Colonization of the Southern Patagonia Ocean by Exotic Chinook Salmon

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Abstract: *Anadromous salmonids have been particularly successful at establishing wild populations in southern Patagonia, in contrast to their limited success elsewhere outside their native ranges. The most recent such discovery is a spawning population of Chinook salmon in the Santa Cruz River, which flows into the Atlantic Ocean from Argentina. We used mitochondrial DNA analysis to discriminate between alternative potential sources of this population and were able to discard in situ introductions of fish imported directly from California in the early twentieth century. Our results showed that the fish most likely came from Puget Sound, Washington, imported into southern Chile for salmon-ranching experiments in the 1980s. This finding provides concrete evidence of colonization of Atlantic rivers from Pacific locations. The southern Pacific and Atlantic oceans provide a favorable marine environment for the success of invading salmon. In particular, the waters associated with fjords, southern channels, and the inshore portion of the Patagonian shelf provide a rather bounded, continuous waterway for exotic anadromous salmonids, rich in diverse forage species.*

Keywords: Chinook salmon, mtDNA analysis, *Oncorhynchus tshawytscha*, Santa Cruz River, species introduction, Patagonia

Colonización del Sur de la Patagonia por el Salmón Exótico *Oncorhynchus tshawytscha*

Resumen: *Los salmónidos anádromos han sido particularmente exitosos en el establecimiento de poblaciones silvestres en el sur de la Patagonia, en contraste con el éxito limitado en otras localidades fuera de sus rangos de distribución nativos. El descubrimiento más reciente es una población reproductiva en el Río Santa Cruz, que fluye al Océano Atlántico en Argentina. Utilizamos análisis de ADN mitocondrial para discriminar entre las diferentes fuentes potenciales de esta población y pudimos descartar introducciones in situ de peces importados directamente de California a principios del siglo veinte. Nuestros resultados mostraron que los peces probablemente provinieron de Puget Sound, Washington, introducidoss al sur de Chile para experimentos de cultivo de salmón en la década de 1980. Este hallazgo proporciona evidencia concreta de la colonización de ríos del Atlántico desde sitios en el Pacífico. Los océanos Atlántico y Pacífico proporcionan un ambiente marino favorable para el éxito de la invasión de salmones. Particularmente, las aguas asociadas con fjords, canales y la porción interior de la plataforma Patagónica constituyen una vía continua, rica en especies presa, para salmónidos anádromos.*

Palabras Clave: análisis de ADNmt, introducción de especies, *Oncorhynchus tshawytscha*, Patagonia, Río Santa Cruz

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Paper submitted December 22, 2006; revised manuscript accepted April 23, 2007.

Conservation Biology Volume 21, No. 5, 1347–1352

DOI: 10.1111/j.1523-1739.2007.00761.x

Introduction

In Patagonia, at the tip of South America, salmonids have been introduced widely and have been very successful at colonizing lakes and rivers (Dyer 2000; Pascual et al. 2002). In addition to these nonanadromous populations, evidence has accumulated in recent years that indicates salmonids have established anadromous populations in various rivers of southern Patagonia. For instance, Chinook salmon spawn in several river basins, both Pacific (Soto et al. 2001) and Atlantic (Ciancio et al. 2005), anadromous rainbow trout (*Oncorhynchus mykiss*) inhabit the Santa Cruz River of Argentina (Pascual et al. 2001), and sea-run brown trout (*Salmo trutta*) support world-class fisheries in the continent, Tierra del Fuego, and Malvinas Islands (McDowall et al. 2001).

Most recently, in Patagonia a spawning population of Chinook salmon (*O. tshawytscha*) was discovered in the Caterina River, a small tributary in the Santa Cruz River basin of Argentina (Fig. 1). Two potential origins have been identified for Caterina's Chinook (Ciancio et al. 2005): in situ introductions of fish imported directly from the United States in the early twentieth century or fish from fish-ranching experiments conducted in the southern Pacific Ocean in Chile during the 1980s. The possibility of a recent origin from ranching experiments raises two important environmental issues. First, it underscores the risks associated with feral fish from net-pen aquaculture (Naylor et al. 2005), a serious concern in Norway, where large numbers of hatchery-produced Atlantic Salmon are overwhelming dwindling native wild populations (Fleming et al. 2000), and in the Pacific Northwest, where increased production of exotic Atlantic salmon has raised the prospect of an invasion of rivers inhabited by native Pacific *Oncorhynchus* species (Volpe et al. 2000). This issue has received much less attention in South America (but see Gajardo & Laikre 2003), even though Chile is expected to soon surpass Norway as the world's leading salmon producer. Second, an origin in Chile would substantiate the occurrence of interoceanic invasions in southern marine ecosystems, an unexplored issue with regionally important environmental implications. We applied mtDNA analysis to discriminate between alternative parental stocks and analyzed the oceanographic setting of southern Patagonia as a backdrop for the biotic connection between the Pacific and the Atlantic Oceans.

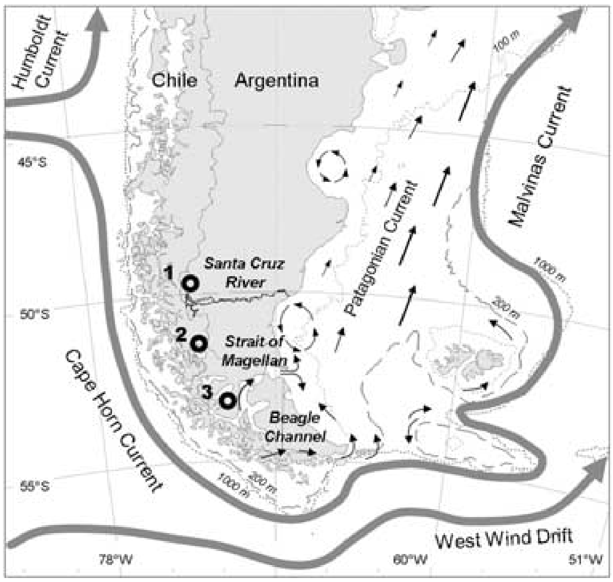

Figure 1. Southern South America and major marine currents (based on Glorioso & Flather 1995; Strub et al. 1998; Palma et al. 2004; Sabatini et al. 2004). Major, stable currents are represented as continuous, thick arrows; variable currents, driven by tides and local winds, are represented as thin, short arrows. Circles indicate streams with established populations of Chinook salmon (1, Caterina River, Santa Cruz River basin) and where ranching experiments were originally conducted (2, Pratt River; 3, Santa María River). For a more detailed map of locations see Ciancio et al. (2005).

Methods

Identification of Potential Parental Stocks and Sources

There were four recorded introductions of Chinook salmon into the Santa Cruz River between 1906 and 1910 (Marini 1936; Table 1) that apparently failed. The exact origin of the eggs is unknown. It is likely they came from hatcheries in the Sacramento River, which at the time were the major producers of Chinook eggs, including those shipped between 1900 and 1906 from Battle Creek Hatchery to found the populations on the South Island of New Zealand (Quinn et al. 1996).

More recently, numerous attempts have been made to introduce Chinook salmon to Chile's Pacific rivers. Of those, all introductions before 1980 occurred north of 45° S, whereas in the 1980s two ranching experiments were conducted in rivers of the southernmost region of Chile, near Puerto Natales and Punta Arenas (Fig.1; Table 1; Basulto 2003). The ova used in these ranching experiments were shipped from the University of Washington Hatchery (Seattle, Washington). According to Donaldson and Joyner (1983), the origin of this stock is a population from the Green River in Puget Sound, Washington. Interest in establishing ocean-ranched salmon populations in Chile dwindled during the late 1990s, when government efforts concentrated exclusively on the development of net-pen aquaculture (Basulto 2003).

Prospects to discriminate between the two possible origins—a century-old source from the Central Valley, California, and a more recent origin from Puget Sound,

Table 1. Introduction events of Chinook salmon in southern Argentina and adjacent areas.

Year	Number and stage	Origin or stock	Destination	Reference
1906–1910	1,000,000 eggs	Battle Creek,* Sacramento River, CA	Santa Cruz and Gallegos rivers, Argentina	Marini 1936
1982	200,000 smolts	University of Washington, Puget Sound, WA	Santa María River, Strait of Magellan, Chile	Donaldson & Joyner 1983
1983–1989	670,000 smolts	University of Washington, Puget Sound, WA	Pratt River, Pto. Natales, Chile	Basulto 2003

*Most probable, but unconfirmed origin.

Washington—based on the genetic structure of Caterina Chinook are good. Coastwide genetic diversity of Chinook salmon from the Pacific Northwest is largely dominated by differences among major geographic and ecological provinces, rather than by life-history variation (Waples et al. 2004). Genetic analyses consistently show that all Chinook populations of the Central Valley are very similar to each other and very different from Puget Sound Chinook (Utter et al. 1989; Myers et al. 1998).

Collection of Samples and mtDNA Analysis

We obtained tissue samples for mtDNA analyses from 46 of 57 adult salmon collected from spawning beds in the Caterina River, Santa Cruz River basin (SC), in 2003 and 2004 (Fig. 1; Table 2; Fig.1 in Ciancio et al. 2005) and from 40 adult salmon from the University of Washington Hatchery (WA), a stock for which molecular sequences were not available. The upper Sacramento River holds four Chinook salmon runs, defined by the timing of upstream migration: fall, late fall, winter, and spring. Nielsen et al. (1994*b*) analyzed two wild populations from that basin (spring and late-fall runs) and five hatchery populations (winter and fall runs). Sample sizes were between 15 and 30 individuals per population. Quinn et al. (1996) compared three New Zealand populations of Chinook (34–39 individuals per population) with those reported by Nielsen et al. (1994*b*) and identified the Sacramento River as their origin.

We extracted total genomic DNA from fin tissue preserved in 70% ethanol with a standard NaCl extraction protocol. We used two primers (S-phe and P2; sequences in Nielsen et al. 1994*a*) and amplified about 180 base pairs (bp) from the highly variable segment of the right-domain of the mtDNA control region, following the protocol in Nielsen et al. (1994*a*).

We purified amplified DNA templates with the QIAquick PCR Purification Kit (Qiagen, California) and used 20 ng of purified PCR product in cycle sequencing reactions following ABI PRISM BigDye Terminator protocols (Applied Biosystems, Foster City, California). Sequences were visualized on an ABI PRISM 377 automated sequencer and were aligned with the BioEdit software (Hall 1999). The sequences we obtained were deposited in GenBank under accession numbers EF531711–EF-531713. We compared the mtDNA sequences obtained from Santa Cruz River Chinook salmon with haplotypes from Sacramento River Chinook salmon (Nielsen et al. 1998) and from the University of Washington Hatchery.

Table 2. Individual Chinook salmon sampled during 2003 and 2004 seasons in the Caterina River, Argentina.*

Year sampled	Sex	n	Mean length (cm)	Mean weight (g)
2003	F	14	78.7 (69–89)	5792 (3400–8,250)
2003	M	10	77.8 (61–95)	6116 (2750–10,500)
2004	F	6	73.3 (40–92)	6200 (1000–10,400)
2004	M	27	61.1 (44–82)	3952 (1200–8,000)

*Ranges in parentheses.

Results

The DNA extraction and sequencing was successfully performed for a total of 70 fish, 32 from the Santa Cruz River and 38 from the University of Washington Hatchery. In total, eleven different haplotypes were recognized for Santa Cruz Chinook and the two putative parental stocks (Table 3). The WA samples had two different haplotypes, both new and different from the nine haplotypes previously described for California salmon (Table 3). Both haplotypes had a new variable site (base pair 1032 for *O. mykiss*; Digby et al. 1992). Only one haplotype was found in all 32 SC fish, identical to the most frequent haplotype in the WA samples (WA1; 24 out of 38). This haplotype was not found in salmon from the Sacramento River analyzed by Nielsen et al. (1998) or in the related New Zealand populations sampled by Quinn et al. (1996). This result discounted California Central Valley as the origin of salmon in the Santa Cruz River and points to modern-day ranching experiments in southern Chile as the most plausible origin.

Discussion

To establish a population, anadromous species have to successfully complete the entire series of transition events in their life cycle, often within narrow temporal

Table 3. Chinook salmon variable sites found by Nielsen et al. (1994*a*) and the variable site we discovered in our survey of Chinook at base pair 1032.

	Base pair number[a]							
mtDNA haplotype[b]	*1006*	*1019*	*1021*	*1032*	*1050*	*1081*	*1089*	*1136*
CA 1	G	T	T	A	T	T	C	C
CA 2	A	T	T	A	T	T	C	C
CA 3	G	T	T	A	T	T	A	C
CA 4	G	T	T	A	T	T	C	A
CA 5	G	T	T	A	T	81i[c]	C	C
CA 6	G	T	C	A	T	T	C	C
CA 7	G	T	T	A	G	T	A	C
CA 8	G	T	T	A	G	T	C	C
CA 9	A	A	T	A	G	T	C	C
WA 1 ($n = 24$)[d]	G	T	T	G	T	T	C	—
WA 2 ($n = 14$)	G	T	C	G	T	T	C	—
SC [= WA1] ($n = 32$)	G	T	T	G	T	T	C	—

[a] *Base pair numbers are equivalent to those given by Digby et al. (1992) for* Oncorhynchus mykiss. *Base pair number 1006 is a nucleotide insertion not found in* O. mykiss *by Digby et al. (1992). Dashes indicate deletions.*
[b] *Abbreviations: CA 1–9, haplotypes for California Chinook (TSA 1–9 in Nielsen et al. 1998); WA 1 and WA 2, Washington haplotypes; and SC, Santa Cruz haplotype.*
[c] *An 81-base-pair insertion was found in Chinook.*
[d] *Sample sizes for our analyses in parentheses.*

windows. The explanation for the many failures in salmon acclimatization attempts should not be sought, therefore, in a single limiting factor; rather, the explanation is in a more complex mismatch between life-cycle requirements, linked by way of elaborate freshwater–marine migrations and conditions encountered in receiving environments (Allendorf & Waples 1996). Indeed, the attempts to explain the failure of salmon-ranching experiments in Chile in the 1960s and 1970s based on freshwater characteristics alone were futile; by all accounts, southern Chilean rivers are ecologically similar to Pacific Northwest streams.

More revealing has been the examination of the oceanography of the southern oceans around South America (Fig. 1). On the basis of oceanographic characteristics and general features of salmon biology, international experts recommended moving ranching experiments in Chile to locations south of 45° S, from the more northerly locations of early attempts (Joyner et al. 1974). This idea was based on the assumption that salmon populations in northern locations would be carried away from rivers and productive areas by the northward Humboldt Current, whereas rivers flowing into the fjords of southern Chile would provide a more direct access to the rich waters of the Antarctic convergence (Fig. 1). Salmon would then be able to feed on highly abundant Antarctic krill. These locations would also facilitate migrations toward the Atlantic Ocean and into the highly productive waters of the Patagonian shelf (Donaldson & Joyner 1983).

Our results provide the first concrete evidence of such a Pacific–Atlantic connection in migrating anadromous salmon. Present-day oceanographic information allowed us to further examine salmon colonization and their ecological links to the Patagonian shelf (Fig. 1). Two branches of the West Wind Drift affect the southern Patagonian shelf: the Cape Horn Current, which provides a direct inflow of cold Antarctic water through the gap between Tierra del Fuego and Isla de los Estados (Strub et al. 1998), and to the west the deep northward jet known as the Malvinas Current. Freshwater discharge in southern Patagonia dilutes the waters of the Magellan Strait (Glorioso & Flather 1995) and together with the drainage of continental rivers along the Atlantic coast of southern Patagonia forms a coastal, low-salinity tongue, known as the Patagonian Current (Sabatini et al. 2004). As revealed by satellite images, salinity ocean fronts dominate this region, making it extremely productive (Rivas et al. 2006). High values of zooplankton biomass are normally recorded during austral summer and early autumn in this region. Consequently, the southern Patagonian Shelf is the habitat for various commercially important planktivorous species, such as Patagonian hoki (*Macruronus maguellanicus*) (Hansen & Wöhler 2000) and fuegian sprat (*Sprattus fueguensis*) (Sánchez et al. 1995). In New Zealand, two related species, *M. novaezelandiae* and *S. muelleri*, constitute major prey items for nonnative Chinook salmon (James & Unwin 1996).

The Southern Pacific and Atlantic oceans provide, therefore, a favorable marine environment for the success of invading salmon. In particular, the water belt around the tip of South America associated with fjords; southern channels, including the Magellan Strait with its direct inflow of diluted waters toward the Atlantic Ocean; and the inshore portion of the Patagonian shelf on the Atlantic, appear to provide a rather bounded waterway for exotic anadromous salmonids, rich in diverse forage species. These characteristics may explain, at least in part, the success of different anadromous species in Southern Atlantic rivers. It also points to the southern Patagonian Shelf as a prime foraging arena for anadromous salmon from spawning populations in both the southern Atlantic and Pacific Oceans.

Will invading salmon have a significant effect on receiving marine communities? Anticipating and evaluating the long-term environmental effects of salmon ranching and net-pen aquaculture is an enormous challenge. The effect will obviously depend on the extent of the colonization, but if salmon prove to be the efficient protein converters that aquaculturists of the past had hoped for, they will do so at the expense of key forage species of the southern oceans. The growing presence of exotic anadromous salmonids in Patagonia calls for studies and methods to quantify the chances of further colonization of rivers in the region and determination of the impacts of salmonids on native communities.

Acknowledgments

We thank R. Waples, T. Quinn, and J. Myers for insightful comments on the manuscript; T. Quinn for tissue samples of UW Chinook; S. Basulto for assistance throughout this project; J. Ciancio, J. Lancelotti, C. Riva-Rossi, N. Olivera, L. Real, and A. Parma for assistance and comments at different stages of this work; P. Dell'Arciprete and A. Rivas for advice and assistance with oceanographic data and maps; APN, Subsecretaría de Pesca de Santa Cruz, PNA, Ea. Cristina S.A, and Fitz Roy Expediciones for access to field sites and support. This work was supported by grants from UNPA and ANPCyT to M.A.P.

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