SAN FRANCISCO ESTUARY & WATERSHED SCIENCE
Sponsored by the Delta Stewardship Council and UC Davis Institute of the Environment

RESEARCH

Ancestry and Adaptation of Resident, Adfluvial, and Anadromous Rainbow Trout (*Oncorhynchus mykiss*) in Putah Creek, an Ecotone Crossing Watershed

Laura C. Goetz [1,2], Eric D. Chapman [3], Cyril J. Michel [2,4], Elena C. A. Correa [2,4], Devon E. Pearse [1,2]

ABSTRACT

Evaluating patterns in the distribution of genetic variation across heterogeneous landscapes provides perspectives on how environmental features contribute to molecular evolution, and how human activities influence populations. Impassable barriers, such as hydroelectric dams, and human-directed movement or propagation of individuals across riverscapes have had strong impacts on the genetic diversity observed in natural populations. We considered the population structure and distribution of adaptive genetic variation in the salmonid species *Oncorhynchus mykiss* throughout Putah Creek, a watershed near Napa Valley, California that was transformed by the 1950's construction of multiple dams and a large artificial reservoir (Lake Berryessa). In addition, hatchery-raised *O. mykiss* has been introduced throughout the watershed over many years, which may have introduced genetic variation into existing Putah Creek populations. To explore the population structure and distribution of adaptive genetic variation in Putah Creek, we analyzed microhaplotypes from eight *O. mykiss* populations above Lake Berryessa and two populations below Lake Berryessa and compared them with 40 reference populations from California Central Valley, coastal, inland, and hatchery rainbow trout lineages. We found distinct patterns of neutral and adaptive variation between populations above Lake Berryessa and those below. Populations below Lake Berryessa resembled various Central Valley populations and hatchery rainbow trout strains, while those above were more similar to coastal *O. mykiss* populations. Additionally, Putah Creek populations below Lake Berryessa possessed significantly different proportions of adaptive variants associated with life-history traits compared to populations above Lake Berryessa, consistent with studies in other populations located above and below barriers to migration.

SFEWS Volume 24 | Issue 3 | Article 5

https://doi.org/10.15447/sfews.2026v24iss2art5

* Corresponding author: *dpearse@ucsc.edu*

1 Department of Ecology and Evolutionary Biology
University of California–Santa Cruz
Santa Cruz, CA USA 95060

2 Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
Santa Cruz, CA USA 95060

3 Fish and Aquatic Science and Technology Team, ICF
Sacramento, CA USA 95691

4 Institute of Marine Sciences' Fisheries Collaborative Program, University of California–Santa Cruz
Santa Cruz, USA 95060

KEY WORDS

population genetics, microhaplotypes, steelhead, adaptation, life-history variation

INTRODUCTION

Landscape genetics, assessing the distribution of genetic variation within and among populations in heterogeneous environments, has become a useful conservation tool with increasing accessibility of molecular techniques (Manel et al. 2003; Robinson et al. 2012; Manel and Holderegger 2013; Gray et al. 2014; Rougemont et al. 2021). Understanding how abiotic features shape population genetic dynamics provides insights into environmental influences on the adaptive evolution of populations and how human activity modifies natural patterns (Pease et al. 2009; Winans et al. 2010; Andrew et al. 2012; Cooke et al. 2014; Winans et al. 2017; Brauer and Beheregaray 2020; Stronen et al. 2022). These results can further inform management of imperiled species and/or populations by both discerning geographic distribution of underrepresented or declining adaptive genetic variation and identifying important external influences on population genetics and phenotypic expression.

One species with strong associations between population variation and environmental features is the salmonid species *Oncorhynchus mykiss*, which possesses highly plastic life-history traits that respond to both abiotic and genetic cues (Nichols et al. 2008; Sloat and Reeves 2014; Kendall et al. 2015; Christie et al. 2018). One of these traits is migration strategy, with some *O. mykiss* remaining in freshwater for their entire lives, while others migrate to the Pacific Ocean as juveniles before returning to their natal freshwater streams to spawn. These distinct ecotypes are known as "Rainbow Trout" (freshwater residents) and "Steelhead" (anadromous migrants). Juvenile *O. mykiss* can mature into residents or migrants, depending on genetic and environmental interactions (Kendall et al. 2015; Phillis et al. 2016). A spectrum of migration patterns exists, including movement through rivers ("fluvial") or within lake and reservoir systems ("adfluvial;" Holecek et al. 2012). In addition to plasticity in overall life-history strategy, migrating *O. mykiss* species also vary when they return to spawning grounds as adults, a trait known as "run timing." Individuals from the same population may return to spawning grounds before spawning season begins as sexually immature ("early", or "summer-run"), just before spawning season begins as sexually mature ("late", or "winter-run"), or at an intermediate time (Quinn et al. 2016). Expression of these traits varies among *O. mykiss* individuals based on internal (biotic) and external (abiotic) conditions, influencing their chances for survival to reproduction. Environmental characteristics such as barriers to migration influence a population's migration patterns and timing by altering life-history tradeoffs (Sloat and Reeves 2014; Phillis et al. 2016; Apgar et al. 2017; Mattocks et al. 2019). Barriers like dams that block access to migration can landlock formerly anadromous populations (Arciniega et al. 2016; Leitwein et al. 2017; Pearse and Campbell 2018; Winans et al. 2018; Abadía–Cardoso et al. 2019) and negatively select against early migrating salmonids by removing access to historic spawning grounds in higher reaches (Quinn et al. 2016; Kannry et al. 2020; Fraik et al. 2021).

In recent years, genomic studies have identified key genes and adaptive genomic regions associated with important life-history traits in several salmonid fish species, providing important information about their underlying genetic basis to inform conservation and management. In particular, two regions in the *O. mykiss* genome have been specifically associated with: (1) expression of anadromous or adfluvial migration (Omy05; Pearse et al. 2014, 2019; Arostegui et al. 2019) and (2) summer vs. winter anadromous run timing (*GREB1L/ROCK1*; Waples et al. 2022). The strength of these associations, and predictive value among populations with varying coastal vs. inland migration distances, genetic lineages, and frequencies of heterozygotes remains unclear (Willis et al. 2020; Collins et al. 2020). Studies investigating the distribution of Omy05 above and below barriers found that landlocked *O. mykiss* populations often rapidly lose anadromous genetic variation with loss

of anadromous migration (Pearse et al. 2014; Phyllis et al. 2016; O'Malley et al. 2026). However, it is less clear how *GREB1L/ROCK1* variation influences resident populations isolated above barriers (Fed Regist 2019). In addition, surveys of Omy05 variation have found that some *O. mykiss* populations landlocked above impassable barriers have maintained anadromous genetic architecture despite their current inability for physical movement to marine habitat (Leitwein et al. 2017; Pearse and Campbell 2018; Abadía–Cardoso et al. 2019). This could be explained by the formation of reservoirs upstream of dams, providing habitat with sufficient capacity for movement to preserve migratory variation (Holecek et al. 2012; Leitwein et al. 2017). Recent successes in rapid *O. mykiss* recolonization following watershed restoration provide additional support for dams negatively impacting *O. mykiss* phenotypic expression but not necessarily genetic variation (Winans et al. 2017; Fraik et al. 2021; Knoth et al. 2022).

Multiple studies have found significant genetic and phenotypic differences in life-history traits between the Central Valley (CV) and coastal lineages within the subspecies *O. mykiss irideus* that reflect regional variation in California (Sogard et al. 2012; Pearse and Garza 2015; Abadía–Cardoso et al. 2019; Goetz et al. 2024). Extensive historic movement of individuals among CV populations has partially homogenized population structure among wild populations, and stocking from hatchery strains also provided opportunities for introgression in wild populations (Pearse and Garza 2015; Pearse and Campbell 2018; Abadía–Cardoso et al. 2019). Additionally, descendants of coastal steelhead propagated in CV watersheds maintain coastal genetic and phenotypic characteristics (California HSRG 2012; Goetz et al. 2024), highlighting the inherited basis of life-history traits. Other studies have found significant environmental effects on *O. mykiss* life-history expression (McMillan 2012), and state-dependent models suggest that high environmental variation in the Central Valley favors altered expression of life-history variation compared with the central coast (Satterthwaite et al. 2009, 2010; Sogard et al. 2012).

Putah Creek is a watershed near Napa Valley, California, that straddles the ecotone between the California coastal and Central Valley environments with *O. mykiss irideus* populations. Located on the natural edges of coastal and CV lineages, the genetic relationships among Putah Creek O. mykiss irideus and other populations in Central California are unclear, but previous genetic analyses have identified genetic similarities among samples from central coast populations such as Calaveras River, Putah Creek, lower American River, and Nimbus Hatchery (Nielson et al. 2005). To investigate patterns of neutral and adaptive genetic variation in *O. mykiss irideus* populations located between central coast and Central Valley ecotones, we utilized genetic samples from above and below barriers in Putah Creek. Specifically, we evaluated and compared the population structure and distribution of adaptive genetic variation among *O. mykiss* in Putah Creek relative to reference populations from both coastal and CV lineages in neighboring watersheds, as well as hatchery strains historically used to stock the Putah Creek watershed. Our results provide important insights into the complex history that has contributed to the present-day distribution of genetic variation in *O. mykiss* in Putah Creek.

METHODS

Study System

With a long history of human modifications, today Putah Creek is impounded in Lake Berryessa, formed by Monticello Dam in 1957 and the third largest reservoir in California. Below Monticello Dam, the creek flows through the eight miles of inter-dam reach (IDR), including Lake Solano, before passing over the smaller Putah Diversion Dam (PDD). Below this final barrier to upstream migration, it continues downstream past Davis, California, and into the Yolo Bypass before joining the Sacramento River and flowing out to the ocean via San Francisco Bay. The segment of watershed above Lake Berryessa is highly variable spatially, with higher water temperatures and low gradient (Jang et al. 2017; EDAW 2005). Below Monticello Dam, the watershed is wide and shallow with fine sediment substrate and

https://doi.org/10.15447/sfews.2026v24iss3art5

altered flow (Peffer 2013). The watershed has an extensive history of stocking with various strains of hatchery Rainbow Trout by California Department of Fish and Wildlife (CDFW) from at least 1977 until suspension in 2008 (Weaver and Mehalick 2009). Between Monticello Dam and PDD, the IDR possesses naturally reproducing *O. mykiss* (Weaver and Mehalick 2009; Hogan et al. 2013) and was designated as "wild trout" water by CDFW in 2008 (Weaver and Mehalick 2009). However, relative contributions of native Putah Creek and hatchery Rainbow Trout strains to the IDR population today are unknown. While both Monticello Dam and the PDD are impassable to fish, waters downstream of PDD are accessible to anadromous CV Steelhead, which are federally protected as threatened species under the Endangered Species Act (ESA; Fed Regist 2006). To further our understanding of the genetic composition of Putah Creek trout populations, we investigated the distribution of neutral and adaptive genetic variation in Putah Creek populations above and below barriers and compared them with reference populations from various regions.

Sampling

To investigate population structure and distribution of adaptive variation of *O. mykiss* in the Putah Creek watershed, we collected 196 samples from ten sites throughout the watershed above and below Monticello Dam and within Lake Berryessa. Of the sampling sites above Lake Berryessa, only Upper Anderson Creek (UAC; Figure 1) did not have access to Lake Berryessa because of an impassable barrier. Fish were captured using hook-and-line fly fishing or backpack (Smith-Root LR-24) electrofishing. A nonlethal upper caudal clip was collected from each *O. mykiss* and desiccated on blotter paper prior to DNA extraction. We extracted DNA using a BioRobot 3000 with QIAGEN DNeasy 96 Tissue Kits (QIAGEN Inc.), then diluted DNA 1:2 in ddH_2O before genotyping.

In addition to the Putah Creek samples, we used previously collected genotype data from 2,075 samples from multiple reference populations in California, including hatchery Rainbow Trout strains, as a baseline for comparison (Le Gall et al. 2024). Ten Californian regions were considered for this study, with at least two *O. mykiss* populations represented per region (Table 1; Table B1; Figure 1), including coastal and Central Valley lineages, anadromous Steelhead, Rainbow Trout and Redband Trout populations, and five strains of hatchery Rainbow Trout commonly used for stocking in California (Coleman, Shasta, Pit, Kamloops, and Hot Creek).

All genetic data collected for this study were obtained by sequencing a panel of 'microhaplotype' loci (Le Gall et al. 2024), each containing one or more single nucleotide polymorphisms (SNPs). We followed sequencing protocols outlined by Le Gall et al. (2024). Microhaplotypes from 2,075 sampled fish at 124 putatively neutral markers were processed using R package microhaplotopia which utilizes microhaplot (Ng 2022). We removed 14 loci located on chromosome Omy05 from the population genetic dataset, keeping 110 putatively neutral markers for analysis (Table B2). An additional 18 neutral loci with more than 20% problematic genotypes that either did not call confidently or contained deletions compared to the reference genome, (i.e., NX genotypes) were also identified and removed. After filtering loci for genotyping success, microhaplotype sequences for all individual samples were first batch filtered by a minimum haplotype depth of five reads, a minimum total depth of 20 reads, and a 0.3 ratio of second haplotype read depth to first haplotype read depth (allelic balance). This removed 13 samples, reducing the initial 2,075 individuals to 2,062 (Table B3). Seven of these removed individuals were samples from Putah Creek. Filtering individuals missing genotypes for more than 7/92 loci removed an additional 114 samples, retaining only individuals with a minimum of 85 loci (Table B3). Of the 114 removed individuals, 14 were from Putah Creek. The final dataset contained 1,948 genotyped individuals for population genetic analysis, including 175 individuals from the Putah Creek watershed (Table B3).

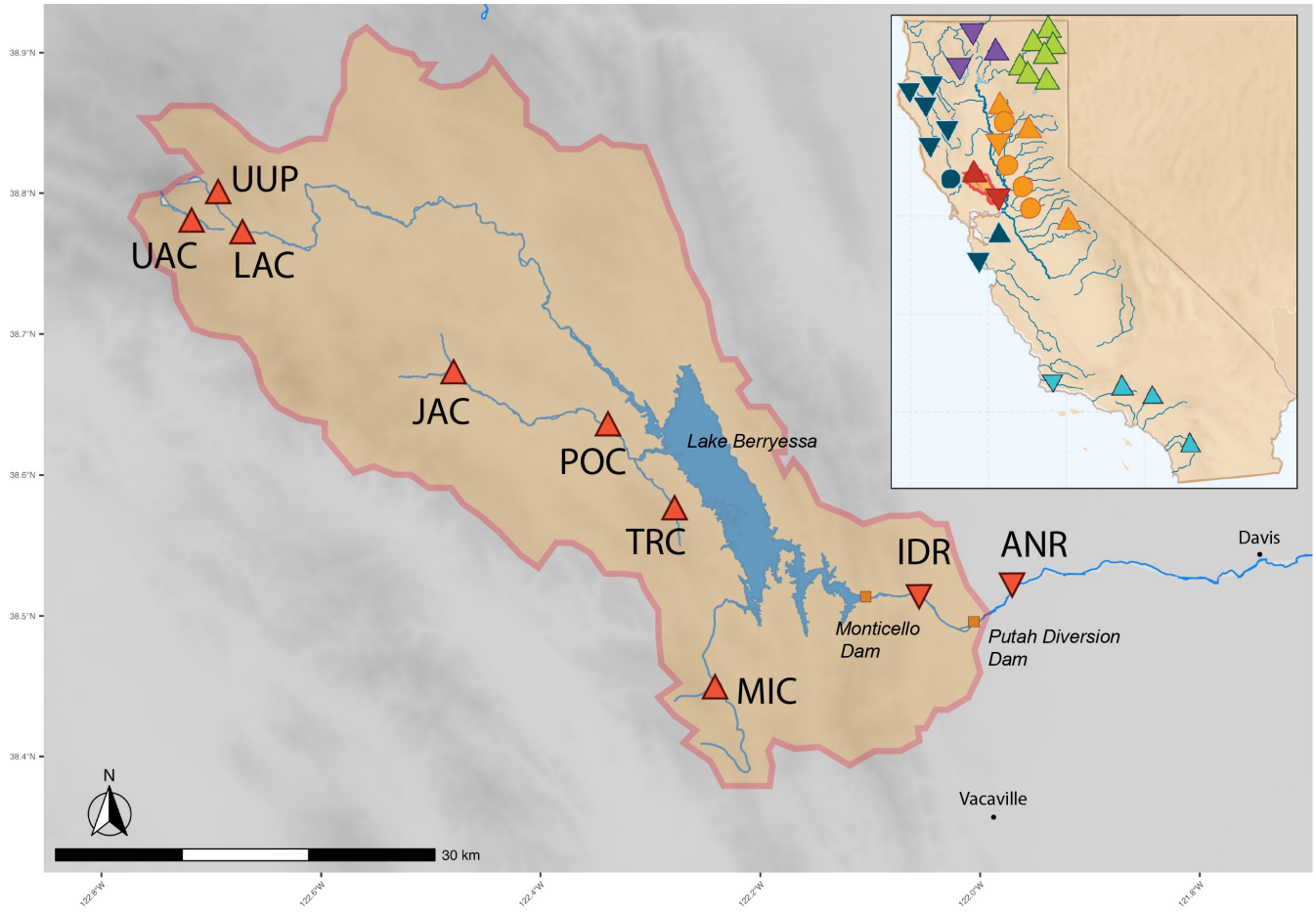


Figure 1 Map of Putah Creek watershed and populations sampled in relation to Davis, California, USA, with *triangles* indicating if the population is above (△) or below (▽) Monticello Dam. *Inset:* A map of California with the reference populations shown with colors corresponding to locations listed in Table B1 and the location of Putah Creek highlighted. *Circles* represent locations of hatchery programs that produce anadromous steelhead.

Table 1 Putah Creek sample populations with sample sizes and population genetics results. Populations are specified as above or below the barrier Monticello Dam. Population genetics statistics included expected (H_E) and observed heterozygosity (H_O), and allelic richness (A_R).

Population	Monticello Dam	Sampled	Genotyped	H_E	H_O	A_R
Anderson Creek, Above Waterfalls (UAC)	Above	33	33	0.282	0.250	1.777
Upper Upper Putah Creek (UUP)	Above	14	12	0.368	0.313	2.100
Lower Anderson Creek (LAC)	Above	4	4	0.345	0.361	1.692
James Creek (JAC)	Above	20	20	0.357	0.347	2.002
Pope Creek (POC)	Above	6	6	0.363	0.317	1.911
Trout Creek (TRC)	Above	16	15	0.200	0.186	1.584
Middle Creek (MIC)	Above	25	25	0.380	0.357	2.108
Lake Berryessa (LBE)	Above	23	7	0.383	0.294	2.241
Putah Creek, IDR (IDR)	Below	27	27	0.301	0.274	1.865
Putah Creek, Anadromous Reach (ANR)	Below	28	26	0.332	0.311	1.976

https://doi.org/10.15447/sfews.2026v24iss3art5

Population Genetics

Heterozygosity (observed [H_O] and expected [H_E]) were calculated among individuals for each population using the R package STRATAG (version 2.0.2; Archer et al. 2017). Pairwise F_{ST} between each population pair was also calculated using 'strataG', with separate analyses on the neutral and adaptive loci (Omy05 and *GREB1L/ROCK1*, see below and Table B2). We calculated mean allelic richness (A_R) per population using rarefication with the R package PopGenReport (version 3.0.7; Adamack and Gruber 2014). Population structure was then visualized using the modeling-based program *STRUCTURE* (version 2.2; Pritchard et al. 2000) with a hypothesized number of populations of K = 2, 3, 4, 6, 8, 10, 12, 14, 16. We selected these K values to explore population structure similarities and dissimilarities among samples and populations. Population structure visualization utilized the subsampled dataset, which consisted of Putah Creek sites and selected reference populations representing Central Valley (Feather River [FER]) and coastal (Dry Creek [DRC]) lineages, and hatchery rainbow trout strains (Pit River [RTPI] and Shasta [RTSH]). A principal component analysis (PCA) was also conducted to determine population structure in the IDR, as well as above and below the impassable Anderson Creek Falls. *STRUCTURE*, with a hypothesized number of populations of K = 2, 3, 4, 6, 10, and accompanying PCAs were also conducted on only populations from the Putah Creek region, and on a subset including all Putah Creek populations, Feather River, Dry Creek, and rainbow trout hatchery populations. *STRUCTURE* figures were constructed using *CLUMPAK* (Kopelman et al. 2015).

Adaptive Genetic Variation

To characterize genomic variation associated with migratory life-history strategies, the Le Gall et al (2024) genotyping panel includes multiple microhaplotypes in both the *GREB1L/ROCK1* genomic region and across the chromosomal inversion on Omy05. To characterize frequencies of the inversion haplotypes on Omy05, we targeted a single SNP within the Omy05 chromosomal inversion (omy5_9_54854574-19) and estimated the frequencies of homozygous and heterozygous inversion haplotypes based on the anadromous (AA), resident (RR), and heterozygous (AR) genotypes at that locus. Similarly, to characterize the distribution of variation in the *GREB1L/ROCK1* genetic region, we focused on a single SNP (mhap8_71, pos. 11667915) that has been used in many recent studies of this genetic region (e.g., Collins et al. 2020; reviewed by Waples et al. 2022). Genotypes at this SNP are associated with the early-migratory (EE) and late-migratory (LL) life-history strategies known as summer- and winter-run Steelhead, respectively, and individuals can also be heterozygous (EL). Adherence to Hardy Weinberg equilibrium for these loci was calculated using the R package HardyWeinberg (Graffelman 2015). Unfortunately, we were unable to obtain this data for the Lake Berryessa samples, so Lake Berryessa samples were excluded from these analyses.

RESULTS

Population Genetics

Genetic diversity at the putatively neutral loci was relatively consistent throughout Putah Creek, but some variation was observed among populations (Table 1). Samples collected from smaller, upstream reaches, such as Upper Anderson Creek above the falls (UAC) and Trout Creek (TRC), had lower genetic diversity values (H_O, A_R). Lake Berryessa (LBE) *O. mykiss* had among the highest allelic richness and expected heterozygosity among all populations, but a lower observed heterozygosity than predicted (Table 1). These results suggest mixed ancestry among Lake Berryessa fish.

Samples from below Lake Berryessa in the IDR and anadromous reach were genetically similar to each other, but distinct from Putah Creek populations above Lake Berryessa. F_{ST} was low between these populations (0.009; Table B4). PCA and *STRUCTURE* model-based results consistently supported close relationships between the IDR and anadromous reach, and between these reaches and CV Steelhead and hatchery Rainbow Trout (Figures 2 and 3; Figures A3 and A5). However, most CV *O. mykiss* below barriers had

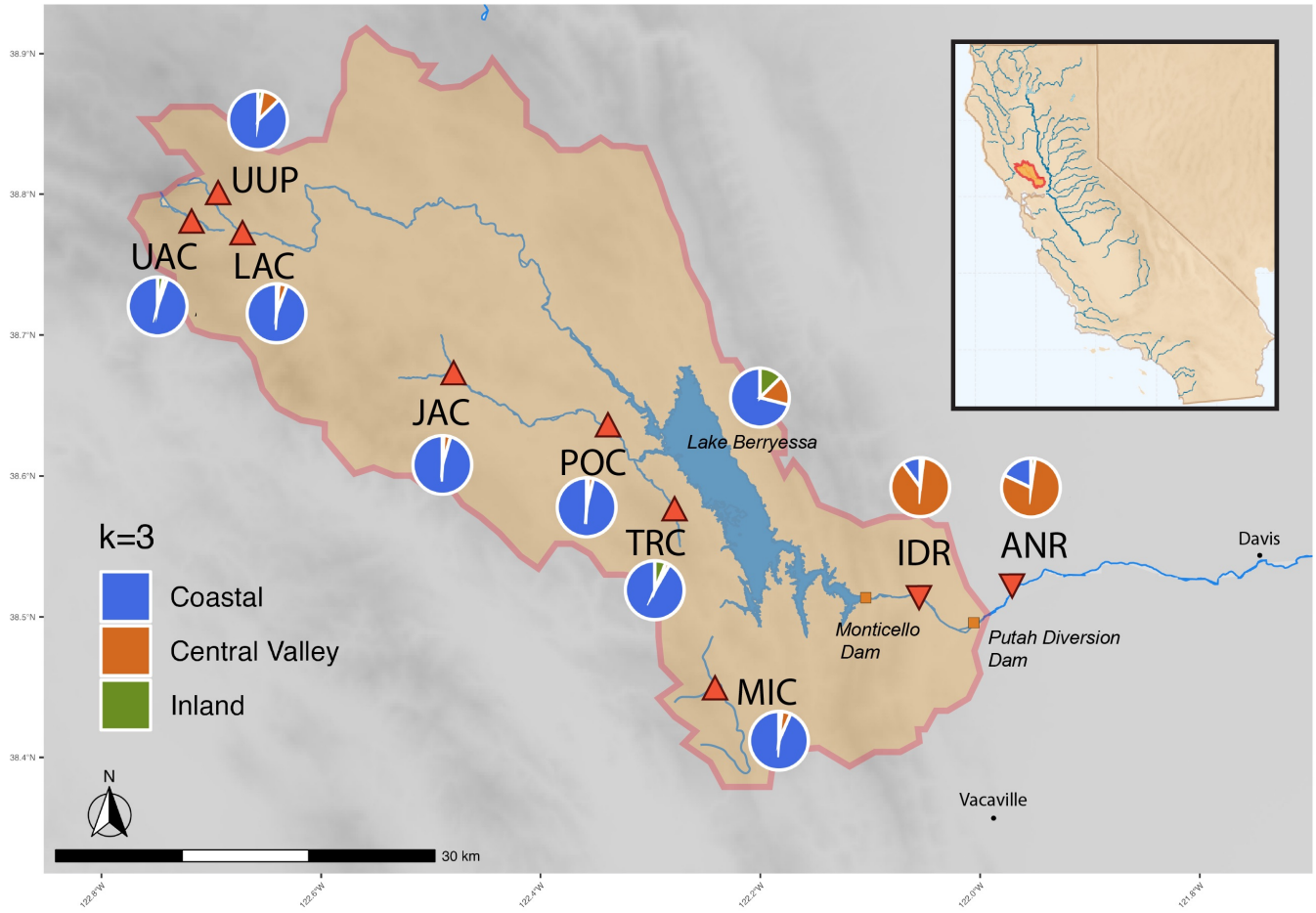
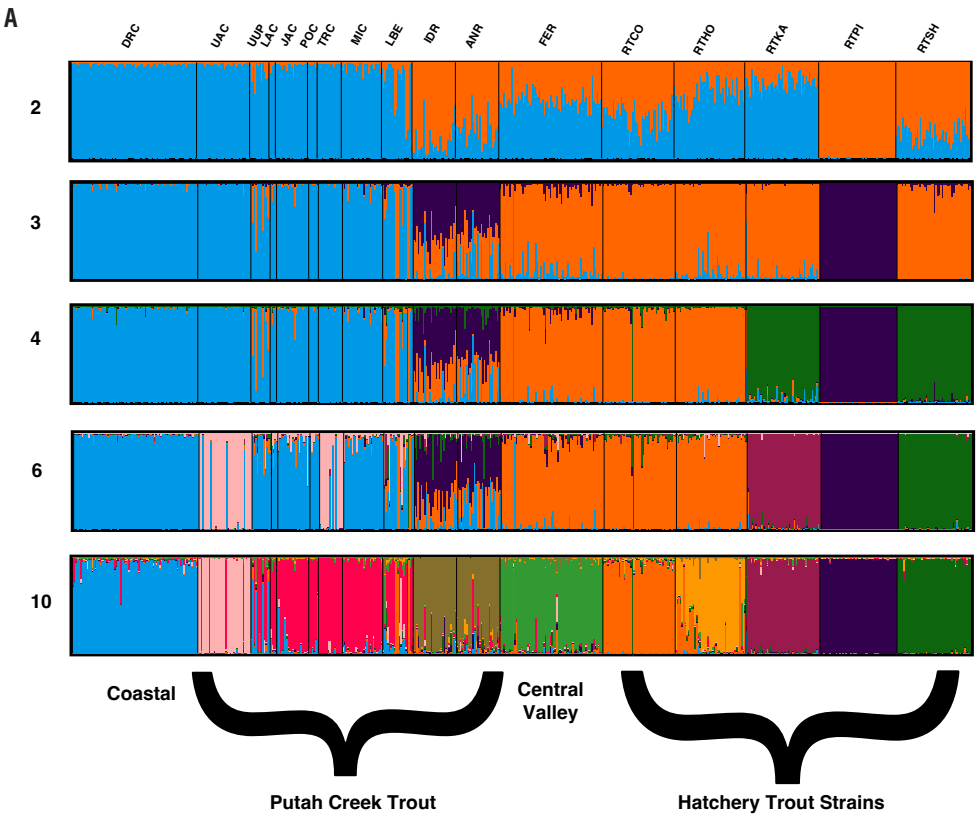


Figure 2 K = 3 STRUCTURE results for Putah populations above and below Monticello Dam divided by Coastal, Central Valley, and inland assignments

high values of H_O and A_R, while the Putah Creek anadromous reach had values similar to the above-barrier IDR. *STRUCTURE* results showed mixed genetic ancestry from multiple CV sources within individuals from the IDR and anadromous reach (Figure 3, $K = 3$). F_{ST} values between these CV populations and the IDR and anadromous reach were also low (Table B4).

In contrast, *O. mykiss* in the Putah Creek watershed above Lake Berryessa were more genetically similar to each other and coastal populations (Figures 2 and 3; Table B4). Smaller hypothesized numbers of populations in *STRUCTURE* (K) assigned individuals sampled from the upper Putah Creek watershed to genetic clusters shared with coastal Steelhead (Figures 2 and 3; Figures A2 and A4). This pattern was also apparent in the low pairwise F_{ST} values between coastal populations and samples from the upper Putah Creek watershed (Table B4). The strong differentiation between coastal-lineage populations above Monticello Dam and CV lineages below is maintained at higher values of K, but subtle differences among Putah populations were observed (Figures 2 and 3). For example, some individuals in upper Anderson Creek (UAC) assign to a distinct genetic cluster at higher values of K, likely indicating further subtle population or family substructure in these small, isolated populations (Figure 3, $K = 6$ and 10). This is consistent with the low allelic richness and observed heterozygosity in the Upper Anderson Creek and Trout Creek samples relative to most upper Putah Creek populations (Table 1).

https://doi.org/10.15447/sfews.2026v24iss3art5



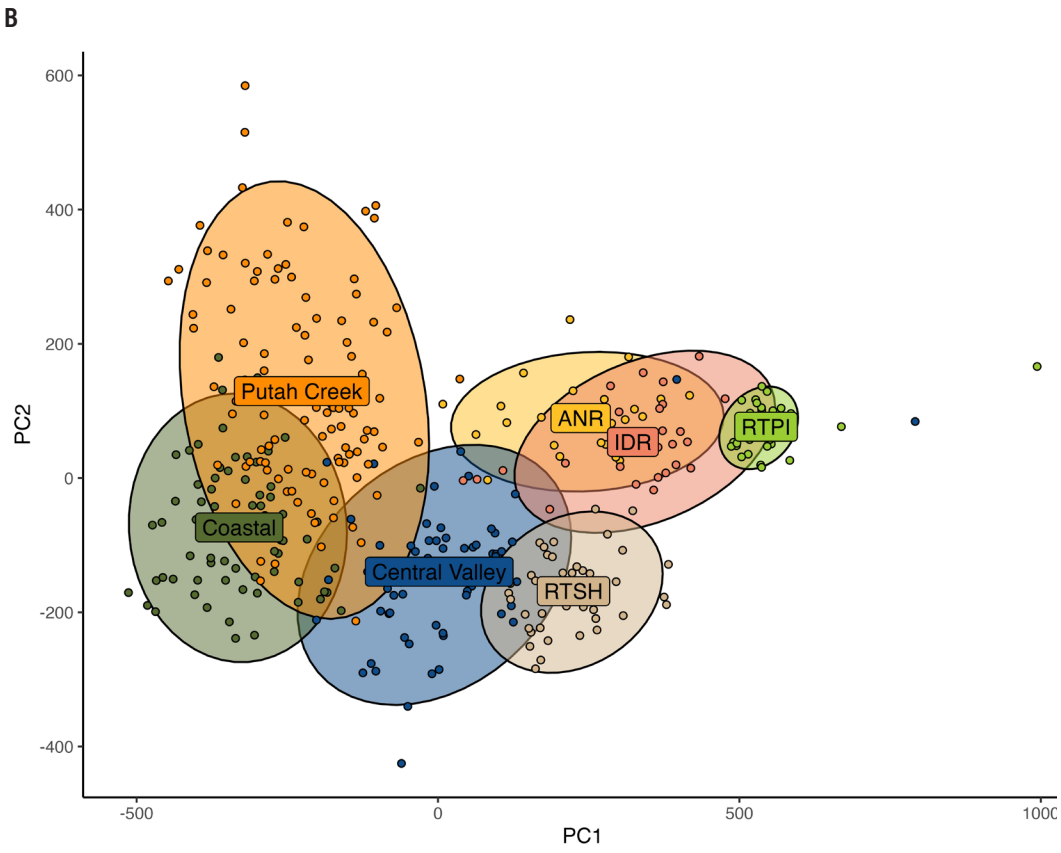


Figure 3 (**A**) *STRUCTURE* (*K* = 2, 3, 4, 6, and 10) and (**B**) PCA results from Putah Creek and subset of reference populations representing Central Valley (Feather River) and coastal (Dry Creek) lineages, and hatchery Rainbow Trout strains (Pit River (RTPI) and Shasta (RTSH). PC1 and PC2 explained 14.4% and 3.6% of the variance.

Adaptive Genetic Variation

We also genotyped microhaplotype markers targeting adaptive genetic variation associated with two life-history traits: residency vs anadromy (Omy05), and summer- vs. winter-run timing in Steelhead (*GREB1L/ROCK1*). An F_{ST} analysis among Putah Creek population pairs based on these adaptive genotypes enabled comparison of neutral and adaptive F_{ST} values among populations (Tables B5 and B6). We found higher F_{ST} values in the adaptive microhaplotypes, with the highest values consistently found between populations above and below Monticello Dam (Table B6).

Among the SNPs genotyped that tag the Omy05 inversion, genotypes were highly concordant across all populations, consistent with their known linkage and locations within the inversion (Pearse et al. 2019; Le Gall et al. 2024). When grouping populations by location above or below Monticello Dam into two groups, there was a significant difference in Omy05 genotype frequencies associated with residency between populations above and below Monticello Dam (RR; Kruskal-Wallis: chi-squared = 18.659, df = 3, *p*-value = 3.216e-4; Figure 4; Table 2). When considering each sample location individually, Putah Creek samples from the upper watershed, such as Upper Anderson Creek (UAC), Trout Creek (TRC), and Upper Upper Putah Creek (UUP), had the highest frequencies of Omy05 resident genotypes (Figure 4; Table 2). Of these populations, only Upper Anderson Creek (UAC) had no access to Lake Berryessa. In contrast, populations near Lake Berryessa maintained variable frequencies of all three Omy05 genotypes through adfluvial movement (Figure 4; Table 2). Omy05 genetic variation associated with anadromy were even more frequent in the

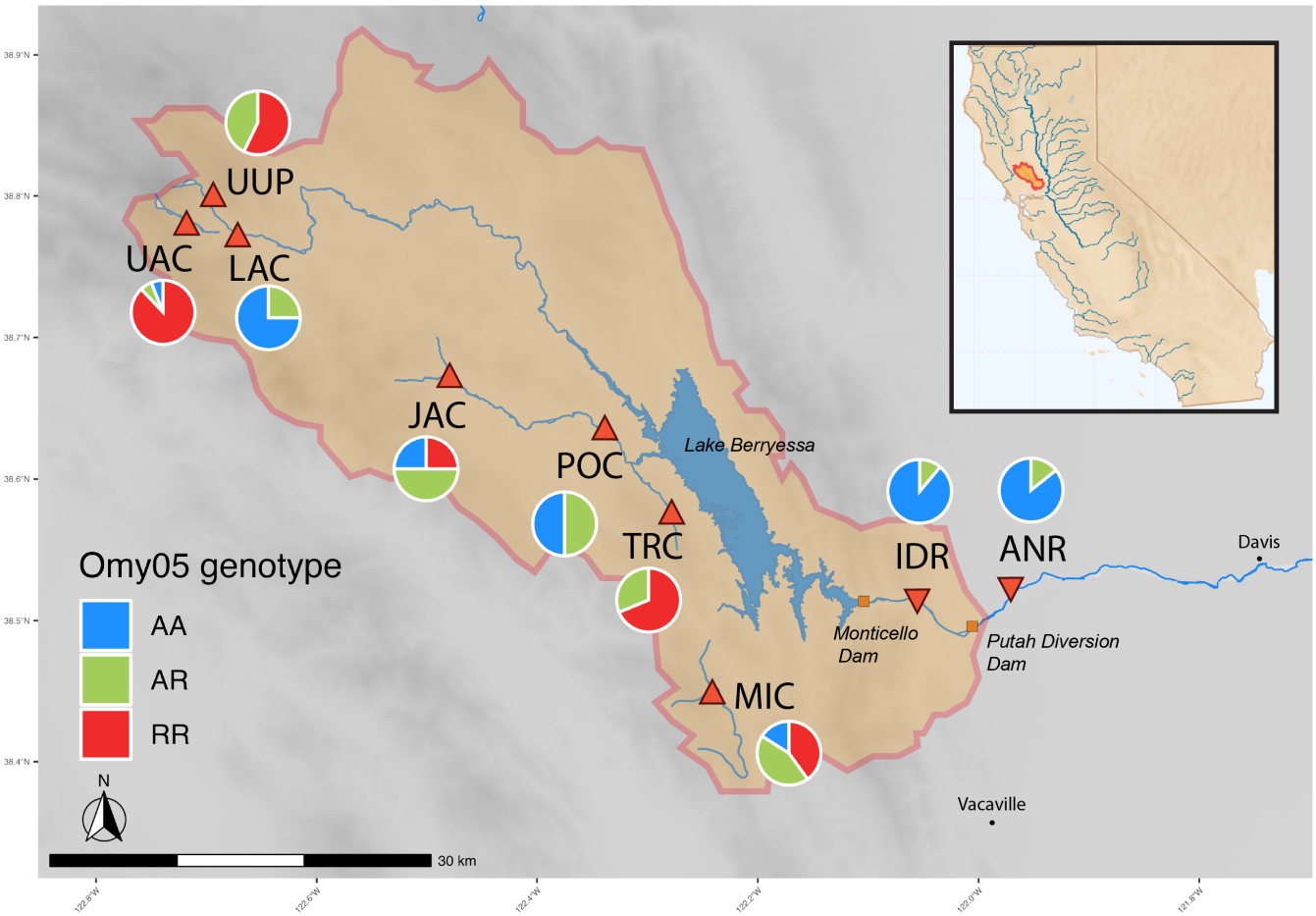


Figure 4 Frequencies of Omy05 genotypes (AA = anadromous, RR = resident, AR = heterozygous) across Putah Creek populations

https://doi.org/10.15447/sfews.2026v24iss3art5

Table 2 Putah Creek populations and adaptive genotype results for Omy05 and *GREB1L/ROCK1*. Omy05 genotype frequencies (AA = anadromous, RR = resident, AR = heterozygous) among Putah Creek populations, and total for above and below Monticello Dam. *GREB1L/ROCK1* genotype frequencies (EE = early-migrant, LL = ate-migrant, EL = heterozygous) in Putah Creek populations, and above and below Monticello Dam. Kruskal-Wallis results are provided for significance in both Omy05 and *GREB1L/ROCK1* genotypes above and below Monticello Dam. Additional details and adherence to Hardy Weinberg equilibrium are provided in Table B1.

	Population		Omy05			*GREB1L/ROCK1*		
			AA	AR	RR	EE	EL	LL
Above Monticello Dam	Anderson Creek, Above Waterfalls	UAC	2	2	29	0	0	33
	Upper Upper Putah Creek	UUP	0	6	8	1	4	7
	Lower Anderson Creek	LAC	3	1	0	0	1	3
	James Creek	JAC	5	10	5	0	0	20
	Pope Creek	POC	3	3	0	0	2	4
	Trout Creek	TRC	0	5	11	0	1	14
	Middle Creek	MIC	4	11	10	0	2	23
Below Monticello Dam	Putah Creek, IDR	IDR	24	3	0	21	6	0
	Putah Creek, Anadromous Reach	ANR	24	4	0	14	12	1
Kruskal-Wallis: Adaptive genotype ~ Above/Below			**chi-squared = 18.659, df = 3, *p*-value = 0.0003216**			**chi-squared = 21.713, df = 3, *p*-value = 7.483e-05**		
Total	Above Monticello Dam		17	38	63	1	10	104
	Below Monticello Dam		48	7	0	35	18	1

IDR and anadromous reach populations below Monticello Dam (chi-squared = 18.659, df = 3, *p*-value = 3.216e-4; Figure 4; Table 2).

There were also significant differences in the distribution of *GREB1L/ROCK1* genotypes in Putah Creek fish populations above and below Monticello Dam. We found that below Monticello Dam, both the IDR and ANR had significantly higher proportions of early-migrating (EE) genotypes (i.e., summer run) compared to samples collected from above Monticello Dam, which featured predominantly late-migrating (i.e., winter run) and heterozygous genotypes (Kruskal–Wallis: chi-squared = 21.713, df = 3, *p*-value = 7.483e-5; Figure 5; Table 2).

Compared with reference populations, the distribution of adaptive genetic variation aligned with the inferred ancestry of Putah Creek populations. Samples from the IDR and anadromous reach, which were genetically similar to CV wild populations and hatchery strains in the population structure analyses, had Omy05 and *GREB1L/ROCK1* genotype distributions similar to CV populations like Feather River Fish Hatchery (FER; Figures 4 and 5; Table 2; Table B1). Conversely, populations above Monticello Dam in Putah Creek that are genetically similar to coastal populations had GREB1L/ROCK1 genotype frequencies similar to coastal winter-run Steelhead populations (Figure 5; Table 2; Table B1).

DISCUSSION

Human-directed alterations to population composition and landscapes cause discernable changes to population structure and distribution of adaptive genetic variation. These downstream effects can further affect management by complicating population and lineage identification, as well as disrupting established abiotic patterns that influence important phenotypic traits. This is particularly evident among Californian salmonid populations, including Rainbow Trout, *Oncorhynchus mykiss irideus*. Historic transplanting of individuals

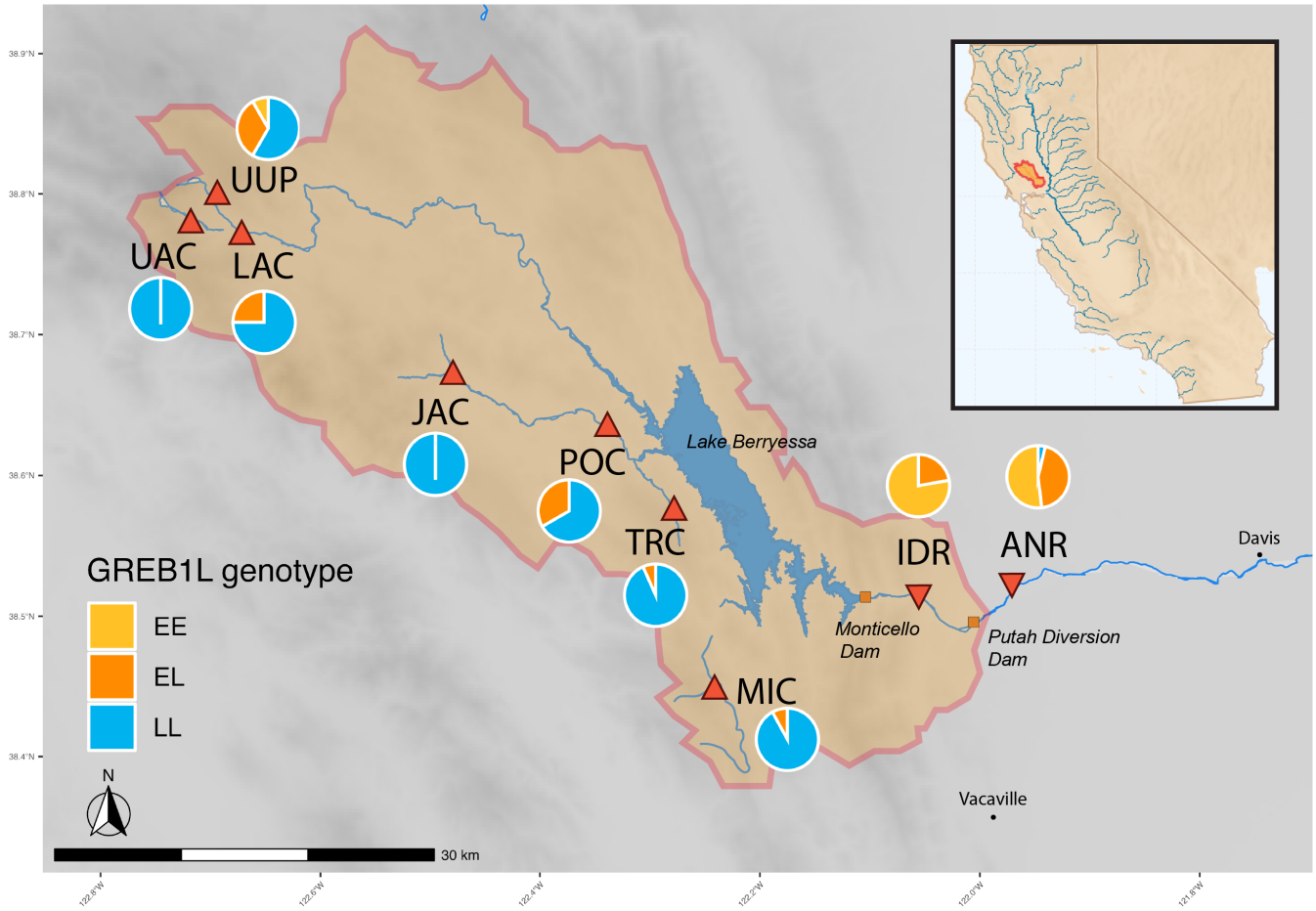


Figure 5 Frequencies of *GREB1L/ROCK1* genotypes (EE = early-migrant, LL = late-migrant, EL = heterozygous) across Putah Creek populations

between watersheds and the operation of hatcheries have significantly affected population structure, and construction of hydroelectric dams has residualized *O. mykiss* populations in upper watershed habitats previously accessible by anadromous Steelhead (Nielson et al. 2005; Pearse and Garza 2015; Phillis et al. 2016).

Population Genetics

Overall, we found that genetic relationships between *O. mykiss* populations inhabiting the Putah Creek watershed reflect larger genetic patterns and environmental influences in major California *O. mykiss* lineages. Our results show that prolonged stocking has provided opportunities for introgression by hatchery Rainbow Trout strains, with individuals sampled downstream of Monticello Dam possessing mixed genetic ancestry primarily from CV Steelhead and hatchery Rainbow Trout. There was a particularly close association with Pit River and Shasta strains that is consistent with past stocking practices.

In contrast, we identified a strong signal of coastal ancestry in the populations above Monticello Dam, consistent with a previous study that noted a curious and difficult to explain genetic relationship between samples from Putah Creek above Lake Berryessa and coastal ancestry in populations from the Calaveras River, the lower American River, and Nimbus Hatchery (Nielsen et al. 2005). Studies using historical samples have shown that, despite decades of extensive stocking with hatchery Rainbow Trout strains, most modern coastal *O. mykiss* populations are genetically similar to historical samples from the same watersheds (Pearse et al. 2011; Sharo et al. 2023). Additionally, previous genetic studies

https://doi.org/10.15447/sfews.2026v24iss3art5

have identified coastal ancestry in San Francisco Bay populations as far inland as the Napa River (Leitwein et al. 2017), which is adjacent to Putah Creek to the West. Thus, one hypothesis is that the coastal-ancestry populations above Monticello are descendants of the trout that were trapped above the dam, suggesting that prior to dam construction the Putah Creek watershed was inhabited primarily by *O. mykiss* of the coastal lineage rather than from the lineage that now dominates the Central Valley. Patterns of *GREB1L/ROCK1* adaptive variation are concordant with this hypothesis, with above dam populations containing adaptive variant genotype frequencies similar to coastal populations.

An alternative hypothesis is that the entire Putah Creek was historically inhabited by CV-lineage *O. mykiss* and that the coastal ancestry we identified above Monticello Dam arrived via stocking with some undocumented coastal lineage hatchery trout strains after dam construction. However, it is important to emphasize that all major hatchery Rainbow Trout strains propagated in California and stocked into Putah Creek over the last century have been developed primarily from inland and CV *O. mykiss* source populations (Leitritz 1970; Barngrover 1988), which would not impart the signals of coastal ancestry and adaptive variation we observed. Thus, evidence suggests that the coastal lineage above Monticello Dam likely reflects native Putah Creek ancestry, potentially introgressed by coastal lineage sources from early stocking efforts (e.g., the Silverado Fisheries Base and East Side Rearing Facility in Napa County, Leitritz 1970).

We identified population substructure among the above dam populations and mixed ancestry within individuals from the upper Putah Creek watershed. At higher hypothesized *K* values in our *STRUCTURE* plots, Upper Anderson Creek (UAC) diverges from the other upper Putah populations, consistent with our analyses suggesting higher genetic divergence in this population. This likely results from Upper Anderson Creek (UAC) possessing an impassable barrier that restricts access to the rest of Putah Creek and Lake Berryessa. Additionally, some individuals sampled above Monticello Dam had mixed ancestry, particularly in Upper Putah Creek (UUP), suggesting some introgression from hatchery trout strains. These details could further support historical stocking above Monticello Dam, but only in certain streams, or it could be evidence of stocking from multiple lineages in different Putah watersheds. Regardless of the origins of the coastal ancestry in populations above Lake Berryessa, our findings are consistent with previous studies that describe distinct genetic differences between *O. mykiss* lineages, particularly between the central coast and Central Valley (Nielsen et al. 2005; Pearse and Garza 2015; Pearse and Campbell 2018; Abadía–Cardoso et al. 2019; Goetz et al. 2024).

Adaptive Genetic Variation

Hydroelectric dams fragment freshwater habitats and disrupt migration routes, landlocking formerly anadromous populations (Phillis et al. 2016; Leitwein et al. 2017; Pearse and Campbell 2018; Winans et al. 2018; Abadía-Cardoso et al. 2019). Before the construction of Monticello Dam and Putah Diversion Dam in 1957, migratory *O. mykiss* spawned throughout the Putah Creek watershed (Shapovalov 1947). Establishing these dams segmented both the watershed and local populations above, between, or below these barriers. Introducing barriers to a watershed can quickly convert populations above barriers to residents, and consequently select for higher frequencies of genetic variation associated with residency (Pearse et al. 2014; Leitwein et al. 2017; Pearse and Campbell 2018; Abadía-Cardoso et al. 2019). Additionally, the distribution of Omy05 haplotypes varies geographically, with evidence of a latitudinal cline: the frequency of Omy05 variation associated with residency increases with latitude (Arostegui et al. 2019; Pearse et al. 2019).

We found that populations below Monticello Dam possessed high frequencies of anadromous-associated Omy05 haplotypes compared with populations above, which is consistent with other studies investigating *O. mykiss* populations above and below barriers (Leitwein et al. 2017; Pearse and Campbell 2018; Abadía-Cardoso et al. 2019; Kannry et al. 2020). Although most sites

above Monticello Dam had higher proportions of genotypes associated with residency (AR and RR), we observed variation among Omy05 microhaplotype frequencies in these populations, with some above-barrier populations possessing genetic variation associated with anadromy, particularly through migratory connectivity to Lake Barryessa. These patterns could reflect Omy05 patterns observed in other southern *O. mykiss* populations (i.e., a latitudinal cline with anadromous genetic variation more frequent in southern populations; Pearse et al. 2019), or they could reflect watershed connectivity differences and the potential for adfluvial movement. Previous studies investigating the distribution of Omy05 haplotypes above and below barriers across watersheds found variation in the frequency of genetic variation associated with anadromy above barriers that suggests increased freshwater connectivity can contribute to retaining a higher frequency of the anadromous variation (Leitwein et al. 2017; Fraik et al. 2021; O'Malley et al. 2026). Additionally, multiple studies found coastal *O. mykiss* ancestry underlying adfluvial individuals possessing genetic variation associated with anadromy (Leitwein et al. 2017; Arostegui et al. 2019; O'Malley et al. 2026). Based on these studies, we hypothesized that we would find a high frequency of residential genetic variation in sampling sites with impassable barriers and little opportunity for adfluvial or anadromous movement. The presence of genetic variation associated with anadromy above barriers may be a reflection on differences among Putah Creek watersheds' accessibility to alternative freshwater habitats, particularly large reservoirs like Lake Berryessa, but without direct evaluation, we cannot make a strong conclusion.

By disrupting migration routes, hydroelectric dams also select against early-returning steelhead by blocking access to upstream spawning habitats, decreasing stream flows, and increasing temperatures (Quinn et al. 2016), thus changing the tradeoffs underlying migration timing. Return timing in salmonids is highly heritable (Quinn et al. 2016; Waples et al. 2022), with salmonid species and populations often responding differently to altered watershed characteristics in a shared environment (Kovach et al. 2013). This suggests that molecular and lineage-specific effects contribute significantly to patterns in the distribution of adaptive genetic variation and return timing. Prior to major dam construction, many of the major Central Valley rivers had habitat that supported early-run salmonids, including spring-run Chinook Salmon and summer-run Steelhead. In Putah Creek, we found higher frequencies of the late-returning, winter-run, *GREB1L/ROCK1* allele in populations above Monticello Dam, and higher frequencies of the early-returning, summer-run allele in populations below Monticello Dam. This pattern likely reflects population structure before the introduction of barriers, consistent with the patterns of population structure, but could also reflect environmental variation within the Putah Creek watershed, as well as the influence of migrant CV Steelhead into the below dam reaches. The distribution of *GREB1L/ROCK1* haplotypes below Monticello Dam suggests higher representation of early-returning individuals, which may be consistent with previous observations suggesting that trout in the IDR spawn in early December (Moyle 2002; Salamunovich 2009). However, further work is needed to better understand the associations between the specific alleles at this locus and run-timing phenotypes in the CV-lineage and resident Rainbow Trout populations (Fed Regist 2019).

CONCLUSIONS

Our results show distinct genetic patterns between Putah Creek populations above Lake Berryessa and those below Monticello Dam, and that these above-barrier populations have coastal lineage ancestry despite extensive history of stocking with CV-lineage and other hatchery Rainbow Trout strains. In addition, the striking contrast in the distribution of adaptive genotype frequencies among populations above and below Monticello Dam is consistent with their distinct genetic ancestry and the contrasting selective environments in the upper and lower parts of the Putah Creek watershed. Our results based on adaptive genomic variants in the Omy05 and

https://doi.org/10.15447/sfews.2026v24iss3art5

GREB1L/ROCK1 regions are concordant with the patterns of ancestry identified in the population genetic analyses and the potential for expression of life-history variation (presence or absence of barriers). We found that *O. mykiss* below Monticello Dam showed evidence of introgression from stocking, with most individuals possessing genetic variation from multiple CV-lineage sources. The combination of coastal ancestry and adaptive genetic variation suggests that Putah Creek populations above Monticello Dam are mainly residents with some adfluvial individuals connecting to other freshwater habitats. Additionally, the identification of individuals possessing anadromous genetic architecture above Monticello Dam is consistent with previous observations of the ability for heterogeneous habitat fragments to support maintenance of genetic diversity, particularly when habitat fragmentation is unavoidable (Fahrig 2018). Though this could be maintained neutrally, similar relationships between fish populations divided by dams have been found in other studies like in pygmy perch (Brauer and Beheregaray 2020) and brook lamprey (Rougemont et al. 2021). Together, these results highlight the complexity of *O. mykiss* adaptation to habitat fragmentation (Pearse and Campbell 2018; Winans et al. 2018; Fraik et al. 2021), and genetic considerations for restoring migratory connectivity in fish populations impacted by dams (Meek et al. 2014; Lusardi and Moyle 2017). Results from Putah Creek overall reflect the dynamic nature of these populations and their genomes, which continuously adapt to changing environmental factors and human-driven management practices through migration, drift, and natural selection.

ACKNOWLEDGEMENTS

This work was partially supported by the Solano County Water Agency (Agreement AG-U-51). We thank Dylan Warner and Christopher Yarnes from Putah Creek Trout for volunteering time to hook-and-line sample the IDR, and Charles Knutsen and Jeff Rodzen for samples from Lake Berryessa. Thanks to Tim Salamunovich for permit assistance and allowing us to sample fish captured below the PDD. Thanks to the following members of the team for camping, hiking, and sampling with us in the upper watershed: Benjamin Burford, Maxwell Chesser, Andrew Kalmbach, Jeremy Notch, and Julia Taylor. Thank you to the many landowners for allowing us to access creeks on or through their property: Dennis Kilkenny, Pat Roy, Kevin Reynolds, Peggy Dickson, Lea Jennings, Steve Strickler and the R Ranch. Thanks to Rick Fessenden, Christopher Cahill, and Brent Randol from Napa County Regional Parks for providing access to the Cedar Roughs Wilderness Area and Trout Creek. Finally, we thank the members of the SWFSC Molecular Ecology and Genetic Analysis team for support, particularly Ellen Campbell and Cassondra Columbus for laboratory genetic data collection and Anthony Clemento, Ellen Campbell, and Eric Anderson for assistance with the genetic data analysis.

DATA ACCESSIBILITY STATEMENT

All data are available via DRYAD at the unique digital object identifier (DOI): *https://doi.org/10.5061/dryad.1c59zw49w* and relevant analytical scripts are available via GitHub at *https://github.com/lauracgoetz/OmykissPutah.git*.

REFERENCES

Abadía-Cardoso A, Brodsky A, Cavallo B, Arciniega M, Garza JC, Hannon J, Pearse DE. 2019. Anadromy redux? Genetic analysis to inform Development of an Indigenous American River Steelhead Broodstock. J Fish Wildl Manage. [accessed 2026 Mar 5];10:137–147. *https://doi.org/10.3996/072018-JFWM-063*

Adamack AT, Gruber B. 2014. PopGenReport: simplifying basic population genetic analyses in R. Methods Ecol Evol. 5:384–387. *https://doi.org/10.1111/2041-210X.12158*

Andrew RL, Ostevik KL, Ebert DP, Rieseberg LH. 2012. Adaptation with gene flow across the landscape in a dune sunflower. Mol Ecol. [accessed 2026 Mar 5];21:2078–2091. *https://doi.org/10.1111/j.1365-294X.2012.05454.x*

Apgar TM, Pearse DE, Palkovacs EP. 2017. Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker. Evol Appl. [accessed 2026 Mar 5];10:485–497. *https://doi.org/10.1111/eva.12471*

Archer FI, Adams PE, Schneiders BB. 2017. STRATAG: An R package for manipulating, summarizing and analysing population genetic data. Mol Ecol Res. [accessed 2026 Mar 5];17:5–11. *https://doi.org/10.1111/1755-0998.12559*

Arciniega M, Clemento AJ, Miller MR, Peterson M, Garza JC, Pearse DE. 2016. Parallel evolution of the summer steelhead ecotype in multiple populations from Oregon and Northern California. Conserv Gen. [accessed 2026 Mar 5];17:165–175. *https://doi.org/10.1007/s10592-015-0769-2*

Arostegui MC, Quinn TP, Seeb LW, Seeb JE, McKinney GJ. 2019. Retention of a chromosomal inversion from an anadromous ancestor provides the genetic basis for alternative freshwater ecotypes in rainbow trout. Mol Ecol. [accessed 2026 Mar 5];28:1412–1427. *https://doi.org/10.1111/mec.15037*

Barngrover BG. 1988. Rainbow trout strains in California state hatcheries. [unknown]: California Department of Fish and Game, Inland Fisheries Administration. Report No. 1988: 19 p.

Brauer CJ, Beheregaray LB. 2020. Recent and rapid anthropogenic habitat fragmentation increases extinction risk for freshwater biodiversity. Evol Appl. [accessed 2026 Mar 5];13:2857–2869. *https://doi.org/10.1111/eva.13128*

California HSRG. 2012. California Hatchery Review Report. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission. [accessed 2026 Mar 6];June 2012:1–110. Available from: *https://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/docs/cmnt091412/sldmwa/hsrg_2012.pdf*

Christie MR, McNickle GG, French RA, Blouin MS. 2018. Life history variation is maintained by fitness trade-offs and negative frequency-dependent selection. Proc Nat Acad Sci. [accessed 2026 Mar 5];115:4441–4446. *https://doi.org/10.1073/pnas.1801779115*

Collins EE, Hargrove JS, Delomas TA, Narum SR. Distribution of genetic variation underlying adult migration timing in steelhead of the Columbia River basin. 2020. Ecol Evol. [accessed 2026 Mar 5];10: 9486–9502. *https://doi.org/10.1002/ece3.6641*

Cooke GM, Landguth EL, Beheregaray LB. 2014. Riverscape genetics identifies replicated ecological divergence across an amazonian ecotone. Evolution. [accessed 2026 Mar 5];68:1947–1960. *https://doi.org/10.1111/evo.12410*

EDAW. 2005. Lower Putah Creek Watershed Management Action Plan Phase I - Resource Assessments. Report for Lower Putah Creek Coordinating Committee. [accessed 2026 Mar 6]. Sacramento (CA): Lower Putah Creek Coordinating Committee. 351 p. Available from: *https://scwa2.com/documents/lpccc/Lower_Putah_WMAP_Vol_I_12-05.pdf*

Fahrig L. 2019. Habitat fragmentation: a long and tangled tale. Global Ecol Biogeogr. [accessed 2026 Mar 5];28:33–41. *https://doi.org/10.1111/geb.12839*

Fraik AK, McMillan JR, Liermann M, Bennett T, McHenry ML, McKinney GJ, Wells AH, Winans G, Kelley JL, Pess GR, Nichols KM. 2021. The impacts of dam construction and removal on the genetics of recovering steelhead (*Oncorhynchus mykiss*) populations across the Elwha River watershed. Genes. [accessed 2026 Mar 5];12:89. *https://doi.org/10.3390/genes12010089*

Goetz LC, Nuetzel H, Vendrami DLJ, Beulke AK, Anderson EC, Garza JC, Pearse DE. 2024. Genetic parentage reveals the (un)natural history of Central Valley hatchery steelhead. Evol Appl. [accessed 2026 Mar 5];17:e13681. *https://doi.org/10.1111/eva.13681*

Graffelman J. 2015. Exploring diallelic genetic markers: the HardyWeinberg package. J Stat Soft. [accessed 2026 Mar 5];64:3. *https://doi.org/10.18637/jss.v064.i03*

Gray MM, St. Amand P, Bello NM, Galliart MB, Knapp M, Garrett KA, Morgan TJ, Baer SG, Maricle BR, Akhunov ED, Johnson LC. 2014. Ecotypes of an ecologically dominant prairie grass (*Andropogon gerardii*) exhibit genetic divergence across the U.S. Midwest grasslands' environmental gradient. Mol Ecol. [accessed 2026 Mar 5];23:6011–6028. *https://doi.org/10.1111/mec.12993*

Hess JE, Zendt JS, Matala AR, Narum SR. 2016. Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing. Proc Roy Soc B. [accessed 2026 Mar 5];283(1830):20153064. *https://doi.org/10.1098/rspb.2015.3064*

Holecek DE, Scarnecchia DL, Miller SE. 2012. Smoltification in an impounded, adfluvial Redband Trout population upstream from an impassable dam: does it persist? Trans Am Fish Soc. [accessed 2026 Mar 5];141:68–75. *https://doi.org/10.1080/00028487.2011.651550*

Jang S, Kure S, Ohara N, Kavvas ML, Chen ZQ, Carr KJ, Anderson ML. 2017. Application of WEHY-HCM for modeling interactive atmospheric-hydrologic processes at watershed scale to a sparsely gauged watershed. Sustainability. [accessed 2026 Mar 5];9:1554–1569. *https://doi.org/10.3390/su9091554*

Kannry SH, O'Rourke SM, Kelson SJ, Miller MR. 2020. On the ecology and distribution of Steelhead (*Oncorhynchus mykiss*) in California's Eel River. J Heredity. [accessed 2026 Mar 5];111:548–563. *https://doi.org/10.1093/jhered/esaa043*

Kendall NW, McMillan JR, Sloat MR, Buehrens TW, Quinn TP, Pess GR, Kuzishchin KV, McClure MM, Zabel RW, Bradford M. 2015. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Can J Fish Aquat Sci. [accessed 2026 Mar 5];72:319–342. *https://doi.org/10.1139/cjfas-2014-0192*

Knoth BA, Hargrove JS, Dobos M, Copeland T, Bowersox BJ. 2022. Rapid colonization of upstream habitats by *Oncorhynchus mykiss* following culvert modification. N Am J Fish Manage. [accessed 2026 Mar 5];42:1173–1184. *https://doi.org/10.1002/nafm.10809*

Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I. 2015. CLUMPAK: a program for identifying clustering modes and packaging population structure inferences across *K*. Mol Ecol Res. [accessed 2026 Mar 5];15:1179–1191. *https://doi.org/10.1111/1755-0998.12387*

Kovach RP, Joyce JE, Echave JD, Lindberg MS, Tallmon DA. 2013. Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. PLoS ONE. [accessed 2026 Mar 6];8(1):e53807. *https://doi.org/10.1371/journal.pone.0053807*

Le Gall R, Barthelemy N, Clemento AJ, Columbus CD, Campbell E, Correa ECA, Rodzen JA, Garza JC, Pearse DE. 2024. Development of a microhaplotype panel for steelhead/rainbow trout (*Oncorhynchus mykiss*) and application for phylogenetic analysis in California. Conserv Gen Res.[accessed 2026 Mar 5];17:17-29. *https://doi.org/10.1007/s12686-024-01374-2*

Leitritz E. 1970. A history of California's fish hatcheries 1870-1960. Fish Bulletin 150. Sacramento (CA): California Department of Fish and Game. [accessed 2026 Mar 6]. 89p. Available from: *https://www.noaa.gov/sites/default/files/legacy/document/2020/Oct/07354626232.pdf*

Leitwein M, Garza JC, Pearse DE. 2017. Ancestry and adaptive evolution of anadromous, resident, and adfluvial rainbow trout (*Oncorhynchus mykiss*) in the San Francisco Bay area: application of adaptive genomic variation to conservation in a highly impacted landscape. Evol Appl. [accessed 2026 Mar 05];10:56–67. *https://doi.org/10.1111/eva.12416*

Lusardi RA, Moyle PB. 2017. Two-way trap and haul as a conservation strategy for anadromous salmonids. Fisheries. [accessed 2026 Mar 5];42(9):478-487. *http://doi.org/10.1080/03632415.2017.1356124*

Manel S, Holderegger R. 2013. Ten years of landscape genetics. Trends Ecol Evol. [accessed 2026 Mar 5];28:614–621. *https://doi.org/10.1016/j.tree.2013.05.012*

Manel S, Schwartz MK, Luikart G, Taberlet P. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol. [accessed 2026 Mar 5];18:189–197. *https://doi.org/10.1016/S0169-5347(03)00008-9*

Mattocks S, Hall CJ, Jordaan A. 2017. Damming, lost connectivity, and the historical role of anadromous fish in freshwater ecosystem dynamics. BioScience. [accessed 2026 Mar 5];67:713–728. *https://doi.org/10.1093/biosci/bix069*

Meek MH, Stephens MR, Tomalty KM, May B, Baerwald MR. 2014. Genetic considerations for sourcing steelhead reintroductions: investigating possibilities for the San Joaquin River. San Franc Estuary Watershed Sci. [accessed 2026 Mar 5];12(1). *https://doi.org/10.15447/sfews.2014v12iss1art2*

Ng T. 2022. R package microhaplot. [accessed 2026 Mar 5]. Available from: *https://cran.r-project.org/src/contrib/Archive/microhaplot/*

Nichols KM, Edo AF, Wheeler PA, Thorgaard GH. 2008. The genetic basis of smoltification-related traits in *Oncorhynchus mykiss*. Genetics. [accessed 2026 Mar 5];179:1559–1575. *https://doi.org/10.1534/genetics.107.084251*

Nielsen JL, Pavey SA, Wiacek T, Williams I. 2005. Genetics of Central Valley *O. mykiss* populations: drainage and watershed-scale analyses. San Franc Estuary Watershed Sci. [accessed 2026 Mar 5];3:2. *https://doi.org/10.15447/sfews.2005v3iss2art3*

[Fed Regist] NMFS. 2006. Endangered and threatened species: final listing determinations for 10 distinct population segments of west coast steelhead. Federal Register. [accessed 2026 Mar 6];71:834–859. Available from: *https://www.federalregister.gov/documents/2006/01/05/06-47/endangered-and-threatened-species-final-listing-determinations-for-10-distinct-population-segments*

[Fed Regist] NMFS. 2019. Northern California steelhead DPS-configuration review-panel report. Federal Register. [accessed 2026 Mar 5];2020-02174:6527-6531. Available from: *https://www.fisheries.noaa.gov/action/12-month-finding-petition-list-summer-run-steelhead-northern-california-endangered-under*

O'Malley KG, Hereford ME, Olsen KC, Pearse DE, Tinniswood WR, Ramirez BS, Armstrong JB, Piotrowski SJ. 2026. Characterizing the distribution of *Oncorhynchus mykiss* genetic diversity in the Klamath River Basin before dam removal. Evol Appl. [accessed 2026 Jul 27];19(7):e70297. *https://doi.org/10.1111/eva.70297*

Pearse DE, Barson NJ, Nome T, Gao G, Campbell MA, Abadía–Cardoso A, Anderson EC, Rundio DE, Williams TH, Naish KA, et al. 2019. Sex-dependent dominance maintains migration supergene in rainbow trout. Nat Ecol Evol. [accessed 2026 Mar 5];3:1731–1742. *https://doi.org/10.1038/s41559-019-1044-6*

Pearse DE, Campbell MA. 2018. Ancestry and adaptation of rainbow trout in Yosemite National Park. Fisheries. [accessed 2026 Mar 5];43:472–484. *https://doi.org/10.1002/fsh.10136*

Pearse DE, Garza JC. 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 Franc Estuary Watershed Sci. [accessed 2026 Mar 5];13(4). *https://doi.org/10.15447/sfews.2015v13iss4art3*

Pearse DE, Miller MR, Abadía-Cardoso A, Garza JC. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. Proc Roy Soc B. [accessed 2026 Mar 6];281(1783):20140012. *https://doi.org/10.1098/rspb.2014.0012*

Pease KM, Freedman AH, Pollinger JP, Mccormack JE, Buermann W, Rodzen J, Banks J, Meredith E, Bleich VC, Schaefer RJ, Jones K, Wayne RK. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. Mol Ecol. [accessed 2026 Mar 5];18:1848–1862. *https://doi.org/10.1111/j.1365-294X.2009.04112.x*

Peffer E. 2013. Aquatic Vegetation Assessment of Putah Creek, Lake Solano, the Putah South Canal, and the Terminal Reservoir. Report for Solano County Water Agency. [accessed 2026 Mar 6]. [Davis (CA)]: [unknown]. 123 p. Available from: *https://www.scwa2.com/documents/publications/S-12A-2.UCD_Peffer.SP%20Veg%20Report.pdf*

Phillis CC, Moore JW, Buoro M, Hayes SA, Garza JC, Pearse DE. 2016. Shifting thresholds: rapid evolution of migratory life histories in steelhead/rainbow trout, *Oncorhynchus mykiss*. J Heredity. [accessed 2026 Mar 5];107:51–60. *https://doi.org/10.1093/jhered/esv085*

Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. Genetics. [accessed 2026 Mar 5];155:945–959. *https://doi.org/10.1093/genetics/155.2.945*

https://doi.org/10.15447/sfews.2026v24iss3art5

Quinn TP, McGinnity P, Reed TE. 2016. The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. Can J Fish Aquat Sci. [accessed 2026 Mar 5];73:1015–1030. *https://doi.org/10.1139/cjfas-2015-0345*

Robinson SJ, Samuel MD, Lopez DL, Shelton P. 2012. The walk is never random: subtle landscape effects shape gene flow in a continuous white-tailed deer population in the midwestern United States. Mol Ecol. [accessed 2026 Mar 5];21:4190–4205. *https://doi.org/10.1111/j.1365-294X.2012.05681.x*

Rougemont Q, Dolo V, Oger A, Besnard A-L, Huteau D, Coutellec M-A, Perrier C, Launey S, Evanno G. 2021. Riverscape genetics in brook lamprey: genetic diversity is less influenced by river fragmentation than by gene flow with the anadromous ecotype. Heredity. [accessed 2026 Mar 5];126:235–250. *https://doi.org/10.1038/s41437-020-00367-9*

Salamunovich T. 2009. 2008-2009 Trout spawning/redd surveys in the Putah Creek Interdam reach. Arcata (CA): Thomas Payne & Associates. [accessed 2026 Mar 6]. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=40826*

Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2009. Steelhead life history on California's Central Coast: insights from a state-dependent model. Trans Am Fish Soc. [accessed 2026 Mar 5];138:532–548. *https://doi.org/10.1577/T08-164.1*

Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M. 2010. State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. Evol Appl. [accessed 2026 Mar 5];3:221–243. *https://doi.org/10.1111/j.1752-4571.2009.00103.x*

Shapovalov L. 1947. Report on fisheries resources in connection with the proposed Yolo-Solano development of the United States Bureau of Reclamation. California Fish and Game [accessed 2026 Jul 3]:33:61–8. Available from: *https://babel.hathitrust.org/cgi/pt?id=mdp.39015045826867&seq=69*

Sharo AG, Supple MA, Cabrera R, Seligmann WE, Sacco S, Columbus CD, Pearse DE, Shapiro B, Garza JC. 2025. Recent adaptation in an imperiled salmonid revealed by museum genomics. Mol Ecol. [accessed 2026 Jul 3];34:e70063. *https://doi.org/10.1111/mec.70063*

Sloat MR, Reeves GH. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. Can J Fish Aquat Sci. [accessed 2026 Mar 5];71:491–501. *https://doi.org/10.1139/cjfas-2013-0366*

Sogard SM, Merz JE, Satterthwaite WH, Beakes MP, Swank DR, Collins EM, Titus RG, Mangel M. 2012. Contrasts in Habitat Characteristics and Life History Patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley. Trans Am Fish Soc. [accessed 2026 Mar 5];141:747–760. *https://doi.org/10.1080/00028487.2012.675902*

Stronen AV, Norman AJ, Vander Wal E, Paquet PC. 2022. The relevance of genetic structure in ecotype designation and conservation management. Evol Appl. [accessed 2026 Mar 5];15:185–202. *https://doi.org/10.1111/eva.13339*

Waples RS, Ford MJ, Nichols K, Kardos M, Myers J, Thompson TQ, Anderson EC, Koch IJ, McKinney G, Miller MR, Naish K, Narum SR, O'Malley KG, Pearse DE, Pess GR, Quinn TP, Seamons TR, Spidle A, Warheit KI, Willis SC. 2022. Implications of large-effect loci for conservation: a review and case study with Pacific Salmon. J Heredity. [accessed 2026 Mar 5];113:121–144. *https://doi.org/10.1093/jhered/esab069*

Weaver J, Mehalick S. 2009. Putah Creek summary report. State of California Natural Resources Agency. Rancho Cordova (CA): California Department of Fish and Game. 17 p.

Willis SC, Hess JE, Fryer JK, Whiteaker JM, Brun C, Gerstenberger R, Narum SR. 2020. Steelhead (*Oncorhynchus mykiss*) lineages and sexes show variable patterns of association of adult migration timing and age-at-maturity traits with two genomic regions. Evol Appl. [accessed 2026 Mar 5];13:2836–2856. *https://doi.org/10.1111/eva.13088*

Winans GA, Allen MB, Baker J, Lesko E, Shrier F, Strobel B, Myers J. 2018. Dam trout: genetic variability in *Oncorhynchus mykiss* above and below barriers in three Columbia River systems prior to restoring migrational access. PLoS ONE. [accessed 2026 Mar 6];13(5):e0197571. *https://doi.org/10.1371/journal.pone.0197571*

Winans GA, Baird MC, Baker J. 2010. A genetic and phenetic baseline before the recolonization of steelhead above Howard Hanson Dam, Green River, Washington. N Am J Fish Manage. [accessed 2026 Mar 5];30:742–756. *https://doi.org/10.1577/M09-119.1*

Winans GA, Baker J, McHenry M, Ward L, Myers J. 2017. Genetic characterization of *Oncorhynchus mykiss* prior to dam removal with implications for recolonization of the Elwha River Watershed, Washington. Trans Am Fish Soc. [accessed 2026 Mar 5];146:160–172. *https://doi.org/10.1080/00028487.2016.1249293*