

Chinook salmon invade southern South America

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Abstract We document the invasion of Chinook salmon (*Oncorhynchus tshawytscha*) to southern South America providing historical, current and future perspectives. We conducted field sampling, angler surveys, and analyzed all written records, and found evidence of reproductive populations in more than ten Andean (and many more coastal) watersheds draining mainly to the Pacific Ocean in Chile (39°–53° S), but also to the Atlantic Ocean in Argentina (50° S). Invasion begun ~25 years ago apparently from a few point sources of introduction by ocean ranching operations using spring-run Chinook salmon originated from tributaries of the lower Columbia River, USA. The rapid spread suggests that Chinook salmon were pre-adapted to their novel marine and freshwater environments because of similarities to equivalent North Pacific habitats, and invasion may have been facilitated by low ecological resistance. Preliminary data suggest that populations express a latitudinal gradient in juvenile migration life histories equivalent to that in their native range. Parallels to

the only other establishment of anadromous Chinook salmon outside their native range, New Zealand, suggests a predictable invasion rate. In South America, the invasion is ongoing in southern areas, yet we deem unlikely colonization of rivers north of the range reached thus far. This is the first anadromous salmon species to have invaded such a large range in South America, and it raises many evolutionary, ecological, environmental and socioeconomic issues, with several discussed here.

Keywords Patagonia · Andes · Chile · Introduced fish · Life-history · Propagule pressure · Impacts · Distribution range · Establishment · Colonization · Naturalization · Pre-adaptation

Introduction

Biological invasions¹ have stimulated researchers to develop descriptive and predictive theoretical frameworks (e.g., Moyle and Light 1996; Mack et al. 2000; Richardson et al. 2000; Facon et al. 2006), as well as collect empirical data (e.g., Torchin et al. 2003; Marchetti et al. 2004; Vila-Gispert et al. 2005;

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¹ Herein the terms ‘biological invasion’ and ‘invasive species’ refer to the establishment, naturalization, and un-assisted spread of non-indigenous species population(s) resulting in range expansion (*as per* Richardson et al. 2000; Facon et al. 2006; Falk-Petersen et al. 2006).

Stohlgren et al. 2006) however forecasting invasions remains problematic. Recently, Facon et al. (2006) proposed an eco-evolutionary framework that ordines sequence of events leading to invasiveness. Their framework suggests three non exclusive pathways leading to invasiveness: Introduced species may become invasive quickly if they are pre-adapted to their new range (Scenario 1), or may require time to allow for environmental (Scenario 2) or evolutionary changes (Scenario 3) before their environmental needs match the new environment. Here, we demonstrate that Chinook salmon (ChS; *Oncorhynchus tshawytscha*) from western North America that were introduced to Chile in the period 1978–1989 have now naturalized and are sweeping across a large range in South America—matching the prediction of the species having been pre-adapted. We review the history of the introduction, study the rate of spread, provide phenotypic data, and discuss potential consequences for South America.

Over 3,000 fish introduction events involving > 500 fish species have been recorded worldwide, and more than half of these may have led to the establishment of wild populations (Casal 2006). However, little is known about why some introduced fishes are successful and others are not (Copp et al. 2005). Salmonid fishes, native to the northern hemisphere, are common and popular among invasive fishes (Welcomme 1988; Alcaraz et al. 2005). This may be because of their high aesthetic, sport and commercial value leading to repeated introductions. It may also be that suitable niches for salmonids are widely available outside their natural boundaries (e.g., in the southern hemisphere), and thus salmonids show a high degree of success once moved by humans. Also, many species show high phenotypic plasticity and the capacity for rapid genetic adaptive evolution to new environments (e.g., Adkison 1995; Hendry et al. 2000; Quinn et al. 2001; Waples et al. 2004).

Salmonid invasions have the potential to negatively impact native ecosystems. They are thought to reduce taxonomic diversity (McDowall 2003; Bosch et al. 2006; Dextrase and Mandrak 2006; Ortubay et al. 2006) disrupt native food webs (Townsend 2003; Baxter et al. 2004; Ortubay et al. 2006), modify the cycling of nutrients (Bilby et al. 1996), alter the transmission of diseases (Muratov and Posokhov 1989) and re-distribute pollutants (O'Toole et al. 2006). Thus, while the socioeconomic benefits

of salmonid introductions may seem large, the biodiversity and environmental costs must also be taken into consideration (Crawford 2001).

One of the most preferred salmon species to humans is the ChS, also called the King salmon because it is the largest bodied of the North American salmonids, reaching typically 5–11 kg but often much higher weights. It is found from California north to Alaska and also in eastern Asia south to Kamchatka (Augerot 2005). Chinook salmon are the least abundant of the five North American *Oncorhynchus* species and are capable of spawning in both mainstream rivers and small tributaries and headwaters. Freshwater populations are also known but most are anadromous, utilizing rivers for spawning and early juvenile development and marine waters for growth to adulthood (Healey 1991; Behnke 2002). After 3–6 years and when nearing maturity, the semelparous adults return to their natal river for reproduction although some 'stray' into neighbouring rivers (Unwin and Quinn 1993). Their life histories vary greatly both within river basins and across the range of the species (Waples et al. 2004; Augerot 2005) reflecting their capacity for local genetic adaptation, made possible in part by their high site fidelity (Quinn 2005). The juveniles of some populations migrate to the ocean in their year of birth (ocean-type), while others migrate after spending typically 1 year in their freshwater stream (stream-type; Healey 1991). The two types use different ocean rearing habitat, but both are highly piscivorous feeders. Spawning time varies among populations and is most often in the fall with late spring and summer runs. Shortly after spawning the males and females die and the embryos develop for two to six months (depending on water temperature) in the gravel nest before emerging as fry.

The first human introductions of ChS into the southern hemisphere began in 1875 with approximately annual shipments of embryos from the Sacramento River system of California to New Zealand. These apparently failed until a 1904 shipment produced the first adult returns to the river of release in 1906–1907 (McDowall 1994). These adults, along with subsequent shipments to 1907, founded an anadromous population in the river of introduction. Stray individuals from this population have since gone on to colonize several other New Zealand drainages. Currently, about seven river

systems (43–45° S) of the Canterbury region in the east coast of the southern island have regular and substantial runs, and smaller rivers of other regions feature smaller and intermittent populations (Unwin 2006; Deans et al. 2004). The main populations have diverged significantly in terms of genetically based life history traits in both adults (e.g., fecundity and migration behaviour; Kinnison et al. 2002; Kinnison et al. 2003) and juveniles (e.g., growth rates; Unwin et al. 2000).

Successful introductions of ChS are the exception rather than the rule, and most introductions have failed for unknown causes. For example, during the time of the introductions into New Zealand, shipments were also made to Latin America, including Argentina, Brazil, Chile, Nicaragua and Mexico (Joyner 1980; Welcomme 1988). However, these introductions were believed to be unsuccessful and efforts were later abandoned.

In the 1960s, Norway initiated commercial practices in salmon aquaculture using the concept of ‘ocean ranching’, in which Atlantic salmon (*Salmo salar*) smolts produced by hatcheries were released to the sea and homing adults were used both for brood stock and commercial sales. However, it proved difficult to regulate the harvest when ranched fish commingled with wild populations. Therefore, in the 1980s the industry shifted to ‘net-pen farming’, in which the smolts were reared to adulthood in floating net cages. Chile, which has no native salmonids but has environmental characteristics in common with Norway and British Columbia (productive oceans, cold and mountainous rivers), began ocean ranching in the late 1970s and 1980s using ChS as well as other species. Despite promising results, by 1990 the industry switched entirely from ocean ranching to net pen farming, largely due to the absence of physical and legal means to control the capture of returning adults by local fishermen (Basulto 2003). A similar sequence of events is also true in North America. Currently, Chile and Norway are the two largest producers of farmed salmonids in the world (FAO Fishery Information 2006). Chinook salmon were originally farmed in Chile but soon the industry became dominated by Atlantic salmon, coho salmon (*O. kisutch*), and rainbow trout (*O. mykiss*). Chinook salmon were more difficult and expensive to raise causing a drop in its production to less than 1% ever since 1994 (FAO Fishery Information 2006).

Although sightings of free ranging ChS in Chile have become more frequent and widespread during the last fifteen years, until recently it was still debatable whether or not they had established self-sustaining populations (Fundación Chile 1990; Soto et al. 2001a; Behnke 2002; Soto et al. 2006). Chinook salmon have not been stocked into nature since the late 1980s, but escapees from farming facilities (e.g., Soto et al. 2001a; Anonymous 2004) have been regarded as possible source of wild-spawning ChS (Soto et al. 2001a; Behnke 2002). Yet, the minimal production of ChS by fish farms contrasts starkly with their conspicuous annual spawning migrations in Chilean and Argentinean rivers (see Results). Recently, J. Ciancio et al. (2005) reported an established self-sustaining population of anadromous ChS in a river that drains into the Atlantic Ocean in southern Argentinean Patagonia, and in Chile, D. Soto and her colleagues (2007) reported the establishment of the species in several river systems that drain into the Pacific Ocean in the lakes district. However, the Chilean government has not yet acknowledged their naturalization, nor regulated the ChS (incipient) fishery, which so far is traded at low value in the local black market by artisan fishermen.

The purpose of the present study is to: (1) document the history of ChS introductions in South America; (2) provide evidence for establishment and self-sustainability; (3) map the progress of the invasion revealing approximate invasion rate; (4) document the putative phylogenetic origin; (5) describe the adult body size and weight, spawning date, and juvenile migration behaviour and compare this to North American and New Zealand populations; (6) attempt to answer why ChS have been successful (as per Facon et al. 2006), and where they may eventually end their range in South America; and finally (7) discuss potential ecological, evolutionary, and socioeconomic consequences of this invasion.

Materials and methods

Literature review

We conducted an intensive literature review to find all known records of both introductions and free-ranging ChS in South America, with particular focus

on records from Chile. We reviewed any technical report of fish surveys (particularly in fresh water), including peer-reviewed journal articles, books, unpublished base-line studies, and publicly funded agency reports. This review spanned the past century, encompassing the entire period of known South American salmonid introductions. We also reviewed media reports during the period 2000–2004 documenting angler trophy catches or ChS runs, but because of the non-technical nature of these reports they were used only to supplement the angler interview survey (see below). For each record of salmon sighted in the wild, we recorded the sampling site, date, number of individuals collected, ontogenetic stage, and observations. Records of stockings were also reviewed from the same body of literature, and we tabulated stocking sites, date, number of individuals released, ontogenetic stage, origin of the fish, institutions and people involved, results, and observations.

Angler interview survey

We interviewed sport-fisherman in Chile and documented their personal observations of ChS between the years of 2000 and 2004. Interviewees were 26–56 years of age and were skilled anglers. In order to reach the people who were most familiar with the basins of interest, most of the interviews were conducted locally, between February and March 2003, throughout the south of Chile (from Santiago to Cochrane). During the interviews, we gathered basic information on specific sites and dates where ChS were observed. To avoid false positives, each interviewee was first tested on his ability to identify images of several salmonid species. For our analysis we considered only those interviewees who correctly identified ChS and who had sighted them freeranging in South America. Most of the interviewees provided photographs of their ‘trophy-fish’, and these were scanned and examined to confirm the correct identification of ChS.

Field Sampling

From February 19th to May 1st, 2004, we conducted a field survey of ChS in southern Chile (39° to 48° S).

Five major basins were chosen for sampling: the Toltén, Petrohué, Palena, Aysén, and Baker Rivers. These were chosen to confirm information from interviewees and records, and to sample a broad range of the current ChS distribution. Each basin was sampled at two to four sites or river portions (main river or tributaries), which often included salmon spawning areas. The Palena River basin was sampled less intensively due to poor weather conditions. An additional remote southern basin (Pascua, 48° S) was visually inspected in March 2007 only to confirm the presence of a ChS run.

A variety of fish sampling methods were used, depending on the ontogenetic stage, decay stage and abundance of the fish, as well as on the physical conditions of the river. Juveniles were always angled (fly-fishing and spinning), and were weighed, photographed and released (if alive). No hatchery existed that could explain the presence of the juveniles in the rivers studied. Adults were also collected in the rivers and euthanized for examination; collection techniques included gill-nets (5.5 inch monofilament), gaff hooks, and sink lines with multiple treble hooks. Carcasses were also located on the banks or obtained from anonymous fishermen. Our sampling was not intended to provide CPUE data. Every fish was examined within 24 h of capture (most within 12 h). Variables reported here include: ontogenetic stage; sex (adults); presence/absence of foods in stomachs (adults), fork length (adult lengths tape-measured to the nearest 0.5 cm, juvenile fork lengths estimated from images using digital callipers calibrated to scales of reference accurate to the nearest 1 mm); and wet weight (adults to the nearest 250 g, juveniles to the nearest 0.5 g).

Results

Chinook salmon introductions

The many introductions to Latin American rivers from 1891 to 1989 are summarized in Table 1. Chinook salmon were introduced to five Latin American countries: Mexico, Nicaragua, Brazil, Argentina, and Chile. However, extant wild populations are known only in Argentina and Chile.

Argentina—Recently, Ciancio et al. (2005) reported finding a population of anadromous ChS

Table 1 Chinook salmon releases in Latin American rivers from 1891 to 1989

Country, year(s) Basin, latitude River stocked	Number of individuals released	Ontogenetic stage	Stock origin	Adult returns	Comments
Mexico 1891–1900 Unknown	50,000 ¹²	Unknown	USA ¹¹ ; Sacramento river basin (?) ¹²	No ^{11,12}	From [1872–1930] the [US] Bureau of Fisheries, with benevolent intent, supplied over 100 million eggs of Pacific salmon (Chinook) to people in other countries, with the idea of establishing new salmon runs there—a considerable attempt to bring in the New World to right the Rest ¹³
Mexico 1901–1910 Unknown	50,000 ¹²	Unknown	USA ¹¹ ; Sacramento River basin (?) ¹²	No ^{11,12}	
Nicaragua 1901–1910 Unknown	20,000 ¹²	Unknown	USA ¹¹ ; Sacramento river basin (?) ¹²	No ^{11,12}	
Argentina 1906 Santa Cruz, 50° S ¹⁶ Gallegos, 52° S ¹⁶	300,000 ¹⁶	Unknown	USA; Sacramento River basin (?) ¹⁶	No (?) ¹⁸	
Argentina 1908 Chico, 50° S ¹⁷ Santa Cruz, 50° S ¹⁷	300,000 ¹⁷	Unknown	USA; Sacramento River basin (?) ¹⁷	No (?) ¹⁸	
Argentina 1909 Chico, 50° S ¹⁷ Santa Cruz, 50° S ¹⁷	200,000 ¹⁷	Unknown	USA; Sacramento river basin (?) ¹⁷	No (?) ¹⁸	
Argentina 1910 (Rivers of Santa Cruz Province ¹⁷)	200,000 ¹⁷	Unknown	USA; Sacramento river basin (?) ¹⁷	No (?) ¹⁸	
Argentina 1904 + ¹¹ –1910 ¹² Unknown	1,058,000 ¹²	Unknown	USA ¹¹ ; Sacramento river basin? ¹²	No? ^{11,18}	The last Argentinean entry (1904–1910) may include the previous four
Brazil, 1958 Jaquari, 30° S Rio Cai ¹⁴ Rio Tainhos ¹⁴ Rio dos Antos ¹⁴	400,000 ¹⁴	Fertilized eggs ¹⁴	USA; American river, California ¹⁴	No (?) ¹⁴	Although there were no reports of salmon returning to the Rio Jaquari, large fish of a species unknown to local residents were seen leaping falls in the Rio Uruguay in 1962 ¹⁴
Chile, 1924 Imperial, 39° S Rio Cautin ^{2,20} Maullin, 42° S ^{2,20} Rio Maullin ^{2,20} Cochamo, 42° S Rio Cochamo ²⁰ Puelo, 42° S Rio Puelo ^{2,20}	200,000 ¹ (little less than 50% died during transport ²⁰)	Fingerlings (4-months ²⁰)	USA; Sacramento river basin; McCloud river Hatchery (?) ¹	No (?) ^{1,2}	The U.S. government presented the government of Chile with 200,000 ^{1,20} fertilized CHS eggs. The embryos arrived at a recently built hatchery in Rio Blanco (near Santiago) just prior to hatching ^{2,20} . After four months, fingerlings were transported by rail and released ²⁰

Table 1 continued

Country, year(s) Basin, latitude River stocked	Number of individuals released	Ontogenetic stage	Stock origin	Adult returns	Comments
Chile 1969, 1970 Bueno, 40° S Río Chirri ^{3,4}	54,500 (1969) ³ 269,180 (1970) ³	Subyearlings ³	USA ^{3,4}	No (?)	Coordinated efforts by the Agriculture and Livestock Service of the Government of Chile and the U.S. Peace Corps. This was the first shipment by plane ^{3,4}
Chile 1969, 1970 Bueno, 40° S Río Chirri ^{1,5}	100,000 ^{1,5}	Fingerlings ^{1,5}	Unknown	No (?) ¹	It is unclear if this refers to the stocking event described above
Chile, 1978 Coastal, 42° S Curaco de Vélez, Chiloé Island ^{1,6,8}	120,000 ⁶ 170,000 ^{1,8}	Smolts (1+) ^{6,8}	USA; Cowlitz River (lower Columbia River basin, Washington) ⁷	Yes ⁶	Domsea Pesquera Chile Ltd., (subsidiary of the Union Carbide Corporation, USA) began salmon ocean-ranching experimentation ^{1,6,7} . In 1979, 334 fish were trapped, returning to their home stream ⁶
Chile, 1979 Coastal, 42° S Curaco de Vélez, Chiloé Island ⁶	190,000 ⁶	Smolts (1+) ⁶	USA; Cowlitz River (lower Columbia River basin, Washington) ⁶	Yes ⁶	Domsea Pesquera Chile Ltd. ⁶
Chile, 1980–1982 Coastal, 42° S Curaco de Vélez, Chiloé Island ⁸	40,000–90,000*	Smolts (1+) ⁸	Same as the above entry (?); gametes from returns ¹	Yes ⁶	In 1981, Domsea Pesquera Chile Ltd. was sold to Fundación Chile (a private, non-profit organization), and renamed Salmones Antártica Ltd. ¹ Through the winter of 1981, returnees totalled 817 adult individuals ⁶
Chile, 1981 or 1982 Southern Channels zone ¹⁵	Unknown	Smolts (?)	USA; University of Washington ¹⁵	Yes ¹⁵ (May refer to success in Río Prat.)	Two years later, returns of adult ChS far exceeded the modest expectations of the Chilean and U.S. sponsors of the project. These provided gametes for further stockings. ¹⁵ May refer to entries below
Chile, 1982 San Juan, 54° S Río Santa María ⁹	200,000 ⁹	Smolts ⁹	Same as the above entry (?) ⁹ ; gametes from returns in Curaco de Vélez (?)	No (?) ⁹	Fundación Chile through Salmones Antártica Ltd. ⁹

Table 1 continued

Country, year(s) Basin, latitude River stocked	Number of individuals released	Ontogenetic stage	Stock origin	Adult returns	Comments
Chile, 1983 Prat, 51° S Río Prat ¹⁰	5,000 ¹⁰	Smolts (1 +) ¹⁰	USA ¹⁰ ; University of Washington ¹⁵ (?)	Yes (~2.3%) ¹⁰	Fundación Chile through Salmones Antártica Ltd. ⁹
Chile, 1987 Same location ¹⁰	335,009 ¹⁰	Smolts (1 +) ¹⁰	Chile ¹⁰ ; gametes from returns of the above stocking (?)	Yes (~0.07 until 1989) ¹⁰	Fundación Chile through Salmones Antártica Ltd. ⁹ In 1998 Fundación Chile and Salmones Antártica created Salmotec S.A. ¹⁹
Chile, 1983–1989 Same location ⁹	670,000 (ChS & coho) ⁹	Smolts ⁹	(?)	Yes (> 2% ChS) ⁹	Fundación Chile through Salmones Antártica Ltd. ⁹ This entry would include the above two records. The source of ref. ⁹ was a personal communication by Cristián Jelvéz. The ocean ranching program closed in 1989

Some stocking efforts may have been tabulated twice due to difficulties combining incomplete records from different sources. The number of individuals released may be less than reported due to mortality during transport. Latitude is given at the river mouth

¹ Fundación Chile 1990, ² Golusda (1927), ³ Snyder 1971 in Basulto (2003), ⁴ Ellis and Salo 1969 in Basulto (2003), ⁵ Vila et al. (1978), ⁶ Lindbergh (1982), ⁷ Anonymous (1989), ⁸ Méndez-Zamorano and Munita 1989 in Grosman (1992), ⁹ Basulto (2003), ¹⁰ Salmotec Ltd. in Sakai (1989), ¹¹ Welcomme (1988), ¹² Davidson and Hutchinson (1938), ¹³ Elton (2000), originally published in 1958, ¹⁴ Joyner (1980), ¹⁵ Donaldson and Joyner 1983, ¹⁶ Tullian 1908 in Ciancio et al. (2005), ¹⁷ Marini and Mastrarrigo 1963 in Ciancio et al. (2005), ¹⁸ Marini 1936 in Davidson and Hutchinson (1938), ¹⁹ United Nations (2006), ²⁰ Barros (1931). (?) Indicates probable but unconfirmed. * This value is from an estimation of 400,000 for 1978–1982 (Ref. ⁸) from which is subtracted the 1978 + 1979 values

that spawn in the headwaters of the Santa Cruz River. This is the only known record of ChS utilizing the Atlantic ocean of South America. Its origin could be individuals released between 1906 and 1910 in the Santa Cruz River, but recent evidence from mitochondrial DNA points to origin from the ocean ranching program at the Magellan region in southern Chile in 1982–1989 (see below; Becker et al. [in press](#)).

Chile—Early attempts sponsored by the Governments of Chile, France, and the USA failed to establish ChS. The very first of a series of attempts was in 1,886 involving 39 juvenile ChS shipped to Santiago of Chile from Paris (where the species was previously introduced from the USA). These fish were kept in captivity, however, and never stocked in the wild (Basulto [2003](#)).

In 1924, ova travelled for three months in a cargo-steamer transport ship from the USA, and after reaching land were reared to the fingerling stage and then released into four basins in southern Chile (Barros [1931](#)). However, no returnees were found. Mann ([1954](#)) and De Buen ([1959](#)) found no evidence of establishment by ChS from any of these early introductions.

In 1969, a new program to introduce ChS in Chile involved cooperative efforts by the Chilean government and the US Peace Corps. Embryos were now flown from the USA to Chile and arrived in excellent condition (Basulto [2003](#)). Several hundred thousand fingerlings were introduced in the Chirri River (1969–1970). This project was suspended, however, and its results were never officially assessed. No returnees were reported during the following decade.

In 1976, the first commercial ocean-ranching experiment was conducted near Ancud on the island of Chiloé (Anonymous [1979](#); Joyner [1980](#)). A simple hatchery was built on a small island (Qhinchao) in the village of Curaco de Vélez, from which several hundred thousand ChS smolts were stocked between 1977 and 1982 in a stream flowing to the Pacific Ocean (Fundación Chile [1990](#)). Jon Lindbergh of the famous US aviation family held a senior position in the company that performed the introduction, and published a paper on the salmon enterprise but unfortunately did not mention the origin of the transplanted embryos (Lindbergh [1982](#)). The only reference that addresses the origin of these fish is an interview with Jon Lindbergh for a US corporate publication (Anonymous [1989](#)) where he is quoted as

saying: “We brought both coho and Chinook to the Chiloé area in 1975...We took down two or three [Chinook] strains, primarily Cowlitz Spring Chinook”.

Although the return rate was minimal (see next section), adult ChS did return to the hatchery. In 1979, several hundred adult ChS returned from the ocean, demonstrating for the first time the viability of the species in the southeast Pacific. Returnees provided the gametes to support the hatchery program (Fundación Chile [1990](#)).

In the 1980s, additional releases of ChS for ocean-ranching were carried out further south in the Magellan region (south of 51° S), with several hundred thousand smolts released between 1982 and 1989. The stock for the Magellan introductions appear to be different yet phylogenetically related to those used at Curaco de Vélez on the island of Chiloé. Donaldson and Joyner ([1983](#)) report that in 1980, eyed eggs were sent to Chile from the University of Washington. After a rearing period, these were released into ‘waters leading to the Southern Channel zone’, and unexpectedly high returns were observed two years later. They also state that the gametes of these returns would be used for future stockings in the Magellan region. Basulto ([2003](#)) assumes that Donaldson and Joyner ([1983](#)) refer to the stockings conducted by Fundación Chile in the Magellan region, first in Río Santa María, and then in Río Prat. Data from a company created by Fundación Chile (in Sakai [1989](#)) indeed show that ChS imported from the USA were stocked in 1983 in Río Prat and after 2–4 years, > 2% of the fish returned and provided gametes for further stockings in the same river in 1987. It is difficult to reject the possibility that the company also used gametes from Curaco de Vélez. Nevertheless, the Curaco de Vélez’ and the University of Washington’s stock are closely related phylogenetically (Waples et al. [2004](#)) as both populations are derived from the lower Columbia River watershed, USA (Donaldson and Joyner [1983](#); Anonymous [1989](#)). This was the last stocking for ocean ranching in Chile.

Since 1991, Fundación Chile has incorporated ‘closed’ production systems using ocean netpens to rear adults, which have had considerable success and now comprise the modern Chilean salmon-farming industry (Fundación Chile [1990](#)). Escapees from netpens in the early to mid-1990s may have contributed to the freeranching ChS currently in Chile. Soto and

colleagues (2007) estimate that in the period from 1994 to 1996, escaped ChS could have numbered as many as 50 thousand yearlings or older fish. However, it is our contention that most if not all of the original stock of the wild ChS populations that we document in Chile have stemmed from early ocean ranching.

Chinook salmon establishment

Over the last 25 years, sightings of freeranging ChS in the freshwaters of Chile have increased in frequency and distribution. Below we summarize the chronology and pattern of ChS observed (Fig. 1; Table 2; see also presence-absence database in Appendix A).

1979 and 1980s—The first confirmed sighting of freeranging ChS was in 1979, when several hundred adults returned to the stream in Curaco de Vélez, Chiloé (42° S), where stocking of smolts for ocean ranching began 1 year earlier (Lindbergh 1982). During the 1980s, returns continued to be observed

in Curaco de Vélez (Lindbergh 1982; Reyes 1982; Munita 1988). Further south, stocking of smolts in Río Prat in the Magellan region (51° S) also produced returnees (Sakai 1989; Basulto 2003). The number of returning adults never exceeded 3% of the released smolts (Table 1).

During this period, ChS were being reported in the headwaters in Argentina of two unstocked Pacific slope rivers (Yelcho and Palena). The mouths of these rivers in Chile are located less than 200 km southeast of the first ocean ranching site at Curaco de Vélez (Fig. 1). Spawning ChS have been observed there every austral summer/fall since 1984 (Grosman 1992; Pascual et al. 2002; Baigún and Ferriz 2003). However, except for the returnees from the smolt stocking at Curaco de Vélez, no freeranging ChS were reported anywhere in Chile throughout the 1980s. Substantial fish sampling efforts in ten large basins spanning from 39° to 45° S (including the Chilean portions of the Yelcho and Palena basins) did not detect ChS at this time (Campos et al. 1984; Zama and Cárdenas 1984; Campos 1985; Campos et al. 1985a, b). This suggests that only a few

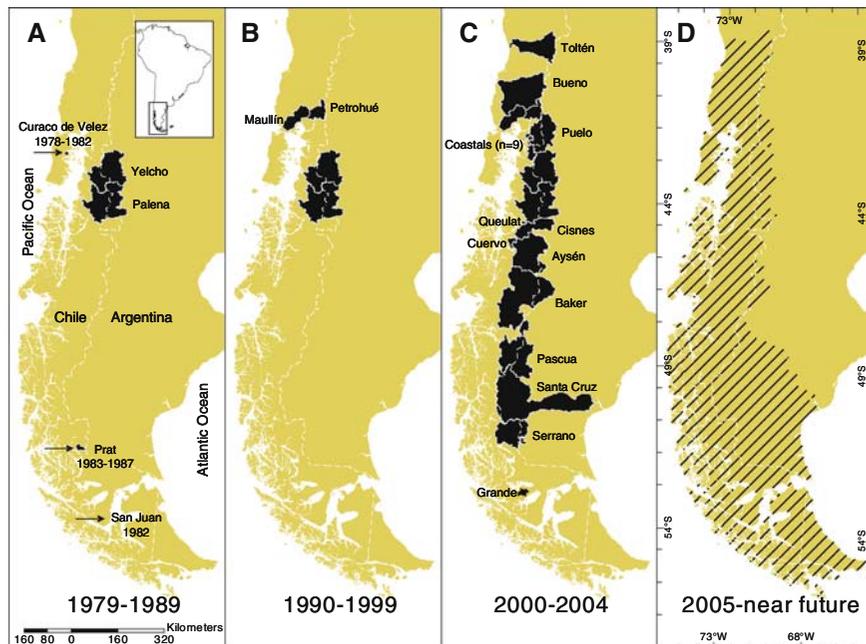


Fig. 1 Range expansion of Chinook salmon in South America. Locations and years of smolt releases for ocean ranching are shown with arrows in panel A. The black areas are basins (only labeled when first noted) where the species has been captured freeranging as (A, B) reported in empirical studies, and (C) based on empirical studies, angler interview surveys, media

reports and field sampling conducted in this study. The dashing in panel D illustrates the general area where we suggest future range expansion and population growth during the next few generations (e.g. within 15 years). The white dashed line represents approximate position of political border between Chile and Argentina

Table 2 Chinook salmon presence in South American basins in the period 2000–2004

Basin name	Type of basin ^b	Drain to ocean	Basin area (km ²)	Mean discharge (m ³ s ⁻¹)	Season(s) of peak discharge ^f	River distance (km)	HASL (m) ^h	Latitude South	Literature	Interv. & media reports	Field surveys
Imperial	Andean	Pacific	12054	240	W	<220 ^g	?	38°47'		j	
Tolón	Andean	Pacific	7886	572	W	200	400–520	39°15'			
Bueno	Andean	Pacific	17210	570	W	150	80–200	40°15'			
Maulín	Andean	Pacific	4298	73	W	120	60	41°36'			
Petrohué ^a	Andean	Pacific	2644	278	LF, (S)	25 or 35	50 or 120	41°23'			
Puelo	Andean	Pacific	8817	670	LF, S	<140 ^g	?	41°39'			
Three small basins	Coastal	Pacific	300 ^c	?	W?	<15 ^g	?	42°			
Six small basins	Coastal	Pacific	1,700 ^c	?	W?	<30 ^g	?	42°			
Fjords (Sea)	n/a	Pacific	n/a	n/a	n/a	n/a	n/a	42°			
Yelcho	Andean	Pacific	10979	363	W, S	170	350	42°57'			
Palena	Andean	Pacific	12887	130	W	200 or 160	360 or 490	43°46'			
Queulat	Coastal	Pacific	180	?	Su?, W?	<10 ^g	?	44°32'			
Cisnes	Andean	Pacific	5196	240	LF, (LS)	<160 ^g	?	44°45'			
Cuervo	Coastal	Pacific	688	126 ^e	(F)	<10 ^g	?	45°20'			
Aysén	Andean	Pacific	11674	628	F, S	80 or 140	150 or 440	45°25'			
Fjords (Sea)	n/a	Pacific	n/a	n/a	n/a	n/a	n/a	44°–45°			
Baker ^a	Andean	Pacific	26726	875	Su	50	50	47°47'			
Pascua	Andean	Pacific	14760	574	Su?	35	30	48°12'			
Serrano	Andean	Pacific	7347	61	W, (Su)	40	20	51°25'			
Grande in Riesco I.	Coastal	Pacific	600 ^c	?	W?	<25 ^g	?	53°00'			
Santa Cruz	Andean	Atlantic	24000 ^d	691 ^d	LSu ^d	460	180	50°00'			
Grande Bay (Sea)	n/a	Atlantic	n/a	n/a	n/a	n/a	n/a	49°–52°			
Grande (T. del Fuego)	Andean	Atlantic	8821	15+	?	<150 ^g	?	54			

Presence is determined from different sources of information including an extensive literature review, interviews with anglers, media reports, and original field surveys. Shaded cells represent presence; empty cells represent no Chinook salmon recorded. Approximate values for river distance from sea to known spawning grounds and height above sea level of the latter (HASL) are also provided. Variables for each basin extracted from Niemeyer and Cereceda (1984) unless otherwise indicated with superscripts. See the complete presence/absence database and references are in Appendix A

^a Below falls. ^bPre- and Trans-Andean watersheds where reclassified into Andean. ^cBasin area (to the nearest 100 Km²) and river distance measured from features produced by hydrological modelling tool SWAT (Di Luzio et al. 2000) using remotely sensed elevation data as input (Void-filled seamless SRTM data V1, 2004). ^dGaiero et al. (2002). ^eCentro de Ecología Aplicada Ltda. (2001). ^fSpring (S), summer (Su), fall (F), winter (W), late season (L), small peak indicates in parentheses. ^gLikely river distance given unknown locations of spawning grounds. ^hElevation data from ref. in superscript^c (see above). ⁱOceanic range not represented in Fig. 1. ^jInsufficient records available; not represented in Fig. 1. ^kWe confirmed this run in 2007; the remaining sites where visited in 2004

relatively small spawning populations, close to the smolt stocking site, existed during this period.

1990s—ChS sightings were documented in five Pacific basins during the 1990s. Runs continued in the headwaters of the Yelcho and Palena Rivers (Grosman 1992). Although ChS adults were not reported in Curaco de Vélez after 1988 (Munita 1988), returns may have continued. Adult ChS were reported for the first time in the Bueno, Maullín and Petrohué Rivers (40–42° S). Particularly conspicuous runs were observed in April of 1995 and 1996, in a short section of a branch of the Petrohué River (at a site called Los Patos), where many presumably anadromous adult ChS exhibited reproductive behaviour (Jara and Soto 1996; Soto et al. 2007). Toward the north, in the Bueno River (40° S) and particularly in Puyehue Lake, gillnetting resulted in the capture of many ChS across two years (1998–1999), and one juvenile was also fished in a tributary of this lake (Cassigoli 1999; Soto et al. 2001b, 2007; see below). Adult ChS were also captured sporadically in fjords near the coast of Chiloé, Puerto Montt, and in continental Chiloé (~42° S), but not further south in Aysén (45° S) (Soto and Jara 1996; Soto et al. 2001a). In Tierra del Fuego (54° S), intensive electrofishing in four basins revealed no salmon (Vila et al. 1999).

2000–2004—Information for the period 2000–2004 comes from published and media literature, but mostly from the results of our field sampling and angler interview survey. Since 2000, published technical records of ChS became more common and adults were confirmed in eight major basins flowing into the Pacific Ocean, four small coastal basins, and in fjords of two distant areas. Combined, these reports suggest a latitudinal range of 40–45° S on the Pacific slope of South America. However, adding our angler interview survey and media reports extends the potential ChS distribution north and especially south to a range encompassing 39–53° S (Table 2). Two new records of ChS presence in major basins outside the range reported in the literature were confirmed by our field survey in 2004 (Table 3)—and an additional southern basin was confirmed in 2007—supporting the information provided by angler interviewees. Below, we describe the current general pattern of ChS distribution, integrating information from across all of our sources.

The northernmost basin that anglers use to fish anadromous adult ChS in summer and fall is Toltén,

particularly in the Allipen River and its tributaries. We confirmed the presence of a small spawning run in the fall of 2004, but we did not observe juveniles at this site despite substantial snorkelling and angling effort (Table 3). In the proximal northward basin (the Imperial River), adults are rarely seen (and juveniles have never been seen) by anglers and we therefore consider the Toltén River to be the current northernmost basin being colonized (Fig. 1). We did not find any report of ChS in the Valdivia River basin (40° S, the proximal basin south of Toltén). Between the Bueno and Serrano rivers (40–51° S), however, the species is often reported in technical literature or by anglers revealing a nearly continuous range in Andean basins (interrupted by ice fields between Pascua and Serrano on the Pacific slope; Fig. 1).

The Bueno River basin appears to host both anadromous and landlocked ChS populations (Soto et al. 2007). This basin was surveyed intensively during 2000 and 2001 (Soto et al. 2001b; Soto 2002). Both juveniles and adults were collected in every sampled area. Juveniles were caught in different seasons in eight tributaries of three lakes (Ranco, Puyehue and Rupanco), but always comprised only a small fraction of the overall number of fish collected. In lakes Ranco and Rupanco, and in the Bueno River, gillnetting sporadically revealed a few adults, whereas adults were collected year-round in Puyehue Lake in high proportions relative to other species (averaging 28% of the total catch). Size structure, full stomachs, and examination of reproductive traits in the Puyehue Lake population strongly suggest a landlocked life history. Within 10 kms of the outlet of Puyehue Lake is a 17 m natural waterfall and a hydroelectric power plant that has operated since 1944 (CADE-IDEPE Ltda. 2004a), preventing upstream salmon migration.

Intensive surveys in the Maullín River basin revealed low abundance of ChS, but hundreds of adults were seen and sampled while spawning in the nearby Petrohué River (42° S) in the fall of 2001 (Soto 2002), but especially in 2004 (Soto et al. 2007). Several hundred juveniles were also electro-fished in spring of 2000, 2001 and 2004 (Soto 2002; Soto et al. 2007). Soto and collaborators have been annually observing ChS reproductive events at this site since 1995 (Soto et al. 2007). Angler interviewees also identified this site, and a site in the lower Petrohué basin, as containing large numbers of adult ChS each

Table 3 Results of the 2004 field survey. Description of sampling sites and dates of collections, number, sex, developmental stage, fork length and weight (Mean \pm SD, Range, *N*) of Chinook salmon sampled in southern Chile. None of the individuals exhibited the abraded fins typically observed in pen-raised fish; no adult had food items in its stomach

Variable	Total			
	Basin	Palená	Aysén	Baker
	Tollén	Petrohué		
Description of sampling sites & collection dates ^a	April 16–29. Rivers Peuco, Truful-truful, Viluco, Llaïma (38°51–53' S, 71°40–49 W). All rivers are shallow (max. 2 m deep), 2nd order tributaries of Allipen River, the northern branch of Tollén River basin. Scattered spawning redds observed	April 7–12. Petrohue River at Los Patos (41°11' S, 72°28' W): short (1 km), deep (max. 2 m deep), shallow loop of Petrohué River with many spawning redds approximately 1 km below the main river's waterfall. River Huñu-hueñu (41°16' S, 72°29' W): shallow, 3rd order tributary of Petrohué with scattered redds observed	February 28–March 9. Simpson River (45°43–44' S, 72°05–10' W): shallow and deep, 5th order, important southern affluent of Aysén River. March 30. Ñireguao River (45°10' S, 72°07' W): shallow, 4th or 5th order, with many redds, tributary of Mañiguales River, an important northern affluent of Aysén River	March 13–24. Jaramillo River (47°42' S, 73°03' W): shallow, 2nd order river with many redds, that flows for a few km leading to Vargas Lake and then to the next sampling site. Vargas River (47°42' S, 73°05' W): deep, 3rd order, affluent of Baker River. Tortel (47°49' S, 73°33' W): intertidal creek near Baker River mouth (one juvenile)
<i>Examined</i> (#)				
Adult females	18	8	9	13
Adult males	10	40	21	39
Adults (unsexed) ^c	2	1	0	0
Juveniles ^d	0	0	29	8 + 1 ^e
Total	30	49	59	61
<i>Length</i> (mm)				
Adult females ^g	852 \pm 47, 786–956, 13	914 \pm 96, 750–1022, 6	852 \pm 51, 750–920, 9	887 \pm 71, 760–1015, 13
Adult males	913 \pm 34, 850–950, 6	962 \pm 88, 730–1100, 25	1037 \pm 130, 790–1215, 21	983 \pm 111, 600–1260, 39
Adults pooled	871 \pm 52, 786–956, 19	952 \pm 90, 730–1100, 31	982 \pm 141, 750–1215, 30	959 \pm 110, 600–1260, 52
Juveniles	No data	No data	120 \pm 12, 94–143, 29	103 \pm 18, 90–144, 8
				117 \pm 15, 90–144, 37

Table 3 continued

Variable	Basin					Total
	Toltén	Petrohué	Palena	Aysén	Baker	
<i>Weight (g)</i>						
Adult females	5844 ± 1052, 4000–7750, 8	8292 ± 3299, 3500–13000, 6	?	5991 ± 1785, 3750–9171, 9	7077 ± 2544, 3750–13000, 13	6734 ± 2347, 3500–13000, 36
Adult males	7400 ± 627, 6500–8000, 5	1085 ± 2878, 5000–16000, 25	?	13074 ± 5225, 5000–21500, 21	11099 ± 3946, 2250–23750, 39	1128 ± 4087, 2250–23750, 90
Adults pooled	6442 ± 1182, 4000–8000, 13	10355 ± 3081, 3500–16000, 31	?	10949 ± 5532, 3750–21500, 30	10093 ± 4027, 2250–23750, 52	9985 ± 4207, 2250–23750, 126
Juveniles	No data	No data	No data	21.8 ± 7.4, 10.3–39.5, 29	13.7 ± 9.3, 8.6–36.5, 8	20.0 ± 8.4, 8.6–39.5, 37

Incomplete or rotten carcasses were not measured (and the number of individuals examined therefore does not always match the number of individuals measured). Length did not vary significantly among basins, but males tended to be longer than females (two-way ANOVA followed by unequal N HSD on log normal transformed data: Basin, $DF = 3$, $F = 1.4$, $P = 0.256$; Sex: $DF = 1$, $F = 22.1$, $P < 0.001$; Interaction $DF = 3$, $F = 2.0$, $P = 0.118$). Considerable variation in fish weight, particularly in females, was due to their spawning status; un-spawned individuals were heavier than spent ones, with gonads weighing 15–26% of total female weight ($N = 6$) and 2–7% of male total weight ($N = 43$). Most adults sampled in this study were partially or totally spawned, especially toward the end of the field survey in Petrohué and Toltén basins. Juveniles from Aysén were significantly longer (and hence heavier) than those from Baker (Mann-Whitney test: $U = 0.05(2)$, 8 , $29 = 41$, $P < 0.01$)

^a See basin variables (type, area, mean discharge, season of max. discharge, and latitude), river distance and height above sea level in Table 2. ^bSalmon restricted by waterfalls to lower portion of Petrohué and Baker basins. ^cEvery adult was sexed unless eviscerated by fishermen; both ripe and spent individuals, as well as a few carcasses, were examined. ^dJuveniles were never sexed. ^eOne juvenile, 72 mm long and 5.3 g in weight (the smallest), was found in a brackish intertidal creek near Baker River mouth [weight estimated from the calculated function: $Weight = 0.7293 * EXP(0.2768 * Length)$]. This individual was excluded from the calculation of length and weight mean and SD. ^fRotten carcass—not measured. ^gFor 9 females which had eroded anal and caudal fins from nest-building, the fork length was calculated from the function: $Female FL = 1.3134 * posterior\ ocular\ orbit\ to\ posterior\ hypural\ complex - 4.8377$, obtained from measurements on the remaining females

year. We confirmed spawning runs at these two sites during our field survey. Juveniles (Soto et al. 2001b) and adults (our interview survey) have also been sighted in small coastal basins of this same general area. Adults are occasionally caught in nearby fjords (Soto et al. 2001a).

Toward the south, in the Argentinean headwaters of the large Puelo, Yelcho and Palena Rivers (42° S, 43° S and 44° S, respectively), sightings of anadromous ChS adults continue (Pascual et al. 2002; Baigún and Ferriz 2003; Soto et al. 2007). These three basins have not been intensively surveyed in the Chilean territory, but sampling in a tributary of the Puelo detected juveniles (Soto et al. 2007), and sampling in Lake Yelcho and three of its tributaries in 2001 revealed one adult (Soto 2002). Anglers, by contrast, report catching many adults in the Chilean portion of these rivers. We attempted to sample the Palena River basin, but were hampered by difficult weather; we recorded one adult carcass near the Argentinean border.

The next Andean basin southward, the Cisnes River (45° S), also contained adult ChS, though only in low numbers. This basin was surveyed in fall 2001, but only a few adult ChS were caught near the Argentinean border (Niklitschek and Aedo 2002). Anglers reported the presence of ChS in this basin.

The southernmost basin in which ChS have been reported in the literature is that of the Aysén River (45°25' S). In summer 2001, Behnke (2002) observed adults (assumed to have been on a spawning run) and juveniles (hatched the previous year) in the Simpson River, an observation consistent with surveys conducted by local researchers in the same area and at the same time (Niklitschek and Aedo 2002; Niklitschek et al. 2002). We confirmed the simultaneous presence of both adults and juveniles in the same sub-basin during the late summer and early fall of 2004, as well as a large spawning run in a northern tributary of the Aysén River (Table 3). Anglers also supported these observations. Near the estuary of the Aysén River, a few ChS smolts and adults were sampled in both a coastal basin (Cuervo) and in an adjacent fjord (Centro de Ecología Aplicada Ltda. 2001).

We could not find printed records of field surveys finding ChS further south in Chile, but interviewees in our study reported adults in several systems further south. Our field study confirmed two of these reports: In 2004 we observed and sampled a conspicuous

adult run, as well as some juveniles in Baker River (47°47' S; Table 3), and in March 2007 we witnessed the same and another spawning run further south in the remote Pascua River basin (48°12' S). Similarly, interviewees reported ChS presence in Serrano River (52° S), and this was corroborated by sport-fishing outfitters (CADE-IDEPE Ltda. 2004b). Near Punta Arenas (the southernmost Chilean provincial capital), a ChS run on the Grande River of Riesco Island (53° S) was documented and broadcasted by a Chilean mainstream TV news program (Teletrece 2004).

It may be possible for wild ChS to stray through the Magellan Strait (or around Tierra del Fuego Island) to the Atlantic Ocean and colonize Argentinean watersheds. While a recent review of freshwater fishes in Argentinean Patagonia found no ChS in Atlantic basins (Pascual et al. 2002), Ciancio and collaborators (2005) recently documented a spawning population in the Caterina River, a tributary of the Santa Cruz River (50° S), in 2003 and 2004. Five sub-adults were also caught in nearby ocean waters by bottom trawlers during 2002 and 2003 (Ciancio et al. 2005). These are the first known records of ChS utilizing the Atlantic Ocean of South America. This population largely consists of a stream-type life history, migrating to the ocean after a full year in freshwater, and spending an average of three years in the ocean (range 2–4 years) before returning in mid-March at an average weight of 4.35 kg and 77 cm fork length (range 47–104 cm) to spawn and die. The population is small, numbering perhaps a couple of hundred adults (Ciancio et al. 2005). An interviewee photographed the capture of one large adult ChS, and another interviewee reported the presence of groups of 'presumable' ChS adults in the Grande River in Tierra del Fuego, a river which also drains into the Atlantic Ocean (54° S). However, these records represent insufficient evidence of establishment.

Discussion

Distribution and biology

Currently, ChS are established across a large range in South America, mainly in the Pacific basin, but also in the Atlantic basin. Printed records from Pacific drainages suggest a latitudinal distribution from

40° S to 46° S, and our information extends this range to 39–53° S (spanning > 1,500 km of lineal N–S distance). The strongest previous evidence for self-sustaining ChS populations in Pacific watersheds is provided by D. Soto and collaborators who located a land-locked population in Puyehue Lake, consistent annual runs and subsequent juvenile production in the Petrohué River, and the presence of juveniles or adults in the Puelo, Yelcho and Palena basins and in a few coastal basins (Soto et al. 2001b, 2007; Soto 2002). Printed records from Atlantic drainages provide strong evidence of only one established population in a tributary of the Santa Cruz River (Ciancio et al. 2005). We now know that ChS reproduce in > 10 Andean basins draining into the South Pacific Ocean (39–53° S), and in at least one draining into the South Atlantic Ocean (50° S).

We confirmed runs in a total of five basins chosen from the ~ 10 basins identified by our interviewees as hosting relatively large populations of ChS. These included three basins located outside the range reported in the literature, and thus our confidence in our interviewees is high. We observed typical (e.g., Healey 1991) reproductive behaviour such as upstream migration, territory defence, nest building, mate-guarding, and intra-sexual agonistic interactions by both sexes. Adults were never feeding as revealed by stomachs dissections, and their mean size (fork length) is similar to or perhaps slightly higher than that observed in the anadromous populations described for Argentina (Ciancio et al. 2005), New Zealand (Kinnison et al. 1998), and North America (Roni and Quinn 1995). No southern South American freshwater fish reaches a body size as large as anadromous ChS. Thus, the adult ChS sampled in this study were anadromous (mature male parr may exist; e.g., Unwin et al. 1999). In our field survey we also observed juveniles from previous years but only in the southernmost basins, suggesting a stream-type life history—a trait prevailing (92%, $N=46$) in the single Argentinean population (Ciancio et al. 2005). This suggests a strong latitudinal cline with the ocean-type dominating at lower latitudes and the stream-type at higher latitudes, as is the case in the ChS's native North American range (Healey 1991). At a smaller scale, the influence of lakes on water temperature at rearing sites may accelerate development facilitating an ocean-type life history (Soto et al. 2007). Interestingly, most ChS from the

putative source population in North America are ocean-type (Waples et al. 2004) consistent with high plasticity of age at sea entrance affected by growth rate, photoperiod, or other factors (see Quinn et al. 2001; Waples et al. 2004, and references cited therein).

Chinook adults in most South American rivers are found in spring and summer, and spawn in late summer and fall (from March through May). Salmon are usually observed in clear, shallow water in the upper portions of the basins, unless physical barriers prevent upstream migration, in which case fish congregate in nearby habitats. For example, the Petrohué and Baker rivers feature waterfalls that apparently restrict salmon to the lower portions of these basins. Although salmon entrance to the river is difficult to observe, silver-coloured and thus fresh from the ocean ChS are often caught in the spring in the lower portions of the Toltén and Aysén River, and near the border with Argentina in the Palena River.

Origin and colonization

Current populations of ChS in South America are likely derived from ocean ranching operations in Chile. During the decade starting in 1977, approximately 1.5 million ChS (mostly yearlings) were stocked, initially in a stream on Chiloé Island (42° S), and later in rivers of the Magellan region (52° S) (Sakai 1989; Fundación Chile 1990). The former ranching operation was the only possible source of colonists establishing in Yelcho and Palena River basins in the 1980s. These fish were, in turn, apparently derived from the lower Columbia River basin, the former from the Cowlitz River and the latter from the Kalama River (Donaldson and Joyner 1983; Anonymous 1989) which are phylogenetically related (Waples et al. 2004). There is a correspondence between the reproductive timing of ChS in South America and the reproductive timing of the putative source population in Cowlitz River (spring run with fall spawning). However, this is a weak evidence of recent ancestry because run timing is a labile trait subject to rapid evolution and environmental influence (Quinn et al. 2000; Waples et al. 2004). Alternative or additional routes of introduction are escapes from aquaculture facilities in Chile during the 1990s (with unknown ancestry to us),

and early (1904–1910) stockings in Argentina using Sacramento, CA, fish. However, Becker and colleagues ([in press](#)) recently discarded the latter potential source by comparing mitochondrial DNA sequences obtained from the Santa Cruz River Chinook salmon (Argentina) with haplotypes from Sacramento River Chinook salmon and from the University of Washington Hatchery.

The colonization of New Zealand began when approximately 1.5 million juvenile ChS from the Sacramento River basin were released in the Waitaki River between 1901 and 1907 ([McDowall 1978](#); [Quinn et al. 2001](#)). Hatchery supplementation continued for many years in the same river (using local returns as broodstock), and within fifteen years (four or five generations) the species had naturally strayed and colonized several rivers up to 230 km northward from their point of introduction. These sites in the Region of Canterbury now have the largest current runs ([McDowall 1978](#); [Quinn et al. 2001](#); [Unwin 2006](#)).

Similar to the pattern observed in New Zealand, within 15 years of the introduction programs in Chile, ChS have colonized Andean basins within a radius of 200 km from the two points of introduction—the Yelcho, Palena and Petrohué Rivers in the northern area ($\sim 42^\circ$ S), and the Serrano River in the southern area ($\sim 51^\circ$ S; distances measured as the shortest distance by sea to each river's mouth). In the last 5–10 years, ChS distribution in Chile has continued to expand rapidly. However, since the southern stockings were done several years after the northern stockings, and because we lack information for the Serrano River during the 1990s, we cannot discard the possibility that the southern areas received their colonists from the northern area rather than from the stocking program (molecular genetic analysis may also help to resolve this question). It is even more difficult to ascertain the founders of the Pacific basins of intermediate position (e.g., Aysén and Baker). Yet, we can conclude that ChS not only established, but rapidly colonized many new areas.

After a decade of ocean-ranching experimentation, stocking ceased, and salmon farming (rearing in captivity) begun. Currently, Chile is a leading producer with over 600 thousand tons of farmed salmon and trout harvested every year ([FAO Fishery Information 2006](#)), a quantity so high that it inevitably leads to the speculation that escapees may

create or sustain free ranging populations. There is no conclusive evidence that escaped farmed salmon have given rise to wild populations anywhere in the world ([Volpe et al. 2000](#); [Naylor et al. 2001](#)), but we cannot rule out the possibility that genetic contributions from farm escapees have influenced current wild populations. The low production of farmed ChS in Chile since 1994 ($< 1\%$ of the total production per year; [FAO Fishery Information 2006](#)), the current wild ChS distribution well beyond the range of ChS farming facilities (e.g., in the Toltén, Baker, Pascua and Magellan basins), and the presence of juveniles in rivers indicates that escape from farms does not account for current populations. None of the individuals sampled in our field study had the morphological traits of farmed fish (e.g., abraded pectoral or dorsal fins, [Gross 1998](#)).

A potential ChS population from aquaculture escapement is the land-locked population of Puyehue Lake (41° S) ([Soto et al. 2007](#)). Natural colonization is unlikely since the lake is unreachable by upstream salmon migrants. However, the lake hosted a ChS farming facility ([Soto et al. 2007](#)) and juveniles captured in the lake's tributaries are likely escapees ([I. Arismendi and D. Soto personal communication](#)). Whether this population is self-sustaining remains unclear ([Soto et al. 2007](#)).

What makes Chinook salmon invasive?

The large South American range colonized by ChS in the 25 years since its two successful point-introductions indicates that this species is invasive (See footnote 1). We suggest that pre-adaptation and low ecological resistance (e.g., spare spawning grounds, few enemies and competitors; [Elton 2000](#)) are the two primary characteristics allowing ChS to be invasive in South America and probably in New Zealand. In [Facon et al's. \(2006\)](#) framework for biological invasions, we would say there is a pre-existing match between the ChS strain(s) introduced and the environment encountered in southern South America. Neither evolutionary nor environmental changes seem to have been necessary for their rapid spread. The only factor that prevented an earlier natural colonization by salmon of South America appears to have been the warm waters of the equatorial region. The lack of success of early

transplants before ocean ranching may have been due to the limited number released, or due to vulnerable early life stages stocked rather than release at the smolt stage.

The pre-adaptation hypothesis favouring immediate invasiveness might be challenged by a hypothesis of rapid adaptive evolutionary change. Many introduced species show a time lag before becoming invasive. Facon et al.'s (2006) framework interprets this time lag as necessary for evolutionary and/or environmental change to occur when introduced species do not match the novel environment. Adaptive evolution may arise during the very early stages of colonization when colonists represent a highly selected (non-random) sample of the introduced population (i.e. 'favoured founders effect'; Quinn et al. 2001). This evolutionary change could quickly improve the fitness of the new population, acting as a trigger for invasiveness. The corollary is that most invasive species would undergo this process yet many still need long time lags to become invasive. We therefore emphasize the magnitude of the evolutionary change needed to match the novel environment, and suggest that pre-adapted invasive species require little evolution, and that their source population already possess the required genetic variability to succeed in the new environment. Pre-adapted invasive species can of course also continue to evolve after expanding their range (Facon et al. 2006) as happened with New Zealand ChS (Quinn et al. 2001; Kinnison et al. 2002, 2003).

Anadromy and homing behaviour also play important roles in the invasiveness of ChS. Following point introductions, homing behaviour favours initial establishment by congregating returning adults in the vicinity of their point of introduction. Without homing, anadromous salmon would disperse widely, making reproduction and population growth difficult. Homing also facilitates human production efforts as homing fish are used as broodstock for the next generation. Both in Chile and New Zealand, initial releases were comprised of imported stocks, but after a few years local returns provided the necessary gametes to continue the stocking programs (McDowall 1978; Fundación Chile 1990). Pacific salmon homing/straying rates vary substantially among populations (Quinn 1993). In the Cowlitz River (putative source for stockings in the northern site in Chile) and in the Waitaki River (New Zealand), over 70% of

spawning adults return to their river of origin (Quinn and Fresh 1984; Quinn et al. 1991; Unwin and Quinn 1993). These rivers are relatively short (< 100 km), like many Chilean rivers (Table 2). While homing rates are generally high, low (but non-zero) straying rates have important evolutionary consequences through both founding new runs which may involve 'favoured-founders effect' (Quinn et al. 2001), and increasing gene flow among populations (McDowall 2001).

Colonization of pristine habitats is likely to occur if there is a source population from which colonists may be produced in sufficient numbers. Several interacting factors determine the likelihood that enough strays will meet at a new spawning ground to enable successful reproduction and establishment. The most important factors include: mortality rate, size of the source population, distance between river mouths, river flow (higher flow attracts more strays), degree of dichotomy of river systems (i.e., the more branched a river, the less likely the encounter between strays on new spawning grounds will be), and the physical and chemical properties of the new river (e.g., water temperature, oxygen, and mechanical barriers). A large-scale mark-recapture experiment conducted in New Zealand revealed that 12% of recaptured individuals entered a different river from that in which they were released. These strays were mostly recaptured in rivers located within a distance of 200 km from their river of origin, with a maximal straying distance of 580 km (as measured by sea distance from each river's mouth; Unwin and Quinn 1993). Although hatchery fish may display abnormal behaviour, these empirical observations match the early colonization rate observed both in Chile and in New Zealand populations, where strays appear to have colonized nearby basins (within ~200 km) within a span of 4–5 generations (15 years). This suggests a predictable invasion rate.

Colonization: an ongoing process?

The establishment of ChS populations in South America appears to be an ongoing process. The lower bound of their latitudinal distribution is 39° in both their native North American range (i.e., Sacramento-San Joaquin River system) and their novel South American range (i.e., Toltén River basin). This

fact may not be coincidental, since it has been suggested that oceanographic processes and their effects on climate and biota are comparable and similar between the Northern and Southern East Pacific (Halpin et al. 2004). In Chile, few adult ChS have been sighted in the closest basin north of the Toltén, indicating that, despite the lack of apparent barriers, warmer climate and sub-optimal water conditions may prevent establishment further north (Fig. 1D). Additionally, human population density, irrigation practices, damming, and eutrophication increase considerably toward Santiago of Chile further preventing ChS establishment. However, there are many more rivers in the Pacific and Atlantic drainages of southern South America (particularly south of 50° S) that could be colonized by ChS (if colonization has not already occurred; Fig. 1D). For example, the species has been spotted in the Atlantic basins of the Gallegos River and the Grande River in Tierra del Fuego (F. Valenzuela and G. Cortés, personal communication). The fact that other studies (Vila et al. 1999; Pascual et al. 2002) have not found ChS in that region may reflect the recent spread of the species and the lack of appropriate field surveys. The presence of other anadromous salmonids in the area, including rainbow trout (steelhead; Pascual et al. 2001) and brown trout (sea-trout; Baigún and Ferriz 2003) in the Atlantic rivers of Tierra del Fuego and north of the Magellan Strait to Santa Cruz (50° S) suggest potential for ChS colonization as demonstrated recently by Ciancio et al. (2005). Also, rivers in southern Patagonia are relatively close to each other, facilitating the colonization of new rivers.

The conditions for ChS in rivers north of 50° S on the Atlantic coast may not be as favourable as they are on the Pacific coast at similar latitudes. Rivers become considerably longer, with little slope in most of their course, and the adjacent terrestrial habitat is much drier and warmer, similar to northern Chile (i.e., xeric habitat type; Olson et al. 1998), all of which may result in physiological constraints upon salmon (Fig. 1D). Also, river mouths become farther apart, and basins become larger with several sub-basins, all of which are characteristics that diminish the likelihood of sufficient numbers of strays gathering in particular spawning grounds to facilitate establishment (see above). Finally, the likelihood that ChS in South America may be pre-adapted to relatively short rivers might diminish their capacity

for establishment in longer rivers: Waples et al. (2004) showed that populations from the lower Columbia River (putative origin of South American ChS), and from coastal rivers between California to British Columbia (comparable to Chilean rivers in length), evolved from a different lineage than those in the upper Columbia or Fraser Rivers, which require much longer migration (e.g., <200 km vs. >1,000 km). Each lineage has a suite of life history traits that may favour performance solely for its respective length of river (Waples et al. 2004).

The naturalization of ChS in South America offers an outstanding and unique opportunity to study contemporary evolution, ecology, and invasion biology. The species' broad latitudinal distribution in South America provides an environmental cline comparable to that found in its native range, offering an excellent opportunity to study local adaptation. The presumably monophyletic origin of current populations should assist in the interpretation of evolutionary processes. Recent introductions, the early stage of naturalization, and apparent ongoing colonization, all offer the opportunity to study evolutionary and ecological processes as part of what determines the success of invading species. Finally, this species is a longstanding influential model system elsewhere (e.g., Hendry and Stearns 2004) providing excellent basis to impel advanced future research.

Overview on expected consequences

The invasion of ChS into South America raises issues for native biodiversity and ecosystems, as well as for human socioeconomics. On theoretical grounds, the evolutionary insularity of South American fish fauna from most North American fish fauna may make them especially sensitive to biological invasions (Rodríguez 2001). Each ChS ontogenetic stage and life history type can have particular impacts on the ecosystem and biotic community. For example, fingerlings in fresh water may compete for food with native fish (and with other introduced salmonids), yet may also provide prey for native species. Their impacts may be particularly intense toward higher latitudes, where more juveniles seem to spend a full year in streams (i.e., stream-type; Healey 1991).

In marine waters, Chile is currently experiencing colonization by over 30 non-indigenous marine algae and macroinvertebrates (Castilla et al. 2005), and the addition of anadromous ChS increases stress and perturbation to the food web. Once in the marine environment, sub-adults have the potential to roam several thousand kilometres as they feed and grow for 2–6 years, although ‘ocean-type’ fish tend to reside in deep pelagic zones of coastal areas closer to their river of origin (Healey 1991). Sub-adult ChS are primarily pelagic and benthopelagic fish consumers (Healey 1991; James and Unwin 1996; Behnke 2002). Based on diet data of coho salmon caught in fjords of Chile (Soto et al. 2001a), where ocean-type ChS may forage, predation by ChS on shoaling fishes (including *Engraulis rigens*, *Sardinops sagax*, *Normanichthys crockeri*, *Odontesthes regia* and juvenile *Macruronus magellanicus*, as well as on unspecified crustacean species) is anticipated, since coho and ChS have similar diets in the north Pacific (Healey 1991). However, it is difficult to foresee the impact of tens or hundreds of thousands of ChS foraging at sea. The land-locked ChS population in Puyehue Lake is also mainly ichthyophagous (Soto et al. 2001b). Understanding ChS vertical and horizontal food web interactions and their impacts on local ecosystems and resources demands substantial empirical research.

After the marine growth period, mature adults migrate upstream from the ocean, whereupon they spawn and die. Although ChS cease feeding after entering freshwater (Healey 1991; this study), they can impact aquatic, riverine, and terrestrial ecosystems through the nutrients released on their death (Soto and Campos 1995; Soto et al. 2007) as well as parasites from the ocean (the macro-parasite fauna found in our field survey is described in Bravo 2005). Input of marine-derived nutrients may result in increased basal food web production (Zhang et al. 2003; Wilkinson et al. 2005), and cascade to upper trophic levels (Bilby et al. 1998). These are only a few simple examples of how ChS invasion may impact local ecosystems. A proper environmental impact assessment involving more complex ecological interactions is required.

From the perspective of human socioeconomics, the presence of harvestable wild origin ChS may create commercial and recreational marine and freshwater fisheries comparable to those long

practiced in Pacific waters of North America and Asia. During their upstream migration, ChS in Chile already support a sport fishery with economic and recreational benefits. A commercial marine ChS fishery could also provide a substantial source of employment in remote areas. However, the Government of Chile has not yet officially recognized ChS as a resource available to fisheries, and this results in unknown (but potentially large) economic and environmental losses. Paradoxically, ChS foraging at sea may be harvesting significant proportions of traditional natural resources, which are subject to restrictive harvestable quotas to local fishermen (e.g., *M. magellanicus*, *Merluccius australis*). Stakeholders need to develop management policies to address the dilemmas posed by these fish—policies that recognize the capacity to provide important economic benefits, but also recognize the potential to cause significant biological changes to local ecosystems. Decision-making should acknowledge the inherent complexities of the tradeoffs between protection and economic opportunities (Pascual et al. 1998). Chile has to be particularly cautious in this matter given the high importance of its aquaculture industry, which has long been criticized for being environmentally subsidized (Naylor et al. 1998; Gajardo and Laikre 2003). Future research should provide insights for management strategies, address environmental impacts in marine and freshwater ecosystems, and address ecological and evolutionary processes related to the naturalization of ChS in South America.

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Appendix A Review of Chinook salmon sighted freeranging in Chile (presence-absence database). For each basin, basin portion, or group of coastal basins, presence (P), absence (A), or total number of individuals reported (#) is presented for four time periods

Basin (Type)*	Source type	1979	1980s	1990s	2000–2004
<i>Pacific Ocean and watersheds draining to the Pacific Ocean</i>					
Imperial, 39° S (Pre-Andean)**	Tech	A ^a	A ^a	No study	No study
	Int				Pa ^{1,2}
Toltén, 39° S (Andean)	Tech	A ^a	A ^{a,b}	No study	No study
	Int				Pa ^{1,2,3,4,5,6} ; Pj ^{1,2,4,5}
	News				Pa ^{i,ii}
	Field				30a
Valdivia, 40° S (Trans-Andean)	Tech	A ^a	A ^a	No study	No study
Bueno, 40° S (Andean)	Tech	A ^a	A ^c	61a ^{d+e} ; 1j ^e	207a ^{e+f} ; 151j ^e
	Int				Pa ^{7,8}
	News				Pa ⁱⁱⁱ
Maullín, 42° S (Pre-Andean)	Tech	A ^a	No study	A ^{d,g,h} ; 3j ⁱ	3a ^f ; 31j ^f
Petrohué, 41° S (Andean)	Tech	No study	No study	36a ^j	> 500a ^{f+ad} ; > 1000j ^{f+ad}
	Int				Pa ^{9,10,11,12} ; Pj ¹¹
	News				Pa ^{iv,v}
	Field				49a
Puelo, 42° S (Trans-Andean)	Tech	No study	No study	No study	Pa ^k ; Pj ^{ad}
	Int				Pa ¹⁰
	News				Pa ^{vi,vii}
Pichicolo, Cuchildeo and Negro, 42° S (Coastals)	Tech	No study	No study	No study	155j ^c
	Int				Pa ^{2,6,13,14}
	News				Pa ^{vii}
Blanco, Cholgo, Quintupeu, Cahuelmo, Huinay, and Vodudahue, 42° S (Coastals)	Tech	No study	No study	No study	No study
	Int				Pa ^{2,6,13,14}
Stream near Curaco de Vélez, 42°S (Coastal)	Tech	[Few hundred]a ^a ; 334a ^f	818a ^{l+tm} ; Pa ^{n,o}	No study	No study
Fjords ~42° S (Sea)**	Tech	No study	No study	17a ^p	2a ^e
Yelcho, 43° S (Trans-Andean)	Tech	No study	A ^q ; 1a ^r	6a ^r	> 10a ^{ad} ; P ^s
	Int				Pa ^{15,16,17,18}
Palena, 44° S (Trans-Andean)	Tech	No study	A ^q ; 3a ^r	3a ^r	25a ^{ad} ; Pa ^{s,ac}
	Int				Pa ^{15,16,17,19}
	Field				1a
Queulat, 45° S (Coastal)	Tech	No study	A ^q	No study	No study
	Int				Pa ²⁰
Cisnes, 45° S (Trans-Andean)	Tech	No study	A ^q	No study	2a ^t
	Int				Pa ^{11,15,19,21}
Cuervo, 45° S (Coastal)	Tech	No study	No study	No study	5j ^u
Aysén, 45° S (Trans-Andean)	Tech	No study	A ^{q,w}	No study	9a ^{t+y} ; Pa ^x ; Pj ^x
	Int				Pa ^{15,20,22} ; Pj ^{15,20}
	Field				30a ; 29j
Fjords 44–45° S (Sea)**	Tech	No study	No study	A ^p	3a ^u

Appendix A continued

Basin (Type)*	Source type	1979	1980s	1990s	2000–2004
Baker (lower, below waterfalls), 48° S (Trans-Andean)	Tech	No study	No study	No study	No study
	Int				Pa ^{18,20,22,23,24}
	News				p ^{viii}
	Field				52a; 9j
Pascua, 48° S (Trans-Andean)	Tech	No study	No study	No study	No study
	Int				Pa ²⁵ , see also ref. ad.
	Field				> 10a; 1j***
Serrano 51° S (Trans-Andean)	Tech	No study	No study	No study	Pa ^{ab} (but see note after reference)
	Int	No study	No study	No study	Pa ^{18, 26, 27}
Prat, 51° S (Coastal)	Tech	No study	346a ^{aa} ; Pa ^o	No study	No study
Grande in Riesco Island, 53° S (Coastal)	Tech	No study	No study	No study	No study
	News				Pa ^{ix} (but see note after reference)
Cóndor and Bueno in Tierra del Fuego, 54° S (Coastals)	Tech	No study	No study	A ^v	No study
<i>Atlantic Ocean and watersheds draining to the Atlantic Ocean</i>					
Santa Cruz 50° S (Andean)	Tech	No study	No study	No study	57a ^z
Grande Bay 49–52° S (Ocean)**	Tech	No study	No study	No study	5a ^z
Grande in Tierra del Fuego 54°S (Trans-Andean)**	Tech	No study	No study	A ^v	No study
	Int				Pa ^{18,26}

Ontogenetic stage of observed fish is also provided: juveniles (j) or adults (a). The information is classified by type of source, namely technical reports (Tech), angler interview survey (Int), media news reports (News), or field sampling in this study (Field). References are indicated in superscript letters (literature), numbers (interviewees), and roman numerals (news reports) as listed at the bottom of the table. Technical reports were reviewed for every time period and basin, whereas interviews, news reports and field sampling provided supplementary information only for 2000–2004. Basins with presence are listed from north to south

Cited literature: ^aCampos (1985); ^bCampos et al. (1985a); ^cCampos et al. (1985b); ^dCassigoli (1999); ^eSoto et al. (2001a); ^fSoto (2002); ^gSoto et al. (1993); ^hSoto et al. (1997); ⁱWood (1997); ^jJara and Soto (1996); ^kPascual et al. (2002); ^lLindbergh (1982); ^mReyes (1982); ⁿFundación Chile (1990); ^oBasulto (2003); ^pSoto and Jara (1996) or Soto et al. (2001a); ^qCampos et al. (1984); ^rGrosman (1992); ^sPascual et al. (2002); ^tNiklitschek and Aedo (2002); ^uCentro de Ecología Aplicada Ltda. (2001); ^vVila et al. (1999); ^wZama and Cárdenas (1984); ^xBehnke (2002); ^yNiklitschek et al. (2002); ^zCiancio et al. (2005); ^{aa}Salmotec S.A. in Sakai (1989); ^{ab}CADE-IDEPE Ltda. (2004b) (This last study reports presence of the species based on interviews to sport fishing outfitters.); ^{ac}Baigún and Ferriz (2003); ^{ad}Soto et al. (2007)

Sport fishermen personal communications (2003–2006): ¹Francisco Javier Nualart, Temuco; ²Patricio Salas and Claudio Fuentes, Temuco; ³Fermín (Rubén) Buchhorsts, Villarica; ⁴Mario Alarcón, Pucón; ⁵Sergio Maza, Sergio de la Fuente and Leonardo Ortega, Temuco; ⁶Antonio Vasquez and Jorge Meriño, Los Angeles; ⁷Sergio Santana, Entrelagos; ⁸Hernan Fuentealba, San Pablo; ⁹Francisco Castaños, Pto. Varas; ¹⁰Carlos Bretón, Pto. Varas; ¹¹Robert Parker, Llanquihue; ¹²Javier Gebauer, Ranco; ¹³Jorge Espindola, Hornopirén; ¹⁴Alfredo Stanke, Hornopirén; ¹⁵Stephan Weber, Chaiten; ¹⁶Roberto Matamala, Palena; ¹⁷Pablo Schlegel, Palena; ¹⁸Gonzalo Cortés, Santiago; ¹⁹Gustav Basedow, Coyhaique; ²⁰Eduardo Otarola, Coyhaique; ²¹Alfredo Torres, Coyhaique; ²²Claudio Urrejola, Coyhaique; ²³Carlos Benes, Cochrane; ²⁴Alejandro Brautigam, Pto. Guadal; ²⁵Emilio Marquez, Pto. Bertrand; ²⁶Francisco Valenzuela, Santiago

News reports: ⁱEl Diario Austral Osorno: 5 January 2001; ⁱⁱEl Diario Austral La Araucanía: 21 November 2000, 5 and 24 February, and 19 December 2001, 26 December 2003, 28 March 2004; ⁱⁱⁱEl Diario Austral Osorno: 23 and 24 January, 19 March 2001 and 18 March 2002; ^{iv}El Diario Austral Osorno: 13 March 2004; ^vEl Mercurio: 11 May 2004; ^{vi}El Diario Austral Osorno: 9 March 2004; ^{vii}El Diario Austral La Araucanía: 25 March 2004; ^{viii}El Diario Austral Osorno: 20 February 2002; ^{ix}El Diario Austral La Araucanía: 13 March 2004; ^xTeletrece news report (open TV): 2 June 2004 (the video shows only a few decaying Chinook salmon and fresher coho salmon)

Notes: * Type of basin *sensu* Niemeyer and Cereceda (1984). ** Not included in Fig. 1, see text. *** We confirmed this run in March 2007

References

- Adkison M (1995) Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? *Can J Fish Aquat Sci* 52:2762–2777
- Alcaraz C, Vila-Gispert A, Garcia-Berthou E (2005) Profiling invasive fish species: the importance of phylogeny and human use. *Divers Distrib* 11:289–298
- Augerot X (2005) Atlas of Pacific salmon. University of California Press, Berkeley, California
- Anonymous (1979) Operación “salmones en Chiloé”. *Chile Pesquero* 6:12–13
- Anonymous (1989) Coho in Chile: an interview with Jon Lindbergh. *Egg Smolt US Salmon Digest* 2(2):1
- Anonymous (2004) 1 million salmon escape in Chile. In: *The Salmon Farm Monitor*, International News, Available at <http://www.salmonfarmmonitor.org>, Accessed August 2004
- Baigún C, Ferriz R (2003) Distribution patterns of native freshwater fishes in Patagonia (Argentina). *Org Divers Evol* 3:151–159
- Barros R (1931) Introducción de un nuevo salmón en Chile. *Rev Chil Hist Nat* 35:57–62
- Basulto S (2003) El largo viaje de los salmones. Una crónica olvidada. Propagación y cultivo de especies acuáticas en Chile. Maval Ltd, Santiago
- Baxter CV, Fausch KD, Murakami M, et al. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663
- Becker LA, Pascual MA, Basso NG (in press) Colonization of the southern Patagonia Ocean by exotic Chinook salmon. *Conserv Biol*. doi:10.1111/j.1523-1739.2007.00761.x
- Behnke RJ (2002) Trout and salmon of North America. The Free Press, New York
- Bilby RE, Fransen BR, Bisson PA (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: Evidence from stable isotopes. *Can J Fish Aquat Sci* 53:164–173
- Bilby RE, Fransen BR, Bisson PA, et al. (1998) Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to addition of salmon carcasses to two streams in southwestern Washington, USA. *Can J Fish Aquat Sci* 55:1909
- Bosch J, Rincón PA, Boyero LUZ et al (2006) Effects of introduced salmonids on a montane population of Iberian frogs. *Conserv Biol* 20:180
- Bravo A (2005) Fauna esperada de parásitos metazoos y análisis cuantitativo de helmintos de salmón Chinook (*Oncorhynchus tshawytscha*) recientemente asilvestrado en el sur de Chile. Tesis para obtener el título de Médico Veterinario. Universidad de las Américas
- CADE-IDEPE Ltda. (2004a) Diagnóstico y clasificación de los cursos y cuerpos de agua según objetivos de calidad; cuenca del Río Bueno. In: Dirección General de Aguas (ed). Ministerio de Obras Públicas. Gobierno de Chile, Santiago, p 141
- CADE-IDEPE Ltda. (2004b) Diagnóstico y clasificación de los cursos y cuerpos de agua según objetivos de calidad; cuenca del Río Serrano. In: Dirección General de Aguas (ed) Ministerio de Obras Públicas. Gobierno de Chile, Santiago, p 89
- Campos H (1985) Distribution of the fishes in the Andean rivers in the south of Chile. *Arch Hydrobiol* 104:169–191
- Campos H, Arenas J, Jara C et al (1984) Macrozoobentos y fauna íctica de las aguas limnéticas de Chiloé y Aysén continentales (Chile). *Medio Ambiente* 7:52–64
- Campos H, Arenas J, Steffen W et al (1985a) Investigación de la capacidad de cultivo de salmonídeos de las principales hoyas hidrográficas de país; II antecedentes limnológicos hoyo lago Villarrica. In: Corporación de Fomento de la Producción—Instituto de Fomento Pesquero—Universidad Austral de Chile
- Campos H, Arenas J, Steffen W et al (1985b) Investigación de la capacidad de cultivo de salmonídeos de las principales hoyas hidrográficas del país; III antecedentes limnológicos hoyo lago Rupanco. In: Corporación de Fomento de la Producción—Instituto de Fomento Pesquero—Universidad Austral de Chile, p 405
- Casal CMV (2006) Global documentation of fish introductions: the growing crisis and recommendations for action. *Biol Inv* 18:3–11
- Cassigoli J (1999) Catastro de enfermedades de peces nativos circundantes a centros de cultivo de salmónidos. In: Fondo de Investigación Pesquera—Instituto Tecnológico del Salmón—Universidad Austral de Chile—Aquatic Health
- Castilla JC, Uribe M, Bahamonde N et al (2005) Down under the southeastern Pacific: marine non-indigenous species in Chile. *Biol Inv* 7:213–232
- Centro de Ecología Aplicada Ltda. (2001) Estudio de Impacto Ambiental (EIA) proyecto ALUMYSA. Anexo IV.A_1 Caracterización del hábitat acuático del Río Cuervo, Puerto Aysén. In: Comisión Nacional del Medio Ambiente
- Ciancio JE, Pascual MA, Lancelotti J et al (2005) Natural colonization and establishment of a ChS, *Oncorhynchus tshawytscha*, population in the Santa Cruz River, an Atlantic basin of Patagonia. *Environ Biol Fishes* 74:219–227
- Copp G, Bianco PG, Bogutskaya NG et al (2005) To be, or not to be, a non-native fish? *J Appl Ichthyol* 21:242–262
- Crawford SS (2001) Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects, vol 132. Canadian Special Publication of Fisheries and Aquatic Science, Ottawa
- Davidson F, Hutchinson S (1938) The geographic distribution and environmental limitations of the Pacific salmon (genus *Oncorhynchus*). *Bull US Bur Fish* 48:667–692
- De Buen F (1959) Los peces exóticos en las aguas dulces de Chile. *Invest Zool Chilenas* 5:103–137
- Deans N, Unwin M, Rodway M (2004) Sport fishery management. In: Harding J, Mosley P, Pearson C, Sorrell B (eds) *Freshwaters of New Zealand*. New Zealand Hydrological Society and New Zealand Limnological Society, Wellington, pp 41.1–41.16
- Dextrase A, Mandrak N (2006) Impacts of alien invasive species on freshwater fauna at risk in Canada. *Biol Inv* 8:13–24
- Di Luzio M, Srinivasan R, Arnold JG (2000) AVSWAT: an ArcView extension as tool for the watershed control of point and nonpoint sources. In: 20th ESRI International User Conference, San Diego, California

- Donaldson LR, Joyner T (1983) The salmonid fishes as a natural livestock. *Sci Am* 249:50–58
- Elton CS (2000) The ecology of invasions by animals and plants. University of Chicago Press
- Facon B, Genton BJ, Shykoff J et al (2006) A general evolutionary framework for understanding bioinvasions. *Trends Ecol Evol* 21:130–135
- Falk-Petersen J, Bøhn T, Sandlund O (2006) On the numerous concepts in invasion biology. *Biol Inv* 8:1409–1424
- FAO Fishery Information (2006) Aquaculture production: quantities 1950–2004. FISHSTAT Plus—Universal software for fishery statistical time series [online or CD-ROM]. In: Data and Statistics Unit. Food and Agriculture Organization of the United Nations. Available at: <http://www.fao.org/fi/statist/FISOFT/FISHPLUS.asp> Accessed October 2006
- Fundación Chile (1990) El libro del salmón. Ed. Fundación Chile, Santiago
- Gaiero D, Probst, et al. (2002) Riverine transfer of heavy metals from Patagonia to the southwestern Atlantic Ocean. *Reg Env Change* 3:51–64
- Gajardo G, Laikre L (2003) Chilean aquaculture boom is based on exotic salmon resources: a conservation paradox. *Conserv Biol* 17:1173–1174
- Golusda P (1927) Aclimatación y cultivo de especies salmónidas en Chile. *Bol Soc Biol Concepción* 1(1 y 2):80–100
- Grosman F (1992) Algunos aspectos de la biología del salmón del pacífico (*Oncorhynchus tshawytscha*) presente en la Provincia del Chubut (Informe técnico No 8). In: del Valle A, Núñez P, Nagasawa A, Sakai M (eds). CEAN-JICA, Buenos Aires, p 12
- Gross MR (1998) One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Can J Fish Aquat Sci* 55:131–144
- Halpin PM, Strub PT, Peterson WT, et al. (2004) An overview of interactions among oceanography, marine ecosystems, climatic and human disruptions along the eastern margins of the Pacific Ocean. *Rev Chil Hist Nat* 77:371–409
- Healey MC (1991) Life history of ChS (*Oncorhynchus tshawytscha*). In: Groot C, Margolis L (eds) Pacific salmon life histories. UBC Press, Vancouver, BC, pp 311–396
- Hendry AP, Stearns SC (2004) Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford UK
- Hendry AP, Wenburg JK, Bentzen P et al (2000) Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–518
- James GD, Unwin MJ (1996) Diet of ChS (*Oncorhynchus tshawytscha*) in Canterbury coastal waters, New Zealand. *N Z J Mar Freshw Res* 30:69–78
- Jara F, Soto D (1996) Recaptura de salmónes retornantes en el Río Petrohué. In: Universidad Austral de Chile, Laboratorio de Ecología Acuática, Puerto Montt, p 19
- Joyner T (1980) Salmon ranching in South America. In: Thorpe JF (ed) Salmon ranching. Academic Press Inc, London
- Kinnison M, Unwin M, Boustead N et al (1998) Population-specific variation in body dimensions of adult ChS (*Oncorhynchus tshawytscha*) from New Zealand and their source population, 90 years after introduction. *Can J Fish Aquat Sci* 55:554–563
- Kinnison MT, Bentzen P, Unwin MJ et al (2002) Reconstructing recent divergence: evaluating nonequilibrium population structure in New Zealand ChS. *Mol Ecol* 11:739–754
- Kinnison MT, Unwin MJ, Quinn TP (2003) Migratory costs and contemporary evolution of reproductive allocation in male ChS. *J Evol Biol* 16:1257–1269
- Lindbergh JM (1982) A successful transplant of Pacific salmon to Chile. *Proc Gulf Caribb Fish Inst* 34:81–87
- Mack RN, Simberloff D, Lonsdale WM et al (2000) Biotic Invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Mann G (1954) Vida de los peces en aguas chilenas, 2nd edn. Ministerio de Agricultura. Universidad de Chile, Santiago, p 342
- Marchetti MP, Light T, Moyle PB et al (2004) Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecol Appl* 14:1507–1525
- McDowall (2001) Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? *Fish Fisher* 2:78–85
- McDowall R (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 (1978) New Zealand freshwater fishes. Heinemann Educational Books Ltda, Auckland
- McDowall RM (1994) The origins of New Zealand's ChS, *Oncorhynchus tshawytscha*. *Mar Fish Rev* 56:1–7
- Moyle PB, Light T (1996) Biological invasions of freshwater: empirical rules and assembly theory. *Biol Conserv* 78:149–161
- Munita C (1988) Acuicultura, breve itinerario histórico. *Chile Pesquero* 50:39–42
- Muratov IV, Posokhov PS (1989) Epidemiologic characteristics of diphyllobothriasis in the lower Amur River valley. *Med Parazitol (Mosk)* 4:53–57
- Naylor RL, Goldberg RJ, Mooney H et al (1998) Nature's subsidies to shrimp and salmon farming. *Science* 282:883–884
- Naylor RL, Williams SL, Strong DR (2001) Aquaculture—a gateway for exotic species. *Science* 294:1655–1656
- Niemeyer H, Cereceda P (1984) Geografía de Chile—Hidrografía. In: Instituto Geográfico Militar (ed) Colección Geografía de Chile, vol VIII, Santiago, p 320
- Niklitschek E, Aedo E (2002) Estudio del ciclo reproductivo de las principales especies objetivo de la pesca deportiva en la XI región. In: Fondo de Investigación Pesquera—Universidad Austral de Chile, p 75
- Niklitschek E, Niklitschek M, Aedo E (2002) Manejo y administración para la sustentabilidad y el mejoramiento cuantitativo y cualitativo de la pesca deportiva en ríos de gran atractivo turístico en la región de Aysén. In: Fondo de Desarrollo e Innovación (FDI)—Universidad Austral de Chile, Coyhaique
- O'Toole S, Metcalfe C, Craine I et al (2006) Release of persistent organic contaminants from carcasses of Lake Ontario ChS (*Oncorhynchus tshawytscha*). *Environ Pollut* 140:102–113

- Olson D, Dinerstein E, Canevari P et al (1998) Freshwater biodiversity of Latin America and the Caribbean: a conservation assessment. Biodiversity Support Program, Washington, DC, p 61
- Ortubay S, Cussac V, Battini M et al (2006) Is the decline of birds and amphibians in a steppe lake of northern Patagonia a consequence of limnological changes following fish introduction? *Aqua Conserv: Mar Freshw Ecosyst* 16:93–105
- Pascual M, Bentzen P, Rossi CR et al (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, Urbansky J et al (2002) Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. *Biol Inv* 4:101–113
- Pascual MA, Orensanz JM, Parma AM et al (1998) The Patagonian challenge: melding conservation with development. In: Fiedler PL, Kareiva PM (eds) *Conserv Biol for the coming decade*, 2nd edn. Chapman & Hall, New York, pp 410–425
- Quinn T, Kinnison M, Unwin M (2001) Evolution of ChS (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112–113:493–513
- Quinn T, Unwin M, Kinnison M (2000) Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced ChS populations. *Evolution* 54:1372–1385
- Quinn TP (1993) A review of homing and straying of wild and hatchery-produced salmon. *Fish Res* 18:29–44
- Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. American Fisheries Society in association with University of Washington Press
- Quinn TP, Fresh K (1984) Homing and straying in ChS (*Oncorhynchus tshawytscha*) from Cowlitz River hatchery, Washington. *Can J Fish Aquat Sci* 41:1078–1082
- Quinn TP, Nemeth RS, McIsaac DO (1991) Homing and straying patterns of fall ChS in the lower Columbia River. *Trans Am Fish Soc* 120:150–156
- Reyes X (1982) Presencia de *Hepatoxylon trichiuri* (Holten, 1802) (Cestoda: Trypanorhyncha) en *Oncorhynchus tshawytscha* y *Somniosus pacificus* capturados en Chile. *Invest Marín Valparaíso* 10(1–2):40–45
- Richardson DM, Pysek P, Rejmánek M (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6:93–107
- Rodríguez JP (2001) Exotic species introductions into South America: an underestimated threat? *Biodivers Conserv* 10:1983–1996
- Roni P, Quinn TP (1995) Geographic variation in size and age of North American ChS. *N Am J Fish Manag* 15:325–345
- Sakai M (1989) Final report of aquaculture project in Chile. In: Japan International Cooperation Agency (JICA), p 138
- Soto D (2002) Estudio del ciclo reproductivo de las principales especies objetivo de la pesca deportiva en la X región. In: Fondo de Investigación Pesquera—Universidad Austral de Chile, p 153
- Soto D, Arismendi I, Jara F et al (2001b) Evaluación, ordenamiento y manejo del potencial biológico para la pesca deportiva de la región de los lagos. In: Fondo Nacional de Desarrollo Regional, Región de los Lagos—Universidad Austral de Chile, p 320
- Soto D, Arismendi I, González J et al (2006) Southern Chile, trout and salmon country: invasion patterns and threats for native species. *Rev Chil Hist Nat* 79:97–117
- Soto, Arismendi I, Prinzió CD, et al. (2007) Establishment of ChS (*Oncorhynchus tshawytscha*) in Pacific basins of Southern South America and its potential ecosystem implications. *Rev Chil Hist Nat* 80:81–98
- Soto D, Campos H (1995) Los lagos oligotróficos asociados al bosque templado húmedo del sur de Chile. In: Armesto J, Khalin M, Villagrán C (eds) *Ecología del bosque Chileno* Ed. Universitaria, Santiago
- Soto D, Campos H, Steffen W et al (1993) Estudio del potencial impacto ambiental de las actividades productivas y de servicio sobre el Lago Llanquihue. In: Fondo Nacional de Desarrollo Regional, Región de los Lagos—Universidad Austral de Chile, p 143
- Soto D, Jara F (1996) Evaluación de salmonídeos de vida libre en aguas interiores de las regiones X y XI. In: Fondo de Investigación Pesquera—Universidad Austral de Chile, p 159
- Soto D, Jara F, Moreno C (2001a) Escaped salmon in the inner seas, southern Chile: facing ecological and social conflicts. *Ecol Appl* 11(6):1750–1762
- Soto D, Palma R, Arismendi I (1997) Investigación para el manejo sustentable de la biomasa íctica de salmonídeos en el Lago Llanquihue. In: Fondo Nacional de Desarrollo Regional, Región de los Lagos—Universidad Austral de Chile, Pto. Montt
- Stohlgren TJ, Barnett D, Flather C, et al. (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol Inv* 8:427–447
- Teletrece (2004) Magallanes: El regreso de salmones silvestres. In: Teletrece (open TV news show) Broadcasted 2 Jun 2004, Santiago
- Torchin ME, Lafferty KD, Dobson AP et al (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- Townsend CR (2003) Individual, population, community and ecosystem consequences of a fish invader in New Zealand streams. *Conserv Biol* 17(1):38–47
- United Nations (2006) Transfer of technology for successful integration into the global economy; A case study of the salmon industry in Chile. In: United Nations conference on trade and development. United Nations, New York and Geneva
- Unwin MJ (2006) Assessment of significant salmon spawning sites in the Canterbury region. In: NIWA Client Report CHC2006-097. Unpublished report prepared for Environment Canterbury, Christchurch, New Zealand, p 33
- Unwin MJ, Kinnison MT, Quinn TP (1999) Exceptions to semelparity: postmaturation survival, morphology, and energetics of male ChS (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci* 56:1172–1181
- Unwin MJ, Quinn TP (1993) Homing and straying patterns of ChS (*Oncorhynchus tshawytscha*) from a New Zealand hatchery: spatial distribution of strays and effects of release date. *Can J Fish Aquat Sci* 50:1168–1175
- Unwin MJ, Quinn TP, Kinnison MT et al (2000) Divergence in juvenile growth and life history in two recently colonized

- and partially isolated ChS populations. *J Fish Biol* 57:943–960
- Vila-Gispert A, Alcaraz C, García-Berthou E (2005) Life-history traits of invasive fish in small Mediterranean streams. *Biol Inv* 7:107–116
- Vila I, Fuentes L, Saavedra M (1999) Ictiofauna en los sistemas límnicos de la isla grande, Tierra del Fuego, Chile. *Rev Chil Hist Nat* 72:273–284
- Vila I, Zeiss E, Gibson H (1978) Prospecciones de sistemas hidrográficos para la introducción del “salmón” en Chile. *Biología Pesquera* 10:61–73
- Void-filled seamless SRTM data V1 (2004) International Centre for Tropical Agriculture (CIAT). Available from the CGIAR-CSI SRTM 90 m Database: <http://srtm.csi.cgiar.org> and <http://www.ambiotek.com/topoview> Accessed 20 April 2006
- Volpe JP, Taylor EB, Rimmer DW et al (2000) Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. *Conserv Biol* 14:899–903
- Waples R, Teel D, Myers J et al (2004) Life-history divergence in ChS: historic contingency and parallel evolution. *Evolution* 58:386–403
- Welcomme RL (1988) International introductions of inland aquatic species. In: *FAO Fisheries Technical Paper*, p 318
- Wilkinson CE, Hocking MD, Reimchen TE (2005) Uptake of salmon-derived nitrogen by mosses and liverworts in coastal British Columbia. *Oikos* 108:85–98
- Wood J (1997) The distribution of feral salmonids in inland Chilean waters. Dissertation to obtain the degree of M.Sc. in Aquaculture. Institute of Aquaculture, University of Stirling
- Zama A, Cárdenas E (1984) Introduction into Aysén Chile of the pacific salmon. N°9 Descriptive catalogue of marine and freshwater fishes from the Aysén region, southern Chile, with zoogeographical notes on fish fauna. In: *Servicio Nacional de Pesca—Japanese International Cooperation Agency*, p 82
- Zhang Y, Negishi JN, Richardson JS et al (2003) Impacts of marine-derived nutrients on stream ecosystem functioning. *Proc R Soc Lond B* 270:2117–2123