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Ancestry and genetic structure of resident and anadromous rainbow trout (*Oncorhynchus mykiss*) in Argentina

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Abstract

Since the first introduction from North America more than a century ago, rainbow trout (*Oncorhynchus mykiss*) have rapidly established self-sustaining populations in major river basins of Patagonia. Many generations later, only the freshwater resident life history is expressed in the Chubut and Negro rivers of northern Argentinian Patagonia, whereas both the resident and anadromous life histories are found in the Santa Cruz River of southern Argentina. Despite previous studies that have tried to identify the sources of these introduced populations, uncertainty still exists. Here we combined data from many single-nucleotide polymorphisms and microsatellite loci in *O. mykiss* populations from Argentina and North America to evaluate putative source populations, gene flow between Argentinian river basins, and genetic diversity differences between Argentinian and North American populations. We found that populations from northern and southern Patagonia are highly differentiated and have limited gene flow between them. Phylogeographic analysis also confirmed that they have separate origins, with the northern populations most closely related to the domesticated rainbow trout strains that are raised worldwide and the Santa Cruz River populations most closely related to North American populations from California and Oregon that have an anadromous component. In addition, fish with different life histories in the Santa Cruz River were found to constitute a single interbreeding population. No evidence was found of reduced genetic variation in introduced rainbow trout, suggesting multiple contributing sources. In spite of these advances in understanding, significant questions remain regarding the origins and evolution of the introduced *O. mykiss* in Patagonia.

KEYWORDS
anadromy, Argentina, microsatellite, rainbow trout, SNPs, steelhead

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1 | INTRODUCTION

Rainbow trout and steelhead, the non-anadromous and anadromous forms of *Oncorhynchus mykiss*, have a native distribution extending from the Kamchatka Peninsula in eastern Russia eastward to southern Alaska and coastal and interior regions of British Columbia, Washington, Oregon, California, and northwestern Mexico (Behnke, 1992).

The parallel evolution of anadromy and residency across different phylogeographic lineages of *O. mykiss* has led to a complex network of populations with anadromous and resident life histories, and has led to inconsistencies in the delineation of conservation units based on migratory life-history traits (Clemento et al., 2009). Presently, there is general consensus that rather than distinct evolutionary lines, the relationship between anadromous and resident rainbow trout appears to be more concordant with geography than with life-history strategy (Clemento et al., 2009; Docker & Heath, 2003; Garza et al., 2014; McEwan, 2001; Olsen et al., 2006; Pearse et al., 2019). For example, large genetic differences have been reported between populations of *O. mykiss* in some major river systems (Busby et al., 1996; Hendry et al., 2002). However, within these river systems, anadromous and resident fish in a given tributary are usually more closely related to one another than to populations of the same life history in other tributaries and river systems, supporting the view that within a geographic area, alternative forms share an evolutionary legacy (Allendorf, 1975; Busby et al., 1996; Currens et al., 1997). Conversely, substantial genetic divergence has been recorded between non-anadromous/resident and anadromous trout in areas where the two forms have been isolated by long-standing natural barriers, allowing for independent evolution (Busby et al., 1996; Deiner et al., 2007; Kostow, 2003; Nielsen et al., 2003). In sympatry, the relationship between steelhead and resident rainbow trout may vary from complete genetic isolation to genetically indistinguishable groups (Busby et al., 1996; McPhee et al., 2007; Narum et al., 2004; Zimmerman & Reeves, 2000).

The complex relationship between anadromous and resident forms of trout in different river systems has led many authors to propose that the expression of alternative life histories in *O. mykiss*, and in salmonids more generally, is the outcome of interacting genetic variation and environmental factors. Whether an individual migrates or not depends on a combination of its genetic constitution and specific environmentally triggered threshold traits (Phillis et al., 2016; Thrower et al., 2004). This concept also holds true for other salmonid species, including Arctic charr (Jonsson & Jonsson, 1993), brook charr (Thériault & Dodson, 2003), Atlantic salmon (Thorpe et al., 1998), and others (Aubin-Horth & Dodson, 2004; Garant et al., 2002). Because threshold values for traits that lead to different strategies may differ among populations, due to environmental selection pressures (Aubin-Horth & Dodson, 2004) or random genetic drift (e.g., Moczek et al., 2002; Roff, 1996), the incidence and expression of anadromy often vary among individuals, populations, and environments. For example, a relationship has been described between juvenile body size and the proportions of mature parr and smolts in white-spotted charr across various latitudes (Yamamoto et al., 1999).

Historical records reveal rainbow trout propagation and exports commencing in 1870, when the California Acclimatization Society initiated artificial propagation in the San Francisco Bay area (Behnke, 2002). In contrast to the long-standing belief that the McCloud River was the exclusive source of early hatchery rainbow trout domestication, the origin of hatchery trout strains is notably diverse (Behnke, 2002). After the initial domestication of trout from the San Francisco Bay area, later contributions to hatchery strains came from Clear Lake, California, and the McCloud River, in 1873 and 1877, respectively (Leitritz, 1970). Interestingly, the initial translocations of rainbow trout beyond their native range, to New York and Michigan, occurred in 1874 and 1876, but did not originate from the McCloud River area (Behnke, 1992; Wales, 1939). However, by 1888, *c.* 2.5 million rainbow trout eggs of anadromous and resident stocks sourced from the Baird Station hatchery on the McCloud River and coastal rivers in northern California and southern Oregon were shipped to establish broodstocks in other US hatcheries (Behnke, 1992, 2002; Busack & Gall, 1980; Leitritz, 1970). Early overseas exports of rainbow trout to Japan and Europe occurred in 1877, and these exports extended to various global destinations, including Sri Lanka, New Zealand, China, and Argentina (MacCrimmon, 1971; Stanković et al., 2015).

The introduction of rainbow trout across the geographical gradient of Patagonia, Argentina, provides an opportunity to evaluate the establishment of new populations and the maintenance of anadromy and residency in this species. In Patagonia, rainbow trout were first introduced in the early 1900s, reportedly from the McCloud River in northern California, and then later between 1950 and 1970, with imports from Denmark using strains sourced from secondary and tertiary transfers of rainbow trout within Europe in the late 1800s (see below, MacCrimmon, 1971; Pascual et al., 2001; Riva Rossi et al., 2004; Stanković et al., 2015). These introductions led to the establishment of self-sustaining populations in the major river basins of northern Patagonia, the Negro (38° S) and Chubut rivers (43° S), and in the Santa Cruz River (50° S) in southern Patagonia (Figure 1). Over 10–25 generations after these introductions, both resident and migratory (anadromous) life histories are found in the Santa Cruz River, whereas only the resident life history has been recorded in northern Patagonian populations (Pascual et al., 2001; Riva Rossi et al., 2004). In the Santa Cruz River, the anadromous and resident forms are genetically similar (Pascual et al., 2001), and both forms can give rise to each other, suggesting a single population with alternative phenotypes (Riva-Rossi et al., 2007).

Understanding the origins of *O. mykiss* populations in Argentina will help to clarify whether current life-history diversity is a consequence of introduction from populations with life-history variation or whether this variation has arisen de novo in the recipient environments. Previous analysis of the mtDNA control region indicated that *O. mykiss* populations from the Santa Cruz River and northern Patagonia derived from different source populations (Riva Rossi et al., 2004). However, considerable uncertainty exists regarding the origin of the Santa Cruz River population and specifically if it was established from a single source in the McCloud River, California, United States, or if it resulted from multiple mixed sources, possibly from California or elsewhere on the West Coast of North America. In addition, it is unclear whether the source population(s) consisted only of individuals with a single life history or with both resident and anadromous life histories (Behnke, 2002; Nielsen et al., 2005; Pascual et al., 2002; Riva Rossi et al., 2004).

Here, we survey genetic variation at 93 single-nucleotide polymorphisms (SNPs) and 14 microsatellite loci to investigate the evolutionary relationships among and between steelhead and rainbow trout populations from Argentina and the West Coast of North America. Because of the differences in migratory life history found among Argentinian populations and the uncertainty about their origins, we evaluate if Argentinian populations came from the same or different ancestral populations from North America and, more specifically, whether they came from the California Central Valley (where the McCloud River is located), hatchery strains or other populations from California and Oregon. We also study gene flow between the populations of *O. mykiss* in Argentina, as it may be an important factor to maintain population structure. In some rivers, the presence of different migratory ecotypes is indicative of separate populations, so here we investigate whether the anadromous and resident ecotypes found in the Santa Cruz River represent different populations and if they share ancestral origins. Genotype data from a locus within a large chromosomal inversion on chromosome Omy5 associated with migratory life-history variation in some steelhead populations (Pearse et al., 2019) offer further potential insights into the evolution of anadromy in *O. mykiss* in Patagonia. Finally, when populations are founded by a few individuals, founder effects and bottlenecks can produce a decrease in genetic diversity, so we also evaluate whether introduced *O. mykiss* populations in Argentina have reduced genetic variation in contrast with native populations.

2 | METHODS

2.1 | Stocking history

Introductions of *O. mykiss* in Patagonia started in the early 1900s, mainly with eggs exported from the United States, but with occasional imports from Germany and France (Riva Rossi et al., 2004). Within a few generations of the original introduction, successful populations of presumably resident trout were well established, and natural reproduction was observed in every basin in the region where they had been introduced (Valette, 1922). In the Santa Cruz River, imported rainbow trout presumably from California or Oregon, United States, were stocked between 1906 and 1910, and naturalized populations were well established and widely distributed throughout the basin by the 1920s (MacCrimmon, 1971; Pascual et al., 2001; Riva Rossi et al., 2004; Valette, 1924). Because trout introductions in the Santa Cruz River occurred over a decade after the Baird Station hatchery on the McCloud River had closed (Pascual et al., 2002), Behnke (2002) proposed that the introduced stock may actually derive from multiple sources from the McCloud River and various coastal rivers in northern California and southern Oregon, including the Klamath River, Redwood Creek, Kern River, and Rogue River, as well as from hatcheries in Caledonia, New York, and Northville, Michigan, containing different varieties of *O. mykiss*, including redband trout, golden trout, and coastal steelhead trout, all of which were commonly utilized during the early 1900s as broodstock sources (Behnke, 1992, 2002; Busack & Gall, 1980; Colihueque et al., 2019).

Rainbow trout introductions to Argentina briefly restarted in 1930 from Chile (of German origin, Colihueque et al., 2019) but intensified in the period 1950–1970, mostly with stocks raised in Denmark. Danish hatchery rainbow trout stocks also have complex ancestry. The first translocation of rainbow trout to Europe was when eggs from the Baird Station were shipped to Paris in 1879 and then to Germany in 1882 (Baird, 1886; Behr, 1882; Clark, 1884). Rainbow trout were then transferred extensively across Europe, particularly from German hatcheries to Austria, Bulgaria, Denmark, Poland, Sweden, Switzerland, Russia, Slovakia, Slovenia, and the Czech Republic (Crawford & Muir, 2008). Rainbow trout most likely arrived in Danish trout farms from Germany around 1894. Since then, eggs from the United States, Canada, New Zealand, and France have been imported to Patagonia (MacCrimmon, 1971; Stanković et al., 2015).

These imports were maintained by the Bariloche hatchery in Argentina, which propagated them extensively throughout Patagonia, particularly into northern basins (e.g., Negro and Chubut rivers) for commercial (aquaculture) and recreational fishery purposes, including stock enhancement of public and private waters. Descendants of the Danish strain from the Bariloche hatchery were utilized as the broodstock source of the Piedra Buena hatchery, a small aquaculture facility established on the Santa Cruz River in 1991, dedicated to the production of trout for human consumption and to a lesser extent for stock enhancement. These fish were used for trout farming rather than river stocking, but they were planted in low abundances in small tributaries of the upper Santa Cruz River basin, including small creeks flowing into Lake Roca and the De las Vueltas River (R. Hudson, Manager Piedra Buena Hatchery, personal communication).

2.2 | Sample collection

Pelvic-fin clips and scales were taken from adult anadromous ($n = 113$) and non-anadromous trout ($n = 115$) at three sites in the mainstem Santa Cruz River during March–April 1997, 1998, 2000, and 2001 (fall in the Southern Hemisphere); September–October 1999, 2000, and 2001 (spring); and May–September 2004 (fall to spring). In addition, dry pelvic tissue and scale samples were taken from adult resident trout during the period 1994–2000 from the Negro ($n = 21$) and Chubut rivers ($n = 18$) in northern Patagonia, as well as Lake Argentino ($n = 18$), Lake Roca ($n = 7$), La Leona River ($n = 7$), and De las Vueltas River ($n = 5$) in the upper basin of the Santa Cruz River (Figure 1; Table 1). Fish ecotype (e.g., anadromous, non-anadromous) was determined using scale pattern analysis (Pascual et al., 2001; Riva-Rossi et al., 2007). Although Argentina did not have specific regulations for care or use of nonnative animals in

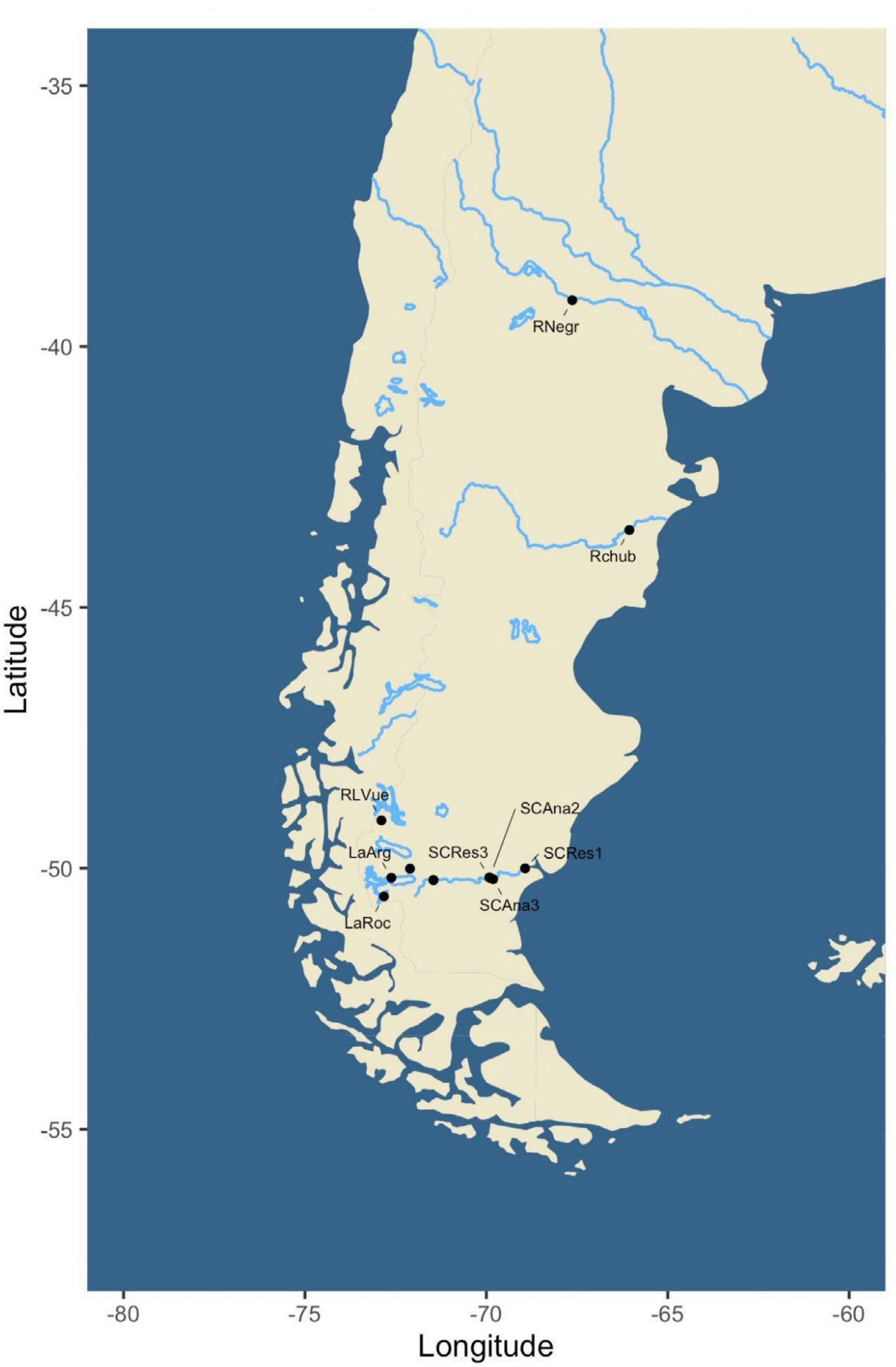

FIGURE 1 Geographic locations of *Oncorhynchus mykiss* sampling sites in Argentina. From north to south—Negro River: RNegr, Chubut River: RChub, Las Vueltas River: RLVue, La Leona River: LaLeo, Lake Argentino: LaArg, Lake Roca: LaRoc, Santa Cruz River-Resident: SCRes, and Santa Cruz-Anadromous: SCAna.

place at the time of this study, all fish capture and handling procedures were approved by the Ministerio de Agricultura, Ganadería y Pesca of Río Negro Province; by the Instituto Provincial del Agua, Administración General de Recursos Hídricos of Chubut Province; and by the Subsecretaría de Pesca y Asuntos Portuarios of Santa Cruz Province and were conducted using the best-available science and veterinary practices for minimizing stress and ensuring fish survival.

In addition, to investigate the ancestry and origins of these introduced fish, data from 54 natural and hatchery *O. mykiss* populations from the native range (California and Oregon; Table 1) were included in this study. These samples were collected and analysed as part of studies of population structure and evolutionary history of *O. mykiss* throughout the southern portion of their native range (Abadía-Cardoso et al., 2016; Arciniega et al., 2016; Clemento et al., 2009; Garza et al., 2014; Pearse & Garza, 2015).

2.3 | Microsatellite and SNP procedures

DNA was extracted from all the samples using DNeasy 96 tissue extraction kits on a BioRobot 3000 (Qiagen, Inc.) following the manufacturer's procedures.

TABLE 1 Summary statistics of the 93 SNPs and 14 microsatellite assays in *Oncorhynchus mykiss* populations from Argentina and North America.

O. mykiss

River-sampling site	Population code	Sample size	Loci typed	H_e	H_o	A_R	% Polymorphic loci	Omy05 ancestral haplotype freqency
Patagonia Argentina								
Rio Negro-Paso Córdoba/Curso inferior	RNegr	21	107	0.40	0.37	2.0	88	77
Rio Chubut-Curso inferior/Dique	RChub	18	107	0.39	0.39	2.5	87	78
Río de las Vueltas-SC	RLVue	5	107	0.38	0.39	N/A	63	60
La Leona-Santa Cruz	LaLeo	7	107	0.31	0.33	N/A	60	42
Lago Argentino-Santa Cruz	LaArg	18	107	0.33	0.32	2.9	74	47
Lago Roca-Santa Cruz	LaRoc	17	107	0.36	0.35	3.2	87	41
Santa Cruz River-Resident	SCRes	113	107	0.35	0.34	2.5	92	48
Santa Cruz River-Anadromous	SCAna	112	107	0.34	0.34	3.0	86	56
North America								
Columbia River-Still Creek/Summer	ColSC	24	100	0.30	0.29	3.4	84	7
Columbia River-Wiley	ColWy	23	100	0.25	0.26	2.0	78	0
Umpqua River-Winter	UmpWi	24	101	0.34	0.32	3.0	92	73
Umpqua River-Summer	UmpSu	21	101	0.33	0.31	2.9	89	86
Rogue River-Lobster Creek/Winter	RouLb	17	100	0.36	0.35	2.9	97	47
Rogue River-Lawson Creek/Winter	RouLw	23	100	0.36	0.35	2.8	94	64
Smith River-South Fork Rowdy Creek	SmiSF	48	107	0.38	0.37	2.8	94	39
Klamath-Horse Linto Creek	KlaHL	72	107	0.34	0.35	2.0	96	56
Klamath-New River/Summer	KlaNR	47	101	0.35	0.34	3.6	96	52
Mad River-Canon	MadRC	48	107	0.38	0.38	2.0	100	69
Mattole River	Matto	31	106	0.39	0.40	3.3	97	61
Eel River-Hollow Tree Creek	EelHT	45	107	0.39	0.38	2.3	95	84
Eel River-Willits Creek	EelWC	38	107	0.41	0.41	2.0	98	41
Eel River-Middle Fork Summer	EelMF	24	100	0.39	0.39	3.1	96	59
Noyo River-Little North Fork	NoyLF	64	107	0.40	0.40	2.4	99	86
Gualala River	Guala	61	106	0.43	0.44	2.9	99	75
Central								
Russian River-Willow	RussW	64	107	0.40	0.42	2.0	97	71
Lagunitas Creek-Olema Creek	LagOC	56	107	0.41	0.41	2.3	98	96
San Francisquito Creek-Los Trancos Creek	SaFLT	24	106	0.40	0.40	2.9	96	77

TABLE 1 (Continued)

O. mykiss

River-sampling site	Population code	Sample size	Loci typed	H_e	H_o	A_R	% Polymorphic loci	Omy05 ancestral haplotype freqency
South-Central/South								
Scott Creek	Scott	64	107	0.42	0.42	3.7	99	80
San Lorenzo-Boulder	SanLB	50	107	0.41	0.43	3.0	98	60
Carmel River	CarmR	32	106	0.41	0.41	4.0	98	95
Big Sur River	BigSR	46	107	0.41	0.42	3.4	98	89
San Simeon Creek	SimeC	31	106	0.41	0.43	3.3	98	79
Santa Maria-Sisquoc/Manzana	SmSiM	47	107	0.33	0.34	2.2	87	16
Santa Ynez-Salsipuedes Creek	SYSal	47	107	0.37	0.35	3.3	95	83
Santa Ynez-Santa Cruz Creek	SYSt	34	107	0.38	0.37	3.0	92	18
Ventura-North Fork Matilija Creek	VenMC	46	107	0.37	0.37	2.7	96	39
Santa Clara-Sespe Creek	SClSe	39	105	0.36	0.35	3.7	98	63
Santa Clara-Sta Paula	SClPa	45	107	0.41	0.40	4.2	97	34
Santa Ana-Coldwater Canyon Creek	SACaC	19	105	0.12	0.12	2.0	31	0
San Luis Rey-West Fork	LuRWF	12	105	0.25	0.26	3.0	65	21
Santa Domingo-Mexico (O. m. nelsoni)	SaDom	38	107	0.18	0.16	2.0	54	76
Central Valley								
McCloud River-Butcherknife Creek	McClB	21	107	0.21	0.21	2.4	66	0
McCloud River-Claiborne Creek	McClC	33	107	0.37	0.36	2.0	92	0
Clear Creek	ClrCk	94	107	0.39	0.37	2.5	100	25
Battle Creek	Battl	92	107	0.41	0.40	2.6	100	39
Feather River-Upper	FeaUp	47	107	0.37	0.32	2.4	100	3
Yuba River-Upper	YubUp	26	107	0.42	0.42	2.7	100	4
Yuba River-Pauley Creek	YubPC	24	107	0.33	0.32	2.8	89	0
Mokelumne River-North Fork	MokNF	51	107	0.38	0.37	2.6	100	12
Mokelumne River-South Fork	MokSF	49	107	0.35	0.35	3.1	100	24
Stanislaus River-Upper	StanUp	52	107	0.38	0.35	2.4	99	31
Tuolumne River-Upper	TuoUp	47	107	0.38	0.35	2.7	99	17
Merced River-Upper	MrdUp	35	107	0.39	0.34	2.8	100	40

(Continues)

TABLE 1 (Continued)

River-sampling site	Population code	Sample size	Loci typed	H_e	H_o	A_R	% Polymorphic loci	Omy05 ancestral haplotype freqency
O. mykiss								
Hatchery Strains								
Coleman-Fillmore	ColeM	47	107	0.37	0.36	2.0	98	35
Mt Whitney Early-Fillmore	MtWhE	24	106	0.37	0.37	3.0	93	54
Mt Whitney Late-Fillmore	MtWhL	24	106	0.36	0.35	2.8	92	54
Virginia-Fillmore	VirgM	48	107	0.31	0.29	2.9	90	35
Wyoming-Fillmore	WyomM	47	107	0.37	0.37	2.5	93	30
Kamloops-Hot Creek	HCKml	47	106	0.28	0.27	2.6	80	0
Moccasin Creek-Hot Creek	Moccs	47	107	0.30	0.29	1.7	87	28
Eagle-American River	EaglM	47	107	0.29	0.28	3.0	99	6
Shasta-American River	ShasM	47	106	0.35	0.34	3.0	91	52

Note: Reported are the expected heterozygosity (H_e), observed heterozygosity (H_o), allelic richness (A_R), and percentage of polymorphic loci (%PI). Chromosome Omy05 ancestral (noninversion) haplotype frequency was estimated from SNP locus Omy_114448-87. A_R was not estimated for sample sizes <10. NA means not applicable for this parameter for the two populations.

Abbreviation: SNP, single-nucleotide polymorphism.

A total of 93 SNPs and 14 microsatellite loci were used for the current study, including markers described by different authors (Table S1). The 14 microsatellite loci were previously optimized for use in *O. mykiss* (Garza et al., 2014). Extracted DNA was diluted *c.* 10:1 and used for PCR amplification using the conditions described by Garza et al. (2014). PCR products were electrophoresed on ABI 377 sequencers, and microsatellite genotypes were called using Genescan 3.0 and Genotyper 2.1 software (Applied Biosystems, Inc.). All the SNP loci were genotyped using TaqMan 5′-nuclease chemistry (Applied Biosystems) on an EP1 system, with the SNP Genotyping Analysis software, version 3.1.1 (Fluidigm Corporation), used to call all genotypes. All genotypes were checked independently by two people to ensure correct and consistent calling. The few discrepancies found between the two calls were resolved by consensus, by re-genotyping, or by deletion of that genotype from the data set.

2.4 | Population genetic analyses

Within-population genetic diversity at microsatellite and SNP loci was evaluated using descriptive statistics, including unbiased heterozygosity (H_E), observed heterozygosity (H_O), and the mean number of alleles per locus, all employing the *Microsatellite Toolkit* (Park 2001). Allelic richness (A_R) was calculated using the *diveRsity* R package (Keenan et al., 2013). The proportion of polymorphic loci is also reported. Hardy–Weinberg equilibrium (HWE) was also evaluated using Pearson's χ^2 test from the *genetics* R package (Warnes & Leisch, 2005), and pair-wise population differentiation for the 62 populations was quantified for each locus based on average F_{ST} values obtained using the *strataG* R package (Archer et al., 2017). Pair-wise linkage disequilibrium between all the loci was calculated using the *genetics* R package (Warnes & Leisch, 2005).

Evolutionary relationships and population genetic structure between and within native and introduced *O. mykiss* populations and hatchery strains were estimated using several methods. Because the Argentinean populations have been established over a period of only *c.* 100 years, which equates to *c.* 25–30 generations, changes in microsatellite allele frequencies through mutation (at rates of 10^{-3}–10^{-4} per locus per generation) are not likely to have a major influence on allele frequencies compared to the effects of genetic drift. Therefore, methods that are based on evolutionary models of genetic drift rather than mutation were favored (e.g., Tessier & Bernatchez, 1999; Wenburg et al., 1998). As such, evolutionary relationships between the North America and Argentinian populations were summarized using pair-wise chord distances (Cavalli-Sforza & Edwards, 1967), which were then used to construct neighbor-joining (NJ) trees with PHYLIP (Felsenstein, 1993). Bootstrap-consensus trees were built using 1000 bootstrap replicates to confirm consistency of the tree structure obtained. All trees were plotted using Dendroscope, version 3 (Huson & Scornavacca, 2012).

Discriminant analysis of principal components (DAPC; Jombart et al., 2010) was used to identify patterns of genetic relatedness among populations and performed using the *adegenet* R package

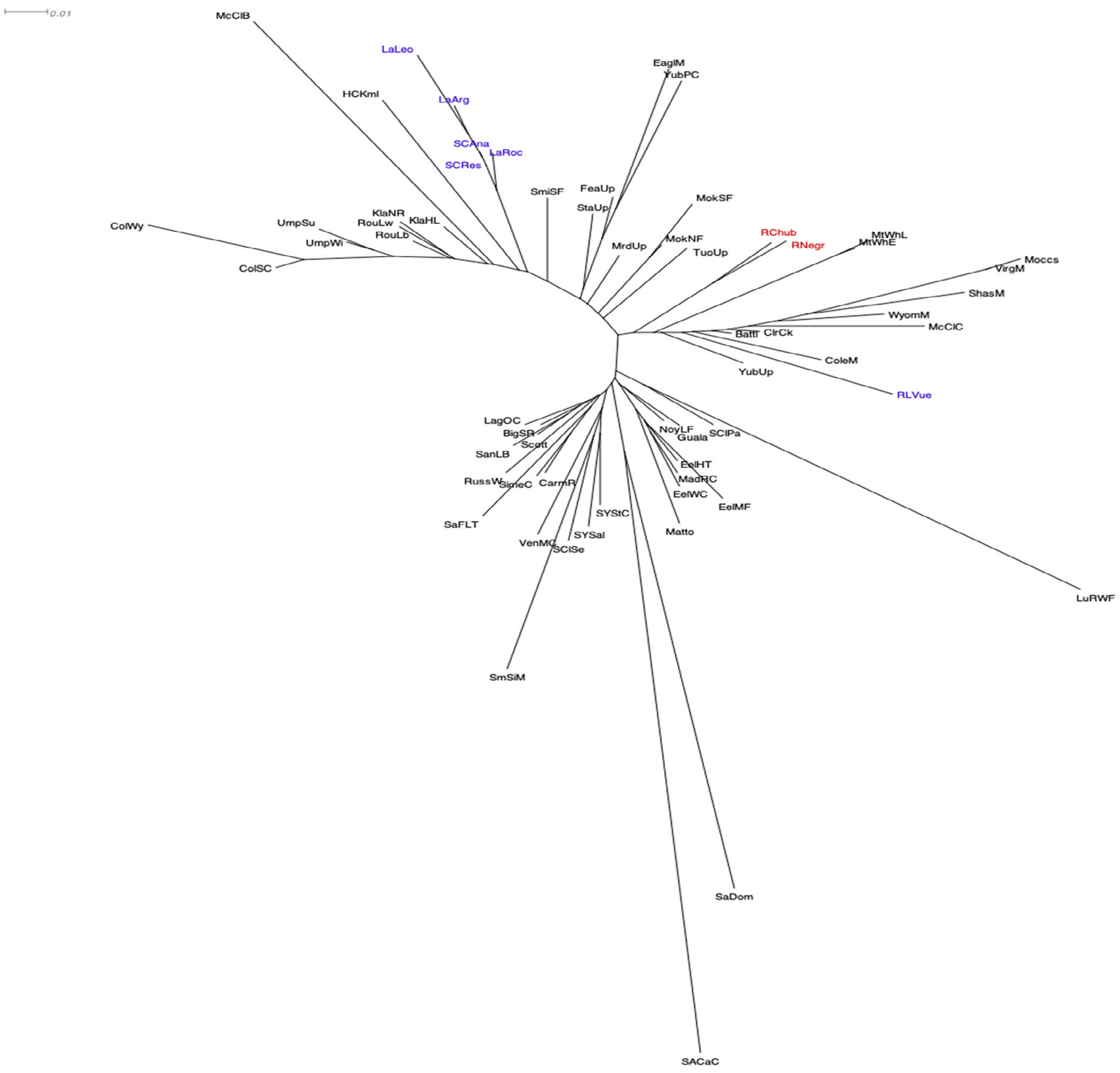

FIGURE 2 Neighbor-joining tree of all populations is included in the analysis. Northern Patagonian populations are in red, and southern Patagonian populations are in blue.

(Jombart, 2008). The Bayesian model–based clustering method from *structure* (Pritchard et al., 2000) was used to look for evidence of admixed ancestry and multiple origins, and to infer population clusters from the multilocus genotype data of both Patagonian and North American fish. A series of evaluations were performed using different numbers of potential genetic clusters ($k = 2$–6) to guide an empirical estimate of the number of identifiable genetic groups in Argentina, under a model assuming admixture and correlated allele frequencies. The probability of how the data best fit into each number of assumed clusters was estimated in each case (ln probability of the data) without using any prior population information (USEPOPINFO = 0), so that individuals were assigned to a cluster based on only their multilocus genotypic profile. The admixture parameter, α, estimated with each k value was also estimated. Burn-in was set at 5000, with the next 15,000 iterations used for data collection, and each test yielded a log-likelihood value of the data (ln probability). The ad hoc statistic based on the rate of change in the log likelihood of the data (Δk) was used as proposed by Evanno et al. (2005) to accurately determine the level of structure. Runs were replicated five times at each k value to confirm consistency of log-likelihood probabilities. Individuals were assigned probabilistically to a population based on qi values, or to multiple populations, if their genotype profile indicated admixture. For

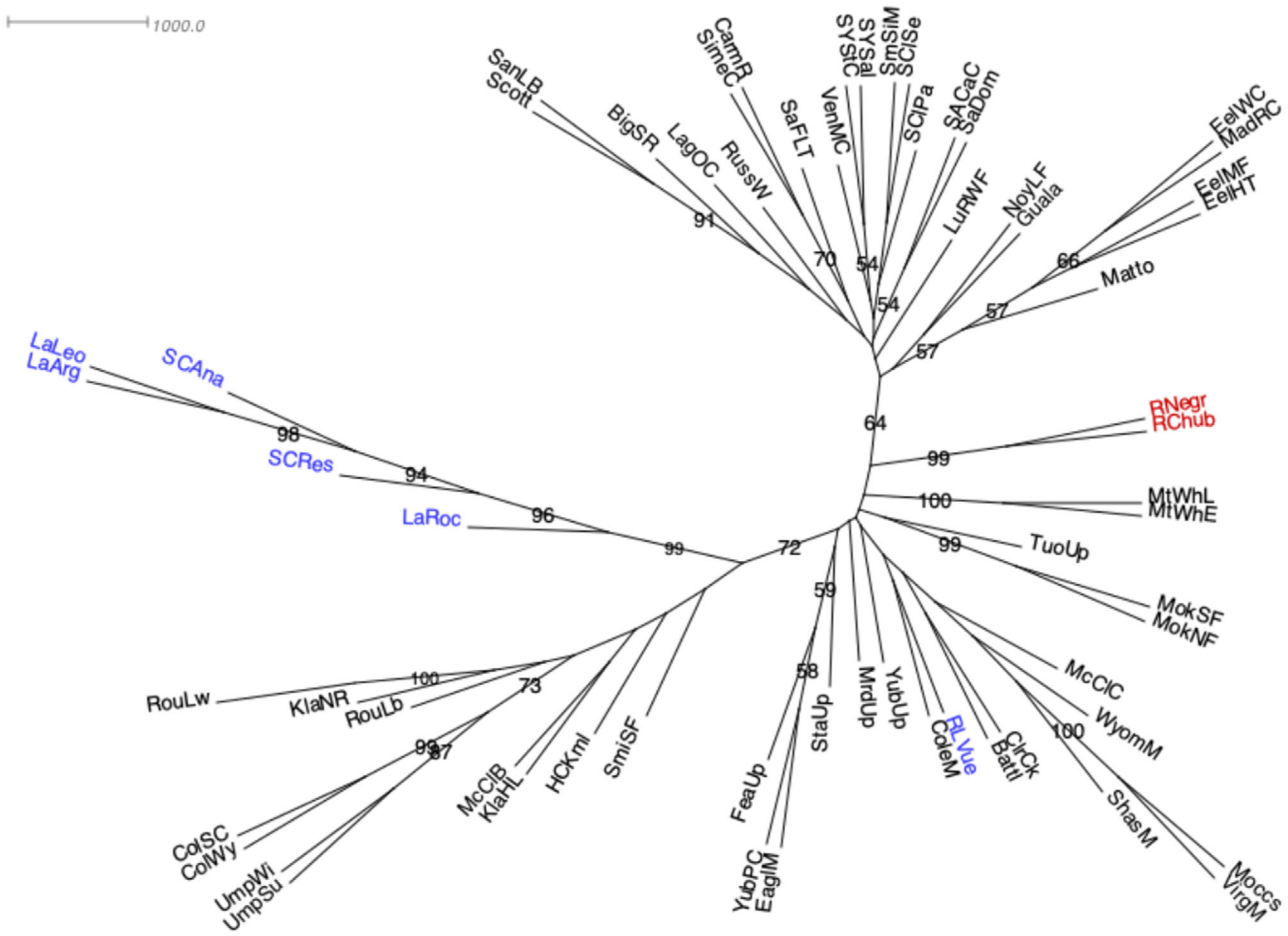

FIGURE 3 Bootstrap-consensus tree of all populations included in the analysis, with bootstrap support for internal branches of greater than 50% indicated. Northern Patagonian populations are in red, and southern Patagonian populations are in blue.

visualization purposes, CLUMPP (Jakobsson & Rosenberg, 2007) and Distruct (Rosenberg, 2004) were used to reorder clusters and plot individual qi values.

One of the SNP loci (Omy_114448-87) is located within an inverted region of the genome on chromosome Omy5 that is strongly associated with life history in some *O. mykiss* populations (Abadía-Cardoso et al., 2011; Pearse et al., 2014; Pearse et al., 2019). Here, we use the allele frequencies for Omy_114448-87 to estimate the frequencies of the Omy5 inversion haplotypes for the populations in the present study.

3 | RESULTS

Newly generated and previously published (Abadía-Cardoso et al., 2016; Arciniega et al., 2016; Clemento et al., 2009; Garza et al., 2014; Pearse et al., 2019; Pearse & Garza, 2015) microsatellite and SNP data from 2568 fish in Argentina and North America were combined for this study. The standard descriptive statistics for these genotypes of 100–107 loci and for all the populations included in this study are presented in Table 1. Among the North American populations, the expected heterozygosity (H_E) ranged from 0.12 (Santa Ana-Coldwater Creek, SACaC) to 0.43 (Gualala River, Guala), whereas the observed heterozygosity (H_O) ranged from 0.12 to 0.44 at the same locations. For the Argentinian populations, H_E ranged from 0.31 (La Leona, LaLeo) to 0.40 (Negro River, RNegr), and H_O values ranged from 0.32 (Lake Argentino, LaArg) to 0.39 (Chubut River, RChub).

For the native range, microsatellite allelic richness (A_R) ranged from 1.7 (Moccasin Creek-Hot Creek, Moccs) to 4.2 (Santa Clara-Sta Paula, SClPa), and the proportion of polymorphic SNPs ranged from 31 (SACaC) to 100% (Mad River-Canon, MadRC, and multiple populations from the California Central Valley). For the Argentinean populations, A_R values ranged from 2.0 (RNegr) to 3.2 (Lake Roca, LaRoc), and the proportion of polymorphic loci ranged from 60 (LaLeo) to 92% (Santa Cruz River-Resident, SCRes) (Table 1). Overall, the values obtained for both A_R and the proportion of polymorphic loci in Argentinean populations were marginally lower than those obtained for the native-range populations.

Among the Argentinian populations, test results indicated that only the Santa Cruz River resident fish had a significant departure

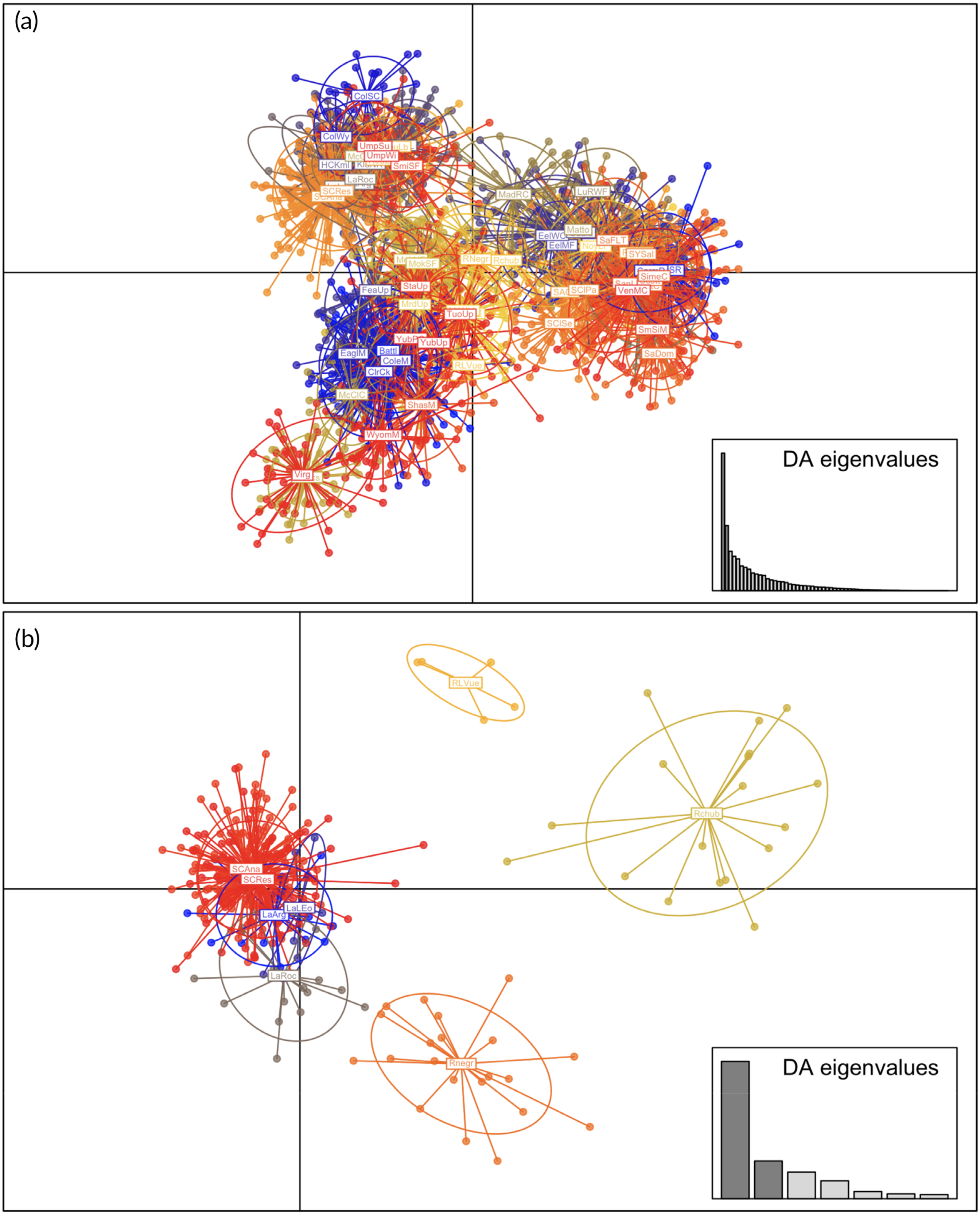

FIGURE 4 Discriminant analysis of principal components plot with (a) all populations and (b) Argentinian populations only.

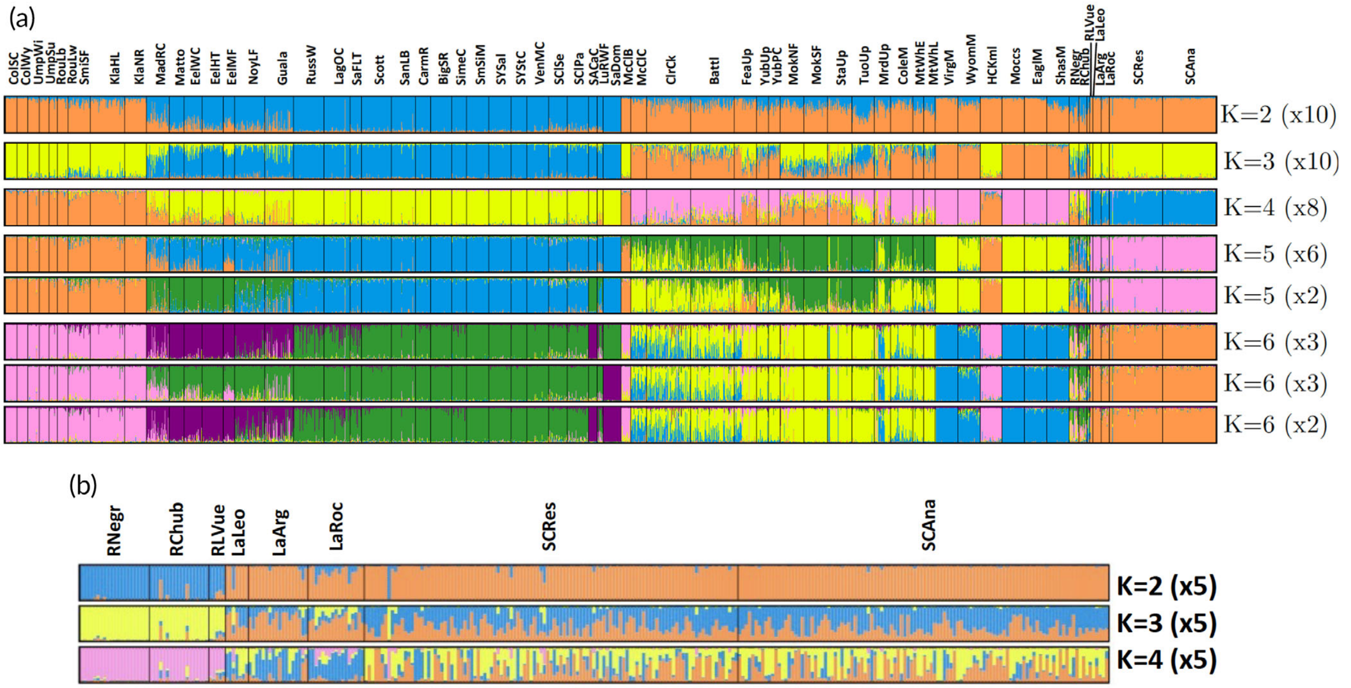

FIGURE 5 Results from *structure* showing ancestry and genetic relationships of (a) all populations and (b) the Argentinian populations only. Each vertical line represents the genetic relationships between an individual and each potential genetic cluster (k). Populations are aligned from north to south.

from HWE following Bonferroni correction for multiple tests ($p < 0.01$).

F_{ST} among Argentinian populations showed a high degree of differentiation in the northern populations of Patagonia, RNegr and RChub, from the southern populations in the Santa Cruz River basin (Table S2). The exception to this is the De las Vueltas River (RLVue) population, which is also differentiated from all other Santa Cruz River populations and slightly more similar to the two northern populations. In contrast, the two northern populations are genetically differentiated from each other, but with a much smaller F_{ST} value between them, than with the southern populations. Similarly, in the Santa Cruz River basin, most populations were modestly differentiated, with the exception of the mainstem resident (SCRes) and anadromous (Santa Cruz River–Anadromous, SCAna) groups, which were not significantly differentiated. F_{ST} among all the populations, native and Argentinean, showed that northern Patagonian populations are more similar to California Central Valley and hatchery rainbow trout strains, whereas southern Patagonian populations are more similar to populations from coastal North America, including California and Oregon.

Genetic differentiation (F_{ST}) among populations within the introduced range was far less than that between introduced and native populations. Overall F_{ST} among Argentinean populations was 0.061 ($p = 0$), and that between native and introduced samples was 0.189 ($p = 0$).

NJ tree relationships (Figure 2) were supported by the bootstrap-consensus tree with bootstrap values greater than 50% (Figure 3). Both grouped the northern Argentinean populations RChub and RNegr with the hatchery strains and populations from the Central Valley of California (with bootstrap values of 99%), whereas the southern populations from the Santa Cruz River basin—SCRes, SCAna, LaArg, LaLeo, and LaRoc—clustered with natural populations from northern California and Oregon (with bootstrap values greater than 90%). RLVue was grouped separately from all other Argentinian populations and was also related to the hatchery strains and Central Valley populations.

The results obtained using the DAPC analysis (Figure 4) were consistent with the NJ and bootstrap-consensus tree results. When looking at all the populations (Figure 4a), the northern Patagonian populations were grouped with hatchery strains, and the southern Patagonian populations were grouped with northern California and Oregon populations, with nominal clustering by one hatchery strain domesticated from a Canadian source and a McCloud River population, and the RLVue fish were grouped with the California Central Valley and the hatchery rainbow trout strains that were domesticated from California source populations. The DAPC plot for the Argentinian populations (Figure 4b) showed only four different groups, where the two northern populations (RChub and RNegr) represent different groups.

The individual-based analysis performed using *structure* assigned fish to their population and also identified ancestry (Figure 5). Using Δk as calculated following Evanno et al. (2005), the greatest rate of change was found when $k = 2$, indicating that this level of structure is the most appropriate to describe Patagonian populations. Also, at this level we obtained an $\alpha = 0.016$, indicating that fish in Argentina are best characterized as essentially from either the northern Patagonia or the Santa Cruz River basin cluster.

In general, and regardless of *k* values, the results indicate that populations from northern and southern Patagonia have different origins. Santa Cruz River populations (SCRes and SCAna), LaArg, and LaRoc seem to share ancestry with populations from northern California and Oregon in the native range, whereas RNegr and RChub populations have ancestry from the hatchery trout strains. RLVue, as in the other analyses, was not grouped with the other southern populations, and its ancestry was closer to the hatchery strains. These results are consistent with the clusters obtained from the NJ and bootstrap-consensus trees, as well as the patterns observed on the DAPC plots, which suggest different origins for northern and southern Patagonian *O. mykiss* populations. Even though it is clear that Argentinian populations constituted two clearly differentiated clusters, separating RNegr and RChub from the rest of the populations, these results do not allow us to clearly identify the ancestral populations.

Frequencies of the A (ancestral/anadromy-associated) allele at the locus Omy_114448-87 were highly variable among populations (Table 1). Within the native range, ancestral allele frequencies ranged from 0% to 96% for natural populations and from 0% to 54% for hatchery strains. Frequencies of the same allele in the Santa Cruz basin populations ranged from 41 (LaRoc) to 56% (SCAna), whereas for the northern Patagonian populations, the frequencies were 78% (RChub) and 77% (RNegr), considerably higher than in the hatchery strains.

Linkage disequilibrium (LD) for all the other loci in the Argentinean populations was generally not significant after Bonferroni correction. However, a modest but significant excess of LD, beyond that expected due to type 1 error of 0.05, remained in the LaRoc (5.1%) and Santa Cruz River (8.1%) populations.

4 | DISCUSSION

The principal results that emerged from this study are as follows: (i) introduced *O. mykiss* from northern and southern Patagonia had separate origins, possibly with different genetic capabilities for anadromy; (ii) fish with alternative life-history forms (resident and anadromous) within the Santa Cruz River basin are not genetically differentiated, and there is high gene flow between them; (iii) low levels of gene flow occur among basins in Patagonia; and (iv) Santa Cruz River fish may have originated from multiple sources, as there is not a clear relationship between them and any potential progenitor population.

The present study confirms the genetic relationships between populations of introduced *O. mykiss* in Argentina, as well as relationships with their potential sources from North America. Even so, significant questions regarding origins and life-history evolution of Patagonian trout remain.

4.1 | Ancestral origins of rainbow trout in Patagonia

Combined microsatellite and SNP data demonstrate multiple and separate sources for the northern Patagonian basins (Chubut and Negro rivers) and for the Santa Cruz River populations.

Northern Patagonian populations formed a separate cluster from the southern populations and were strongly associated with hatchery rainbow trout strains and with California Central Valley populations. Southern Patagonian populations from the Santa Cruz River basin, on the contrary, clustered distinctly from the northern populations and with populations from coastal basins of California and Oregon in North America. These potential progenitor populations are comprised predominantly of anadromous steelhead forms. Although the present results clearly demonstrate multiple origins for *O. mykiss* populations in Patagonia, the lack of clear clustering of Argentinean populations with any specific native populations does not allow strong conclusions about the specific ancestral sources. Previous work with mitochondrial DNA also supported the idea that the Santa Cruz River populations were founded by a mixture of multiple sources from California and did not originate from a single source (Riva Rossi et al., 2004).

NJ trees based on chord distances supported a close genetic relationship between Santa Cruz River *O. mykiss* and various populations from California and Oregon (Figure 2). F_{ST} values were consistent with this and also supported closer genetic relationships with some California Central Valley populations, notably the McCloud River populations (Table S2). The NJ tree also suggests an ancestral contribution from the McCloud River redband trout to the Santa Cruz River population, a result concordant with previous studies that indicated that this relictual *O. mykiss* stock, broadly propagated around the world by the turn of the 20th century and now almost extinct locally, is one of the original sources from which anadromous and resident Santa Cruz River rainbow trout evolved (Pascual et al., 2002; Riva Rossi et al., 2004). However, the Claiborne Creek-McCloud population is also known to have been introgressed with nonnative rainbow trout since the Baird Station closed at the beginning of the 20th century (Simmons et al., 2010).

Together, these results also confirm Behnke's (2002) suggestion that the McCloud River was not the only source used in early propagation of rainbow trout in Argentina and, in particular, for the Santa Cruz River. Indeed, the present study suggests several sources (likely representing a mixture of anadromous and non-anadromous life histories) for the Santa Cruz River and supports the idea that anadromous coastal populations of *O. mykiss* (e.g., from San Francisco Bay, the Klamath, Rogue, and/or Willamette rivers; Behnke, 2002) made a significant contribution to the genetic foundation of these populations.

4.2 | Gene flow among and within Patagonian basins

NJ trees, the distribution of alleles and genotypes across fish, and the associated clustering results (DAPC; Figure 4b, *structure*; Figure 5) were all consistent with high divergence between northern Patagonia and the Santa Cruz River, providing strong support for the idea of independent historical colonization and current geographical isolation between basins. Tests of genetic differentiation were significant for most of the between-population comparisons, with the highest significant values recovered between northern Patagonian basins and the

Santa Cruz River, and a low but still significant F_{ST} between the RChub and RNegr populations (Table S2). These results were also consistent with the *structure* analysis that used no prior information about geographic origin of the samples, which found that the northern Patagonian populations (RNegr and RChub) formed one group and the Santa Cruz River populations formed another, with a hypothesis of two genetic groups present in the eight Argentinian populations (Figure 5).

In addition, no genetic differentiation was detected between fish with anadromous and resident life histories within the Santa Cruz River, with non-significant F_{ST} and close associations on NJ trees and with clustering methods. Also, both the resident and anadromous fish from the Santa Cruz River have intermediate frequencies of the anadromy-associated allele of the migration-associated inversion polymorphism on chromosome Omy05 (Pearse et al., 2019). This suggests that expression of life-history strategy in this population is mostly environmental and that individuals of the two types consist of a single polymorphic population, in agreement with previous studies (e.g., Liberoff et al., 2014; Riva-Rossi et al., 2007). Consistent with previous work (Abadía-Cardoso et al., 2016, 2019), the association between the inversion polymorphism and migratory life history breaks down in hatchery rainbow trout strains, which is reflected in the relatively high frequency of the ancestral haplotype in the northern Patagonian populations, in spite of their predominant resident life history.

Within the Santa Cruz River, almost all individuals had nonadmixed genotypes assigned to the "Santa Cruz" cluster by DAPC and *structure*, a result consistent with the lack of clear genetic divisions between the life-history forms and further indicating that they are not derived from separate genetic lineages nor from multiple colonizations by allopatric populations. The one exception is the De las Vueltas River (RLVue) population, which forms a distinct group from the rest of the Santa Cruz River populations and shared ancestry with Central Valley and hatchery rainbow trout strains. This is the furthest upriver population, separated from the main Santa Cruz River populations by several hundred river kilometers, and these fish are likely the results of transplants from the Piedra Buena fish farm at the mouth of the Santa Cruz River that were released in the area for angling purposes and kept isolated from downstream locations by an impassable waterfall (R. Hudson, Manager Piedra Buena Hatchery, personal communication).

Two individuals from the main Santa Cruz River populations had a high degree of ancestry from the cluster of northern Patagonian populations, derived from hatchery rainbow trout. One resident fish had entirely hatchery trout ancestry and may have come downriver from the RLVue population or upriver from the Piedra Buena hatchery. One other resident fish was clearly admixed and may have been a first-generation hybrid between Santa Cruz River and hatchery parents. The presence of these individuals likely explains the significant departures from HWE found in the SCRes fish.

Individuals from La Leona (LaLeo) and Lake Roca (LaRoc) also showed some degree of ancestry from hatchery rainbow trout, whereas two individuals from RChub had signals of ancestry from fish similar to those in the Santa Cruz basin. The LaLeo and LaRoc admixed individuals may reflect introgression with hatchery rainbow trout from RLVue or other historic introductions.

In contrast, the admixed individuals in the northern populations may reflect the occurrence of recent introgression of anadromous fish that migrated to northern Patagonia and hybridized with the resident trout there, or the presence of ancestry from introduced fish that were originally hybrids. The *structure* analysis that includes North American populations shows that those admixed individuals have ancestry very similar to the Santa Cruz populations, supporting the idea that they are the result of anadromous migrants from southern Patagonia, as other salmonid species introduced in Patagonia have also expanded their range to the north (Figueroa-Muñoz et al., 2023). Consistent with this idea is the observation of multiple incidental marine catches of *O. mykiss* occurring along the Atlantic coast between the two river estuaries (J. Ciancio, personal communication).

Such introgression could disrupt any local adaptation that has arisen in these resident populations since introduction or colonization of these basins. Conversely, gene flow among basins could introduce new alleles, allowing more phenotypic variation and increases in population fitness.

4.3 | Genetic diversity in Santa Cruz River rainbow trout

When populations are founded by a small number of individuals from the same source, founder effects are expected to reduce the genetic diversity of the resulting populations in relation to their source populations and theoretically also reduce their capacity to adapt to novel conditions (Lee, 2002; Sakai et al., 2001). This study found no evidence to support the hypothesis that introduced rainbow trout populations in northern Patagonian basins and in the Santa Cruz River have reduced genetic variation due to founder effects during the initial colonizations.

Heterozygosity levels in the introduced populations were relatively high ($H_O = 0.32–0.39$) and overlapped completely with the native populations analysed in this study and those reported elsewhere in the literature surveyed at the same loci (Abadía-Cardoso et al., 2016; Pearse & Garza, 2015). The high overall genetic diversity of the introduced populations further supports the idea that Patagonian populations were founded by a mixture from multiple North American sources. Even the northern Patagonian populations that are genetically similar to, and were founded by hatchery rainbow trout, have higher heterozygosity than their source hatchery strains.

In contrast, the patterns of allelic variation are more complicated. The proportion of polymorphic SNP loci (Table 1) is slightly lower in the Argentinean populations than in most of the North American populations but overlaps with the less diverse native populations. However, some of the native populations are those that were used to ascertain these SNP markers (Abadía-Cardoso et al., 2011), so this small difference might be entirely due to ascertainment bias (Albrechtsen et al., 2010). Values of allelic richness (A_R) for Argentinean populations were also slightly lower but still overlapping with values obtained for the North American populations. This suggests that naturalized *O. mykiss* populations in Argentina do not have lower genetic diversity due to bottlenecks or founder effects.

In the Santa Cruz River, another potential factor that could have maintained relatively high genetic variation in the introduced fish is the coexistence of resident and migratory forms. Different life-history forms can have different reproductive success in different circumstances, and interbreeding between life-history forms might buffer fluctuations in the effective population size (N_E). For example, if abundance of one life-history form fluctuates widely, whereas that of the other form is relatively stable, then overall N_E will be stabilized through time by interbreeding between forms (Araki et al., 2007). In the Santa Cruz River, where anadromous and non-anadromous forms interbreed, it could be possible that a genetic compensation for N_E (and hence genetic variation) exists between life-history forms, in which the N_E per generation is augmented by the reproductive contribution between life-history forms.

4.4 | Anadromy in the Santa Cruz River rainbow trout: Evolution or re-creation

The Santa Cruz River rainbow trout has received attention among evolutionary biologists interested in salmonid conservation, because initial work postulated that this population may represent a case in which introduced non-anadromous rainbow trout have developed anadromy in situ. However, the results from the present study suggest that Santa Cruz River populations result from an introduction of individuals from populations with both life-history strategies, resident and anadromous. As such, it is likely the case that Santa Cruz River fish have just expressed these life-history strategies in a novel environment, which was facilitated by the underlying genetic variation and flexibility present in their ancestral populations. Although it seems likely that the Santa Cruz River populations were founded by fish from populations with both resident and anadromous life histories (Behnke, 2002; Pascual et al., 2002; Riva Rossi et al., 2004), other questions remain.

First, introduced rainbow trout in Patagonia and the Santa Cruz River have widely varying physiological, behavioral, and life-history responses to environmental variables (e.g., Liberoff et al., 2013, 2014, 2015, 2019). To what extent fish from each ancestral source contributed to the basis and genetic legacy of Santa Cruz River fish is unknown. However, at the time of initial propagation (the turn of the 20th century), historical runs in the upper McCloud River, one of the potential sources, sustained both anadromous and resident forms (Nielsen, 1999). It has been found that in some tributaries of the Columbia River basin, sympatric steelhead and rainbow trout are genetically more similar to each other than to their corresponding forms in other basins (Docker & Heath, 2003; McCusker et al., 2000). Similar results have been found elsewhere in the North American range of *O. mykiss* (Clemento et al., 2009; Pearse & Garza, 2015; Thrower et al., 2004). Thus, it is likely that diversity of ancestral life-history forms could have provided the genetic basis for a partially migratory rainbow trout population, where a fraction of the population expresses an ocean migratory behavior and the rest are resident (Zimmerman & Reeves, 2000).

In addition, there is documented differentiation between native and introduced rainbow trout populations in behavioral traits that may reflect modifications resulting from directional selection in the new environment. For example, in the Santa Cruz River, anadromous rainbow trout have apparently evolved increased iteroparity and associated post-reproductive survival (Pascual et al., 2001; Riva-Rossi et al., 2007), traits directly associated with fitness and possibly under selection (Crespi & Teo, 2002; Fleming & Reynolds, 2004; Willson, 1997). Although iteroparity is a naturally occurring reproductive strategy in *O. mykiss*, its prevalence is highly variable. In pristine populations from Kamchatka, it is expressed with rates as high as 79% (Savvaitova et al., 1999). Relatively high rates of iteroparity have also been reported for *O. mykiss* populations in rivers from Oregon and California (Busby et al., 1996). In contrast, much lower iteroparity rates for hatchery steelhead than for natural-origin fish have been reported in populations throughout the native range (Abadía-Cardoso et al., 2013; Hallock, 1989; Keefer et al., 2008), which may explain such highly variable rates in the different populations studied. Construction of hydropower dams in the United States during the 20th century has greatly reduced iteroparity rates across native populations, mainly due to high mortality of downstream-migrating kelts (Hatch et al., 2004). The existence of highly iteroparous native populations and the fact that, despite strong selection against downstream adult passage, iteroparity still remains in several dammed river systems (Narum et al., 2008) suggest that the potential for expressing high levels of iteroparity is an ancestral capability of *O. mykiss* (i.e., a pre-adaptation) and not a novel adaptation unique to the Santa Cruz population. Whether selection for changes in iteroparity in Santa Cruz River steelhead actually occurred and, if so, if it operated directly on anadromy or indirectly on growth-related threshold traits (e.g., Thériault et al., 2007; Thorpe et al., 1998) are unknown.

In the Santa Cruz River, the close genetic relationship between alternative ecotypes and the fact that each type of parent typically gives rise to fish with both anadromous and resident phenotypes (Riva-Rossi et al., 2007) suggest a strong role for the environment in determining the expression of life history in this combined mainstem population (Liberoff et al., 2013, 2014, 2015, 2019). However, because the (additive) genetic and environmental influences on the adoption of the life-history tactic have not been studied for this population, it remains difficult to establish whether the life-history strategy depends on an environmentally cued threshold or constitutes a direct response to the environment. The estimated frequencies of the Omy5 ancestral haplotype in the Santa Cruz River populations do not indicate a clear association with anadromy, but this may be confounded by the variable association of the Omy5 inversion with migratory life history, temperature, and development rate (Nichols et al., 2008; Pearse & Garza, 2015; Pearse et al., 2019). Evidence from a study of the early phases of growth revealed that the expression of anadromy in the Santa Cruz River is linked to fast growth during the first year of life, whereas residency is associated with slow growth, suggesting that alternative forms within this river may result from a body size–based threshold for life-history determination (Liberoff, 2013; Liberoff et al., 2013, 2014; Riva Rossi, 2004). In the introduced range, the fitness value of a tactic for a given condition could be very different from the value in the native range and could also vary along the environmental gradient of Patagonia, resulting in differences in the body size for which anadromy conferred greater advantages and was selected for in the native range (Riva Rossi, 2004).

Finally, *O. mykiss* is considered to have one of the most diverse portfolios of life-history strategies in Salmonidae, including resident, estuarine, adfluvial, and anadromous ecotypes, and a wide range of reproductive strategies including precocity, and highly variable rates of iteroparity (Abadía-Cardoso et al., 2013; Busby et al., 1996; Narum et al., 2008; Willson, 1997). Although there is little doubt that this complex array of life-history variation contributes to persistence in environmental conditions that vary substantially in space and time (Fleming & Reynolds, 2004), there is uncertainty about the potential for (sub)populations with predominantly resident fish (e.g., above waterfalls) to generate anadromous migrants. Indeed, loss of anadromous fitness in landlocked resident populations, and the unidirectional evolution of landlocked populations away from anadromy (Thrower et al., 2004), raises significant questions regarding the ability of resident *O. mykiss* to regain anadromous life history. In light of this and the results from the present study, it appears most likely that the partially anadromous *O. mykiss* population in the Santa Cruz River was founded by a collection of fish from populations with anadromous and resident life histories that subsequently evolved in the introduced range in response to the particular environmental conditions of this river. Conversely, this population may be partly the result of unique introduction histories, presumably stemming from features of the specific founding lineages and chance events.

In either case, the apparent distinctiveness of this population raises questions as to whether the re-creation of anadromous life history could be a recurring experiment in this river, if for any reason anadromy is prevented for this population. This question has heightened importance due to the construction of two large hydroelectric dams in the upper and middle portions of the Santa Cruz River that will block the migratory corridor and impede anadromous adults from reaching the current spawning grounds located exclusively farther upstream (Riva-Rossi et al., 2007). In light of this, the Santa Cruz River *O. mykiss* population appears to be on the verge of losing the only trait for which it is unique among introduced trout. Providing ongoing connectivity between life-history forms in this river, at both the ecological and evolutionary time scales, is particularly crucial to preserve the full expression of life-history diversity in this population.

AUTHOR CONTRIBUTIONS

Carolina Lázari, Carla Riva-Rossi, Miguel Pascual, and John Carlos Garza conceived the ideas and designed the methodology; Carla Riva-Rossi, Javier Ciancio, and Miguel Pascual collected biological samples; Carolina Lázari, Carla Riva-Rossi, and Devon E. Pearse collected genetic data; Carolina Lázari, Anthony J. Clemento, and John Carlos Garza analysed the data; Carolina Lázari, Carla Riva-Rossi, and John Carlos Garza drafted the manuscript. All authors contributed critically to the manuscript drafts and gave final approval for publication.

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REFERENCES

Abadía-Cardoso, A., Anderson, E. C., Pearse, D. E., & Garza, J. C. (2013). Large-scale parentage analysis reveals reproductive patterns and heritability of spawn timing in a hatchery population of steelhead (*Oncorhynchus mykiss*). *Molecular Ecology*, *22*, 4733–4746. https://doi.org/10.1111/mec.12426

Abadía-Cardoso, A., Brodsky, A., Cavallo, B., Arciniega, M., Garza, J. C., Hannon, J., & Pearse, D. E. (2019). Anadromy Redux? Genetic Analysis to Inform Development of an Indigenous American River Steelhead Broodstock. *Journal of Fish and Wildlife Management*, *10*(1), 137–147. https://doi.org/10.3996/072018-jfwm-063

Abadía-Cardoso, A., Clemento, A. J., & Garza, J. C. (2011). Discovery and characterization of single-nucleotide polymorphisms in steelhead/rainbow trout, *Oncorhynchus mykiss*. *Molecular Ecology Resources*, *11*, 31–49. https://doi.org/10.1111/j.1755-0998.2010.02971.x

Abadía-Cardoso, A., Pearse, D. E., Jacobson, S., Marshall, J., Dalrymple, D., Kawasaki, F., Ruiz-Campos, G., & Garza, J. C. (2016). Population genetic structure and ancestry of steelhead/rainbow trout (*Oncorhynchus mykiss*) at the extreme southern edge of their range in North America. *Conservation Genetics*, *17*, 675–689. https://doi.org/10.1007/s10592-016-0814-9

Aguilar, A., & Garza, J. C. (2008). Isolation of 15 single nucleotide polymorphisms from coastal steelhead, *Oncorhynchus mykiss* (Salmonidae). *Molecular Ecology Resources*, *8*, 659–662. https://doi.org/10.1111/j.1471-8286.2007.02038.x

Albrechtsen, A., Nielsen, F. C., & Nielsen, R. (2010). Ascertainment biases in SNP chips affect measures of population divergence. *Molecular Biology and Evolution*, *27*, 2534–2547. https://doi.org/10.1093/molbev/msq148

Allendorf, F. (1975). *Genetic variability in a species possessing extensive gene duplication: Genetic interpretation of duplicate loci and examination of genetic variation in populations of rainbow trout*. Dissertation. University of Washington.

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science*, *318*, 100–103. https://doi.org/10.1126/science.1145621

Archer, F. I., Adams, P. E., & Schneiders, B. B. (2017). Stratag: An r package for manipulating, summarizing and analysing population genetic data. *Molecular Ecology Resources*, *17*, 5–11. https://doi.org/10.1111/1755-0998.12559

Arciniega, M., Clemento, A. J., Miller, M. R., Peterson, M., Garza, J. C., & Pearse, D. E. (2016). Parallel evolution of the summer steelhead ecotype in multiple populations from Oregon and northern California. *Conservation Genetics*, *17*, 165–175. https://doi.org/10.1007/s10592-015-0769-2

Aubin-Horth, N., & Dodson, J. J. (2004). Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic Salmon. *Evolution*, *58*, 136–144. https://doi.org/10.1111/j.0014-3820.2004.tb01580.x

Baird, S. F. (1886). Report of the commissioner. In *Report of the commissioner for 1884. Washington: United States Commission for Fish and Fisheries* (pp. XII–LXXI). Government Printing Office.

Behnke, R. L. (1992). *Native trout of western North America*. American Fisheries Society.

Behnke, R. L. (2002). First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina: Response to comment. *Transactions of the American Fisheries Society*, *131*, 585–588. https://doi.org/10.1577/1548-8659(2002)131<0582:CFDCOA>2.0.CO;2

Behr, H. (1882). Five American Salmonidae in Germany. *Bulletin of the United States Fish Commission*, *2*, 237–246.

Busack, C. A., & Gall, G. A. E. (1980). Ancestry of artificially propagated California rainbow trout strains. *California Fish and Game*, *66*(1), 17–24.

Busby, P. J., Wainwright, T. C., Bryant, G. J., Lierheimer, L. J., Waples, R. S., Waknitz, F. W., & Lagomarsino, I. V. (1996). *Status review of west coast steelhead from Washington, Idaho, Oregon, and California*. NOAA Technical Memorandum NMFS-NWFSC-27 https://www.webapps.nwfsc.noaa.gov/assets/25/5592_06172004_122523_steelhead.pdf

Campbell, N. R., Overturf, K., & Narum, S. R. (2009). Characterization of 22 novel single nucleotide polymorphism markers in steelhead and rainbow trout. *Molecular Ecology Resources*, *9*, 318–322. https://doi.org/10.1111/j.1755-0998.2008.02376.x

Cavalli-Sforza, L. L., & Edwards, A. W. (1967). Phylogenetic analysis. Models and estimation procedures. *American Journal of Human Genetics*, *19*, 233–257. https://doi.org/10.2307/2406616

Clark, F. N. (1884). Report of work at the United States hatchery, Northville, Mich., 1881–’82. In *Report of the commissioner for 1882* (pp. 1037–1062). United States Commission for Fish and Fisheries, Government Printing Office.

Clemento, A. J., Anderson, E. C., Boughton, D., Girman, D., & Garza, J. C. (2009). Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. *Conservation Genetics*, *10*, 1321–1336. https://doi.org/10.1007/s10592-008-9712-0

Colihueque, N., Estay, F. J., Crespo, J. E., Arriagada, A., Baessolo, L., Canales-Aguirre, C. B., Marín, J., & Carrasco, R. (2019). Genetic differentiation and origin of naturalized rainbow trout populations from southern Chile, revealed by the mtDNA control region marker. *Frontiers in Genetics*, *10*, 1–14. https://doi.org/10.3389/fgene.2019.01212

Crawford, S. S., & Muir, A. M. (2008). Global introductions of salmon and trout in the genus Oncorhynchus: 1870–2007. *Reviews in Fish Biology and Fisheries*, *18*(3), 313–344. https://doi.org/10.1007/s11160-007-9079-1

Crespi, B. J., & Teo, R. (2002). Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution*, *56*, 1008–1020. https://doi.org/10.1111/j.0014-3820.2002.tb01412.x

Currens, K. P., Hemmingsen, A. R., French, R. A., Buchanan, D. V., Schreck, C. B., & Li, H. W. (1997). Introgression and susceptibility to disease in a wild population of rainbow trout. *North American Journal of Fisheries Management*, *17*, 1065–1078. https://doi.org/10.1577/1548-8675(1997)017<1065:iastdi>2.3.co;2

Deiner, K., Garza, J. C., Coey, R., & Girman, D. J. (2007). Population structure and genetic diversity of trout (*Oncorhynchus mykiss*) above and below natural and man-made barriers in the Russian River, California. *Conservation Genetics*, *8*, 437–454. https://doi.org/10.1007/s10592-006-9183-0

Docker, M. F., & Heath, D. D. (2003). Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. *Conservation Genetics*, *4*, 227–231. https://doi.org/10.1023/A:1023355114612

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*, 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Felsenstein, J. (1993). PHYLIP (phylogeny inference package). version 3.5 c. https://evolution.genetics.washington.edu/phylip.html

Figueroa-Muñoz, G., Olivos, J. A., Arismendi, I., Fabiano, G., Laporta, M., Silveira, S., González-Bergonzoni, I., Pavez, G., Ernst, B., & Ciancio, J. E. (2023). Contemporary distribution of non-native Chinook salmon (*Oncorhynchus tshawytscha*) in South America. *Biological Invasions*, *25*, 2727–2735. doi:10.1007/s10530-023-03083-7

Fleming, I. A., & Reynolds, J. D. (2004). Salmonid Breeding Systems. In A. P. Hendry & S. C. Stearns (Eds.), *Evolution illuminated - Salmon and their relatives* (pp. 264–294). Oxford University Press.

Garant, D., Fontaine, P. M., Good, S. P., Dodson, J. J., & Bernatchez, L. (2002). The influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). *Evolutionary Ecology Research*, *4*, 537–549. https://www.evolutionary-ecology.com/issues/v04n04/ffar1352.pdf

Garza, J. C., Gilbert-Horvath, E. A., Spence, B. C., Williams, T. H., Fish, H., Gough, S. A., Anderson, J. H., Hamm, D., & Anderson, E. C. (2014). Population structure of steelhead in coastal California. *Transactions of the American Fisheries Society*, *143*, 134–152. https://doi.org/10.1080/00028487.2013.822420

Hallock, R. J. (1989). Upper Sacramento River steelhead, *Oncorhynchus mykiss*, 1952–1988. In *Report to U.S. Fish and Wildlife Service* (p. 86). US Fish and Wildlife Service. https://nrm.dfg.ca.gov FileHandler

Hatch DR, Branstetter RD, Whiteaker J (2004) *Kelt reconditioning: A research project to enhance Iteroparity in Columbia Basin steelhead (Oncorhynchus mykiss)*, 2004 Annual Report. Office of Scientific and Technical Information (OSTI). Bonneville Power Administration, US Department of Energy. https://doi.org/10.2172/903055

Hendry, M. A., Wenburg, J. K., Myers, K. W., & Hendry, A. P. (2002). Genetic and phenotypic variation through the migratory season provides evidence for multiple populations of wild steelhead in the Dean River, British Columbia. *Transactions of the American Fisheries Society*, *131*(3), 418–434. https://doi.org/10.1577/1548-8659(2002)131<0418:GAPVTT>2.0.CO;2

Huson, D. H., & Scornavacca, C. (2012). Dendroscope 3: An interactive tool for rooted phylogenetic trees and networks. *Systematic Biology*, *61*, 1061–1067. https://doi.org/10.1093/sysbio/sys062

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*, 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Jombart, T. (2008). Adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics*, *11*, 1–15. https://doi.org/10.1186/1471-2156-11-94

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, *3*, 348–365. https://doi.org/10.1007/BF00043384

Keefer, M. L., Wertheimer, R. H., Evans, A. F., Boggs, C. T., & Peery, C. A. (2008). Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): Implications for conservation. *Canadian Journal of*

Fisheries and Aquatic Sciences, *65*, 2592–2605. https://doi.org/10.1139/F08-160

Keenan, K., Mcginnity, P., Cross, T. F., Crozier, W. W., & Prodöh, P. A. (2013). DiveRsity: An R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods in Ecology and Evolution*, *4*, 782–788. https://doi.org/10.1111/2041-210X.12067

Kostow, K. (2003). *Factors that influence evolutionarily significant unit boundaries and status assessment in a highly polymorphic species, Oncorhynchus mykiss, in the Columbia Basin*. Oregon Department of Fish and Wildlife https://www.semanticscholar.org/paper/Factors-that-Influence-Evolutionarily-Significant-a-Kostow/dc7f753bc9cb04cf9859025a98926417f03a868a

Lee, C. E. (2002). Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, *17*, 386–391. https://doi.org/10.1016/S0169-5347(02)02554-5

Leitritz, E. (1970). A history of California's fish hatcheries,1870–1960. *Fish Bulletin*, *150*, 1–87. http://escholarship.org/uc/item/2z8648k3

Liberoff AL (2013) *Bases ambientales del comportamiento migratorio de la trucha arco iris (Oncorhynchus mykiss) del río Santa Cruz. Ph.D. Thesis*. Universidad Nacional de Córdoba. http://hdl.handle.net/11086/5530

Liberoff, A. L., Leal, A. A., Díaz De Vivar, M. E., Riva-Rossi, C. M., & Pascual, M. A. (2019). Maternal influence on early lipid content in an introduced partially anadromous population of *Oncorhynchus mykiss*. *Journal of Fish Biology*, *95*, 959–964. https://doi.org/10.1111/jfb.14062

Liberoff, A. L., Miller, J. A., Riva-Rossi, C. M., Hidalgo, F. J., Fogel, M. L., & Pascual, M. A. (2014). Transgenerational effects of anadromy on juvenile growth traits in an introduced population of rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 398–407. https://doi.org/10.1139/cjfas-2013-0466

Liberoff, A. L., Quiroga, A. P., Riva-Rossi, C. M., Miller, J. A., & Pascual, M. A. (2015). Influence of maternal habitat choice, environment and spatial distribution of juveniles on their propensity for anadromy in a partially anadromous population of rainbow trout (*Oncorhynchus mykiss*). *Ecology of Freshwater Fish*, *24*, 424–434. https://doi.org/10.1111/eff.12157

Liberoff, A. L., Riva Rossi, C. M., Fogel, M. L., Ciancio, J. E., & Pascual, M. A. (2013). Shifts in δ15N signature following the onset of exogenous feeding in rainbow trout *Oncorhynchus mykiss*: Importance of combining length and age data. *Journal of Fish Biology*, *82*, 1423–1432. https://doi.org/10.1111/jfb.12063

MacCrimmon, H. R. (1971). World distribution of rainbow trout (*Salmo gairdneri*). *Journal of the Fisheries Research Board of Canada*, *28*, 663–704. https://doi.org/10.1139/f71-098

McCusker, M. R., Parkinson, E., & Taylor, E. B. (2000). Mitochondrial DNA variation in rainbow trout (*Oncorhynchus mykiss*) across its native range: Testing biogeographical hypotheses and their relevance to conservation. *Molecular Ecology*, *9*, 2089–2108. https://doi.org/10.1046/j.1365-294X.2000.01121.x

McEwan, D. R. (2001). Central Valley steelhead. In R. L. Brown (Ed.), *Contributions to the Biology of Central Valley Salmonids Fish Bull* (Vol. 179, pp. 1–43), California Department of Fish and Game. UC San Diego: Library - Scripps Digital Collection. https://escholarship.org/uc/item/6sd4z5b2

McPhee, M. V., Utter, F., Stanford, J. A., Kuzishchin, K. V., Savvaitova, K. A., Pavlov, D. S., & Allendorf, F. W. (2007). Population structure and partial anadromy in *Oncorhynchus mykiss* from Kamchatka: Relevance for conservation strategies around the Pacific rim. *Ecology of Freshwater Fish*, *16*, 539–547. https://doi.org/10.1111/j.1600-0633.2007.00248.x

Moczek, A. P., Hunt, J., Emlen, D. J., & Simmons, L. W. (2002). Threshold evolution in exotic populations of a polyphenic beetle. *Evolutionary Ecology Research*, *4*, 587–601. https://scholarworks.umt.edu/biosci_pubs/189

Morris, D. B., Richard, K. R., & Wright, J. M. (1996). Microsatellites from rainbow trout (*Oncorhynchus mykiss*) and their use for genetic study of salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 120–126. https://doi.org/10.1139/f95-161

Narum, S. R., Contor, C., Talbot, A., & Powell, M. S. (2004). Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, U.S.A. *Journal of Fish Biology*, *65*, 471–488. https://doi.org/10.1111/j.0022-1112.2004.00461.x

Narum, S. R., Hatch, D., Talbot, A. J., Moran, P., & Powell, M. S. (2008). Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Biology*, *72*, 45–60. https://doi.org/10.1111/j.1095-8649.2007.01649.x

Nichols, K. M., Edo, A. F., Wheeler, P. A., & Thorgaard, G. H. (2008). The Genetic Basis of Smoltification-Related Traits in Oncorhynchus mykiss. *Genetics*, *179*(3), 1559–1575. https://doi.org/10.1534/genetics.107.084251

Nielsen, C., Aarestrup, K., Nørum, U., & Madsen, S. S. (2003). Pre-migratory differentiation of wild brown trout into migrant and resident individuals. *Journal of Fish Biology*, *63*, 1184–1196. https://doi.org/10.1046/j.1095-8649.2003.00237.x

Nielsen, J. L. (1999). The evolutionary history of steelhead (*Oncorhynchus mykiss*) along the US Pacific coast: Developing a conservation strategy using genetic diversity. *ICES Journal of Marine Science*, *56*, 449–458. https://doi.org/10.1006/jmsc.1999.0452

Nielsen, J. L., Pavey, S. A., Wiacek, T., & Williams, I. (2005). Genetics of Central Valley *O. Mykiss* populations: Drainage and watershed scale analyses. *San Francisco Estuary and Watershed Science*, *3*. https://doi.org/10.15447/sfews.2005v3iss2art3

Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B., & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of Freshwater Fish*, *15*, 446–452. https://doi.org/10.1111/j.1600-0633.2006.00176.x

Pascual, M., Kinnison, M., & Riva Rossi, C. (2002). First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina: Response to comment. *Transactions of the American Fisheries Society*, *131*, 585–588. https://doi.org/10.1577/1548-8659(2002)131<0585:FDCOAI>2.0.CO;2

Pascual, M., Kinnison, M., Riva Rossi, C., Mackey, G., Kinnison, M. T., & Walker, R. (2001). First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. *Transactions of the American Fisheries Society*, *130*, 53–67. https://doi.org/10.1577/1548-8659(2001)130<0053:FDCOAI>2.0.CO;2

Pearse, D., & Garza, J. C. (2015). You can't unscramble an egg: Population genetic structure of *Oncorhynchus mykiss* in the California Central Valley inferred from combined microsatellite and single nucleotide polymorphism data. *San Francisco Estuary and Watershed Science*, *13*(4). https://doi.org/10.15447/sfews.2015v13iss4art3

Pearse, D. E., Barson, N. J., Nome, T., Gao, G., Campbell, M. A., Abadía-Cardoso, A., Anderson, E. C., Rundio, D. E., Williams, T. H., Naish, K. A., Moen, T., Liu, S., Kent, M., Moser, M., Minkley, D. R., Rondeau, E. B., Brieuc, M. S. O., Sandve, S. R., Miller, M. R., … Lien, S. (2019). Sex-dependent dominance maintains migration supergene in rainbow trout. *Nature Ecology & Evolution*, *3*, 1731–1742. https://doi.org/10.1038/s41559-019-1044-6

Pearse, D. E., Miller, M. R., Abadía-Cardoso, A., & Garza, J. C. (2014). Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20140012. https://doi.org/10.1098/rspb.2014.0012

Phillis, C. C., Moore, J. W., Buoro, M., Hayes, S. A., Garza, J. C., & Pearse, D. E. (2016). Shifting thresholds: Rapid evolution of migratory life histories in steelhead/rainbow trout, *Oncorhynchus mykiss*. *The Journal of Heredity*, *107*, 51–60. https://doi.org/10.1093/jhered/esv085

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*, 945–959. https://doi.org/10.1093/genetics/155.2.945

Riva Rossi, C. M. (2004). *Origen y desarrollo de historias de vida alternativas en poblaciones introducidas de trucha arco iris (Oncorhynchus mykiss) en Patagonia*. Ph.D. Thesis. Universidad Nacional del Comahue.

Riva Rossi, C. M., Lessa, E. P., & Pascual, M. A. (2004). The origin of introduced rainbow trout (*Oncorhynchus mykiss*) in the Santa Cruz River, Patagonia, Argentina, as inferred from mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*, 1095–1101. https://doi.org/10.1139/F04-056

Riva-Rossi, C., Pascual, M. A., Babaluk, J. A., García-Asorey, M., & Halden, N. M. (2007). Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. *Journal of Fish Biology*, *70*, 1780–1797. https://doi.org/10.1111/j.1095-8649.2007.01449.x

Roff, D. A. (1996). The evolution of threshold traits in animals. *The Quarterly Review of Biology*, *71*, 3–35. https://doi.org/10.1086/419266

Rosenberg, N. A. (2004). DISTRUCT: A program for the graphical display of population structure. *Molecular Ecology Notes*, *4*, 137–138. https://doi.org/10.1046/j.1471-8286.2003.00566.x

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., & McCauley, D. E. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, *32*, 305–332.

Savvaitova, K. A., Kuzishchin, K. V. A., & Pavlov, D. S. (1999). Population structure of Mikizha *Parasalmo mykiss* from Rivers of northwestern Kamchatka and North America. *Journal of Ichthyology*, *39*, 504–516.

Scribner, K. T., Gust, J. R., & Fields, R. L. (1996). Isolation and characterization of novel salmon microsatellite loci: Cross-species amplification and population genetic applications. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 833–841. https://doi.org/10.1139/f95-254

Simmons, R. E., Lavretsky, P., & May, B. (2010). Introgressive hybridization of Redband trout in the upper McCloud River watershed. *Transactions of the American Fisheries Society*, *139*, 201–213. https://doi.org/10.1577/T08-245.1

Stanković, D., Crivelli, A. J., & Snoj, A. (2015). Rainbow trout in Europe: Introduction, naturalization, and impacts. *Reviews in Fisheries Science & Aquacultur*, *23*(1), 39–71. https://doi.org/10.1080/23308249.2015.1024825

Tessier, N., & Bernatchez, L. (1999). Stability of population structure and genetic diversity across generations assessed by microsatellites among sympatric populations of landlocked Atlantic salmon (*Salmo salar* L.). *Molecular Ecology*, *8*, 169–179. https://doi.org/10.1046/j.1365-294X.1999.00547.x

Thériault, V., & Dodson, J. J. (2003). Body size and the adoption of a migratory tactic in brook charr. *Journal of Fish Biology*, *63*, 1144–1159. https://doi.org/10.1046/j.1095-8649.2003.00233.x

Thériault, V., Garant, D., Bernatchez, L., & Dodson, J. J. (2007). Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). *Journal of Evolutionary Biology*, *20*, 2266–2277. https://doi.org/10.1111/j.1420-9101.2007.01417.x

Thorpe, J. E., Mangel, M., Metcalfe, N. B., & Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology*, *12*, 581–599. https://doi.org/10.1023/A:1022351814644

Thrower, F. P., Hard, J. J., & Joyce, J. E. (2004). Genetic architecture of growth and early life-history transitions in anadromous and derived freshwater populations of steelhead. *Journal of Fish Biology*, *65*, 286–307. https://doi.org/10.1111/j.0022-1112.2004.00551.x

Valette, L. H. (1922). *Apuntes sobre la industria pesquera nacional: someras consideraciones*. Tall. Gráf. del Ministerio de Agricultura de la Nación.

Valette, L. H. (1924). Servicio de piscicultura. Sus resultados hasta 1922 inclusive. Ministerio de Agricultura de la Nación, Circular 338, Buenos Aires.

Wales, J. H. (1939). General report of the investigation on theMcCloud river drainage in 1938. *California Department of Fish and Game*, *25*, 272–309.

Warnes, G., & Leisch, F. (2005). Genetics: Population genetics. R Package Version 1.2.0. https://cran.r-project.org/web/packages/genetics/genetics.pdf

Wenburg, J. K., Bentzen, P., & Foote, C. J. (1998). Microsatellite analysis of genetic population structure in an endangered salmonid: The coastal cutthroat trout (*Oncorhynchus clarki clarki*). *Molecular Ecology*, *7*, 733–749. https://doi.org/10.1046/j.1365-294x.1998.00386.x

Williamson, K. S., Cordes, J. F., & May, B. (2002). Characterization of microsatellite loci in chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. *Molecular Ecology Notes*, *2*, 17–19. https://doi.org/10.1046/j.1471-8286.2002.00129.x

Willson, M. (1997). Variation in salmonid life histories: patterns and perspectives. USDA Research Paper 498. https://www.fs.fed.us/pnw/pubs/pnw_rp498.pdf

Yamamoto, S., Morita, K., & Goto, A. (1999). Marine growth and survival of white-spotted charr, *Salvelinus leucomaenis*, in relation to smolt size. *Ichthyological Research*, *46*, 85–92. https://doi.org/10.1007/BF02674951

Zimmerman, C. E., & Reeves, G. H. (2000). Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: Evidence from surveys and otolith microchemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 2152–2162. https://doi.org/10.1139/f00-192

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