

Disentangling the contributions of ocean ranching and net-pen aquaculture in the successful establishment of Chinook salmon in a Patagonian basin

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Abstract The presence of Chinook salmon in Patagonia is an example of a successful invasion by a Pacific salmon species. The combination of historical records and genetic data can help to determine the origin of invasive / introduced species and allow the identification of the sources and dispersal process. We analyzed the genetic structure of Chinook salmon in the Futaleufú River (Pacific slope basin of Patagonia) using single nucleotide polymorphism genotypes and a recently described baseline dataset of native North American Chinook salmon populations. Our results revealed that Chinook salmon established in the Futaleufú River have high levels of within-population genetic diversity compared with populations from across the native range. Based on genetic similarity and historical reports, our results indicate that the Futaleufú population was first established by colonizing fish derived from the Lower Columbia River Basin, imported into Chile for ocean ranching purposes during the 1970s and 1980s, and

afterward it was strongly supplemented by escaped fish from net pen aquaculture that used broodstock imported during the 1990s from various sources, including the California Central Valley (via New Zealand), the Middle Oregon Coast, and Vancouver Island. The higher incidence of fish derived from the most recent introductions in our sample suggest that the contribution of escaped salmon from these posterior stockings on establishment success must have been particularly strong because included different sources. Subsequent admixture and hybridization among these multiple independent source stocks is likely responsible for the high level of standing genetic variation, which may be facilitating local adaptation and augmenting the opportunity for successful invasion and further colonization.

Keywords Chinook salmon · Potential origin · Pacific slope basin of Patagonia

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Introduction

The presence of Chinook salmon (*Oncorhynchus tshawytscha*) in the Futaleufú (also called the Grande) and Corcovado rivers, two basins with headwaters in the Argentinean Andes that drain to the Pacific Ocean, was first reported in 1984 (Grossman 1991; Di Prinzio and Pascual 2008). This invasion generated a complicated situation with ecological, social, political, and economic implications in the region. As salmonids are one of the most pervasive exotic species in the world (Pascual et al. 2009), there are many examples of their invasion that

have been well documented and large-scale direct and indirect alterations of the recipient ecosystems are expected to occur (Naylor et al. 2005). In addition, this invasion creates conflict between anglers, and associated sport fishing tourism, and those who are concerned with the native aquatic fauna, due to the scarce information about the state of these ecosystems before the introduction (Pascual et al. 2007, 2009). This lack of information may also make it more difficult to understand the impacts generated by this invasive fish.

Pacific salmon species were introduced in Chile during the 1970s for ranching and aquaculture-fishery purposes (Basulto 2003) and within two decades it became a globally important center for salmonid aquaculture (FAO 2011). In the 1980s, the salmon industry began to expand with net-pens in the inlets and fjords of the Lakes Region (40–44°S; Soto et al. 2006). Although Chinook salmon constituted less than 5 % of the total farmed fish production in Chile (SERNAPESCA 2006), it is the only exotic salmon species (not including trout) that successfully established naturalized populations (Sepúlveda et al. 2013) in Patagonian rivers with a Pacific outlet (Soto et al. 2001, 2007; Di Prinzio and Pascual 2008).

Two opposing views have emerged to explain the origin of the invasive Chinook salmon in Patagonian rivers. Astorga et al. (2008) used variation at microsatellite loci to identify the sources of naturalized Chinook salmon in the Petrohué River Basin (Chile) and found that this population derives from individuals imported during early ocean ranching activities in the 1970s. Conversely, Riva Rossi et al. (2012) used mitochondrial DNA sequence data to concluded that invading Chinook salmon in both Argentinean and Chilean rivers likely originated from both early ocean ranching activities and recent net-pen operations in Chile. However, both studies had limited power to fully discriminate the geographic origins of naturalized Chinook salmon populations, both because of the molecular genetic methods and data then available, and because their analyses were mainly focused on establishing the contribution of local aquaculture facilities to the naturalized population in the Petrohué River (Astorga et al. 2008) or validating official records of Chinook salmon imports into Chile (Riva Rossi et al. 2012). However, the identity of the specific population sources, their life history and demographic characteristics, their tolerance of environmental conditions and, therefore, their invasive potential have not been fully resolved.

Genetic stock identification (GSI) techniques are particularly applicable to salmonids; anadromous salmonid species return to their natal streams with high fidelity, promoting local adaptation and the formation of genetically distinct populations (Shaklee et al. 1999; Quinn 2005). GSI uses the observed allelic frequencies of known origin fish from baseline populations to infer the natal origin of fish captured in mixed stock fisheries or in ecological investigations (Milner et al. 1985; Utter and Ryman 1993; Beacham et al. 2014). GSI has been used in studies of stock composition, population structure, migration and distribution patterns, and in applications to fishery management in many Pacific salmonids (e.g., Habicht et al. 2010; Tucker et al. 2011; Larson et al. 2013; Satterthwaite et al. 2014). Recently, single-nucleotide polymorphisms (SNPs; Morin et al. 2004; Schlötterer 2004; Hauser and Seeb 2008) have become the genetic marker of choice for GSI. Compared with microsatellites and other genetic markers, SNPs can be assayed more quickly and cost-effectively, and the resulting genotypes are easily combined among laboratories, and so are ideal for developing shared data sets (Seeb et al. 2011). Here, we use genotypes from 96 SNP markers and a recently described baseline dataset from Chinook salmon populations in North America (Clemento et al. 2014) to identify the potential origins of the Chinook salmon spawning in the Futaleufú River, a Patagonian basin that drains into the Pacific Ocean.

Material and methods

Study area and sample collection

The Futaleufú River runs 246 km from its headwaters (43°08'S; 71°35'W) within Los Alerces National Park, Argentina, where it is regulated by a dam, before draining into the Pacific Ocean in Chile, in a region highly impacted by salmon aquaculture (Fig. 1).

Muscle tissue samples for genetic analysis were taken from adult Chinook salmon individuals ($n=53$; total length 77–120 cm and weight 5.3–20.0 kg) captured by sport fishermen in the Argentinean section of the Futaleufú River during 2010 and 2011. Tissue samples were preserved in 95 % ethanol and DNA was later extracted using QIAGEN DNEasy 96 kits on a BioRobot3000 (QIAGEN, Inc., Valencia, CA) according to the manufacturer's protocols. Samples were then genotyped with 96 SNP genetic markers using 5'

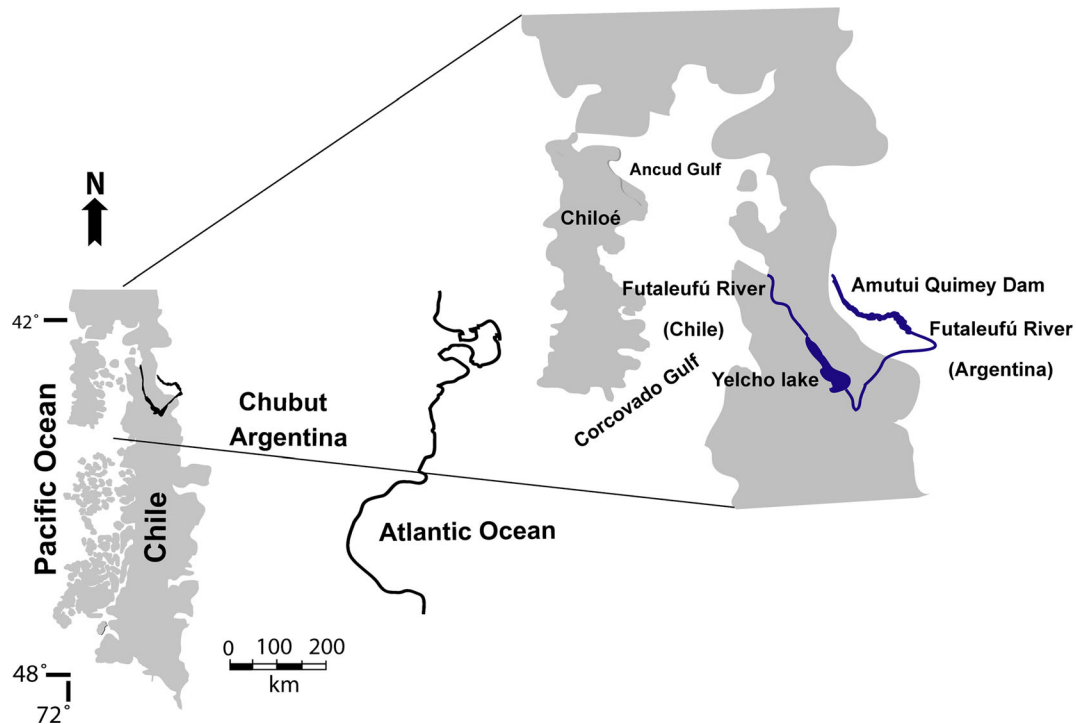


Fig. 1 Study area detailing the Futaleufú River drainage in both Argentinean and Chilean territory

nuclease (TaqMan; Applied Biosystems, Inc) chemistry on 96.96 Dynamic Arrays™ and with an EP-1 visualization system (Fluidigm Corporation, South San Francisco, CA) following Clemento et al. (2014).

Genetic variation

The software GENEPOP V4 (Rousset 2008) was used to perform exact tests for departures from Hardy–Weinberg equilibrium (HWE) and genotypic linkage equilibrium expectations between each pair of loci across samples. Mean expected and observed heterozygosity by locus and population were calculated using FSTAT v2.9.3.2 (Goudet 1995, 2001), while allelic richness, a measure of the number of alleles independent of sample size, was calculated for all populations using HP-RARE v1.0 (Kalinowski 2005).

Identification of the stock of origin

The most likely stock of origin and its associated posterior probability was estimated for each fish using the *gsi_sim* software (Anderson et al. 2008) combined with a baseline dataset, described by Clemento et al. (2014), that includes genotypes of 8031 fish from throughout

the eastern part of the species native range in North America, including 69 populations from Alaska, British Columbia, Washington, Oregon, and California. This baseline also includes data from a coho salmon population to discriminate fish from this species, which are often misidentified as Chinook salmon, particularly as juveniles. Because of low genetic differentiation among some populations in the baseline, population-specific assignment was not feasible; therefore, assignments were conducted at the level of the 38 reporting groups (RUs) that combine genetically similar populations in the baseline dataset. Then, the probability of ancestry for each Patagonian salmon to each reporting group was estimated. Clemento et al. (2014) used a simulation-based method implemented in *gsi_sim* to define low-confidence assignments. Because the Patagonian fish could not be directly from any of the populations in the baseline, we used different criteria than Clemento et al. (2014) for classifying assignments as low confidence. Whereas they considered individuals that had a z -score < -3.0 and either a reporting unit posterior probability < 0.9 or < 90 loci successfully genotyped as assigned without sufficient confidence, we used a z -score < -6.0 , and either reporting unit posterior probability < 0.6 , or > 80 loci

successfully genotyped as confidence criteria, following the sensitivity analysis performed by Anderson E. (pers. comm.) for this particular population.

We also used Discriminant Analysis of Principal Components (DAPC; Jombart et al. 2010) as an alternative method to infer population origin. DAPC is free of assumptions about Hardy-Weinberg and linkage equilibria (Jombart et al. 2010) and it does not rely on any particular population genetic model. DAPC uses genetic data in a Principal Component Analysis (PCA) with pre-defined groups, and then using the output of the PCA as variables in a Discriminant Analysis (DA) that attempts to maximize between-group variation. We performed DAPC using the *ade4* package for R (Jombart 2008) and using pre-defined groups corresponding to native range RUs (the source populations) and then we applied the *predict.dapc* function to position the Futaleufú River individuals (that were not used in constructing the model) onto these discriminant functions (DFs). On the basis of these DFs, we derived for each individual fish a membership probability to original RUs. These posterior probabilities provide a type of “assignment measure” of individuals to predefined groups, similar to the assignments from the GSI analysis. The procedure was also used to estimate the posterior probability with which the DA recovers the true group membership of the known-origin (source) individuals. To avoid over-fitting, which could bias our results, we used the functions *xvalDAPC* and *optim.a.score* to calculate the optimal number of principle components to retain for the DAPC analysis. Both methods indicated that 82 principle components (out of 300), representing 94 % of the total variation in our dataset were the optimal number of PCs to retain.

We also conducted an intensive literature review (Basulto 2003; Correa and Gross 2008; Riva Rossi et al. 2012; Arismendi et al. 2014) for a priori identification of potential candidate stocks for the invasive Chinook salmon in Patagonia and compared the results with the outcomes of the genetic analyses.

Results

Genetic analysis

Tests for HWE deviations in the Futaleufú River population revealed that only locus *Ots_112208-722*

deviated significantly after Bonferroni correction (0.521, $P=0.000$), due to a heterozygote deficiency compared with HWE expectations. For linkage equilibrium, the percentage of significant comparisons after Bonferroni correction was 0.16 %, which is less than the proportion expected by chance alone. Diversity estimates for the Futaleufú River Chinook salmon were high ($H_z=0.375$, $A=1.98$) and higher than values reported for most populations in the native range with these same SNP loci (average $H_z=0.316$, range 0.191–0.377; average $A=1.925$, range 1.630–2.000; Clemento et al. 2014).

Of the 53 fish, 30 were assigned with posterior probabilities >60 %. The assignments were to eight Chinook salmon reporting units: East Vancouver Island, Central Valley fall, Lower Columbia fall, Lower Columbia spring, Central Valley spring, Willamette River, Deschutes fall and Middle Oregon Coast. The RU with the largest number of fish assigned (11) was the Lower Columbia fall, which is represented by the Cowlitz River tributary. The 23 fish that had a posterior probability lower than 60 % were assigned to these same reporting units (except the Willamette River); however, as they did not satisfy the criteria for high confidence, considerable error in their assignments is to be expected (Table 1 and 2).

For DAPC analysis, 82 PCA axes and 37 DFs were retained (94 % of variance). The scatterplot of the first two components of the DA (Fig. 2) showed considerable overlap between the native RUs and the Futaleufú River population. The first DF (representing 31.75 % of the discriminating power) separated the RUs from California to Washington (and Vancouver Island) from those of British Columbia and Alaska, placing the California Central Valley RUs closer to Columbia River Basin RUs than to coastal RUs from California, Oregon, Washington and British Columbia, as has been observed previously (Seeb et al. 2007; Moran et al. 2013; Clemento et al. 2014). The second DF (representing 21.34 % of the discriminating power) resolves a north to south cline from Alaska to California (Fig. 2).

With DAPC, the mean reassignment to the actual predefined native groups was 88.6 %, ranging from 41.9 % (for the mid Oregon Coast RU) to 100 % (for the Thompson River RU) (Fig. 3a). For the 53 Futaleufú individuals, 50 were positioned in the space delimited by the California Central Valley RUs and the Columbia River Basin RUs. Of the

Table 1 Introduction events of Chinook salmon in the area surrounding the Futaleufú River outlet in the Patagonia region of the Pacific Ocean

Year	Origin/stock	Basin	Country	Destination	Latitude	Purposes	Reference
1886–1924	Sacramento River	Sacramento River	USA	X Region	39°–42°S	Ranching Recreational fishing	Basulto 2003; Correa and Gross 2008; Arismendi et al. 2014
1968–1971; 1969–1970	Washington			Reloncavi Seno	40°S	Ranching	Dufflocq 1981; Oyarzo 2006
1974–1979	Cowlitz River	Columbia River	USA	X Region (Curacao de Velez)	42°S	Ranching	Oyarzo 2006
1970–1983	Kalama River	Columbia River	USA	X Region	40°–42°S	Ranching	Correa and Gross 2008; Donaldson and Joyner 1983; Basulto 2003
1982–1989	Univ. Washington Hatchery, Puget Sound	Columbia River	USA	X Region, XII Región		Ranching	Oyarzo 2006; Correa and Gross 2008
1980–1988, 1988–1995	Oregon coast-Siuslaw River, Vancouver Island & Puget Sound		USA, Canada	X Region, XI Regions	39°–44°S, 44°–49°S	Net pen rearing	Riva Rossi et al. 2012
1998–2000	California		New Zealand	X Region, (Pto Montt, Reloncavi Seno)	40°S	Ocean net pen	Riva Rossi et al. 2012

Table 2 Results of the individual assignments to reporting units (RUs) of Chinook salmon in the Futaleufú River in Patagonia using gsi_sim. High-quality assignments when the RUs posterior probability was greater than 0.6

RUs	P<0.6
CVfa	0.43
COlowsp	0.44
CVfa	0.45
CVfa	0.48
CVfa	0.49
CVspSac	0.50
eVancI	0.50
COlowsp	0.52
COlowfl	0.53
CVspSac	0.54
CVspSac	0.55
COlowsp	0.57
COlowfl	0.58
eVancI	0.59
COlowfl	0.59
mOR	0.60
COlowfl	0.61
COlowfl	0.61
COlowfl	0.62
eVancI	0.63
CVfa	0.64
COlowfl	0.64
COlowsp	0.65
COlowsp	0.70
CVspSac	0.72
COlowsp	0.72
COlowfl	0.74
CVfa	0.80
COlowsp	0.81
mOR	0.81
Deschutes	0.86
COlowsp	0.87
Deschutes	0.88
CVfa	0.89
CVfa	0.89
Willamette	0.90
CVfa	0.91
COlowfl	0.92
COlowfl	0.93
COlowfl	0.94
CVfa	0.95
CVspSac	0.95

Table 2 (continued)

RUs	$P < 0.6$
eVancI	0.96
CVfa	0.96
COlowfl	0.97
COlowsp	0.98
COlowfl	0.98
CVfa	0.99
COlowfl	0.99
CVfa	1.00
eVancI	1.00

remaining three fish, two were closer to RUs from the California and mid Oregon Coasts, whereas the third was apparently a coho salmon (Fig. 2). Of these 53 individuals, 48 had mean membership probability > 0.6 to a single RU, while the remaining five appeared to have mixed ancestry from two or three different RUs. Of the 48 individuals with posterior probability > 0.6 , the vast majority were assigned to the California Central Valley fall RU, The other fish were assigned to the east Vancouver Island, Central Valley spring and the lower Columbia River RUs, as well as the one apparent coho salmon noted above (Fig. 3b; Table 3). Individual assignments from DAPC were only 54 % congruent with those from *gsi_sim*, which is consistent with the signal of multiple sources for the Patagonian fish and the relatively low population differentiation observed between some of these RUs in the native range.

Candidate sources of Chinook salmon in southern Patagonia

Seven different egg sources originating in the USA, Canada and New Zealand were used for Chinook salmon importations into Southern Chile between 1886 and 2000 (Table 1). Two main considerations are relevant when evaluating the history of this activity: the magnitude of the introduction efforts and the purposes of the introductions. In the first case, we took into account the number of introduction events and their fate, as the number of eggs and fish are often reported incorrectly. In Chile, there were some Patagonian sites with a single Chinook salmon introduction event in 1924, such as the Cautin, Cochamó, Maullín and Puelo rivers, from a

single source (McCloud River Hatchery, Sacramento River Basin, USA) and other sites, such as Curacao de Velez, Rupanco Lake, Quellón, Puerto Montt, Pichicolo, Llanquihue Lake, and Chiloé Island, with multiple introduction efforts (between 1978 and 1990) from several stocks: Cowlitz River and Kalama River Hatchery, both in the lower Columbia River Basin; Siuslaw River, Oregon (through Domsea Farms Inc.); Vancouver Island, British Columbia (through Sea Spring Salmon Farms); Puget Sound, Washington (through Fish Pro Farms Inc.); the Yaquina and Big Elk rivers, Oregon (through Oregon Aquafarms Inc.); and from the Green River, Washington (through Aqua Seed Corporation; Aedo E. pers. comm.).

The introduced fish in Chile were used in two primary ways; before 1990, they were primarily used for ocean ranching, in which smolts produced by hatcheries were released to the sea and harvested as homing adults. After 1990, they were used primarily for ocean net-pen aquaculture, in which the smolts were reared to adulthood in floating net cages and then harvested. Records indicated that the earliest attempts to introduce Chinook salmon to Chile were probably unsuccessful, as it was not until the end of 1979 when adult fish were trapped returning to their home stream in the Chiloé area (see Lindbergh 1982).

Discussion

Analysis of SNP genotypes revealed that the Futaleufú River Chinook salmon population derived from stocks in the Lower Columbia River and the California Central Valley (introduced via New Zealand), with minor contributions from stocks from the Mid Oregon Coast, the Puget Sound area and Vancouver Island. This indicates that the invasive population was founded by fish from both the introductions for ranching operations during the 1970s and 1980s (Lower Columbia River) and those introduced for net pen rearing during the 1990s (other stocks). These results are consistent with those of Riva Rossi et al. (2012) who found that the Chinook salmon invasion in Patagonia was the result of contributions by multiple stocks imported from northwestern North America and New Zealand.

The potential sources identified are in agreement with aquaculture and ranching records which

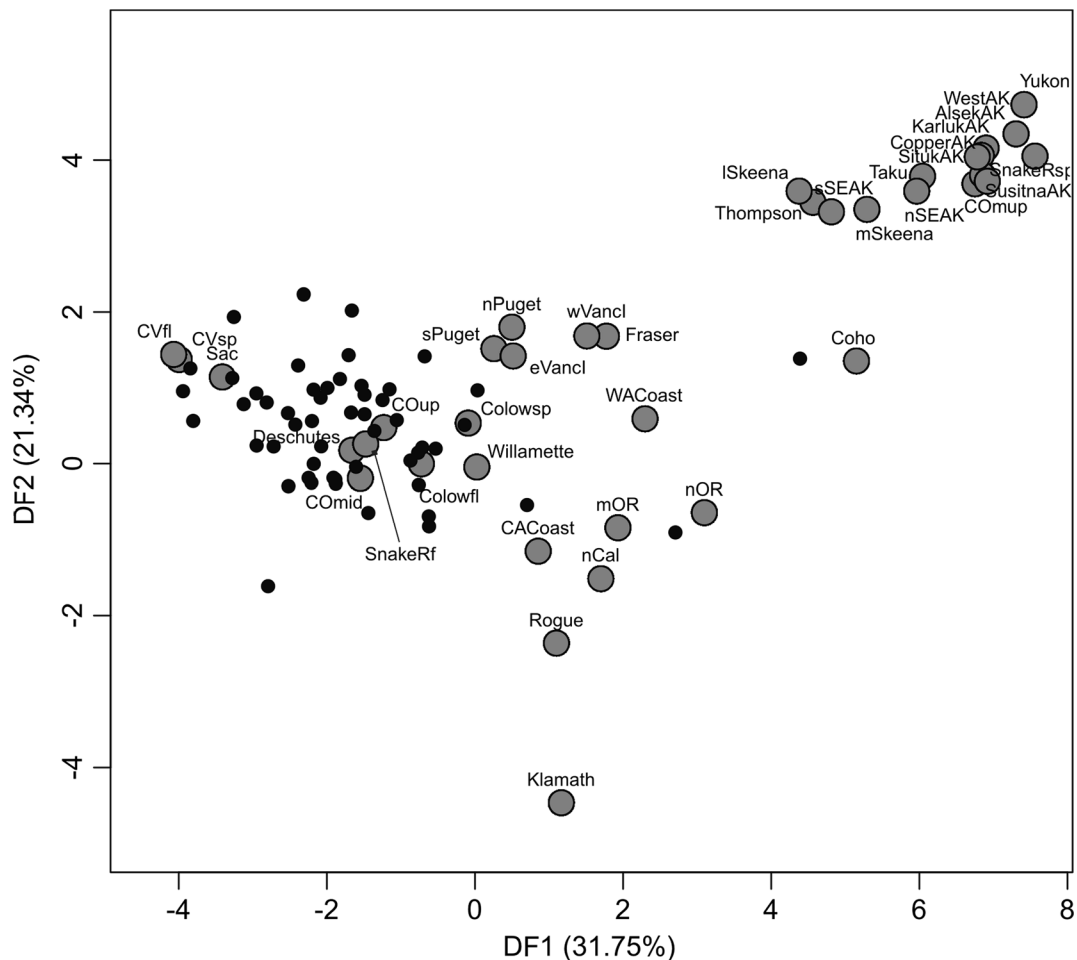


Fig. 2 Scatterplots from the DAPC. Mean sample coordinates (gray-filled circles) of the first and second discriminant functions (DF) compared with the predefined Chinook salmon RUs from across the native range. Introduced individuals are plotted as black small circles. Population codes follow the nomenclature of Clemente et al. (2014). –*CVspSac* Central Valley spring, *CVfl* Central Valley fall, *CACoast* California Coast, *Klamath* Klamath River, *nCal* N. California/S. Oregon, *COMid* Mid Columbia R. Tule, *COup* Upper Columbia River summer/fall, *COMup* Mid/Upper Columbia River spring, *SnakeRf* Snake River fall, *SnakeRsp* Snake River spring, *WACoast* Washington Coast, *sPuget* South Puget Sound, *nPuget* North Puget Sound, *Fraser*

Lower Fraser River *Thompson* Lower Thompson River *eVancI* Eastern Vancouver Island, *Rogue* Rogue River, *mOR* Mid Oregon Coast, *nOR* North Oregon Coast, *Willamette* Willamette River, *Deschutes* Deshutes River, *Colowfl* Lower Columbia River fall, *Colowsp* Lower Columbia River spring, *wVancI* Western Vancouver Island, *ISkeena* Lower Skeena River, *mSkeena* Mid Skeena River, *sSEAK* S. Southeast Alaska, *AlsekAK* N. Gulf Coast Alsek River, *Karluk* N. Gulf Coast Karluk River, *Taku* Taku River, *nSEAK* N. SE Alaska Chilkat River, *SitukAK* N. Gulf Coast Situk River, *CopperAK* Copper River, *SusitnaAK* Susitna River, *WestAK* Lower Kuskokwim/Western AK, *Yukon* Mid. Yukon River, *Coho* Coho

indicate imports from Washington State (spring- and fall-run from the Cowlitz and Kalama rivers, in the Lower Columbia River Basin, and the University of Washington Hatchery, whose broodstock was also derived from Lower Columbia River stocks, introduced from 1978 to 1983 and 1982 to 1989, respectively), from the Oregon coast (spring- and fall-run derived from the Siuslaw, Yaquina and Coos rivers, introduced from 1981 to 1988), from Vancouver

Island, British Columbia (fall-run introduced from 1988 to 1995) and from New Zealand (ancestrally California Central Valley fall-run introduced from 1988 to 2000). Further, these results corroborate previous ideas (e.g., Correa and Gross 2008) that this river was colonized by fish derived from escapees from both earlier ocean ranching and more recent net pen operations in Chile. It seems that following the first colonization in the 1980s by fish

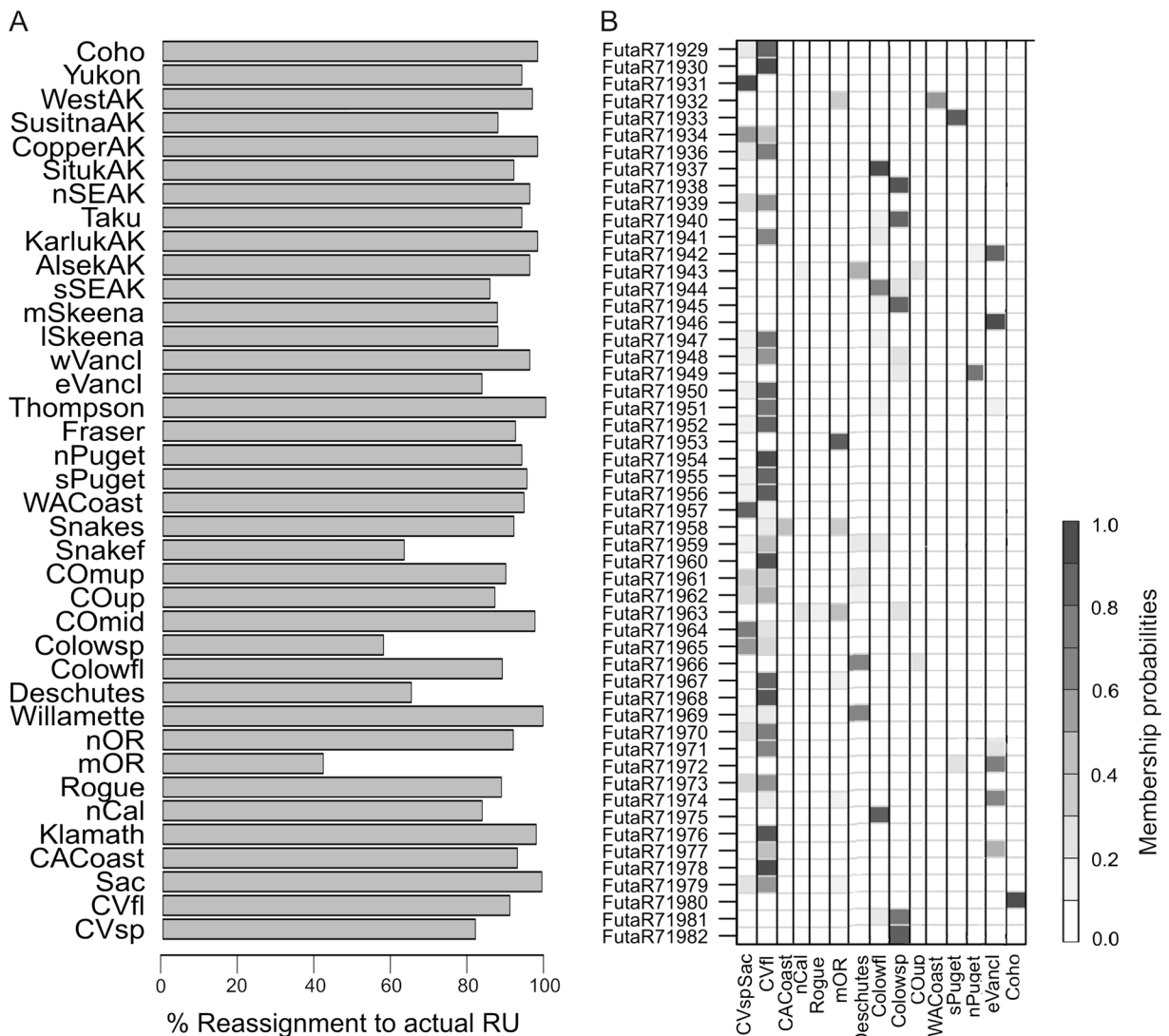


Fig. 3 Estimated group (population sources) and individual (introduced individuals) membership probabilities using the DAPC. A) Percent of individuals that are assigned to their actual RU; B)

Posterior probabilities of assignment of Futaleufú individuals to the different native RUs

that strayed from ranching programs (Table 1), successful establishment of an invasive salmon population was reinforced by subsequent pulses of fish escaped from more recent aquaculture activities.

In agreement with a previous study (Riva Rossi et al. 2012), we found that Chinook salmon in the Futaleufú River have higher within-population genetic variation than that reported for most populations in the native range (Clemento et al. 2014). This is consistent with the finding that the Futaleufú salmon population derived from multiple donor stocks. Our study also showed that the naturalized population of Chinook salmon in the

Futaleufú River has not lost within-population genetic diversity, as both measures of genetic diversity, allelic richness and expected heterozygosity, displayed levels similar to those of populations from the native range. This observation is consistent with other studies of human-mediated introductions, which found similar or even higher levels of within-population genetic diversity in introduced populations that are the product of high propagule pressure, multiple introductions or admixture (Consuegra et al. 2011; Arismendi et al. 2014). Riva Rossi et al. (2012) proposed that the genetically diverse Chinook salmon population in Patagonia was the result

Table 3 Futaleufú Chinook salmon individual assignments to native RUs provided by DAPC ($*P<0.6$) and genetic stock identification with their posterior probability of assignment

Assignment	DAPC	gsi_sim
CACoast		
FutaR71958 *	0.455664304	0.60242307
Coho		
FutaR71980	1	0.97155851
Colowfl		
FutaR71937	0.9886011	0.98830324
FutaR71944	0.741755827	0.62276609
FutaR71975	0.935181484	0.93262546
Colowsp		
FutaR71938	0.947947154	0.77316187
FutaR71940	0.877783529	0.64485969
FutaR71945	0.890762324	0.42088494
FutaR71981	0.780773977	0.98254102
FutaR71982	0.927620985	0.68360004
CVfl		
FutaR71929	0.82464355	0.36351329
FutaR71930	0.997071779	0.45795828
FutaR71936	0.756098305	0.60480913
FutaR71939	0.659207515	0.48840661
FutaR71941	0.728892899	0.60874531
FutaR71947	0.800540424	0.59024244
FutaR71948	0.64291239	0.529106
FutaR71950	0.875379523	0.66993513
FutaR71951	0.781420831	0.3440392
FutaR71952	0.849498024	0.94276461
FutaR71954	0.98664348	0.53075277
FutaR71955	0.821947007	0.60571179
FutaR71956	0.914427219	0.65572885
FutaR71959 *	0.469858504	0.57787896
FutaR71960	0.963396349	0.33476027
FutaR71961 *	0.373294939	0.40993538
FutaR71962 *	0.503933089	0.33139816
FutaR71967	0.863414864	0.7448154
FutaR71968	0.956059271	0.67232823
FutaR71970	0.75368264	0.53377383
FutaR71971	0.676339479	0.72132746
FutaR71973	0.669973968	0.84929098
FutaR71976	0.957483859	0.92118815
FutaR71978	0.994333693	0.40036552
FutaR71979	0.625503525	0.32605567
CVsp		
FutaR71931	0.994987298	0.63058988
FutaR71934	0.592947734	0.32355632

Table 3 (continued)

Assignment	DAPC	gsi_sim
FutaR71957	0.873906746	0.44041072
FutaR71964	0.766214779	0.92976316
FutaR71965	0.628295006	0.50275651
Deschutes		
FutaR71943 *	0.510735972	0.47916393
FutaR71966	0.679014603	0.88343937
FutaR71969	0.674411427	0.86440557
eVancI		
FutaR71942	0.890542983	0.58615618
FutaR71946	0.989713183	0.99982161
FutaR71972	0.759589468	0.95619189
FutaR71974	0.704713814	0.6263873
FutaR71977 *	0.480929412	0.89506406
mOR		
FutaR71953	0.931045186	0.80826026
FutaR71963 *	0.417616517	0.64870227
nPuget		
FutaR71949	0.796080127	0.69936065
sPuget		
FutaR71933	0.920840916	0.57388834
WACoast		
FutaR71932	0.602063475	0.93262546

of multiple introductions, which is consistent with the finding that Chinook salmon in the Futaleufú River is a genetic mixture from previously isolated lineages. The rapid dispersal and successful invasion of Chinook salmon in Patagonia could have been facilitated by this admixture from multiple introduction events, as well as the associated variability in life history traits, characteristics influenced by genetic and environmental factors (Healey 1991; Quinn et al. 2001).

Understanding the effects of biological invasions is one of the most important tasks in ecology. The analyses presented here helped to elucidate the origins of Chinook salmon in the Futaleufú River of Patagonia and allowed the identification of the sources of the invasive population and the process of colonization. The colonization of Patagonian rivers by Chinook salmon provides an interesting framework to understand biological invasion, the factors that determine success of an invading species, and ecological responses to invasion in an ecosystem with contemporary challenges facing many aquatic ecosystems.

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