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The invasion of an Atlantic Ocean river basin in Patagonia by Chinook salmon: new insights from SNPs

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Abstract Chinook salmon spawning was first reported in the 1980s in the Caterina River tributary of the Santa Cruz River basin of Patagonia, which drains into the Atlantic Ocean. A naturalized population now persists and its source has been debated. Chinook salmon from California populations was directly released into the Santa Cruz River in the early twentieth century, but ocean ranching experiments on the Pacific coast of Patagonia (Chile) also released Chinook salmon of lower Columbia River origin

(University of Washington hatchery stock) in the late twentieth century. We used genetic stock identification with single nucleotide polymorphisms to explore the origin of this Chinook salmon population. The genotypes of salmon that invaded the Santa Cruz River were compared with those derived from 69 known populations from the Northern Hemisphere. Chinook Salmon of the Santa Cruz River were found to be most similar to those from the lower Columbia River. This supports the hypothesis that the Santa Cruz River population was founded from the ocean ranching in southern Chile and the river was invaded by fish straying from Pacific coast basins. Moreover, we find that the life history of these naturalized fish, as inferred from scale analysis, was similar to that of the progenitor stock. We suggest that the successful invasion of the Caterina River in Patagonia by Chinook salmon was aided by pre-adaptations of some of the stocks used in the ocean ranching experiments to conditions in the new environment, rather than a post-colonization adaptation.

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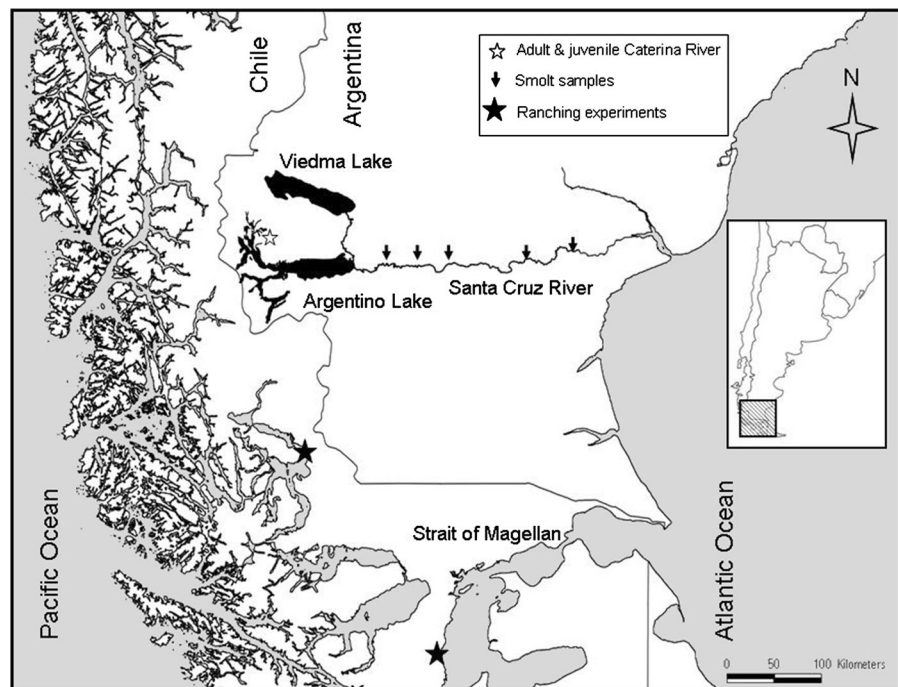
Introduction

The anadromous salmonid life cycle includes foraging migrations to the ocean (Groot and Margolis 1991)

which allow these fishes to invade isolated basins in search of suitable spawning and rearing habitat. The Chinook salmon (ChS, *Oncorhynchus tshawytscha*) establishment in Patagonia constitutes the largest anadromous salmonid invasion documented to date (Pascual and Ciancio 2007). During the last 40 years, at least 10 large basins in Chile and Argentina from latitudes 39° to 54° S were colonized by this species, either directly due to human stocking or indirectly by natural establishment from straying fish (Correa and Gross 2008). Many basins were colonized from nearby rivers, but some isolated basins seem to have been colonized by long-distance noncontiguous dispersal (Riva Rossi et al. 2012). Such is the case of the Santa Cruz River (Fig. 1), the only Atlantic basin colonized by ChS, where the species was first observed about 30 years ago, at the onset of the Patagonia invasion (Ciancio et al. 2005). The ecological effects of the invasion on the receiving ecosystems have been substantial (Arismendi and Soto 2012; Ciancio et al. 2010; Montory et al. 2010; Niklitschek et al. 2013). Understanding the origin of and relationships between Patagonian populations of ChS could lead to a better understanding of the traits that affect success in colonizing new environments, and may help predict future invasions.

Aquaculture records and historical information indicate two potential origins for Santa Cruz River ChS: (1) importation of fish from California in the early twentieth century and direct stocking into the mainstem Santa Cruz River, or (2) oceanic colonization by fish straying from ocean ranching experiments conducted during the 1980s in the southern channels of Chile, which used hatchery stocks imported mainly from the University of Washington hatchery (Becker et al. 2007). Previously, genetic analysis with mitochondrial DNA (mtDNA) was used in combination with historical records to analyze the origin, relationships and invasion patterns of ChS populations throughout Patagonia, including the Santa Cruz River, and its tributary the Caterina River. The Caterina River is both the most remote stream within the invaded range, and the first location of documented spawning of ChS in the Santa Cruz River basin (Becker et al. 2007; Riva Rossi et al. 2012). Although the previous genetic analysis identified multiple sources of introduction and potential areas of admixture between lineages in many river basins in Patagonia, Caterina River fish were monomorphic at the mtDNA control region (Becker et al. 2007; Riva Rossi et al. 2012) and it was therefore not possible to determine their genetic origins and relationships.

Fig. 1 Locations of sample collection and Chilean ranching experiments



Recently, single polynucleotide polymorphisms (SNPs) have been developed for a large array of salmonid species and have become the gold standard for use in salmon population genetics (Seeb et al. 2011), including genetic stock identification (GSI). For example, SNP data is used on a regular basis to predict the stock composition of the world's largest salmon fishery, for sockeye salmon (*O. nerka*) migrating into Bristol Bay (Habicht et al. 2010). The ability of GSI with SNPs to resolve both broad- and fine-scale population structure for ChS across its native range (Clemento et al. 2011; Hess et al. 2011; Templin et al. 2011), as well as to identify the composition of ocean mixtures (Habicht et al. 2010; Larson et al. 2012; Satterthwaite et al. 2014), has been well documented. In this paper, we use GSI to identify the origin of ChS spawning in the Santa Cruz River Basin in Argentina. We employ a stock identification baseline of genotypes from a panel of 96 SNP markers typed in over 8000 known-origin ChS from 69 populations ranging from California to Alaska (Clemento et al. 2014). We also investigate the life history characteristics of the identified potential sources that may have facilitated the invasion and establishment of this population in this remote and relatively isolated river basin.

Methods

Sample collection and locations

The Santa Cruz River (50°S; 70°W) originates in two large oligotrophic to ultra-oligotrophic glacial lakes, Viedma and Argentino, within Argentina's Los Glaciares National Park. This river collects water from the Patagonian ice fields of the Andes Mountains and flows eastward about 500 km to the Atlantic Ocean (Fig. 1). Average flow is $691 \text{ m}^3 \text{ s}^{-1}$, with an average minimum of $278.1 \text{ m}^3 \text{ s}^{-1}$ (September) and an average maximum of $1278 \text{ m}^3 \text{ s}^{-1}$ (March). The Caterina River (49°54'01''S 73°10'11''W) is a medium size (mean discharge 10 m^3) tributary of the Santa Cruz River and flows for 7.72 km from Lake Anita to Lake Argentino (Fig. 1). ChS spawning activity was first reported in the Caterina River about 1980 (Ciancio et al. 2005).

Fin clips were collected from 44 spawning adult fish (years 2003–2004) and 8 juveniles (2008) in the

Caterina River (Fig. 1, for details see Ciancio et al. 2005), and from 24 smolts in the main stem Santa Cruz River during Austral spring (September–November) in the years 2005–2010. Fin clips were dried at air temperature and stored on blotter paper.

SNP genotyping and analysis

DNA was extracted using DNeasy 96 Tissue kits on a BioRobot3000 (QIAGEN, Inc., Valencia, CA) and genotypes collected from 96 SNP loci using 96.96 SNP Genotyping Dynamic ArraysTM with an EP1 system (Fluidigm Corporation, South San Francisco, CA) according to the manufacturer's protocols. Genotypes were called using the Fluidigm SNP Genotyping Analysis Software (version 2.1.1). This panel of SNP markers included 95 loci polymorphic in ChS and one for identification of coho salmon (*O. kisutch*), which are sometimes misidentified as ChS (Clemento et al. 2014).

Genetic variation

The software GENEPOP (version 4; Rousset 2008) was used to perform exact tests for departures from Hardy–Weinberg equilibrium (HWE) genotypic expectations and linkage equilibrium between each pair of loci across samples. These tests can detect the presence of factors altering genotype frequencies from their expected values, including nonrandom mating (due to inbreeding or outbreeding), hidden population structure, selection, or migration. GenAlEx 6.5 (Peakall and Smouse 2012) was used to calculate the number of alleles (N_a) and expected and observed heterozygosities (H_e and H_o , respectively) for each locus and population, as well as the percentage of polymorphic loci for each population.

Identification of the stock of origin of Santa Cruz River Chinook salmon

Two approaches were used to infer the origins of invasive ChS in the Santa Cruz River. First, a literature review was performed in an attempt to identify translocations of fish that may have given rise to the population spawning in the Santa Cruz River Basin. Second, GSI analysis was used with the *gsi_sim* software (Anderson et al. 2008) and a baseline that includes 8031 fish from 69 populations grouped into

38 reporting units (reporting units are generally composed of multiple populations that are genetically similar or are subject to similar management regimes) from Alaska, British Columbia, Washington, Oregon, and California. This method was described and validated in Clemento et al. (2014). Coho salmon are occasionally misidentified as ChS (and vice versa) in fisheries and ecological sampling. The *gsi_sim* program identifies coho salmon both with the diagnostic marker mentioned above, but also with genotype data from a collection of 47 coho salmon from California (Clemento et al. 2014). GSI is typically applied in situations where samples are obtained from mixtures of fish that are all directly and very-recently descended from a population represented in the baseline. This situation is somewhat different, because the ChS population in the Caterina River may have experienced a relatively large degree of genetic drift from the original progenitor population and/or the progenitor population may not be represented in the baseline dataset. We conducted simulations to assess the reliability of stock identification in this context. Specifically, the simulations were designed to verify that:

1. Genetic drift between the time of founding and of sampling in the Caterina River population was unlikely to lead to spurious inferences.
2. There are no sources outside of the Lower Columbia and the Willamette reporting unit areas (see “Results” section) that would have yielded the results obtained.
3. Even though the exact progenitor population might not be in the baseline, the assignments back to reporting unit are accurate.

The simulations were conducted as follows: each of the 69 ChS populations in the baseline was removed sequentially from the dataset, and the allele frequencies in that population recorded. Then, to simulate genetic drift, six new sets of allele frequencies were drawn from the beta distribution at values of:

$$f = t/(2N_e) \in \{10^{-6}, 0.01, 0.025, 0.05, 0.1, 0.2\}$$

where t is number of generations and N_e is the effective population size. Briefly, if the allele frequency at locus ℓ in the removed population was estimated to be p_l [p_l was estimated in each population as the posterior mean, given a uniform prior on allele frequency; see

for example Rannala and Mountain (1997)], then “drifted” allele frequencies were simulated by drawing from a beta distribution with parameters α and β defined as

$$\alpha = p_l \frac{1-f}{f}$$

$$\beta = (1 - p_l) \frac{1-f}{f}.$$

For each of the 6 values of f , 10 new sets of allele frequencies were simulated and genotype data for 76 fish then simulated from those new allele frequencies, assuming independence between alleles within and between loci. These fish were then assigned to reporting unit using the baseline in which the focal population had been removed. The output was then summarized by recording the fraction of fish simulated from each replicate that were assigned to either the Willamette River, Lower Columbia Spring, or Lower Columbia Fall reporting units—the three reporting units to which fish in the Caterina River ChS population were assigned.

Estimates of pairwise genetic differentiation (F_{ST}) between native and introduced populations, and permutation tests of their significance, were generated with FSTAT v2.9.3.2 (Goudet 1995). Additionally, an unrooted neighbor-joining tree was constructed with Cavalli-Sforza and Edwards (1967) chord distances (DCE) with PHYLIP v3.66 (Felsenstein 2005). Consistency of tree topology was assessed by bootstrapping over loci again with PHYLIP, to create 10,000 pseudo-replicate datasets and the resulting consensus tree was visualized in TREEVIEW v1.6.6 (Page 1996).

Once the putative reporting units of origin in the native range were identified, the ecotypes of the adult fish from the Caterina River were compared with the ecotypes of fish from the reporting unit to which they were assigned. Ecotype was inferred from scale analysis of adult fish captured in years 2003–2004 only, following the method described in Ciancio et al. (2005). Individual fish were classified as “stream” or “ocean” ecotype based on criteria for the pattern of circuli in the freshwater nucleus. Traditionally, literature dealing with ChS life histories describes two ecotypes: “stream-type”, or yearling migrants, are those individuals that migrate to sea after a full year of residence in freshwater, whereas “ocean-type”, or

subyearling migrants, migrate in their first year of life (Healey 1991). In many populations in the central and southern part of the species' North American range, these juvenile life history patterns co-vary with the timing of adult return to freshwater. Ocean-type juveniles typically return as adults in the fall, shortly before spawning, whereas stream-type juveniles typically return as adults earlier in the season, with a more protracted period of freshwater holding prior to spawning (Healey 1991; Quinn 2005). Many characteristics, including marine migration patterns (Sharma and Quinn 2012) and juvenile growth and behavior (Taylor 1990), differ between ocean-type and stream-type fish, although there is a spectrum of phenotypic combinations, and there is no genetic support to consider them as different lineages (Moran et al. 2013; but see Waples et al. 2004). Consequently, in the present study, we use ocean- and stream-type to refer to the freshwater life history of individual juvenile fish rather than to imply ancestry.

Results

Tests for HWE deviations revealed that only three loci (Ots_118938-325, Ots_129144-472, and Ots_102867-609) had a significantly negative F_{IS} after Bonferroni correction (-0.765 to -0.667 , p value <0.001) in the Santa Cruz River population. These negative F_{IS} values could reflect chance differences in allele frequencies between males and females, resulting from low effective number of breeders in the founding population or population bottlenecks (Cornuet and Luikart 1996; Luikart and Cornuet 1999). The percentage of locus pairs in significant disequilibrium after Bonferroni correction was 0.72 %, which is less than the proportion expected by chance alone. In the Santa Cruz River population, 91 % of the loci were polymorphic on average. Genetic diversity values for Caterina River ChS (mean $H_e = 0.290$, mean $H_o = 0.298$, and $N_a = 1.916$) fall within the reported ranges measured at the same SNP loci for natural populations and hatchery stocks of ChS from across the native range (Clemento et al. 2014; mean $H_e = 0.307$, range 0.191–0.377; mean $H_o = 0.305$, range 0.195–0.376; mean $N_a = 1.925$, range 1.630–2.000; %P = 92 %, range 62–100 %).

Assignments to northern hemisphere stocks

All of the assignments of Santa River River fish were to stocks from rivers within the lower Columbia River Basin (Oregon and Washington states; Table 1, Supplementary material 1 and 2) corresponding to three reporting units. Most of the fish (79 %) were assigned to the Willamette River Basin reporting unit (McKenzie River Hatchery stock) with posterior probabilities higher than 0.95. The remaining assignments were with lower posterior probabilities (range 0.65–0.88), and included one fish assigned to the Willamette River Basin reporting unit (North Santiam River Hatchery stock), eight to the Lower Columbia River fall-run reporting unit Cowlitz Hatchery fall-run stock), and, finally, seven fish assigned to the Lower Columbia River spring-run reporting unit (five to the Cowlitz Hatchery and two to the Kalama Hatchery spring-run stocks).

While Caterina River fish were assigned to these three reporting units only, assignments of smolts collected in the main Santa Cruz River basin were more diverse. Most of these fish (91 %), both smolts and adults, were assigned to reporting units dominated by spring-run phenotype (stream ecotype) fish (Table 1) and scale analysis showed that 39 out of 46 (84 %) adult salmon were stream-type ecotype. Finally, one smolt from the lower basin was identified as a coho salmon, the first report of the species for any Atlantic basin.

The results of simulations to assess the reliability of the stock identification analyses (summarized in Supplementary material 3) clearly indicated that the observed assignments of fish from the Caterina River, with more than 80 % of the fish assigned to the Willamette reporting unit, would only occur if these fish originated from a Willamette River population. However, as many as 60 % of the fish simulated from the Kalama River with $f = 0.2$ were assigned to the Willamette River reporting unit, which may not be surprising given the history of fish transfers between hatcheries in the lower Columbia River region. So the results obtained with the Caterina River fish indicate that a large fraction of them originated from a Willamette River, or possibly another Lower Columbia River stock, and are not consistent with an origin of these fish from the Sacramento River in the California

Table 1 Results of the genetic stock identification analysis using *gsi_sim*

Reporting unit	Populations	Run	Caterina river		Santa Cruz river	
			Adult	Juvenile	Smolt	Total
Lower Columbia R. spring	Kalama Hatchery spring	Spring			2 (0.88)	2
Lower Columbia R. spring	Cowlitz Hatchery spring	Spring	1 (0.68)	4 (0.65)		5
Lower Columbia R. fall	Cowlitz Hatchery fall	Fall	4 (0.83)		4 (0.77)	8
Willamette River	McKenzie Hatchery	Spring	41 (0.97)	4 (0.97)	16 (0.95)	61
Willamette River	North Santiam Hatchery	Spring			1 (0.81)	1
Coho	Coho Salmon California				1 (0.99)	1
Total			46	8	24	78

Average posterior probabilities are shown in brackets. Only Chinook salmon assigned to the McKenzie stock in the Willamette River Basin have mean posterior probabilities >90 %

Central Valley, which was the source of most early salmon egg imports.

Pairwise F_{ST} values indicated a similar pattern, with the invasive Caterina River ChS population most similar to native populations from the Willamette River ($F_{ST} = 0.119$) and lower Columbia River basin ($F_{ST} = 0.131$ with spring-run stocks, $F_{ST} = 0.140$ with fall-run stocks), and more divergent from all other native populations (0.161–0.448) (Supplementary material 2). The population tree was concordant with the stock assignments and F_{ST} results, grouping the Santa Cruz River fish with those from the Willamette River and two other reporting units from the lower Columbia River Basin. Santa Cruz River fish did not group with populations from the California Central Valley (Fig. 2), again indicating that they were not sources for this invasion. The tree also highlighted the distinctiveness of the Santa Cruz River population from native salmon populations in the Pacific Northwest (California, Oregon, Washington, and British Columbia, Canada) and Alaska, presumably as a result of genetic drift and selection since they were introduced to Patagonia.

Historical review of potential sources

Chinook salmon were first reported in the Caterina River in the early 1980s (Ciancio et al. 2005). This was well before the large aquaculture expansion in Chile in the late 1990s and leads to two primary candidates for the source of these invading fish: Sacramento River Basin fish stocked in the Santa Cruz Basin by the Argentinean government at the beginning of the twentieth century, or fish originated from the sea

ranching experiments in southern Chile in the late twentieth century, primarily in the 1980s. These ranching experiments used hatchery stocks from the University of Washington, USA (Riva Rossi et al. 2012). The origins of the University of Washington Hatchery stock are complex and diverse. It was founded with fish from a hatchery on the Green River (Puget Sound), which used broodstock originally from the Kalama Hatchery on the lower Columbia River (Donaldson and Joyner 1984). The Kalama Hatchery was one of the main exporters of ChS fry and eggs in the late 1800s, and its broodstock was originally founded by fish produced at the nearby Cowlitz and Carson hatcheries. However, eggs and adults were brought in from numerous other lower Columbia River hatcheries, including Eagle Creek, Willamette River and Little White Salmon River hatcheries (Anonymous 2009). Although all of these hatcheries are in the lower Columbia River Basin, the Kalama River is very close to the Cowlitz River, and there is a fair amount of straying between them (Pascual and Quinn 1994; Quinn et al. 1991). In spite of the apparent diversity of broodstock sources for the ranching experiments in southern Chile, they were all closely related phylogenetically (Clemento et al. 2014; Seeb et al. 2011), as they were all derived from stocks in the lower Columbia River Basin.

Discussion

Here, we establish that the founding individuals of the invasive Caterina River Chinook salmon (ChS) population were from stocks native to the lower Columbia

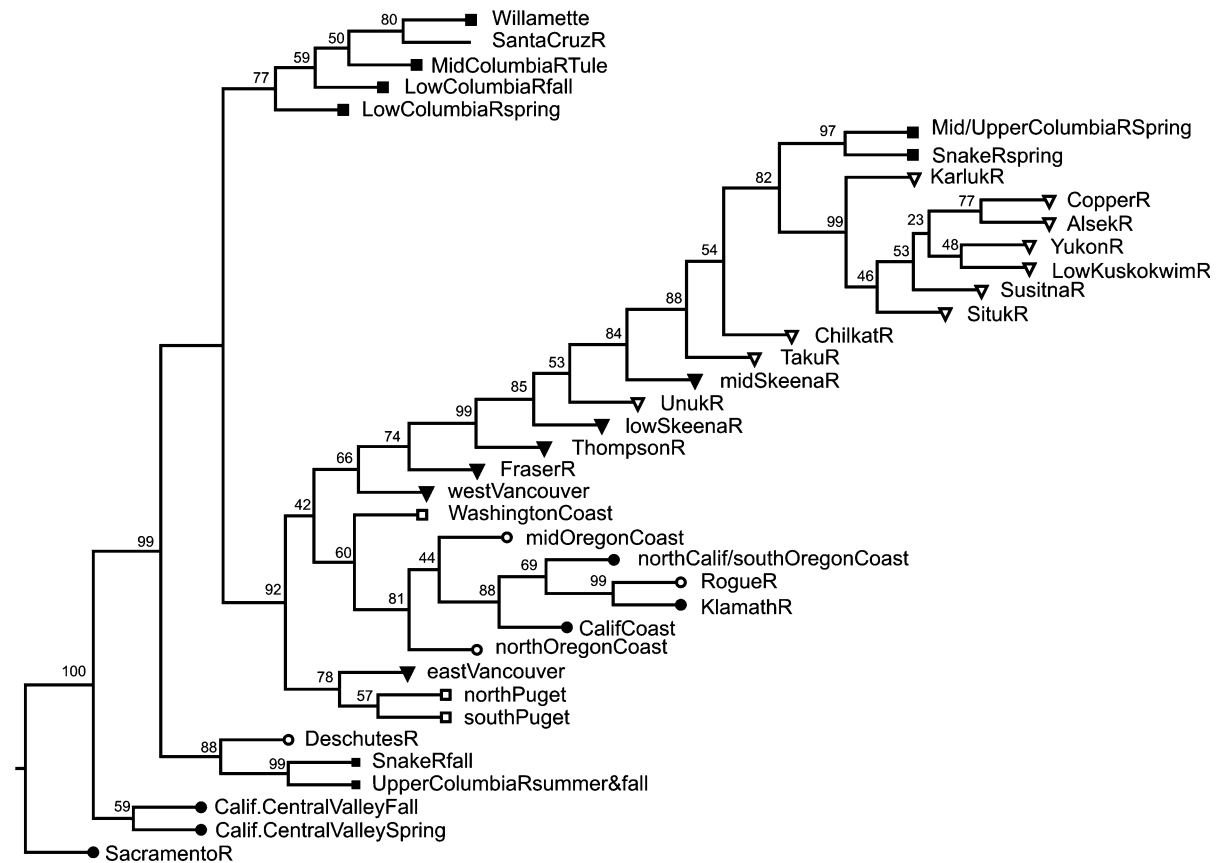


Fig. 2 Neighbor-joining dendrogram of Cavalli-Sforza and Edwards (1967) chord distances from genotype data of 95 SNPs for over 38 reporting units of Chinook salmon from the native range and the population from the Santa Cruz River, Argentina. Bootstrap values indicate the percentage of 1000 trees, constructed from bootstrap samples, where populations beyond the node clustered together. Native reporting unit labels follow Clemento et al. (2014), with full names described in

Supplementary material 1. Invasive Chinook salmon code: SantaCruzR—Santa Cruz River. Symbols represent the location of the River in USA and Canada, regardless of their phylogenetic relationship, from north to south: Alaska (*open inverted triangle*), British Columbia (*filled inverted triangle*), Washington (*open square*), Oregon-Washington (*filled square*), Oregon (*open circle*), California (*filled circle*)

River Basin. This result was indicated by three different methods: pairwise genetic differentiation, neighbor-joining tree, and GSI assignments. Previous studies of this population with mtDNA could not confidently identify its genetic origins (Becker et al. 2007; Riva Rossi et al. 2012). Due to the higher resolution of the current genetic dataset and the robust SNP marker-based GSI baseline, we were able to discriminate potential sources. None of the genotyped fish were assigned to a Californian reporting unit, supporting the hypothesis that the Santa Cruz River ChS population originated from more recent ocean ranching experiments in southern Chile with the intention to exploit the vast resources of the Antarctic and Patagonian Shelf oceans

for salmon production (Donaldson and Joyner 1984). The fish released in these efforts have their origin in stocks from the lower Columbia River Basin, which are the product of inter-hatchery translocations involving at least five hatcheries, and apparently began to stray into the Santa Cruz River Basin during the years 1981–1985. We found similar levels of genetic variation in the invasive and native range ChS populations, most likely due to admixture resulting from multiple source populations of ChS salmon introduced into Chile, similar to what was found with introduced rainbow trout in Patagonia (Consuegra et al. 2011).

There was also correspondence between the ecotypes inferred from scale patterns of the ChS in the

Caterina River and those of their source populations. Caterina River ChS are dominated by stream-type fish and have primarily spring-run ancestry (the phenotype of most stream-type fish). This pattern contrasts with that of introduced ChS populations in New Zealand (NZ), where temporally divergent ecotypes evolved from a single ancestral source (the fall-run from the Sacramento River) within >30 generations after the original introduction (Quinn et al. 2001). Present-day NZ ChS exhibit mixtures of stream- and ocean-type fish in different proportions; some are dominated by ocean-type fish, others by stream-type and few have a mix of the two ecotypes (Kinnison et al. 2011; Quinn et al. 2001). Significant genetic differentiation between NZ populations has also been found at two genes associated with migration and spawn timing in salmon (O'Malley et al. 2007).

The Caterina River ChS population is the product of a secondary colonization. Founders that strayed and survived to spawn probably represent only a small subset of the fish originally introduced for the ranching experiments. The characteristics of the Caterina River (e.g., temperature, flow, and productivity) and distance to the sea (about 500 river km) are typically of spawning and rearing habitat of fish with spring-run and stream-type life histories in the native range (Ciancio et al. 2005). Therefore, the rapid and successful establishment of a stream-type ChS population and apparent utilization of an existing ecotype in this river could be the result of selection on the founders. Several studies support the view that colonization is most likely to be successful under conditions requiring little adaptive change (pre-adaptation: Correa and Gross 2008; Dlugosch and Parker 2007; Facon et al. 2006). The GSI analysis of smolts in the Santa Cruz River Basin found a small number of lower confidence assignments to stocks with different phenotypes and hinted at a higher diversity of sources in the larger basin. This suggests that there may be additional spawning areas in the Santa Cruz River Basin which reflect the diversity of the fish released in the original ranching experiments (see Historical Review Section).

It is also remarkable that this population was established from just a few invading fish, naturalized from a few stocking events in southern Chile (Donaldson and Joyner 1984). Other attempts to introduce semelparous *Oncorhynchus* species in Patagonia involved millions of fish or eggs (Pascual and Ciancio

2007). In comparison to other semelparous *Oncorhynchus*, ChS exhibit a relatively wide array of life history tactics (e.g., timing; Teel et al. 2014). Together with standing genetic variation, diverse life history traits and life history plasticity have been proposed to be important for successful invasion by salmonids in Patagonia (Valiente et al. 2010). The only other species in this genus to have invaded the Santa Cruz River basin is *O. mykiss* (steelhead/rainbow trout), which displays the most diverse set of life history strategies in the genus. Furthermore, ChS have continued to expand their range in this geographically remote and isolated basin and are currently colonizing other tributaries, as suggested by genetic analysis of smolts and angler reports.

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