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First Documented Case of Anadromy in a Population of Introduced Rainbow Trout in Patagonia, Argentina

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Abstract.—The examination of population-specific adaptations of introduced salmonids to the wide range of environments found in Patagonia (southern South America) can help unveil some of the genetic and environmental contributions to life history variation. The rainbow trout *Oncorhynchus mykiss* introduced into Argentina originated from a few parental stocks. Although some of these stocks were anadromous, all of the dozens of established populations described until now have been freshwater resident. In this paper we provide the first documentation of the presence of an anadromous run of rainbow trout in the Santa Cruz River, the second largest river of Argentinean Patagonia. Microsatellite analysis revealed that anadromous and resident fish from the Santa Cruz River are genetically indistinguishable, probably representing alternative life histories within the same population. Both wild types are very different from the fish of Danish origin that were reared in a local hatchery, suggesting that they are descended more directly from California stocks or that they have been affected by strong drift or selection. Marine growth and freshwater residence are comparable to those of California steelhead. River entrance peaks in early fall. Population age structure and scale pattern analysis indicate that fish enter the river at age 3 but that most do not spawn until their next river entry as 4-year-olds. An unusual aspect of Santa Cruz anadromous fish is that they are long-lived and highly iteroparous. For instance, 20% of the fish analyzed had experienced as many as five spawning events.

Few aquatic animal groups have been as extensively exported outside of their native range as salmonids. Among them, rainbow trout *Oncorhynchus mykiss* have been among the most successfully introduced species (MacCrimmon 1971; Lever 1996). Trout shipments to Patagonia, the southernmost region of South America (Figure 1), started early in the 20th century with the primary goal of establishing wild populations. In Argentina, introductions started in 1904 (Tulian 1908), and over the following 70 years the fish were distributed throughout the region by federal and provincial government agencies as well as private landowners. Rainbow trout have become the most conspicuous freshwater fish in Patagonia, inhabiting every basin in the region.

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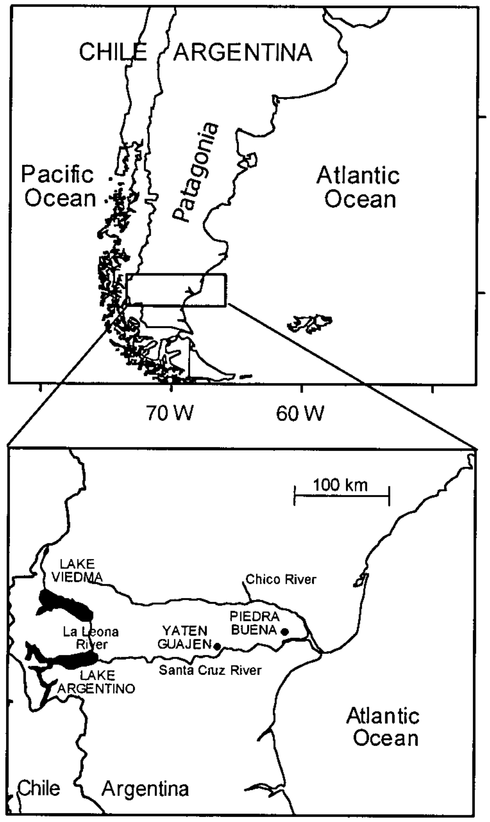

FIGURE 1.—The Patagonia region in southern South America, with the Santa Cruz River and other locations mentioned in the text.

Typical Patagonian rainbow trout remain resident in freshwater throughout their lives, with a life history similar to that of the landlocked populations of lakes and rivers in western North America (Wydoski and Whitney 1979). Although there are informal accounts of marine occurrences of rainbow trout in South America (Guernsey 1998), unambiguous scientific reports of anadromous populations are nonexistent even though trout populations in some of these rivers sustain world-class sport fisheries (Leitch 1991).

In this paper we provide the first documentation of an anadromous run of rainbow trout in the Santa Cruz River, an Atlantic basin of southern Patagonia, Argentina. We describe the basin and some of the basic biological characteristics of anadromous and resident rainbow trout. We present genetic data and explore historical records on fish transplants to identify genetic affiliations of resident and anadromous fish. We compare the life cycle of Santa Cruz anadromous fish with typical steelhead populations from North America. Here we show that Santa Cruz trout are unique with respect to several life history characters.

The Santa Cruz River and the Sport Fishery

The Santa Cruz River (50°S, Figure 1) extends for 382 km, from the Andes Mountains to the Atlantic Ocean. It is the second largest river in Argentinean Patagonia, having a basin area of 24,519 km^2. The river's average flow is 690 m^3/s, with maximum flow in summer (highest flow observed over the period 1955–1980 = 2,000 m^3/s) and minimum flow in winter (lowest flow observed over 1955–1980 = 150 m^3/s). Two large, glacially fed head lakes, Lakes Viedma and Argentino, supply turbid, milky-blue water to the river. From these lakes, the river flows eastward across the Patagonian steppe. The average gradient is moderate (0.53 m/km), with a fast water upper section and a slower, meandering lower section. The main stem has a few small tributaries. Maximum water temperatures are registered in January (average for 1995 in Pavón Island = 15°C) and the minimum ones in July (average for 1995 = 3°C). The river flows into the Atlantic Ocean through a 25-km-long estuary (6 km wide in the widest section), with a large tidal amplitude (average about 8 m) characteristic of the Atlantic coast of southern Patagonia.

Fishing for rainbow trout in the main-stem Santa Cruz River is concentrated on a 20-km stretch adjacent to the town of Piedra Buena (Figure 1). The fishing season starts in December and runs until late May, but captures of large, silvery fish in Piedra Buena tend to occur only in March and April, with a peak in late March and early April. Upriver locations hold trout during the summer (December−March), but fish are small and unattractive from a sportfishing point of view. Fishermen do not move to these upriver locations in search of large fish after the peak of the fishing season in Piedra Buena, mostly because of a lack of incentives to venture far from main roads and populated areas.

The first validated catch of a large rainbow trout in Piedra Buena was in 1982, when a 4.1-kg fish was caught on a lure by a local fisherman (M. Robira, Piedra Buena, personal communication). Whether these large fish were there before then is open to question. The Santa Cruz River is located far from traditional fishing locations and, until recently, it was not recognized as an alluring fishing destination (Leitch 1991). The weight of the largest specimens caught by 14 fishermen who were interviewed ranged from 4.3 to 8.0 kg (average 6 kg), and fish as large as 9.3 kg are reported to have been caught in Piedra Buena.

Methods

Sample collection.—During April 1997, we obtained samples of wild fish from two localities in the Santa Cruz River (Figure 1) and from a local hatchery. The first site was by the town of Piedra Buena, where 26 specimens were caught with rod and reel during the peak of the fishing activity. The fish were measured and, when possible, sexed by direct morphological inspection. Scale and tissue samples were taken, then fish were tagged with spaghetti tags and released. Three of the fish collected during the run were later classified as resident fish by scale pattern analysis. We also obtained scales, along with data on size and sex, from seven anadromous fish captured in March 1996 by sport fishermen.

The second site was at river km 185 (measured from the mouth) in Cañadón Yaten Guajen, where we expected to find only resident fish at that time (April 18, 1997). At this site we used gill nets and hook and line. Eleven fish were caught and sacrificed. We measured, weighed, and sexed them and collected scale and tissue samples. We also obtained fin clips and information on size for two other specimens captured by sport fishermen in Yaten Guajen in January 1997.

We took tissue samples from 34 fish from a municipal hatchery located at Piedra Buena. This hatchery raises rainbow trout for local consumption. While stocking is not conducted on a regular basis, sporadic unintentional releases occur and introgression with the wild population could occur.

Scale pattern analysis and the origins of rainbow trout in the Santa Cruz River.—Scales were removed from both sides of the fish, from an area located approximately five scale rows above the lateral line on an imaginary line extending from the back of the dorsal fin to the front of the anal fin. Scales were cleaned and impressions were made on acetate by means of a press with heated plates (High Seas Salmon Project laboratory, School of Fisheries, University of Washington, Seattle). The impressions were inspected under a binocular microscope and with a microfiche reader. Annuli were counted, and their radii were measured along the anterior–posterior axis of the scale. Because wild fish were not sacrificed, no otoliths were collected.

Ages at spawning events were inferred by the amount of scarring on scales, following general criteria established for North American steelhead (anadromous rainbow trout; Davis and Light 1985). Because Santa Cruz River fish are highly iteroparous (more so than any North American population), we reinforced our interpretation of spawning checks—as compared with simple overwintering checks—with results from other species that have a similar life cycle. The scale patterns of Santa Cruz fish are remarkably similar to those observed for sea-run brown trout *Salmo trutta* from Norwegian and Scottish populations (Lamond 1916; Nall 1930; Richard and Bagliniere 1990).

Although we had no independent verification of marine growth as determined from scales, we identified marine growth using the same criteria used for Northern Hemisphere fish. That is, in anadromous fish, narrowly spaced circuli near the center of the scale were assumed to be freshwater growth and more widely spaced circuli beyond that were assumed to be marine growth. Throughout this paper, we use Shapovalov and Taft's (1954) nomenclature for fish age: for anadromous fish, a slash separates freshwater age from marine age; for resident fish, a period separates maiden age from mature age; and for both types of fish, the letter *s* indicates that the fish has spawned. For example, an anadromous fish that spent 2 years in freshwater and was caught as it returned from the ocean during its third year would receive the age designation 2/1. One that spent 2 years in the river, spawned after its first ocean trip, and was caught as it came from the ocean to spawn for the second time would receive the designation 2/1s.1. And a fish coming into the river for the fourth time and its third spawning would receive the designation 2/1.2s.1. In similar fashion, a resident fish that did not mature in its first 2 years and was caught during its third year would receive the age designation 2.1 (this fish may or may not mature during the current year). A resident fish that matured at age 3 and was caught during its fourth year would receive the designation 2.1s.1. Comparative life history data from North American steelhead were obtained from Busby et al. (1996).

Genetic analysis.—For genetic analysis, a small piece of the pelvic fin was removed and preserved in alcohol. DNA was isolated from 10 mg of fin tissue by standard phenol-chloroform extraction (Bentzen et al. 1990; Ruzzante et al. 1996) and dissolved in tris−EDTA buffer (10 mM tris−HCl, pH 8.0, plus 1mM EDTA). The following seven microsatellite loci were amplified via the polymerase chain reaction (PCR) in two multiplex combinations: *Sfo8* (Angers et al. 1995), *Omy77* (Morris et al. 1996), *Ssa85* (O'Reilly et al. 1996), *Ots100* (Nelson and Beacham 1999), *Omy325* (O'Connell et al. 1997), *Ots103* (Beacham et al. 1998), and *Ots1* (Banks et al. 1999). Reactions were conducted in 10-μL volumes and comprised 10 mM tris–HCl (pH 9.0), 50 mM KCl, 0.8 mM deoxynucleotide triphosphate, 0.5 μg/μL bovine serum albumin, 2.5 mM $MgCl_2$, 0.2 units *Taq* polymerase, and approximately 100 ng trout DNA. The first multiplex contained forward and reverse primers in the following concentrations: *Ssa85* (0.2 μM); *Sfo8* (0.8 μM); *Ots103* (0.05 μM); and *Ots1* (0.7 μM). For the second multiplex, the forward and reverse primer concentrations were as follows: *Ots100* (0.05 μM); *Omy325* (0.05 μM); and *Omy77* (0.1 μM). Amplifications for both multiplex sets were carried out under the following conditions: 1 cycle at 94°C (3.5 min); 6 cycles of ''touchdown'' PCR consisting of 94°C (1 min), variable annealing temperature (30 s), and 72°C (30 s); 41 cycles at 94°C (1 min), 56°C (30 s), and 72°C (30 s); and 1 cycle at 72°C (30 min). The variable annealing temperature during the touchdown phase of the PCR began at 61°C and declined to 56°C in 1-degree increments per cycle. Equal volumes (0.5 μL) of both PCR products were combined and analyzed on an Applied Biosystems, Inc. (ABI) 373A automated DNA sequencer operated in 'Genescan' mode as described in Olsen et al. (1996) and Wenburg et al. (1996). Electrophoretic data were analyzed using ABI Genescan (version 1.1) and Genotyper (version 1.1) software.

We tested for departures from Hardy−Weinberg expectations and heterogeneity of genotype frequencies among populations using probability tests implemented in GENEPOP (version 3.1d; see Raymond and Rousset 1995). In each case, a Markov-chain method was used to obtain an unbiased estimate of the exact *P*-value (Guo and Thompson 1992), except in tests involving fewer than five alleles, in which case an exact test was used. We also used GENEPOP to compute pairwise estimates of F_{ST} among collections, as discussed by Weir and Cockerham (1984).

Identification of stocks that could have given rise to the Santa Cruz populations was done by a literature search encompassing old reports from the federal fishery administration in Argentina and articles in international journals, along with review of shipment records from the federal hatchery in Bariloche, Río Negro Province. This hatchery was the main producer of eggs and alevins destined for lakes and rivers in Patagonia. The origin of the fish kept in the Piedra Buena Hatchery was determined by interviewing the technicians that supervised the establishment of the hatchery.

Results

Origin of Rainbow Trout in Patagonia

The process of salmonid introduction in Argentina started in 1903, when the Ministry of Agriculture hired John Titcomb, then chief of the Division of Fish Culture of the U.S. Bureau of Fisheries, to carry out the undertaking (Tulian 1908; Marini 1936; Marini and Mastrarrigo 1963). The first hatchery in Patagonia was established at Lake Nahuel Huapi, Río Negro Province, and the first consignment of eggs from the United States arrived successfully in 1904. It consisted of embryos of brook trout *Salvelinus fontinalis,* lake trout *S. namaycush,* landlocked Atlantic salmon *Salmo salar sebago,* and whitefish *Coregonus* sp. After a second failed shipment, a third consignment containing rainbow trout arrived in 1905. These fish

TABLE 1.—Summary of known introductions of rainbow trout into the Santa Cruz River, Argentina.

Date	Number of shipments	Origin and stock	Destination
1906	1	California (McCloud stock)	Santa Cruz River (through Santa Cruz Hatchery)
1908–1910	3	California (McCloud stock)	Santa Cruz, Gallegos, and Chico rivers (through Santa Cruz Hatchery)
1913–1950	Several	Bariloche Hatchery (Chilean stock?)	Unknown
1950–1980	Several	Bariloche Hatchery (Danish stock)	Several sites in Santa Cruz River basin
1981	2	Lake Bueno and Bariloche Hatchery (Danish stock)	Isla Pavón Hatchery, Piedra Buena

were planted in lakes and rivers around Lake Nahuel Huapi in northern Patagonia.

The introduction of salmonids in southern Patagonia started in 1906 (Table 1) when the fourth shipment arrived in Argentina, bringing rainbow trout eggs and various species of salmon, including chinook salmon *Oncorhynchus tshawytscha*, sockeye salmon *O. nerka*, coho salmon *O. kisutch*, and landlocked salmon, as well as lake trout and brook trout (all from the United States). This shipment also contained brown trout *S. trutta* and Atlantic salmon from England. The eggs were taken to a hatchery on the Santa Cruz River, which then became the distribution center of salmonids in the area (Tulian 1908; Marini 1936; Marini and Mastrarrigo 1963; MacCrimmon 1971). Three more shipments of salmonid eggs arrived at the Santa Cruz Hatchery from the United States during 1908 and 1910. These fish were introduced throughout the whole Santa Cruz River drainage as well as into the Gallegos, a neighboring river (Tulian 1908; Valette 1924; Marini 1936; Marini and Mastrarrigo 1963; Baigún and Quirós 1985; Leitch 1991). The Santa Cruz Hatchery operated until 1913. In the following years, local fishermen reported to the Fishery Office sustained harvests of rainbow and brook trout and other (unspecified) salmonids in Lake Argentino, Lake Viedma, La Leona River, and the Santa Cruz River (Figure 1; Valette 1924).

All early shipments of rainbow trout and Pacific salmon, including those directed to the Santa Cruz Hatchery, came directly from California (Valette 1924; Marini and Mastrarrigo 1963). At that time, most of the eggs exported by the United States were obtained from the Baird Hatchery on the McCloud River in California (Scott et al. 1978), a major distribution center for rainbow trout eggs that operated from 1872 to 1935 (Leitritz 1970). The eggs imported during the early development of the Santa Cruz Hatchery presumably contained a mixture of anadromous and resident rainbow trout, as steelhead runs existed at sites where the Baird Station collected fish (Wales 1939; Busack and Gall 1980; Nielsen et al. 1997a)

In 1930, the Bariloche and Río Cicerone Hatcheries (Tucumán Province) became the main centers of salmonid propagation in Argentinean waters. Introductions into the Santa Cruz drainage from these new sources continued throughout the 1950s, 1960s, and 1970s. Unlike with the initial shipments, however, the stocks of rainbow trout that were favored after 1950 came from transplanted populations in Denmark and Germany (Baigún and Quirós 1985), though these may have originated in California.

Finally, in 1991, the municipality of Piedra Buena built a hatchery on the Santa Cruz River. The fish used to supply this hatchery came from the same Danish stock as those in the Bariloche Hatchery. Piedra Buena Hatchery trout are descendants of fish from Lake Bueno in Chubut Province (D. Wegrzyn, director of fisheries for Chubut Province, personal communication). Additional shipments of the same stock, originating in the Bariloche Federal Hatchery, arrived later (Rubén Hudson, Municipal Pisciculture Facility, Isla Pavón, personal communication). The presumed anadromous run in the Santa Cruz River was observed before the establishment of the Piedra Buena Hatchery, and stocking is not regularly conducted. However, escapes occur regularly, and the hatchery's proximity to the area where anadromous rainbow trout are caught suggests that escaped fish could be interbreeding with wild populations.

Genetics

The genetic analysis was based on small sample sizes and should be considered preliminary. Nevertheless, clear and consistent patterns emerge. Tests of genotypic heterogeneity show no significant differences between anadromous and resident fish, but significant differences between these two groups and hatchery fish at a minimum of six

TABLE 2.—Results of microsatellite analyses. The first four columns show general statistics for the loci analyzed. The last three columns show the results of the statistical tests for homogeneity in genotype frequencies between groups and for different loci; $P < 0.05$*; $P < 0.01$**. The allele frequencies are shown in Appendix 2.

				Probability of homogeneity of genotype frequencies		
Locus	Number of fish	Number of alleles	Allele range	Anadromous versus resident	Anadromous versus hatchery	Resident versus hatchery
Omy325	48	12	102–154	0.370	<0.001**	<0.001**
Omy77	47	16	100–136	0.105	<0.001**	<0.001**
Ots1	49	10	165–249	0.178	<0.001**	0.003**
Ots100	49	12	169–221	0.440	<0.001**	<0.001**
Ots103	49	4	185–221	0.559	0.018*	0.406
Sfo8	49	14	221–297	0.381	<0.001**	<0.001**
Ssa85	46	6	101–123	0.216	0.002**	0.101

out of seven loci (Table 2; see also the allele frequencies in Appendix 2). Likewise, unbiased multilocus estimates of F_{ST} are -0.003 between anadromous and resident fish, 0.123 between hatchery and anadromous fish, and 0.105 between hatchery and resident fish.

The microsatellite data show a tendency towards heterozygote deficits at several loci (Appendix 2). These could stem from the presence of null alleles, nonrandom sampling of the respective populations, or scoring errors. One of the microsatellite loci used in this study, *Omy77*, has been shown to have a null allele in other rainbow trout populations (Ardren et al. 1999). None of these possibilities undermines the basic conclusions that anadromous and resident fish are not genetically differentiated and that both are distinct from the hatchery population; indeed, the patterns of departure from Hardy−Weinberg expectations were similar for anadromous and resident fish and different from those for hatchery fish (Appendix 2).

Differences between the wild and hatchery populations could have arisen either because they have different ancestral stocks (wild fish having a California ancestry and hatchery fish a Danish ancestry) or because strong selection or drift operated on a common ancestral stock. The first scenario implies that wild populations were derived from early introductions based on U.S. fish (Table 1) before European stocks started to be favored. Because records of wild populations precede the appearance of the Danish hatchery population in the Santa Cruz River by many years, this scenario seems the most likely. However, given that most of the rainbow trout populations that were translocated from their native range ultimately derived from the McCloud River of California more than 100 years ago (MacCrimmon 1971; Lever 1996), the difference between the Santa Cruz fish and the Danish hatchery stock may reflect a complex history of differential selection, stock introgression, and genetic drift (including bottlenecks and founder effects) rather than independent evolutionary lineages.

Anadromous and resident fish, on the other hand, do not show significant differences for any of the loci investigated. This lack of differences between the two wild types provides a preliminary indication of the common origin of both groups and, probably, of active gene flow between the two types. Although the small sample sizes could be affecting our power to detect differences, the consistency of the results for all loci provides support for the close relatedness of anadromous and resident fish. Our results are consistent with a scenario in which both groups represent alternative life history types from the same population unit. This situation is analogous to that in many U.S. coastal rivers from Alaska to California, where wild steelhead and resident rainbow trout co-occur and do not seem to be reproductively isolated. Moreover, analyses of the genetic variation of such populations based on allozymes, mitochondrial DNA, and nuclear microsatellites have shown small genetic differences between types (Busby et al. 1996; Nielsen et al. 1997a, 1997b).

Biological Characteristics and Life History of Santa Cruz Rainbow Trout

Adult migration timing.—North American steelhead present two reproductive ecotypes (Busby et al. 1996) based on the state of sexual maturity upon river entrance. Individuals of the stream-maturing type enter rivers early and in an immature condition (fall run in Alaska, summer run in the Pacific Northwest and northern California), while those of the ocean-maturing type enter rivers as mature fish shortly before spawning (spring run in Alaska and

TABLE 3.—Stream residency patterns (proportion of individuals by freshwater age) of Santa Cruz River rainbow trout as compared with steelhead populations in North America. The number of Santa Cruz River fish in each category is shown in parentheses.

Stream residency (years)	Age frequency						
	Alaska	British Columbia	Washington	Oregon	California	Sacramento River	Santa Cruz River
1		0.008	0.063	0.038	0.251	0.105	0.033 (1)
2	0.131	0.395	0.857	0.775	0.666	0.690	0.900 (27)
3	0.691	0.542	0.080	0.176	0.083	0.186	0.067 (2)
4	0.178	0.055		0.011		0.020	

winter run elsewhere). As indicated by fishing records, the anadromous run in the Santa Cruz River takes place between February and May, peaking in late March and early April (early fall). Allowing for the 6-month shift in seasonality associated with the change in hemispheres, this run occurs somewhat later than typical summer runs in California and the Pacific Northwest. However, the Sacramento River has an early winter run that occurs at a comparable time (August to November), and the rivers of southern Oregon and northern California are known for the so-called ''half-pounders'' (juvenile fish that overwinter in freshwater) that enter rivers in September.

Given the information available, we cannot establish whether runs later than the ones we documented occur in the Santa Cruz River. The sportfishing season is closed in late May, but accounts by local fishermen indicate that experimental winter fishing has proven unsuccessful.

Freshwater residence of anadromous fish and ocean migration.—Scale pattern analysis indicated that 27 out of 30 anadromous fish had spent 2 years in freshwater (Table 3; Figure 2). The exceptions are one fish that appeared to have spent 1 year in the river and two that had spent 3 years prior to their first ocean migration. A 2-year stream residency is found in most steelhead populations from Washington, Oregon, and California (Table 3). Longer stream residencies are common among British Columbia and (especially) Alaskan populations, where 3-year residencies predominate.

The freshwater growth of resident fish in Yaten Guajen and anadromous fish at Piedra Buena, as inferred from back-calculation of scale annuli, is comparable (t-test of second annulus radius; N = 26 for anadromous fish, 14 for resident fish; P = 0.847). However, the third annulus in anadromous fish shows a largely significant ($P < 0.001$) increase in growth rate (Figure 2; also see section on growth below).

In most (28 out of 30) of the anadromous fish we analyzed, a distinctive and consistent scale check appears between the second and third annuli (Figure 2). Unlike in annual checks, there is no gradual change in growth rate associated with this check. The change in growth rates suggested by the intercirculi spacing is abrupt and looks very much like the so-called ''tidewater annulus'' reported by Sumner (1948) for Tillamook steelhead. According to this author, such marks correspond to the migration phase between the estuary and the ocean.

Maturation patterns.—Our data provide a firm indication that Santa Cruz River fish re-enter the river during their first year of ocean life, that is, after a few months at sea. Smaller anadromous fish dominate the catch. For instance, half of the fish we collected were entering the river for the first time and had no ocean annuli on their scales (Appendix 1). This pattern is consistent with reports from fishermen indicating that more than half of the fish caught in 1997 were undersized for the regulations in place at that time (less than 450 mm), which corresponds to marine age 1 (see section on growth below). Scale patterns of older fish showed that the ocean-age-1 annuli were very homogeneous, suggesting that all fish follow this same behavior. No indications were found of alternative growth and oceanic residence patterns.

Because we did not sacrifice anadromous fish, age at maturity could be inferred only from scale pattern analysis (Figure 2). The marine section in a scale of a typical Santa Cruz fish shows a first annulus with moderate resorption along the sides and no scarring. Subsequent annuli show strong resorption and scarring all around the scale. This pattern could emerge if fish mature during their first river entry but spend proportionally less energy in reproduction than in subsequent years. Alternatively, the initial weak check could result from overwintering in their first river entrance as immature fish, and subsequent stronger checks from spawning in later river entrances. Although

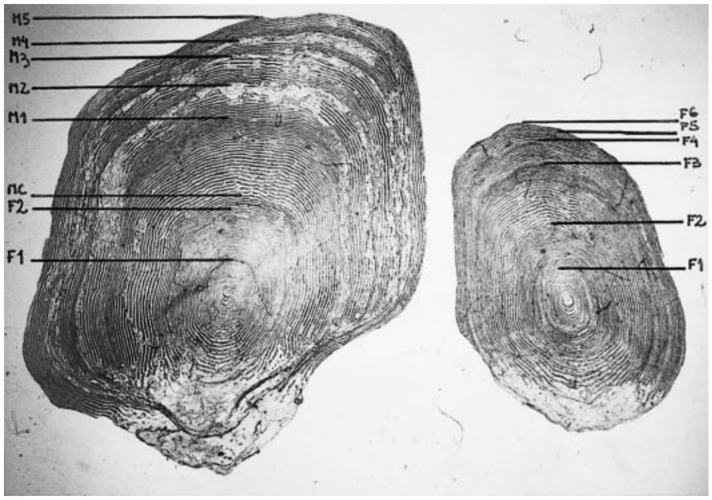

FIGURE 2.—Representative scales of resident (right) and anadromous (left) fish. The letters indicate our interpretation of scale checks, with **F** for river growth annuli, **MC** for migration checks or tidewater growth annuli, and **M** for marine growth annuli. The estimated age of resident fish is 3.2s.1; **F4** and **F5** indicate spawning checks, **F6** the scale border in April. The estimated age of anadromous fish is 2/1.3s.1; **M1** indicates the in-river overwintering mark, **M2** to **M4** spawning checks, and **M5** the scale border in April.

weak spawning checks are not uncommon in winter-run North American steelhead (Davis and Light 1985), Santa Cruz fish show a consistent combination of initial weak checks followed by strong checks. River overwintering of juvenile marine stages of rainbow trout occurs in five rivers of southern Oregon and northern California. In those populations, fish of less than 400 mm (half-pounders) return to overwinter in the river after a few months at sea (Snyder 1925; Kessner and Barnhart 1972). A similar life cycle is found in the coastal cutthroat trout *Oncorhynchus clarki clarki* (Trotter 1989) and in European sea-run brown trout, where immature fish (''whitlings'') return to the river after 2 months in coastal areas (Lamond 1916). In fact, the strong spawning checks observed in Santa Cruz fish scales and the multiplicity of spawning (see below) are very similar to those of sea-run brown trout (Lamond 1916; Nall 1930; Richard and Bagliniere 1990).

In reality, there is no way to validate spawning events from scale inspection alone. Until we are able to certify maturation of young fish by direct inspection of their gonads, we will assume that weak resorption on the sides of the scale indicates overwintering and a strong check with scarring indicates spawning. Following this criterion, most Santa Cruz fish would spawn for the first time on their second river entrance at ocean age 2 (Table 4).

Multiple spawning occurs in North American steelhead, but spawning populations are strongly dominated by first-time spawners (Busby et al. 1996). For example, two spawning migrations rarely occur in fish from British Columbia and Washington, and three are infrequent in Oregon and California populations (Table 5). Among Santa Cruz River steelhead, on the other hand, multiple spawning is the rule. Sixty percent of the fish with spawning events in our samples had experienced three or more spawning events, 33% four or more, and 20% five or more (Table 5). The oldest anadromous fish we found had spent 2 years in freshwater, had already entered the river and spawned on six occasions, and was entering the river for the seventh time. In contrast, we did not find resident fish with more than four spawning events or older than 6 years.

Age and growth.—The size at age of Santa Cruz seagoing and resident fish is shown in Figure 3. During sea life, anadromous trout attain much larger sizes than resident fish at equal ages. The growth rates of anadromous Santa Cruz fish are high compared with those recorded for North American steelhead populations with a comparable life history. For example, typical half-pounders in North America are less than 350 mm (range 250–349 mm) after spending 4–5 months (April−September) in the ocean (Kessner and Barnhart 1972). Assuming that Santa Cruz smolts leave the river in mid-spring, 2/1 fish would also spend 4–5 months in the ocean but reach 412 mm

TABLE 4.—Ocean age patterns at first spawning of the 19 repeat spawners in our samples, as compared with steelhead populations in North America. The number of Santa Cruz River fish in each category is shown in parentheses.

Ocean age at first spawning (years)	Age frequency						
	Alaska	British Columbia	Washington	Oregon	California	Sacramento River	Santa Cruz River
0			0.003				
1	0.030	0.018	0.020	0.075	0.599	0.599	0.211 (4)
2	0.658	0.615	0.650	0.756	0.369	0.401	0.737 (14)
3	0.313	0.360	0.320	0.153	0.032		0.053 (1)
4		0.010	0.010	0.020			

(range, 370–455 mm) by the time they enter the river.

Mature Santa Cruz fish compare well in size with North American populations, even with some that have more extended ocean residencies. For example, the size of Santa Cruz River 2/2 fish, which are entering the river for the second time, is very similar to that of 2/2 fish from Waddell Creek, California, coming into freshwater for the first time after two uninterrupted years in the ocean (Shapovalov and Taft 1954). Large size in North American steelhead results primarily from prolonged marine residence, delayed maturation, and reduced iteroparity. Santa Cruz fish, on the other hand, acquire large size from much shorter and more frequent marine excursions and after multiple spawning events. For example, while a typical 9-kg fish from British Columbia enters the river for the first time to spawn after 2 to 3 years in the river and four consecutive years at sea (total age of 6 to 7 years), a Santa Cruz fish of the same weight is likely to have spent 2 years in freshwater, to have returned to the river seven times, and to be on its sixth spawning migration (total age of 9 years). Trophy steelhead in North America are those that spend as many as 6 years in the ocean before returning to the river (weighing 12 kg or more), a size that is apparently unreachable by the highly iteroparous fish from the Santa Cruz.

Discussion

Tracking the divergence of transplanted fish provides a direct means of assessing the genetic and environmental bases of life history characteristics, as well as an opportunity to estimate the rates at which heritable population characters evolve (Stearns 1983; Reznick et al. 1990; Hendry and Kinnison 1999). As has happened in many other rivers in Patagonia, the Santa Cruz has today established populations of rainbow trout of substantial fishing value. What is peculiar about the Santa Cruz is the presence of an anadromous run, an uncommon behavior in introduced rainbow trout (MacCrimmon 1971) that has not been reported for other Argentinean rivers.

The arrangement of populations within the Santa Cruz River and throughout the rivers along the latitudinal gradient of Patagonia provides a remarkable setting in which to study the genetic and environmental factors that promote anadromy and population differentiation in associated traits. At this point, there are many critical aspects of these populations that we do not know. For instance, we do not know when the anadromous run took hold,

TABLE 5.—Repeat spawning of Santa Cruz River rainbow trout as compared with steelhead populations in North America. The 1997 river entrance of repeat spawners was computed as a spawning event, assuming that all fish sampled would survive to spawn. The number of Santa Cruz River fish in each category is shown in parentheses.

Number of spawning events	British Columbia	Washington	Oregon	California	Sacramento River	Santa Cruz River
1	0.927	0.921	0.814	0.815	0.830	0.269 (4[a])
2	0.063	0.072	0.151	0.170	0.145	0.133 (2)
3	0.010	0.007	0.035	0.015	0.020	0.266 (4)
4				0.000	0.005	0.066 (1)
5						0.133 (2)
6						0.066 (1)
7						0.066 (1)

[a] Estimated number of observed virgin fish of ocean ages 1 and 2 that would spawn that year (from probabilities in Table 4).

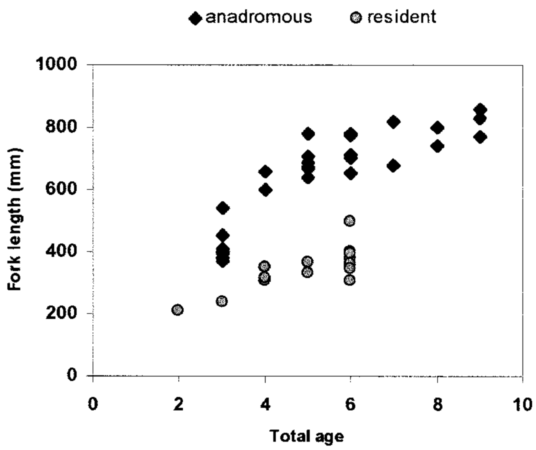

FIGURE 3.—Size at age for resident and anadromous fish. For comparison, the total age of anadromous fish is calculated as 2 (the most common river age) plus the ocean age.

what exactly the parental stock of the Santa Cruz rainbow trout was, to what extent they are segregated from resident populations, and how far from the estuary they range during their marine period. Nevertheless, the information presented in this paper allows us to set the stage for a research program to study the development of alternate life history patterns in the wild.

At different times, the Santa Cruz River has received fish from resident and anadromous stocks. Whether the existing fish are descended from California steelhead and are displaying their characteristic anadromous behavior or are resident fish that developed this behavior secondarily is open to question. Our results suggest that microsatellite analysis could provide a powerful way to discriminate populations founded by California or Danish fish as well as to identify the specific parental stocks of Santa Cruz rainbow trout. Nevertheless, the best way to elucidate the above question may be to combine molecular-genetic approaches with experimental ones, such as rearing experiments.

The way anadromy is expressed in Santa Cruz rainbow trout is extraordinary. Although their freshwater residence, growth patterns, and age at maturity do not differ dramatically from those of North American stocks, the longevity and the frequency of repeat spawning of Santa Cruz fish have no parallel in Northern Hemisphere populations or, for that matter, in resident Santa Cruz fish. This came as a surprise to us because the basic life history plan of archetypal anadromous *Oncorhynchus* populations combines anadromy, fast growth, and reduced iteroparity or strict semelparity (Groot and Margolis 1991). We therefore expected anadromy in introduced salmonids to have a cost in terms of survival and iteroparity. On the contrary, adult Santa Cruz rainbow trout appear to be able to reduce mortality risks by making short marine excursions. This observation has far-reaching implications for the way in which we visualize the coevolution of anadromy and semelparity. It also reinforces the idea that anadromy in introduced populations provides a precious opportunity to unveil how basic life history trade-offs interplay in the evolution of anadromous species.

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Appendix 1. Wild Fish Sampled

TABLE A.1.—Descriptions of the wild fish analyzed in this paper. The following abbreviations are used: ANA = anadromous, RES = resident, PB = Piedra Buena, and YG = Yaten Guajen. The letters Y and N indicate whether or not that fish was included in the genetic analysis. See text for an explanation of age designations.

Type	Genetic analysis	Date	Site	Sex	Fork length (mm)	Weight (g)	Estimated age
ANA	N	15 Mar 1996	PB	F	710	4,670	2/1.2s.1
ANA	N	17 Mar 1996	PB	M	675	3,770	2/1.1s.1
ANA	N	18 Mar 1996	PB	?	775	5,410	2/1.2s.1
ANA	N	18 Mar 1996	PB	F	820	6,400	2/1.3s.1
ANA	N	22 Mar 1996	PB	F	690	3,380	2/1.1s.1
ANA	N	24 Mar 1996	PB	M	640	3,540	2/1.1s.1
ANA	N	25 Mar 1996	PB	F	860	9,100	2/6s.1
ANA	Y	11 Apr 1997	PB	M	742		2/1.4s.1
ANA	N	12 Apr 1997	PB	F	800		2/1.4s.1
ANA	N	12 Apr 1997	PB	?	540		2/1
ANA	N	12 Apr 1997	PB	?	370		2/1
ANA	N	12 Apr 1997	PB	?	455		2/1
ANA	Y	12 Apr 1997	PB	?	380		2/1
ANA	Y	12 Apr 1997	PB	?	395		2/1
ANA	Y	12 Apr 1997	PB	?	380		2/1
ANA	Y	12 Apr 1997	PB	?	780		2/1.2s.1
ANA	Y	12 Apr 1997	PB	?	411		2/1
ANA	Y	12 Apr 1997	PB	F	708		2/2s.1
ANA	Y	12 Apr 1997	PB	F	380		2/1
ANA	Y	12 Apr 1997	PB	F	780		2/1.1s.1
ANA	Y	12 Apr 1997	PB	?	655	3,300	2/1.2s.1
ANA	Y	12 Apr 1997	PB	?	410		2/1
ANA	Y	12 Apr 1997	PB	F	770		1/1.5s.1
ANA	Y	12 Apr 1997	PB	F	830	6,000	2/6s.1
ANA	Y	12 Apr 1997	PB	F	701	4,400	2/1.2s.1
ANA	Y	19 Apr 1997	PB	?	400		3/1
ANA	Y	20 Apr 1997	PB	F	680		3/1.3s.1
ANA	N	23 Apr 1997	PB	?	670		2/2.1
ANA	N	24 Apr 1997	PB	?	660		2/1.1
ANA	N	24 Apr 1997	PB	F	600		2/1s.1
RES	N	11 Apr 1997	PB	F	380		2.3s.1
RES	N	12 Apr 1997	PB	F	400		2.3s.1
RES	N	12 Apr 1997	PB	M	498		3.2s.1
RES	Y	18 Apr 1997	YG	F	360		2.3s.1
RES	Y	18 Apr 1997	YG	F	330		3.1s.1
RES	Y	18 Apr 1997	YG	F	345		3.2s.1
RES	Y	18 Apr 1997	YG	M	395		2.3s.1
RES	Y	18 Apr 1997	YG	M	350		3.1
RES	Y	18 Apr 1997	YG	M	305		3.1
RES	Y	18 Apr 1997	YG	M	305		2.3s.1
RES	Y	18 Apr 1997	YG	M	237		2.1
RES	Y	18 Apr 1997	YG	M	318		3.1
RES	Y	18 Apr 1997	YG	M	365		3.1s.1
RES	Y	18 Apr 1997	YG	M	210		1.1
RES	Y	26 Jan 1997	YG	?	370		
RES	Y	21 Jan 1997	YG	?	340		

Appendix 2. Genetic Analysis

TABLE A.2.—Allele frequencies, observed heterozygosities (H_o), expected heterozygosities (H_e) and probability of departure from Hardy–Weinberg expectations for different loci and fish types.

		Frequencies		
Locus or statistic	Allele	Anadromous Piedra Buena	Hatchery Piedra Buena	Resident Yaten Guajen
Omy325	102			2
	104		1	
	106	5		6
	108	14	9	11
	114	4	7	
	116		1	
	118		3	
	124		4	
	130		9	
	132	1		
	138			1
	154	8		6
H_o		0.44	0.88	0.46
H_e		0.73	0.82	0.74
P		0.037	0.267	0.093
Omy77	100		7	
	102	1	10	
	104	2	2	
	106		1	5
	108			
	112		3	
	114		1	1
	116		1	
	118	9	5	1
	120		1	
	122			
	128		2	
	130	3		
	132			1
	134	2		3
	136	8		5
		7		10
			1	
H_o		0.50	0.76	0.69
H_e		0.82	0.86	0.79
P		0.003	0.648	0.283
Ots1	165	8	9	5
	167	6	7	8
	169		8	
	171		11	5
	173	1		1
	241	9		6
	243	1		
	245	4	1	1
	247	1		
	249	2		
H_o		0.69	0.78	0.62
H_e		0.83	0.78	0.81
P		0.103	0.252	0.547
Ots100	169	16		14
	177	3		4
	187	5	7	2
	189	4		
	195	1		
	199	2	3	1
	203		5	4
	207		2	
	211	1	4	
	215		3	1
	219		4	
	221		5	
			3	

TABLE A.2.—Continued.

Locus or statistic	Allele	Frequencies		
		Anadromous Piedra Buena	Hatchery Piedra Buena	Resident Yaten Guajen
H_o		0.75	0.89	0.77
H_e		0.68	0.90	0.68
P		0.699	0.073	0.733
Ots103	185	2	2	1
	209	21	33	21
	213	3		1
	221	6	1	3
H_o		0.63	0.17	0.38
H_e		0.52	0.16	0.38
P		0.398	1.000	1.000
Sfo8	221	8		
	229	8	2	5
	241	1		3
	245	1	8	
	251		5	4
	257		3	
	259	2	5	
	265		5	
	267	1		2
	271		2	1
	275			3
	291	4		4
	295	5		4
	297		6	
		2		
H_o		0.56	0.89	0.69
H_e		0.85	0.88	0.89
P		0.004	0.078	0.000
Ssa85	101		2	4
	103	9	24	6
	105		2	
	107	16	7	8
	111	7		2
	123		1	
H_o		0.25	0.33	0.40
H_e		0.64	0.53	0.74
P		0.001	0.006	0.015