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Natural colonization and establishment of a chinook salmon, *Oncorhynchus tshawytscha*, population in the Santa Cruz River, an Atlantic basin of Patagonia

Javier E. Ciancio[a], Miguel A. Pascual[a,b], Julio Lancelotti[a], Carla M. Riva Rossi[a] & Florencia Botto[c]
[a]*Centro Nacional Patagónico, CONICET, Blvd. Brown S/N, 9120, Puerto Madryn, Chubut, Argentina (e-mail: uncianci@cenpat.edu.ar)*
[b]*UNPA-UACO, Santa Cruz, and UNPSJB, Puerto Madryn, Argentina*
[c]*UNMdP and CONICET, Mar del Plata, Argentina*

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Synopsis

We report the finding of an established population of exotic Chinook salmon spawning in headwaters of the Santa Cruz River system (Argentina), the first for this species in an Atlantic basin of South America. Spawning takes place in the Caterina River, a small tributary of Lake Argentino, located 488.5 km from the ocean. Anadromy was verified by correspondence of N and C stable isotope ratios with those of fish captured by bottom-trawlers in the ocean and those of anadromous rainbow trout from the same river basin. The scale patterns of most fish examined were consistent with a stream-type life cycle (i.e., seaward migration by juveniles after a full year in fresh water). Two potential origins were identified for this population: in situ introductions of fish imported directly from the USA in the early 20th century or fish from two ranching experiments conducted in southern Chile during the 1980s. In the latter case, colonization would have proceeded through the Strait of Magellan, helped by prevailing eastward currents.

Introduction

To promote commercial and recreational fishing exotic salmonines have been widely propagated and transplanted throughout the world, including Patagonia, the southernmost region of South America, during the last century. For instance, nine species were intentionally imported into Argentina (Pascual et al. 2002), including typically anadromous species (chinook, *Oncorhynchus tshawytscha*, coho, *O. kisutch*, sockeye, *O. nerka*, and Atlantic salmon, *Salmo salar*), facultative anadromous species (rainbow, *O. mykiss*, brown, *S. trutta*, and brook charr, *Salvelinus fontinalis*) and strictly freshwater residents (lake charr, *Salvelinus namaycush*, and lake whitefish, *Coregonus clupeaformis*). While resident ecotypes were very successful at establishing wild self-sustaining populations throughout the region, anadromy is less frequent (Pascual et al. 2002). This pattern is also observed at a global scale (Pascual & Ciancio 2005); for instance, while the success of resident species and varieties in establishing wild populations has been well documented (MacCrimmon 1969, 1971), the only known established anadromous populations in the Southern Hemisphere until a few years ago were those of chinook salmon in eastern rivers of New Zealand (Unwin & James 1998) and brown trout, Atlantic and coho salmon in the Kerguelen Islands (Davaine & Beall 1982, 1997).

In recent years, a number of discoveries have been made of anadromous populations in South America, both in Atlantic and Pacific river basins. In the Pacific, the establishment of anadromous populations has been driven by chilean ocean ranching experiments and net-pen aquaculture; salmon production grew dramatically from 53 metric tonnes (t) harvested in 1981 to 482392 t in 2002 (FAO 2002). As salmon production has increased, so has fish escaping from net pens and straying into Pacific river basins. Spawning populations of chinook salmon have been found in Chile (Soto et al. 2001) and in headwaters of Pacific rivers in Argentina (Grosman 1991, Soto et al. 2001). A growing number of sport fishing destinations in Chile targeting various species of anadromous salmonids[1] suggests that many additional established populations are likely to be formally recognized as rivers are systematically surveyed for spawning fish.

In Atlantic river basins of Patagonia, anadromous salmonids are found in southern locations as alternative ecotypes of populations established early in the 20th century. Rainbow trout populations with a dual anadromous – nonanadromous life history inhabit the Santa Cruz River (Pascual et al. 2001, Riva Rossi et al. 2004) and sea-run brown trout are found in the Gallegos (Southern Santa Cruz Province), Grande and Ewan (Tierra del Fuego) rivers, as well as in rivers of the Malvinas Islands (McDowall et al. 2001).

In this paper we report the discovery of a spawning population of chinook salmon in headwaters of the Santa Cruz River, an Atlantic basin of southern Patagonia. The fish were found in the Caterina River, a small tributary of Lake Argentino (Figure 1). We explore historical records on fish transplants and ranching experiments in the region in search of the origin of this population. We determine general life history traits by scale pattern analysis and we used C and N stable isotopes as evidence for anadromy in this population by comparison with fish captured by commercial trawlers in the ocean. We briefly discuss the implications of this discovery in the context of anadromous salmon ecology.

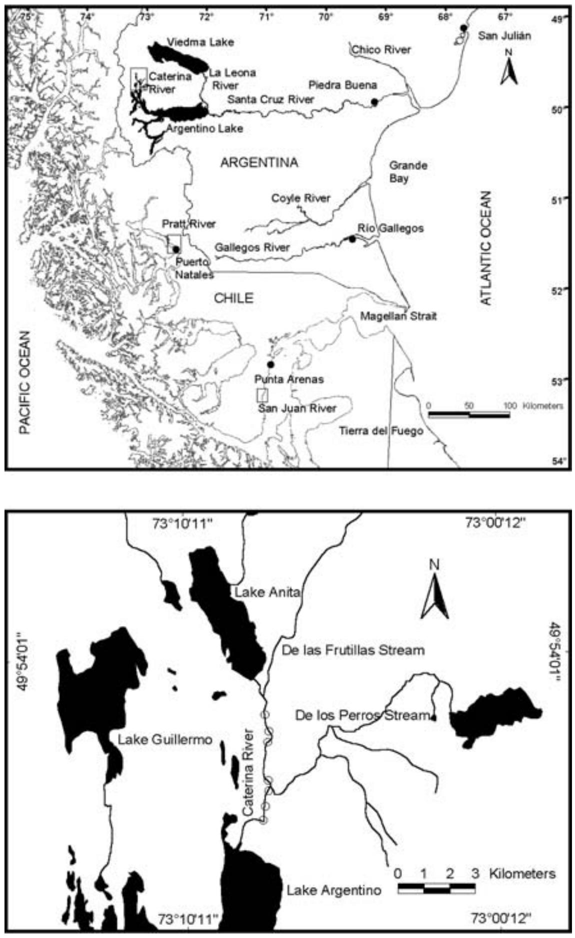

Figure 1. Southern South America, indicating places where chinook were introduced and adjacent marine areas (upper panel) and detail of Caterina River (lower panel); circles indicate main spawning areas.

Materials and methods

The Caterina River is located within Estancia Cristina in Los Glaciares National Park, a lodge accessible only by boat.[2] We conducted the fieldwork in April 2003 and March to April 2004. In 2004, we walked with a GPS between its head at the outlet of Lake Anita and the outflow in Lake Argentino (Figure 1), recording altitude, gradient, and substrate type in different river sections. We detected spawning beds, recorded their locations and approximate surface, and counted both redds and spawners. In 2003 we recorded water temperature, flow, water speed (Global Flow Probe FP 101), and gravel size on spawning beds.

[1] www.theeveninghatch.com/chile

[2] www.upsalaexplorer.com.ar

We obtained samples of 24 fish in 2003 and 33 fish in 2004 from different sections of the river. In total, we caught 20 fish using gillnets (120 and 180 mm net size) and collected 37 dead. We measured (fork and standard length), weighed and sexed the fish, took tissue samples (dorsal muscle) for stable isotopes analysis, and scales and otoliths for ecotype and age determination.

We removed scales from both sides of the fish, from an area located below the anterior margin of the dorsal fin, approximately five scale rows above the lateral line. We cleaned three scales of each of the 24 fish collected in 2003, made impressions on acetate cards and inspected them on a microfiche reader. We used the abrupt change from narrowly spaced circuli near the scale focus or center to wider spaced circuli formed during growth in the ocean to separate the freshwater nucleus from marine growth zones. We classified individual fish as ''stream'' or ''ocean'' type (Healey 1991) based on criteria for the pattern of circuli in the freshwater nucleus developed by Koo & Isarankura (1967) for North American chinook salmon and applied by Unwin & Lucas (1993) to the species in New Zealand. We considered a freshwater growth zone with few and relatively wide circuli that did not contain a slow-growth check as an ocean-type freshwater nucleus, and an area of many circuli including a distinct narrow band of more closely spaced circuli near the outer border as a stream type freshwater nucleus.

As a supplementary criterion to make the ocean/stream distinction, we counted circuli within the freshwater growth zone on the screen of a microfiche reader. We measured the radius of the freshwater nucleus along the anterior–posterior axis of the scale on digital pictures processed with the aid of a shareware image analysis software (imageJ, National Institute of Health),[3] and a custom-made MS Excel macro. We also identified ocean annuli and counted on the microfiche reader, but since significant resorption was apparent we used this data only as an estimate of minimum ocean age.

Anadromous salmon are typically enriched with ^{15}N and ^{13}C relative to the other sources of N and C in watersheds (Rubenstein & Hobson 2004), providing a method to reveal ocean migrations in individuals sampled in freshwater. We conducted C and N stable isotope analysis on 9 fish collected in the Caterina stream in 2003 (4 males and 5 females) and compared them with 5 fish caught in the ocean (Grande Bay, Figure 1) by commercial bottom trawlers during 2002 – 2003 (3 males and 2 females). We also analyzed 13 Santa Cruz River anadromous rainbow trout (13 fish collected between 2001 and 2002) as additional reference values of ^{15}N and ^{13}C for anadromous fish. Dorsal muscle was removed from all fish and tissues were stored frozen for transport to the lab, where all samples were dried at 60 °C for 48 h, ground to a fine powder, and sent for analysis of carbon and nitrogen content and stable isotope signatures (Stable Isotope Facility, University of California, Davis). The stable isotopes ratios are expressed as δ values as ‰: $\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1]\times 1000$ where X is ^{13}C or ^{15}N and R the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. Standards used were Vienna Pee Dee belemnite for C and N_2 for N.

We did a literature review in search of chinook salmon introductions in southern Argentina and Chile and interviewed workers and old settlers of Estancia Cristina in an attempt to establish when chinook salmon were first sighted at the Caterina Stream.

Results

Spawning beds in the Caterina Stream

The Caterina River (49.93 °S 73.12 °W) flows for 7.72 km between glacier-fed Lake Anita (666 m elevation) and Lake Argentino (580 m elevation; Figure 1). It has two small tributaries, ''de las Frutillas'' and ''de los Perros'', both high gradient streams. The average gradient of the Caterina River is 11.13 m km^{-1}, with a 2 km fast flowing upper section and a 6 km lower section with moderate flow and smaller gravel sizes (10 – 100 mm diameter). During 2003 and 2004 we identified 14 distinct spawning beds (average area = 557.14 m^2; range 50 – 2000) in the upper 5 km section of the lower section (Figure 1), as well as some isolated redds. In 2004, we counted 134 fish during a single whole river census. Mean water temperature in April 2003 was 7.8 °C and in March 2004 was 9.23°C. Mean water velocity in

[3] http://rsb.info.nih.gov/ij

2003 (measured at 0.5 m intervals on a transect across the river and over spawning beds) was 0.92 m s^{-1} (min. 0.04; max. 1.57). Mean discharge was estimated at 7.7 m^3 s^{-1}.

Stable isotope analysis

Adult chinook caught in the Caterina River had stable-isotope ratios indicative of marine feeding (Figure 2). The $\delta\ ^{13}C$ (−19.34 – 17.44‰) and $\delta\ ^{15}N$ (17.07 – 18.85‰) signatures of fish in the stream did not differ from those of fish captured at sea (^{13}C: −19.19 – 17.23‰; ^{15}N: 16.8 – 18.15‰; *t*-test ^{13}C p = 0.34 ^{15}N p = 0.33). These values are comparable to those of salmon feeding in the North Pacific and North Atlantic Ocean (Welch & Parson 1993, Doucett et al. 1999a, b, Satterfield & Finney 2002, Kaeriyama et al. 2004) and to those of sea birds feeding on the Argentinean Continental Shelf (Forero et al. 2002, 2004). The chinook salmon isotopic signatures were even more enriched than those corresponding to anadromous rainbow trout from main stem Santa Cruz River (^{13}C: −20.21 – 18.12‰; ^{15}N: 14.41 – 16.08‰; *t*-test ^{13}C p = 0.0005 ^{15}N 5,07695 E-10), providing additional evidence for an anadromous life history in Caterina chinook salmon.

Because the Santa Cruz is an unproductive river (Miserendino 2001), practically untouched by human activities, we consider natural or anthropogenic enrichment of freshwater (Lake et al. 2001) unlikely as an alternative hypotheses to anadromy for explaining the enriched isotope values observed in fish.

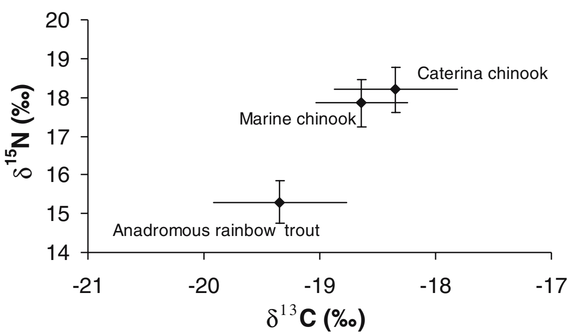

Figure 2. Stable nitrogen and carbon isotope values (mean ± SE) for Caterina chinook, chinook captured in the ocean, and anadromous rainbow trout from Santa Cruz River.

Life cycle and stream residency patterns

We did not sample the population throughout the whole spawning season, but several accounts by estancia managers and workers, as well as by sport fishermen, indicated that the fish arrive to the Caterina River by mid-February (late summer in the Southern Hemisphere) and abundance peaks during mid-March. The mean fork length of fish in our samples was 827 mm (660 – 1040) in 2003 and 712 mm (470 – 990) in 2004. The mean weight of fish caught alive was 5.44 kg (3.9 – 10.5) in 2003 and 3.26 kg (1 – 10.4) in 2004. A large majority of the fish analyzed (22 out of 24) had a stream type freshwater nucleus (Table 1). Mean number of freshwater circuli was 9.5 (9 – 11, SD = 0.2) for ocean type fish and 16.1 (13 – 21, SD = 2.4) for stream type fish (Figure 3); similar values were reported by Unwin & Lucas (1993) for introduced chinook in the Rakaia River, New Zealand (ocean: = 9.4, SD = 1.8; stream: = 16.8, SD = 3.2). Mean freshwater radius was 216.2 μm (201 – 230; SD = 20) for ocean type fish and 393.4 μm (289 – 551, SD = 65) for stream type fish, smaller than those reported for Rakaia River chinook (ocean: = 316 μm, SD = 61; stream: = 421 μm, SD = 81).

The most frequent ocean age was 3 (Table 1), comparable to typical stream type chinook in Southeast Alaska and British Columbia (Roni & Quinn 1995), but older than chinook in New Zealand rivers. The timing of river entrance from the ocean is unknown, since we obtained only one

Table 1. Age and sex frequencies of chinook captured in the Caterina River during the 2003 sampling season.

	Ocean age		
	2	3	4
Females River age			
0		2 (14.2)	
1	3 (21.4)	4 (28.5)	5 (35.7)
Males River age			
0			
1	2 (27.2)	6 (54.5)	2 (18.2)
Total *n*%	5 (20.8)	12 (50)	7 (29.2)

Occurrences are classified according to ocean age, river age (0: ocean, 1: stream), and sex. Number of fish, as well as percentage for each ocean age/river age combination within sexes (in parentheses), are provided.

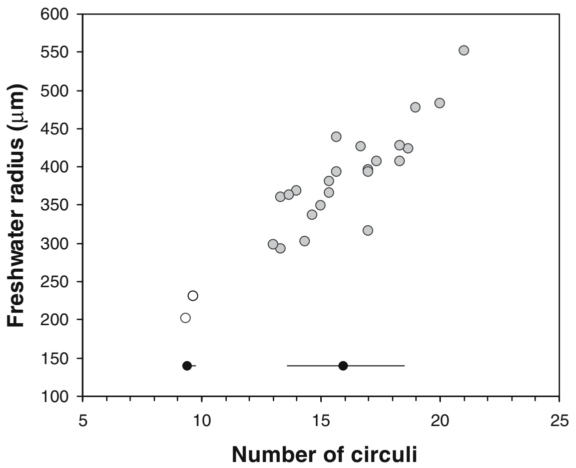

Figure 3. Scales radius versus number of circuli. Grey circles correspond to fish classified as stream type and open circles to fish classified as ocean type. Black circles and lines along the *X*-axis indicate mean number of circuli and standard deviation for each type.

verified record of a Chinook captured in the Santa Cruz River close to the estuary (March 2000). The lack of chinook catches associated to a sport fishery that targets Santa Cruz river steelhead during the summer and fall (January to May; Pascual et al. 2001) hints at an earlier river entry in the spring.

Chinook salmon introductions in southern Patagonia

We were able to find records of nine introduction events involving chinook salmon in South America. Of those, we consider that only the six that took place in Atlantic rivers of Argentinean Patagonia or areas of southern Chile were most likely to have contributed to found the Caterina population (Table 2). We think that ranching and net pen aquaculture enterprises taking place in Chile north of 45–50 °S, an area dominated by the north-bound Humboldt Current (Strub et al. 1998), were less likely to have contributed to the Caterina River population than locations south of 45–50 °S, which are more strongly affected by the Atlantic-bound Cape Horn Current (Fernandez et al. 2000).

The Santa Cruz River was the target of some of the first salmonids importations into Argentina. These first consignments, which resulted in the present-day populations of rainbow trout in this river (Riva Rossi et al. 2004), also contained chinook salmon eggs (Table 2). Between 1906 and 1910, four shipments – a total of 1,000,000 chinook ova – arrived from the USA to a hatchery located at the Santa Cruz River, and were planted primarily in the main Santa Cruz River, and also in the Gallegos and Chico Rivers (Figure 1; Tulian 1908, Marini & Mastrarrigo 1963). At that time, most of the eggs exported by the United States were obtained from the stations situated on the Sacramento River system (Clark 1929) the major distribution center for salmon eggs that operated since 1872 (Leitritz 1970). For example, Battle Creek in the Sacramento River has been identified as the source of New Zealand chinook salmon populations (Quinn 1996).

Two ranching experiments in southern Chile in the 1980s could also have contributed fish to the Santa Cruz River basin (Table 2). The first one was conducted in 1982 in the Santa María River, a

Table 2. Introduction events of chinook salmon in Southern Argentina and adjacent areas.

Year	Number	Origin/stock	Destination	Reference
1906	300,000 eggs	Sacramento, CA (?)	Santa Cruz and Gallegos rivers	Tulian (1908)
1908	300,000 eggs	Sacramento, CA (?)	Santa Cruz and Chico rivers, Lake Argentino	Marini & Mastrarrigo (1963)
1909	200,000 eggs	Sacramento, CA (?)	Santa Cruz and Chico rivers	Marini & Mastrarrigo (1963)
1910	200,000 eggs	Sacramento, CA (?)	Rivers of Santa Cruz Province	Marini & Mastrarrigo (1963)
1982	200,000 smolts	Green River, Puget Sound, WA	Santa María River, Strait of Magellan, Chile	Donaldson & Joyner (1984)
1983–1989	670,000 smolts	Green River, Puget Sound, WA (?)	Pratt River, Pto. Natales, Chile	Basulto (2003)

(?) Indicates probable, but unconfirmed origin.

tributary of the San Juan River (Figure 1), which flows into the Strait of Magellan in southern Chile (Donaldson & Joyner 1984). A total of 200,000 chinook smolts were stocked in this river, but no returns were registered. The fish had been imported from the University of Washington Hatchery (Seattle, WA), based on Green River fish (Puget Sound, WA). The Green River stock had been originally founded with fish from the Kalama River in the Columbia River Basin (Donaldson & Joyner 1984). The second ranching experiment in Chile occurred more recently (Table 2), in the Pratt River, 300 km north from the Santa María. A total of 670,000 smolts were planted over a period of 6 years (1983 – 1989) and returns have been important (Basulto 2003).

We interviewed 10 individuals who lived and worked at the Estancia Cristina at different times to find out whether or not Caterina chinook salmon were already there before 1980 and got ambiguous responses. The earliest report of "big fish" in the Caterina we obtained was in 1973, what would lead us to discard the two ranching experiments in Southern Chile as an origin of chinook populations. All other people, however, reported first sightings between 1979 and 1984, lending some credence to a modern origin for these populations.

Discussion

Caterina chinook salmon constitute the first known spawning population of the species in an Atlantic River basin. The population appears to be relatively modest in size (in the order of hundreds) and visual surveys in three neighboring streams did not yield any other chinook salmon. However, at this time we cannot discount the possible occurrence of spawning in other locations of the Santa Cruz River basin. There are still unexplored streams in the basin, and large rivers (Santa Cruz main stem and La Leona River, Figure 1) are difficult to survey visually because of the low visibility produced by glacial sediments.

The predominance of stream type fish and an apparently early run timing are consistent with the extensive migration that separates the Caterina River and the ocean – about 500 km – and with characteristics of this river that have been associated to lower growth opportunities and stream-type life history in their native range (Taylor 1990): low water temperature and productivity (Miserendino 2001). The divergence between ecotypes has been demonstrated to include a significant environmental component (Unwin et al. 2000) and the predominance of stream-type fish in the Caterina could well be in large part a phenotypic response to local conditions. In fact, chinook salmon displays a broad array of life history tactics, including variation in age at seaward migration, length of freshwater, estuarine and ocean residence, variation in ocean distribution, migration patterns, and age and season of spawning migration (Healey 1991). The aforementioned phenotypic plasticity underlying some of this variation (Healey 1991, Unwin et al. 2000), together with the prospects for rapid evolution in this species (Quinn et al. 2001), could have facilitated the adaptation of chinook life cycle to local conditions. The same characteristics could make chinook intrinsically more invasive than other anadromous salmonids. In particular, the phenotypic variation in timing of critical events throughout the life cycle (i.e., freshwater and ocean residence, ocean-bound migration, river entrance) might be particularly important in facilitating the adaptation to new conditions in invading species. The higher success of chinook as compared to other species provides some support to this observation. In the Southern Hemisphere, for instance, chinook salmon are found in several rivers of the east coast of the Southern Island of New Zealand (McDowall 1994), in at least three Pacific river basins of Chile and Argentina (Grossman 1991, 1992), and, as reported here, in the Santa Cruz River. Meanwhile, there is no comparable record of success for other species that have been at least as intensively transplanted as chinook salmon, such as coho, *O. kisutch*, and sockeye salmon, *O. nerka*, brought together with chinook salmon in early importations into South America (Marini & Mastrarrigo 1963), or coho and Atlantic salmon, *Salmo salar*, two orders of magnitude more important than chinook salmon in Chilean aquaculture production (FAO 2002).

This takes us to the origin of Caterina Stream chinook salmon. Is this a recently established population, founded with fish that colonized the

Santa Cruz from southern Chile in the last 20 years, or is this a century – old population, the result of transplants conducted in situ during the early 20th century? Historical accounts appear to be insufficient to discriminate between these two scenarios, but molecular techniques provide a promising aid to elucidate the origin of Caterina chinook. Such an approach has been successfully applied to identify the most likely parental stocks for New Zealand chinook (Quinn et al. 1996) and for Santa Cruz River rainbow trout (Riva Rossi et al. 2004). Meanwhile, we can set the stage for analyzing the ecological meaning of each of these two alternative scenarios for Caterina chinook origin.

The notion that chinook salmon could have inhabited the Santa Cruz River basin for almost a century, to be discovered only recently, is puzzling. But if we give credence to the one account of the first sightings in the 1970s, then we have to discard the 1980s ranching experiments in southern Chile as the source and accept an origin from early transplants. Although we could not find definite records to establish the origin of those transplants, they might have come from hatcheries in the Sacramento River system, California, as was the case of New Zealand chinook (McDowall 1994, Quinn et al. 1996), for this was a main source of chinook ova at the time. New Zealand chinook has provided a marvelous case study to investigate the pattern, rate and process of evolution among populations that were founded from a single introduction and which are connected through straying (Quinn et al. 2001). The presence of independent chinook "sister" populations in South America would allow an extended natural experiment of global scale to study adaptation and microevolution processes.

A more recent origin of Santa Cruz chinook, as an offshoot of ranching experiments in southern Chile during the 1980s, is suggested by the fact that most reports of chinook sightings in the Caterina are post-1980. Chinook have a high colonizing ability, well demonstrated by the fashion by which this species invaded river basins in New Zealand from a single source (MacDowall 1994); the Magellan Strait provides a direct route from southern Chile to the Santa Cruz River (only 200 km separate the Santa Cruz estuary from the outflow of the Magellan Strait in the Atlantic Ocean). Prevailing eastward currents in the Magellan Strait (as well as around Cape Horn, Krepper 1977), would contribute to a Pacific-to-Atlantic fish movement. From a purely scientific perspective, the prospects for a recent origin of chinook salmon provide an opportunity to study the initial stages of the process of adaptation in real time. From an environmental point of view, it brings in the issue of potential impacts of expanding aquaculture in southern Chile on Atlantic river basins.

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