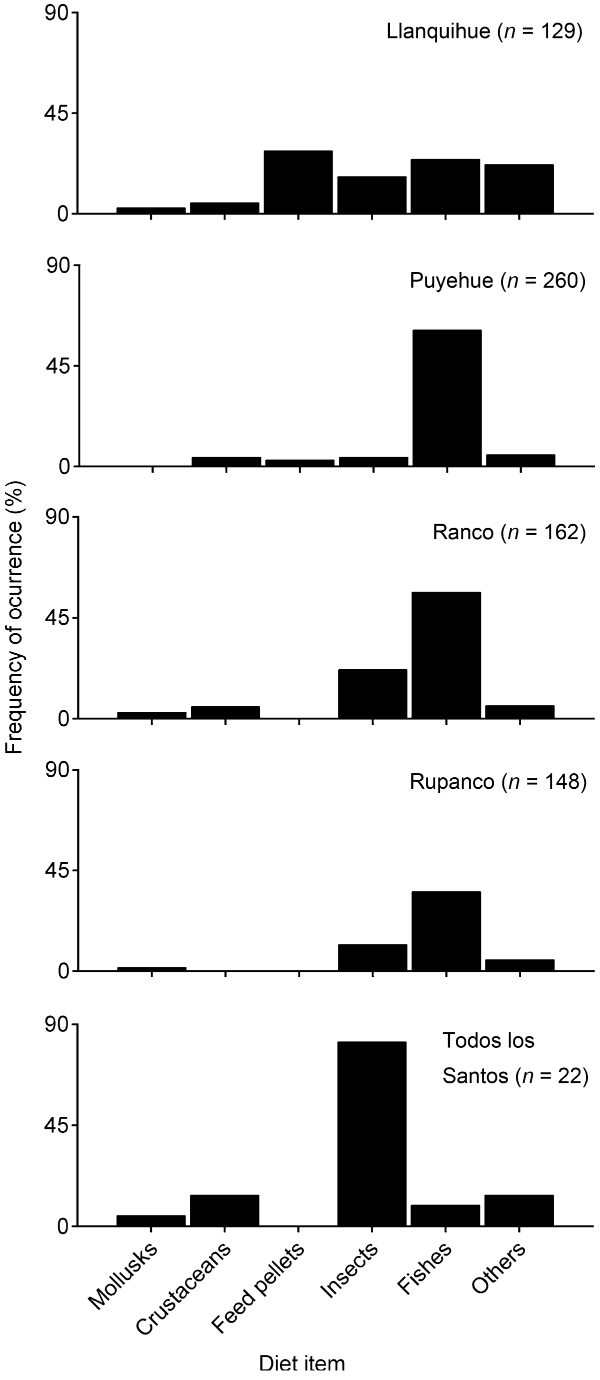

Fig. 6 Frequency of occurrence per diet item for salmonids. Lakes with aquaculture activities and reference lake without aquaculture.

where they are cultivated in salmon farming. Thus far, Atlantic (63%) and coho (17%) salmon comprise the majority of total smolt production in Chile (SERNAPESCA 2005). We found that in lakes with higher smolt production there is a larger population of free living individuals, and over time these free living individuals are increasing in number. Although we do not know what effects these persistent aquaculture escapees are having, impacts may occur regardless of whether or not escapees are reproductively successful (e.g. Weber & Fausch, 2003).

Brown trout and rainbow trout are the most widespread species in southern Chile (Soto *et al.*, 2006) and they are present in every sampled lake, including those without fish farming sites. Brown trout is not a commercially cultivated species, and its presence is explained by stocking before salmon farming was established in Chilean lakes and so it is not a consequence of salmonid aquaculture. Rainbow trout is found in much higher abundance than brown trout, with levels equal to the relative abundance of Atlantic, coho and Chinook salmon combined. Rainbow trout seem to have become well established soon after their introduction in the early 1900s (Campos, 1984; Basulto, 2003), although additional stocking occurred at unknown levels after 1980. Rainbow trout account for an important portion of total salmonid production (SERNAPESCA 2005) and it is reasonable to assume that trout escapees may have contributed to their free living population levels in lakes. Thus, the occurrence of free living trout probably results from a combination of previous self-sustaining populations and escaped individuals.

Interactions between salmonids and native fishes in lakes

Our results suggest a negative impact of salmonids on native fish assemblages, expressed in terms of a negative relationship between the relative abundance of native fishes and salmonids. Further supporting our initial hypothesis, our reference lake, Todos Los Santos, has the lowest abundance of salmonids and one of the highest abundances of native fishes. In the other five lakes with fish farming, we predict this negative trend will continue as growth in salmonid farming production continues to rise. A similar negative association has been shown indirectly in the marine environment and rivers in southern Chile (Soto *et al.*, 2001a, 2006) and in rivers in New Zealand (McIntosh, Crowl & Townsend, 1994; Townsend, 1996) where sites with high abundance of salmonids often have low abundance of native fishes and vice versa.

We propose that the mechanism responsible for the decline in native fishes in lakes is predation by salmonids as indicated by all of the identifiable fishes in their stomach contents being native fishes. This is expected to be especially prevalent in lakes with intensive fish farming where there is higher predation on native fishes because they were the main prey item. Additionally, it is possible that smolt escapees could be a food supplement to resident salmonids which could also be enhancing their populations. Previous studies conducted before fish farming sites were well established in the northern Chilean Patagonia indicate that trout diet consisted mainly of insect and benthic items, followed by fishes (Arenas, 1978; Campos, 1986); in some cases fish did not occur in the diet (Villalobos *et al*., 2003). These results are similar to what we found in our reference lake, and in other lakes without intensive aquaculture in the Patagonia (Macchi *et al*., 1999; Lattuca, Battini & Macchi, 2008). Other types of potential competition between native fishes and salmonids in lakes include resource competition (e.g. same food source or habitat) as seen by the high degree of foraging activity between native fishes and rainbow trout juveniles in Argentine lakes (Lattuca *et al*., 2008).

Our results suggest that salmonids negatively affect native fish relative abundances, with the most pronounced impact on *Aplochiton* spp., a genus classified as at high risk of extinction (Duncan & Lockwood, 2001). The largest populations of *A. zebra* reported for any Chilean lake was found in two remote Andean lakes, Yulton and Meullin, located below 45° and lacking salmonids (Soto *et al*., 2006). Before trout expansion and recent intensive fish farming activities, Eigenmann (1923) described *Aplochiton* spp. as abundant in basins that maintain large headwater lakes, such as the lakes in our studies. Campos (1970) was already suggesting a negative impact of trout on *Aplochiton* spp., and Lattuca *et al*. (2008) suggested the same thing for Argentina. We suspect that, in the long term, the increasing relative abundance of salmonids may alter native fish assemblages in Patagonian lakes. It is probable that the effects of salmonids on native species may provoke cascading effects on food web interactions, as seen elsewhere (Carpenter, Kitchell & Hodgsdon, 1985; Carpenter & Kitchell, 1988; Nyström *et al*., 2001; Simon & Townsend, 2003).

Worldwide net-pen aquaculture is expanding rapidly (FAO 2007). Future management plans for lakes with aquaculture need to consider: (i) reducing the negative impact of salmonids in natural ecosystems; (ii) diminishing the risk of escaped salmonids from aquaculture facilities and (iii) preventing the establishment of future self-sustaining salmonid populations.

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