

**Chapter 18****INTRODUCED ANADROMOUS SALMONIDS IN PATAGONIA: RISKS,  
USES, AND A CONSERVATION PARADOX**

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## Abstract

Because of their peculiar life cycle, introduced anadromous salmonids can have cascading effects on both marine and freshwater communities. From an ecological standpoint, there are three aspects of exotic salmonids that merit special attention: the factors that govern the establishment of wild populations, the impact of the introduced fish on the receiving communities, and their adaptations to the new environments. Here, we examine several case studies dealing with anadromous salmonids introduced in Patagonia, the southern region of Argentina, from these three viewpoints.

## 1. Introduction

Patagonia, the southernmost region of Argentina and Chile (Figure 18.1) has today firmly established populations of trout, red deer, and wild roses, among many other exotic species. While many early introductions were driven by aesthetic or recreational reasons, a new wave of exotic imports is arriving into Patagonia. This time the driving force is development and economic progress--the introduction of exotic species for hatcheries and animal farms.

These new activities differ in several ways from the import of species by European immigrants, who took a favorite plant or animal when they immigrated to South America. The new introductions include freshwater, marine, and terrestrial species. New hatcheries and farms are commercial enterprises that handle large numbers of organisms over wide geographic regions. Once established, these facilities become the source of a persistent influx of exotic organisms, bettering the chances for successful colonization of neighboring communities. Typically, these enterprises are a part of economic development plans that are promoted by governments, funded privately, and highly regarded by society during the initial development stages. In the minds of politicians and the public, the promise for short-term economic progress dwarfs any specter of long-term environmental damage. For the same reasons, the import of species for culture in captivity is bound to increase significantly in coming years.

For creating fishing opportunities and for aquaculture, salmonids have been widely exported around the world from their native ranges in the Northern Hemisphere. In this trade, Argentina and Chile have been assiduous importers (Pascual et al., 2002b). Among salmonids, Pacific species of the genus *Oncorhynchus* are a major target for contemporary marine net-pen aquaculture efforts in Chile; they are actively colonizing coastal and freshwater environments in both Chile and Argentina. As a result, because of their peculiar life cycle, their introgression can have cascading effects on both marine and freshwater communities. Therefore, these fish offer opportunities for analyzing the environmental, economic, and scientific implications of exotic species in Patagonia.

From an ecological standpoint, there are three aspects of exotic salmonids that merit special attention: the factors that govern the establishment of wild populations, the impact of the introduced species on the receiving communities, and the adaptations of these fish to the new environments. In this paper, WE examine different case studies dealing with anadromous *Oncorhynchus* species in the Patagonian region of Argentina from these three viewpoints and propose some avenues to answer the question: What can we scientists do to help mitigate the impact of these new species?

## 2. Salmonids in Argentina's Patagonia

The three first consignments of salmonids that arrived in Argentina in 1904 and 1905 were ordered by the Argentinean Ministry of Agriculture and were destined to establish feral populations in lakes and rivers of northern Patagonia. They consisted of embryos of brook trout (*Salvelinus fontinalis*), lake trout (*S. namaycush*), rainbow trout and steelhead (*Oncorhynchus mykiss*), and landlocked salmon (*Salmo salar sebago*) (Tulian, 1908; Marini, 1936; Marini and Mastrarrigo, 1963).

With the goal of introducing salmonids in rivers of southern Patagonia, a fourth consignment was shipped to Santa Cruz Province in 1906. It consisted of embryos of chinook (*O. tshawytscha*), sockeye (*O. nerka*), coho (*O. kisutch*), and landlocked salmon, as well as lake, brook, and rainbow trout, all from the USA. The Santa Cruz Province received three more shipments of the same species from the USA between 1908 and 1910 (Pascual et al., 2001). Early shipments also contained sea trout (anadromous form of brown trout, *Salmo trutta*) and Atlantic salmon (*Salmo salar*) from England.

The *Oncorhynchus* species contained in these early shipments most likely came from the Baird Hatchery on the McCloud river in California (Scott et al., 1978; Riva Rossi et al., 2004), which distributed eggs all around the USA and to several other countries (Valette, 1924; Marini and Mastrarrigo, 1963; Pascual et al., 2001), but alternative locations in California and Oregon are possible sources as well (Behnke, 2002; Pascual et al., 2002a). The rainbow trout eggs in these early shipments presumably contained a mixture of anadromous and strictly resident stocks of rainbow trout; both varieties occurred at sites where hatcheries such as the Baird Station collected fish for its operations (Wales, 1939; Busack and Gall, 1980; Nielsen et al., 1997). The last imports of salmonids into Argentina occurred between 1950 and 1970, when most of the rainbow trout came from resident hatchery stocks from Denmark and Germany (Pascual et al., 2002b). In summary, rivers in northern and southern Patagonia received fish of typically anadromous species (chinook, coho, sockeye, and Atlantic salmon), facultative anadromous species (rainbow, brown, and brook and trout), and typically freshwater resident species (brook and lake trout).

By the 1930s, salmonid production in Argentina was centered at the Bariloche Hatchery in northern Patagonia, which then became the main center of propagation of salmonids in Argentina. Beginning in the 1980s, the marine net pen culture of salmon in Chile grew dramatically, from a total of 53 metric tons (t) harvested in 1981 to well over 100,000 t today. As salmon production has increased, so have reports of fish escaping from net pens and straying into rivers in the Patagonia region of Chile and Argentina. Although these reports started as early as 1984, it was only recently that we started gathering proof that anadromous salmon are actually spawning in South American rivers. In March and April of 1996 we witnessed, for the first time on record, chinook salmon spawning in South American streams. At that time, one of us (M.P.) found groups of chinook salmon adults spawning in the Futaleufú River (Argentina; Figure 18.1). The following year, Doris Soto and Fernando Jara from the Universidad Austral in Chile found spawning chinooks in the Petrohué River (Chile). Both rivers drain into the Pacific Ocean. Chinook salmon are also present in significant numbers in two other river basins in the region, the Pico and Corcovado Rivers (Figure 18.1); spawning occurs regularly in those rivers (Di Prinzio, 2001). More recently, we found chinook salmon spawning in the Caterina River, Santa Cruz River Basin (Ciancio et al., in press); these fish presumably recently colonized from water bodies used for ranching experiments in southern Chile (Becker, 2004). Interestingly, chinook salmon account for only a small fraction of Chile's salmon production (less than 5%), which is dominated by Atlantic salmon, coho salmon, and rainbow trout.

### 3. The Establishment of Anadromous Populations

Although resident populations of rainbow, brook, and brown trout thrive in lakes and rivers throughout Patagonia, anadromous populations are rare and are limited to rainbow trout, brown trout, and chinook salmon. The same picture arises as we analyze the record of salmonid imports around the world: freshwater-resident species of trout have adapted very quickly to diverse environments (e.g., MacCrimmon and Campbell, 1969; MacCrimmon, 1971) but attempts to establish self-sustaining anadromous populations mostly have been failures (Withler, 1982). As coastal net-pen aquaculture based on exotic species expands in temperate waters of the world, understanding the factors that affect the establishment of anadromous species becomes of paramount importance for pondering the risks associated with these enterprises.

The results of a literature search for, worldwide, reports of attempts to establish anadromous populations of *Oncorhynchus* from North America serves to further illustrate how difficult it is to establish anadromous populations (Table 18.1). Several of the 61 cases recorded consist of multi-year projects in which huge numbers of eggs and juveniles are released. In several of these cases (11, 17-20, 29, 35, 41-42, 49-54), the investment included the construction of costly facilities to incubate imported eggs or to breed the progeny of returning adults. Despite the magnitude of the efforts, the success rate has been dismal. Most attempts failed to produce returning adults. In some other cases (7, 11, 13, 21, 22, 47,49), only isolated returns occurred, while in others (10, 16-18, 29) returns were abundant but insufficient to secure population replacement. Self-sustaining populations were established in only eight cases. Three of them (cases 1, 2, 5) were facilitated by the elimination of geographical barriers that were blocking salmon movements in regions where feral Pacific salmon occur. In four of the five remaining successful cases, the fish established freshwater resident populations, developing what until then had been unrecorded landlocked life cycles (cases 15, 19, 20, 34).

Table 18.1. Details of 61 introduction attempts of *Oncorhynchus* species, worldwide. N. = case number.

N.	Species	Origin	Destination	Years	Effort	Result	References
1	Sockeye ( <i>O. nerka</i> )	Lake Baker, USA	Lake Washing- ton, USA	1940- ??	??	Successful establishment of sport and commercial fishery	Burgner (1991)
2	Sockeye	Neighbor- ing rivers, USA	Dog Salmon River, Alaska, USA	1951- ??	??	Successful establishment of commercial fishery	Kyle et al. (1988), Burgner (1991)
3	Cherry ( <i>O. masou</i> )	Hokkaido, Japan	Lake Westward, Canada	1966	5,500 alevins	FAILURE	Christie (1970)
4	Coho ( <i>O. kisutch</i> )	Washing- ton, USA	South Korea	1970s	??	FAILURE	Sandercock (1991)
5	Coho	Washington and Oregon, USA	Hokkaido, Japan	1973- 1978	??	Apparently successful	Sandercock (1991)
6	Chinook ( <i>O. tshawytscha</i> )	California, USA	East coast, USA	1870- 1880	30,000,000 eggs	FAILURE	Harache (1992)
7	Coho	??	Lake Erie, USA	1873, 1878, 1933	"thousands" of alevins	FAILURE	Sandercock (1991)

8	Coho	Oregon, USA	Maine, USA	1905-1915 (?)	1,300,000 alevins	FAILURE	Harache (1992)
9	Pink ( <i>O. gorbuscha</i> )	Washington, USA	Maine, USA	1906-1908	992,000 alevins	FAILURE	Lear (1980)
10	Pink	Washington and Alaska, USA	Maine, USA	1910-1925	29,165,000 eggs	Initial success, without replacement	Lear (1980), Harache (1992)
11	Chinook	California, USA	Maine and New Hampshire, USA	1920s	5,800,000 eggs	FAILURE	Harache (1992)
12	Chinook	??	Maine, USA	1934-??	??	FAILURE	Harache (1992)
13	Coho	??	Maine, USA	1942-1953	??	FAILURE	Harache (1992)
14	Pink	Skeena River, British Columbia, Canada	Hudson Bay, Canada	1956	738,000 eggs and alevins	FAILURE	Lear (1980)
15	Pink	Skeena River, British Columbia, Canada	Lake Superior, USA	1956	21,000 alevins	Firmly established sport fishery	Kwain and Lawrie (1981), Bagdovitz et al. (1986), Kwain (1987), Heard (1991)
16	Pink	British Columbia, Canada	Newfoundland, Canada	1959-1966	15,000,000 eggs	Initially abundant returns, without natural replacement	Lear (1975), Lear (1980), Harache (1992)
17	Chinook	Washington and Oregon, USA	New Hampshire and Massachusetts, USA	1960s-1986	1,100,000 alevins	Initially abundant returns, without natural replacement	Harache (1992)
18	Coho	Washington and Oregon, USA	New Hampshire and Massachusetts, USA	1960s-1986	3,400,000 alevins	Initially abundant returns, without natural replacement	Harache (1992)
19	Chinook	??	Lake Superior, USA	1966-present	??	Sport fishery established	Healy (1991), Harache (1992)
20	Coho	North Pacific	Lakes Michigan and Superior, USA	1966-1977	51,540,000 alevins	Sport fishery established	Sandercock (1991), Harache (1992)
21	Pink	Alaska, USA	Casco Bay, Maine, USA.	1981-1982	3,000,000 eggs	FAILURE	Harache (1992)
22	Chum ( <i>O. keta</i> )	Washington, USA, and Japan	Casco Bay, Maine, USA	1981-1986	5,000,000 eggs	FAILURE	Harache (1992)
23	Chinook	North Pacific	France	1872-1910	1,053,000 eggs	FAILURE	Harache (1992)
24	Chinook	North Pacific	Germany	1872-1910	955,000 eggs	FAILURE	Harache (1992)
25	Chinook	North Pacific	Italy	1872-1910	100,000 eggs	FAILURE	Harache (1992)

26	Chinook	North Pacific	Holland	1872-1930	900,000 eggs	FAILURE	Harache (1992)
27	Chinook	North Pacific	England	1872-1890	150,000 eggs	FAILURE	Harache (1992)
28	Chinook	North Pacific	Ireland	1891-1910	50,000 eggs	FAILURE	Harache (1992)
29	Pink	Sakhalin Island, Russia	Kola Peninsula, Russia	1956-1980s	200,000,000 alevins	Abundant initial returns, without natural replacement	Heard (1991), Harache (1992)
30	Chum	Sakhalin Island, Russia	Kola Peninsula, Russia	1957-1964	50,000,000 alevins	FAILURE	Harache (1992)
31	Pink	??	Baltic Sea	1973-1976	??	FAILURE	Harache (1992)
32	Chinook	??	North Island, New Zealand	1875-1878	More than 427,000 eggs	FAILURE	Waugh (1980), Flain (1981)
33	Chinook	McCloud River, California, USA, and New Zealand	Tasmania, Australia	1876-1834	725,000 eggs	FAILURE	Stewart (1980)
34	Sockeye	Fraser River, British Columbia, Canada	Waitaki River, New Zealand	1901-1904	95,000 alevins, 18,000 juveniles	Establishment of landlocked population	Waugh (1980), Flain (1981)
35	Chinook	Sacramento River, California, USA	Waitaki River, New Zealand	1902-1907	72,400 juveniles; 1,000,000 eggs	Sport fishery established	Stewart (1980), Waugh (1980), Flain (1981)
36	Sockeye	Canada	Tasmania, Australia	~1900	??	FAILURE	Stewart (1980)
37	Chinook, coho, sockeye	USA	Argentina	1905-1910	377,000 eggs	FAILURE	Joyner (1980), Sandercock (1991)
38	Chinook, sockeye	USA	southern Chile	1905-1938	??	FAILURE	Joyner (1980)
39	Chinook	American River, California, USA	Jaquari River, Brazil	1958	??	FAILURE	Joyner (1980)
40	Coho	Washington and Oregon, USA	Ancud Gulf, Chile	1969	180,000 eggs	FAILURE	Joyner (1980)
41	Cherry	Mena River, Japan	Río Claro River, Aysén fjord, Chile	1973	85,000 juveniles	FAILURE	Joyner (1980)
42	Chum	Tokachi River, Japan	Fiordo Aysén, Coyaique, Chile	1974-1977 (?)	10,000,000 eggs	FAILURE	Anon. (1990), Joyner (1980)
43	Coho	Baker River, USA	Ancud, Chile	1977-1978	100,000 juveniles	FAILURE	Joyner (1980)
44	Coho	?	Kerguelen Islands, Indian Ocean (France)	1980-??	??	Limited population, in fourth generation	Harache (1992)

45	Pink	Baranof Island, Alaska, USA	Santa María River, Chile	1982	600,000 eggs	FAILURE	Heard (1991)
46	Pink	Japan	Aysén fjord, Chile	1982-??	1,350 fry	FAILURE	Anon. (1990)
47	Cherry	Hokkaido, Japan	Lake Carrera, Chile	1987	56,000 fry	Some returns	Sakai et al. (1992)
48	Chinook, coho	University of Washington, USA	Santa María River, Chile	1982	70,000 coho, 200,000 chinook; alevins	FAILURE	Donaldson and Joyner (1984) Basulto (2003)
49	Chinook, coho	University of Washington, USA	Pratt River, Chile	1983-1989	670,000 alevins	5% and 2% coho and chinook returns	Basulto (2003)
50	Chinook	Paris, France	Quinta Normal, Chile	1886	100, alevins	FAILURE	Basulto (2003)
51	Chinook	Washington, USA	Chirri River, Chile	1969-1970	1,126,000 eggs	??	Basulto (2003)
52	Coho	Washington, USA	San Pedro River?, Valdivia, Chile	1901-1910	225,040 eggs	??	Basulto (2003)
53	Chinook, coho sockeye	USA	Chile	1921-1930	200,000 chinook, 225,000 coho, 314,000 sockeye; eggs	??	Basulto (2003)
54	Cherry	Hokkaido, Japan	Claro River, Cohiaique, Chile	1973	85,000 alevins	FAILURE	Basulto (2003)
55	Cherry	Hokkaido, Japan	Simpson River, Don Poli Lake, Chile	1982-1984	61,000 alevins	FAILURE	Basulto (2003)
56	Chinook	USA	Cautín, Maullín, Cochamó, Puelo rivers, Chile	1924	200,000	FAILURE	Dufflocq (1981)
57	Sockeye coho	USA	Chile	1930	114,000 sockeye, 225,000 coho	??	Dufflocq (1981)
58	Chinook	USA	Chirri River, Chile	1968-1971	355,850	??	Dufflocq (1981)
59	Coho	USA	Grisanche River, Kerguelen Islands	1978	5,000	??	Davaine (1997)
60	Coho	Washington USA	Armor River, Kerguelen islands	1984-1990	275,506	??	Davaine (1997)
61	Chinook	University of Washington, USA	Armor River, Kerguelen islands	1987	80,000	FAILURE	Davaine (1997)

The only successful acclimatization of anadromous populations of *Oncorhynchus* of significant size outside of the native range was that of chinook salmon introduced into New Zealand at the turn of the century (case 35). A total population of around 50,000 spawners, established in several rivers of the southern island, today sustains an important sport fishery (McDowall, 1994). The success of this acclimatization project may be a result of the large scale of this effort, which involved millions of juvenile fish planted over several years. But in general the rate of success has not been related to planting efforts (Table 18.1), indicating that more complex processes determine the fate of anadromous

imports. Two extreme cases exemplify the fortuitous nature of anadromous salmon acclimatization. Pink salmon (*Oncorhynchus gorbuscha*) populations in the Great Lakes (USA) originated from the unplanned dissemination of 21,000 alevins (case 15), but a large-scale plan to establish populations of the same species in the Kola Peninsula, Russia, by planting 200 million fish over several years, failed (case 29).

The establishment in Chile and Argentina of apparently self-sustaining populations of chinook salmon that originated from net-pen aquaculture and ranching in Chile constitute only the second case of migrating salmon runs in the Southern Hemisphere to date, underlying the extraordinary uniqueness of the establishment of self-sustaining populations of anadromous salmon. Given this record, it is pertinent to ask what is the reason for the frequent failure of anadromous varieties. The success of freshwater populations in the Southern Hemisphere indicates that rivers are appropriate for salmon. Marine environments in the southern oceans are rich in forage species (e.g., James and Unwin, 1996) similar to those upon which salmon prey in northern oceans (Brodeur, 1990). Moreover, oceanic temperature regimes, which have been proposed as a limitation for Pacific salmon introduced into the North Atlantic (Harache, 1992), are optimal for salmon in the South Atlantic and Pacific oceans. The explanation for failures, therefore, should not be sought in the simplicity of a limiting factor, but in a more complex mismatch between the highly elaborate marine migration of salmon and the conditions encountered by them in the southern oceans.

To explain the lack of success of Atlantic salmon in the Southern Hemisphere, Stewart (1980) proposed that the southern oceans lacked some dynamic oceanographic features characteristic of native oceans, specifically gyres or cyclic currents, that govern marine migration and ensure homing. This explanation, however, does not take into consideration the plasticity of salmon and their ability to adapt to new conditions, which has occurred in some instances of salmon introductions. Over fifty years ago, Ricker (1954) offered a lucid explanation for the difficulty of establishing new anadromous populations: "...homing of a sufficient number of newly-introduced stock to their adopted stream, or to any single stream, may be fraught with hazards. This would be especially true if the salmon's ability to home and become established in a new site depended partly on hereditary factors... If this hereditary component in homing ability exists, then the process of establishing a new run becomes an example of speeded-up adaptation by natural selection. The most obvious by-product of this selection is a poor rate of return during the first generations."

Today we possess strong evidence for the existence of genetic components in migratory behavior, suggesting that a mismatch between genetically determined behaviors and the characteristics of the new environment, such as postulated in the hypothesis advanced by Ricker, could indeed be an impeding factor for the establishment of salmon populations. Different salmon stocks have characteristic migratory patterns in the ocean. Transplanted fish retain this ancestral migratory behavior (Nicholas and Hankin, 1988; Pascual and Quinn, 1994), suggesting that their oceanic movement patterns are largely determined by genetic factors (Figure 18.2). This "hard-wired" behavior could force the introduced fish to follow "inappropriate" patterns of ocean migrations, or they could simply be unable to adjust to new orientation cues and get lost in the ocean. Once in the rivers, olfactory imprinting by juveniles can help surviving fish return to their new home streams (Quinn, 1993; Pascual et al., 1995).

The record of salmon introductions also indicates that some species may be more able to colonize new environments than others. For instance, although several different species were introduced into Australasia and South America, only chinook salmon established anadromous populations on both continents. Chinook salmon are characterized by a high intra- and inter-populational

variability in life-history characteristics (Healy, 1991), a plasticity that may have increased their chances for adapting to the conditions of their new environments. The other species that have developed anadromous runs in South America, rainbow trout and brown trout, also have highly plastic behaviors, particularly in the critically important anadromous behavior. Species with narrower life history requirements, such as sockeye salmon and Atlantic salmon, which were imported into New Zealand (Quinn and Unwin, 1993) and South America without success, may be on the other end of the “invasiveness” spectrum. Nevertheless, ability of some salmonids to rapidly adapt to new environments indicates that this lack of success should not be considered permanent or immutable. The continuous flow of salmon provided through their escape from marine net pens increases the likelihood that critical masses of reproductive fish will be available to adjust to new environments.

After a critical number of fish develop a suitable migratory pattern at sea and reproductive populations are established, the plasticity characteristic of salmonid freshwater life history could allow them to rapidly colonize neighboring rivers. After attempts failed for years, this type of adaptation to a new environment occurred when chinook salmon rapidly colonized neighboring rivers in New Zealand after a population was established (McDowall, 1994). Chinook salmon in Chile and Argentina appear to be experiencing a similar phenomenon; the fish are already present in at least four different river basins.

Most of what we know about the colonization potential of salmon species comes from analyzing patterns of straying in established populations (Quinn, 1993). But only the colonization of new environments (Milner, 1987; Milner and Bailey, 1989) or the recolonization of habitats affected by environmental catastrophes (Leider, 1989) provides opportunities to evaluate the colonization potential of a species. Growing chinook salmon populations in South America presents a new opportunity to examine the colonization process in real time, as well as to evaluate the ecological impacts of the colonization.

#### **4. Evaluating Potential Impacts of Salmon Introgression**

Because anadromous salmon attain most of their growth at sea but return to spawn (and, in many species, also die) in freshwater, they may constitute an important agent for the transport of nutrients from the ocean to freshwater. Large increases in dissolved nutrients occur in streams following the die-off of salmon that have spawned (Kline et al., 1990, 1993) and trout occurring in sympatry with anadromous salmon are known to consume large numbers of salmon eggs and juveniles (Ruggerone and Rogers, 1984; Berejikian, 1992). The list of consumers of freshwater stages of salmon is not limited to fish, but encompasses a long list of wildlife species (Willson and Halupka, 1995). Yet, salmon can compete with local species for food and space during their early life stages and can also prey on those species (Fausch, 1988; Krueger and May, 1991). The complexities of the salmon life cycle indicate that interactions between salmon and sympatric species can propagate through the ecosystem in unforeseen ways.

A typical approach in impact assessment studies is to derive general rules from a retrospective analysis of case studies. Although historical analyses are informative, it is often puzzling to try to apply general rules when considering specific new cases. There is always a measure of uncertainty when extrapolating observations and results from one part of the world to new settings.

In 1997 the Santa Cruz Province fisheries administration in Argentina elaborated a plan to introduce chinook salmon into the Santa Cruz River. The final objective was to provide 200 t of fish per year for harvesting by a coastal fishery. One of us (M.P.) was asked to perform an impact assessment for scenarios in which salmon were successfully established. The general approach

was to develop population models (similar to that of Hankin and Healey, 1986) coupled with a bioenergetic model (Hewett and Johnson, 1992) to predict potential consumption rates by hypothetical salmon populations. The models were then contrasted with the abundances of different candidate prey species or the consumption rates of competitor species that had diets similar to that postulated for chinook salmon that would inhabit the Santa Cruz River region. The demographic model was also used to evaluate the benefits of the proposed introductions in terms of sustainable yields, to calculate how long would it take to build up an exploitable stock, and to estimate how hard it would be to eradicate the introduced chinook salmon if they became a nuisance. With this approach, it was possible to evaluate some of the potential impacts and gains of the proposed introduction as an integrated cost-benefit analysis.

In the analysis, the team that I led considered the interaction of chinook salmon with both freshwater and marine species. We also calculated population standing stock, food consumption, and maximum sustainable yield for introduced populations of different sizes, varying life history characteristics, and recruitment productivity. All of these factors were calculated for chinook salmon inhabiting waters of different temperatures. Figure 18.3 shows an illustration of the type of results obtained for a given set of parameters and settings.

The results of our analysis indicated that large populations (as large as twice the New Zealand population) were needed to produce a harvest of 200 t per year. It also showed that it would take at least two decades to establish these populations and at least 10 years of very intensive harvest (removal of 90% of spawners every year) to reduce them down to an arbitrarily small number (10,000 individuals). The most likely freshwater species to be affected by competition with chinook salmon was the exotic brown trout, an important sport fishery resource in the Santa Cruz River system. In the ocean, likely competitors with salmon were two species with similar diets: the magellanic penguin (*Spheniscus magellanicus*; Frere et al., 1996) and the palometa (*Parona signata*). Susceptible preys included decapod larvae of the valuable southern king crab (*Lithodes santolla*). The estimated consumption of food by the population of breeding penguins in Santa Cruz (270,000 pairs) is comparable to the estimated food consumption of projected salmon populations (Figure 18.3). Given all this information, the provincial government decided not to proceed with the introduction and to apply the resources available to study and promote the exploitation of more traditional resources.

A particular case like this can help illustrate the complexities involved in using an alien species to establish a new fishery better than can a generic ecological discussion. The specific methods used could as well provide some general tools for forecasting the potential effects of planned and unplanned introductions. This analysis was admittedly crude in some aspects. For example, it reduced complex species interactions to ballpark figures of biomass and consumption. But on the other hand, it had the advantage of representing risks in a relatively unambiguous way, thanks to the development of a quantitative framework. More importantly, it considered costs and benefits within the same framework. If the analysis had been based on impact alone, the project might have proceeded, encouraged by groundless calculations.

## 5. A Conservation Paradox?

Perhaps paradoxically, the introduction of salmon in South America provides a chance to contribute to salmon conservation in North America. Because of their homing ability, salmon species are organized into local populations, each with a characteristic geographic distribution and some degree of reproductive isolation from other populations. As a result of this isolation, populations typically display

local characteristics, and much of this variation among populations has a genetic basis (Ricker, 1972; Taylor, 1991). These local adaptations are evident at even very small geographical scales and include morphological traits, behavioral characteristics, developmental and physiological characteristics, disease resistance, and life history traits (reviewed in Taylor, 1991).

Studies on the genetic bases of the geographical variation in salmon populations became the focus of considerable scrutiny as an increasing number of salmon stocks became endangered (Nehlsen et al., 1991). For example, conservation plans for salmonids under the Endangered Species Act rely on identifying "Evolutionarily Significant Units" (Waples, 1991) as the units to which rescue efforts are to be directed. Tracking the divergence of transplanted fish provides a direct means for assessing the genetic and environmental bases of life history characteristics, as well as an opportunity to estimate the rates at which population characters evolve (Stearns, 1983; Reznick et al., 1990). These types of studies can aid decisions on what constitutes "significant" variation (NRC, 1996). The analytical value of contrasting biological characteristics of different introduced populations to one another and/or to their parental populations has been well-demonstrated in recent years (see for example Quinn and Unwin, 1993; Kinnison et al., 1998). Opportunities for such research abound in Patagonia. I present here an example based on the development of anadromy in rainbow trout and discuss the research opportunities presented by the recent introgression of chinook salmon in Pacific basins of Patagonia.

As has occurred in many other rivers of Patagonia, the Santa Cruz River has established populations of rainbow trout of significant fishing value. What is peculiar about the Santa Cruz is the presence of an anadromous run (Pascual et al., 2001), an uncommon behavior in introduced rainbow trout. Anadromy is a pivotal trait in salmonids, not only because of the physiological and behavioral adaptations associated with this behavior (Hoar, 1976), but also because it results in an alteration of the growth and survival opportunities of individuals.

The value of this setting is enhanced by the fact that the Santa Cruz River received, separately and at different times, fish from both resident and anadromous stocks. Our first results suggest that microsatellite DNA analysis (Wright and Bentzen, 1994; Pascual et al., 2001), together with mitochondrial DNA analysis (Riva Rossi, et al. 2004), provides a powerful method to discriminate among the candidate parental stocks, the same stocks that have been extensively used throughout Patagonia as the origin of feral populations.

The new environment had an extraordinary effect on how anadromy is expressed in Santa Cruz River rainbow trout. Whereas freshwater residence time, growth patterns, and age-at-maturity do not differ dramatically from those of North American stocks, Santa Cruz fish live much longer and spawn significantly more times throughout their lives than any known northern hemisphere population (Pascual et al., 2001). The Santa Cruz population presents a fantastic natural experiment to evaluate the trade-offs and coevolution of life history characteristics such as anadromy, longevity, and iteroparity.

The other ongoing unique natural experiment in South America that would allow researchers to study the genetic and environmental bases of life history characteristics is associated with chinook salmon that colonize different Patagonian rivers that flow into the Pacific and Atlantic Oceans. The value of this experiment is heightened by the fact that a parallel setting has been studied for over ten years in chinook salmon that were introduced into New Zealand at the turn of the 20<sup>th</sup> century (reviewed in Quinn et al., 2001). The New Zealand populations vary in several phenotypic traits, including growth in freshwater and at sea, age at maturity, dates of return to fresh water and reproduction, morphology, and reproductive allocation. Strong evidences of trait divergences with likely adaptive bases are found between populations, particularly in freshwater growth rate, date of return, and reproductive output. Since these

salmon populations were all derived from a single source, these data show that considerable variability among populations developed in 90 years, or approximately 25-30 generations.

The colonization of a collection of rivers in Patagonia by the same species provides an opportunity not only to test for the development of local adaptations, but also to track the temporal progression of this phenomenon. Chinook salmon in New Zealand provide researchers with a fantastic opportunity to study the evolution of population characteristics in the time scale of several decades; chinook salmon in South America provide an opportunity to study the same process over a much shorter time scale.

## **6. Concluding Remarks**

The record of intentional salmon introductions unambiguously shows that they more often than not end in failure. The adaptation of some components of the marine migratory behavior of salmon species to conditions in their native range may be responsible for rendering adaptation to new regions difficult. This should not, however, be used as an argument to disregard the risks of invasion posed by salmon net-pen aquaculture. Adaptation of exotic anadromous salmon has occurred and is likely to occur in the future as escapes continue to increase. In fact, southern South America is proving to be a place where anadromous salmonids were particularly successful, compared with the record elsewhere in the world.

But a strategy of crying wolf may not serve the environmental cause either. Ecologists tend to outright combat the use of exotic species, but opposition without supporting data can have a detrimental effect or be simply disregarded. In the eyes of the public and governments, blunt opposition is sometimes regarded as insensitivity to the needs of society and obtuse interference with progress. This is particularly true in developing countries, where the pressure for new productive activities is higher. There is a need to have a proactive approach and to develop quantitative frameworks that include the concept of risk and make explicit economic considerations (cost-benefit analysis) such as those described above. This requires anticipating and evaluating long-term environmental costs.

Whereas refined analytical techniques can help us evaluate hypothetical scenarios, our great ignorance about the likely effects of introduced salmon can only be reduced with documentation of actual cases. There is an urgent need to document ongoing invasions such as those occurring in Patagonia and to monitor changes in the receiving communities as they occur. With time, the information produced will certainly prove precious. These initial stages of colonization also provide a unique opportunity to record the process of adaptation of salmon to new conditions and to evaluate how genetics and environment interplay in the expression of life-history characteristics.

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## Figure Legends

*Fig. 18.1.* Location of Patagonia and the Argentinian locations mentioned in this paper.

*Fig. 18.2.* Marine recoveries of three different stocks of tagged chinook salmon released from two sites along the USA Pacific Coast (relative location indicated with arrows, **R**: Rogue River, **C**: Columbia River). “Native Rogue stock” is composed of native fish from the Rogue River in southern Oregon, reared and released locally at the Cole River Hatchery. “Native Columbia stock” is composed of native fish from the Columbia River, reared and released locally at the Big Creek Hatchery. “Rogue in Columbia” fish are descendants of Rogue River fish, reared and released from the Big Creek Hatchery in the Columbia River. Transplanted Oregon fish display the ancestral tendency to migrate southward in the ocean, which differs markedly from the northward migration characteristic of Columbia River fish. Modified from Pascual and Quinn (1994). CA = California, USA; OR = Oregon, USA; WA = Washington, USA; BC = British Columbia, Canada. Data source: Nicholas and Hankin (1988).

*Fig. 18.3.* Risk analysis of introducing chinook salmon in the Santa Cruz River basin. Upper panel: the gray area represents combinations of population sizes (X-axis) and productivities (Y-axis, slope in stock-recruitment relationship) that produce sustainable yields of at least 200 tons. Average productivity for salmon is about 3. The size of the New Zealand population is 50,000 spawners (indicated with the arrow). Middle panel: years required to arrive at the abundance that produces MSY and years needed to reduce population to 10,000 spawners by harvesting 90% of the run. Lower panel: marine food consumption of populations of different sizes estimated for temperatures of 7 °C and 10°C. The horizontal line shows the food consumption estimated for the population of penguins of Santa Cruz (270,000 pairs, Gandini et al., 1996) during the breeding season.

fig 18.1

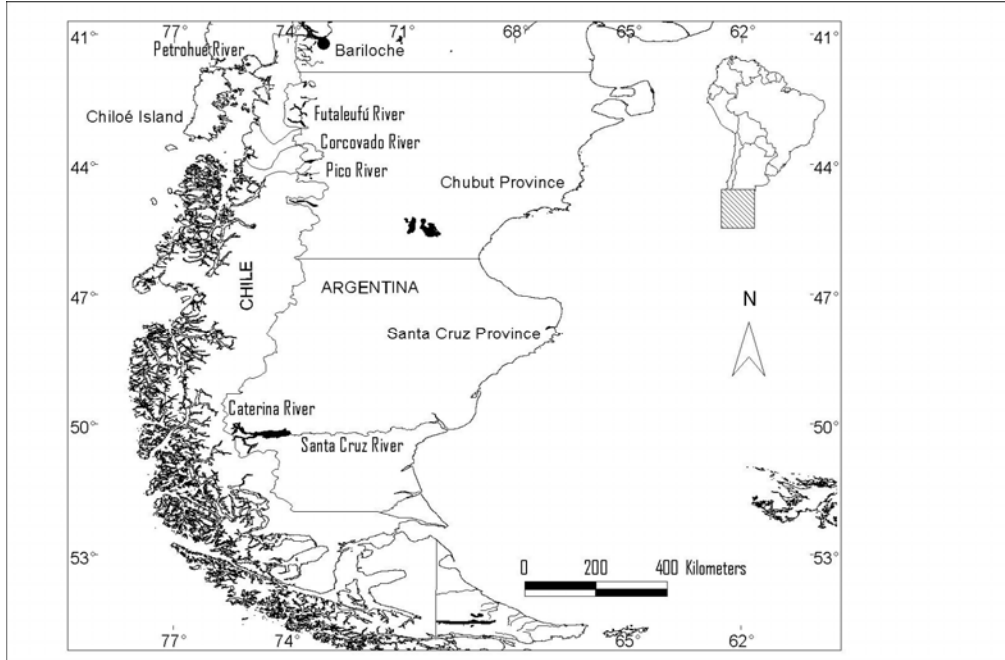


fig 18.2

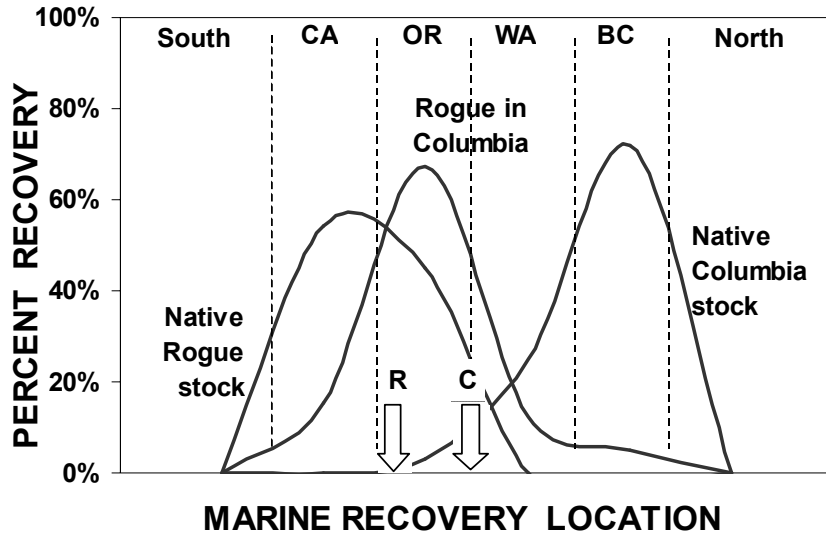


fig 18.3

