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Exploring the Migratory Life-Histories of Pacific Salmonids

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EXPLORING THE MIGRATORY LIFE-HISTORIES OF PACIFIC SALMONIDS

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by

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Abstract

EXPLORING THE MIGRATORY LIFE-HISTORIES

OF PACIFIC SALMONIDS

by

Travis Michael Apgar

Variation in life-history traits within and across species is known to reflect adaptations to different environmental drivers through a diversity of mechanisms. Trait variation can also help buffer species and populations against extinction in fluctuating environments and against anthropogenic disturbances. This recognition has led to a growing interest in applying evolutionary principles to inform ecological restoration actions. In this dissertation, I explored how widespread variation in migratory life-histories in Pacific salmonids (*Oncorhynchus* spp.) is driven by a suite of environmental factors with the goals of shedding light on what drives the frequency of these migratory strategies and creating a restoration framework to aid in the restoration of these imperiled species. In Chapter 1, I examined how anthropogenic disturbance in the form of stream modification influences the frequency of anadromy in steelhead (*O. mykiss*) across California. I found that with an increasing number of instream barriers, the frequency of anadromy was reduced. I then developed an evolutionary restoration framework to guide managers and encourage broader consideration of in situ evolution during the development of habitat restoration projects. In Chapter 2, I quantified distinct juvenile migratory strategies of Chinook salmon (*O. tshawytscha*) and modeled the environmental drivers that influence their frequency. I found two distinct migratory strategies were widespread across these populations and their frequencies were driven a juvenile density, rearing habitat, and flow. In Chapter 3, I examined what environmental and demographic factors influenced spring juvenile migratory strategies in coastal coho salmon (*O. kisutch*). I found that juvenile density, flow, and latitude are strong drivers of these migratory behaviors. As in Chinook salmon, a density-dependent mechanism also appears to operate in coho salmon populations, suggesting a form of bet-hedging might be common across out-migrating Pacific salmon. My dissertation links life-history evolution, environmental variation, and anthropogenic modifications to the landscape, demonstrating that alternative life-history strategies are common in Pacific salmonids and suggesting restoration approaches that can be used to conserve this variation.

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The text of this dissertation includes reprints of the following previously published material:

Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker; TM Apgar, DE Pearse, EP Palkovacs - Evolutionary Applications, 2017

Alternative migratory strategies are widespread in subyearling Chinook salmon; TM Apgar, JE Merz, BT Martin, EP Palkovacs - Ecology of Freshwater Fish, 2020

The co-author listed in this publication directed and supervised the research which forms the basis for the dissertation

Introduction

Human alterations of the Earth's surface is extensive, roughly 1/3-1/2 has been altered by human actions in some way (Vitousek et al. 1997). Urban development, agricultural productions, and water transportation have fundamentally changed ecosystems, which has led to many populations and species declining or becoming extinct (Graff 1999, Shurin et al. 2002, Selle 2014, Alberti 2015). Climate change has also exacerbated these problems by amplifying annual variability in weather patterns leading to more extreme conditions (Scavia et al. 2002). Many already stressed populations cannot evolve or adapt on a quick enough time-scale, leading even further population declines (Stockwell et al. 2003, Carroll et al. 2007, 2014). Freshwater ecosystems have been impacted by climate change and anthropogenic disturbance more than any other around the world, with a roughly 83% decrease in the average abundance of taxa since 1970 (WWF/ZSL 2020). Additionally, since they are highly reliant on precipitation to keep them functioning, regional changes or variability in precipitation patterns can cause the loss of multiple trophic levels (Woodward 2010, Ledger et al. 2012). This has led to freshwater fish populations becoming imperiled worldwide, as they occupy the higher trophic levels in these ecosystems (Firth and Fisher 1992, Scavia et al. 2002, Moyle et al. 2013). Anadromous fish, most notably *salmonids*, are particularly susceptible to these forces as they rely on freshwater for the most critical parts of their life history (juvenile development and adult spawning) (Quinn and Myers 2005). Human alterations, such as large impassible dams and water diversions, have reduced available habitat for fish and has led to large-scale population declines (The Heinz Center 2002, Brown et al. 2013). More than 45,000 large dams are operated around the world blocking access for migratory fish (Poff et al. 2007). Climate change amplifies these stresses, especially in times of drought, as water releases by dams are reduced to reserve water for irrigation (O'Neal 2002), potentially leading to increased stream temperatures, dewatering of spawning areas, and further habitat fragmentation (Gasith and Resh 1999, Meixler et al. 2009). All of these stressors have led to a global decline in anadromous fish populations, many of which play important ecological and economical roles (Willson and Halupka 1995, Schindler et al. 2003, 2010, Finstad and Hein 2012).

The decline in anadromous salmonid populations is widespread (Wilcove and Wikelski 2008, Limburg and Waldman 2009). Atlantic salmon populations in Europe and North America have declined by as much as 90% of their historic levels from the early 20th century (Nicola et al. 2018). Many populations in Central Europe have been extinct for so long due to dam construction, many communities have completely forgot they previously existed (Andreska and Hanel 2015). Pacific salmon are following a similar trend, especially at the southern edge of their range (Moyle et al. 1995, Katz et al. 2013). Salmonids play a crucial role in the transportation of marine-derived nutrients into freshwater ecosystems, which are typically nutrient-poor

(Naiman et al. 2002, Twining et al. 2016). These nutrients are released through excretion, gamete release, and decomposition of adult mortalities (Schindler et al. 2003) and play an important role in aquatic and riparian productivity (Naiman et al. 2002, Hocking and Reynolds 2011). Loss of this crucial nutrient transport vector can have cascading consequences throughout aquatic and the adjacent riparian ecosystems (Merz and Moyle 2006).

Along with population declines, alterations to freshwater ecosystems can fundamentally change life history traits of salmonids. Blockage from historic spawning grounds can cause the loss of unique migratory life histories (winter and spring run chinook) (Gustafson et al. 2007), reducing overall portfolio effects (Schindler et al. 2010). Changes in temperature and flow may alter spawn timing, juvenile growth rates and outmigration timing (Bisson and Davis 1976, Caudill et al. 2007). During the course of my dissertation I aimed to answer some key questions related to the migratory life-histories of Pacific salmonids. In **Chapter 1,** I explore how anthropogenic disturbance in the form of stream modification influences the frequency of anadromy in steelhead *(Oncorhynchus mykiss)* across California. In **Chapter 2**, I quantifying distinct juvenile migratory strategies of Chinook salmon *(Oncorhynchus tschawytscha)* and model the environmental drivers that influence their frequency. And finally in **Chapter 3**, I examine the distribution and drivers of coho salmon *(Oncorhynchus kisutch)* spring juvenile migratory life-histories.

In **Chapter 1,** “Evolutionary restoration potential evaluated through the use of a trait-based genetic marker”, I used an expansive genetics dataset that ranged across 39 populations in Coastal California to explore what environmental factors influences the frequency of the anadromous haplotype in steelhead (*Oncorhynchus mykiss)*. I hypothesized that impediments along the migratory corridor would act as a form of selection against anadromy, and that populations with the greatest number of impediments would have the lowest allele frequencies. Using geospatial analyses, I modeled the number of instream barriers, along with other geographic features that influence the frequency of anadromous alleles across of our populations. I found that complete barriers to anadromy imparted the greatest reduction in frequency, but that small partial barriers while having a reduced overall effect, could add up to be equal to or greater than complete barriers. Migration distance also played an important role as well, as the greater this distance from the ocean, the lower the frequency of anadromy. I also created an evolutionary restoration framework where I modeled potential stream restoration scenarios to evaluative which would give the greatest increase in anadromy for the lowest price. Surprising, while large barrier (dam) removal would be effective at restoring anadromy, it is extremely expensive. So an alternative approach which is more affordable and equally effective is to remove multiple smaller barriers to achieve similar results.

In **Chapter 2,** “Alternative migratory strategies are widespread in subyearling Chinook salmon”, I quantified distinct juvenile migratory strategies and what environmental factors influenced their frequency. Historically it was believed that juvenile Chinook had one main successful migratory strategy, and all others were ‘surplus’ fish destine to not survive. However, new evidence arose suggesting this may not be the case. I evaluated juvenile migratory data across 16 populations ranging from California to Washington to establish if these alternative migratory strategies were ubiquitous and what influenced their frequency. I found that two distinct migratory strategies existed in all the populations, an early ‘non-natal rearing’ form which hatch and quickly leaves the natal stream. And a ‘natal rearing’ form which utilized the natal rearing habitat for up to six months. I also found that the frequency of these migratory strategies varied across years and populations, and were strongly influenced by relative juvenile density, available raring habitat, and flow regime. This was an important discovery as these alternative strategies could act as a form of diversified bet-hedging under fluctuation environmental conditions, increasing overall mean fitness and buffering populations against extinction.

In **Chapter 3**, “Exploring spring migratory diversity in juvenile coho salmon at the southern extent of their range”, I explored what environmental and demographic factors influences the frequency of different spring migratory strategies in coastal coho salmon. I found that juvenile density, latitude, and flow regime strongly influenced the frequency of alternative migratory strategies across populations in California and Oregon. This result shows that a density-depended mechanism may also exist in coho population similar to their closest relatives Chinook, where juvenile densities strongly influenced the frequency of each migratory type. This suggest a model of diversified bet-hedging might be common across out-migrating Pacific salmon.

The results of this dissertation highlight the importance of studying what factors can influence the alternative life-history strategies of ecologically and economically important species. By gaining a better understanding of how these traits are expressed across different populations, it affords the opportunity to inform manager and conservationist how best to approach restoration of struggling populations. Additionally, the widespread nature of these alternative migratory strategies may shed light on a broader evolutionary pattern suggesting these species may share a form of diversified bet-hedging to help buffer them against fluctuating environmental conditions which are common along the Pacific Coast.

Chapter 1: Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker

Abstract

Human-driven evolution can impact the ecological role and conservation value of impacted populations. Most evolutionary restoration approaches focus on manipulating gene flow, but an alternative approach is to manipulate the selection regime to restore historic or desired trait values. Here we examined the potential utility of this approach to restore anadromous migratory behavior in coastal California steelhead trout (*Oncorhynchus mykiss*) populations. We evaluated the effects of natural and anthropogenic environmental variables on the observed frequency of alleles at a genomic marker tightly associated with migratory behavior across 39 steelhead populations from across California, USA. We then modeled the potential for evolutionary restoration at sites that have been impacted by anthropogenic barriers. We found that complete barriers such as dams are associated with major reductions in the frequency of anadromy-associated alleles. The removal of dams is therefore expected to restore anadromy significantly. Interestingly, accumulations of large numbers of partial barriers (passable under at least some flow conditions) were also associated with significant reductions in migratory allele frequencies. Restoration involving the removal of partial barriers could be evaluated alongside dam removal and fishway construction as a cost-effective tool to restore

anadromous fish migrations. Results encourage broader consideration of *in situ* evolution during the development of habitat restoration projects.

Introduction

There is an increasing recognition that human-driven evolution can shape the ecological role and conservation value of impacted populations (Palumbi 2001; Stockwell et al. 2003; Hendry et al. 2008; Hendry et al. 2011; Palkovacs et al. 2012). This recognition has led to a growing interest in applying evolutionary principles to inform ecological restoration actions (Hendry et al. 2011, Carroll et al. 2014, Smith et al. 2014). In some cases, human activity shifts traits such that important ecological functions are altered or lost (Palkovacs et al. 2011; Audzijonyte et al. 2013; Audzijonyte et al. 2014). In such situations, evolutionary strategies can be applied to achieve ecological restoration. Calls to apply evolutionary restoration techniques have largely focused on managing gene flow to increase fitness in threatened populations (Aitken and Whitlock 2013, Leger 2013, Frankham 2015, Whiteley et al. 2015). A somewhat different approach that has received less attention is to estimate the effects of anthropogenic impacts on key traits and then to manipulate selection regimes in ways that restore trait values. In this study, we develop an approach to restoration planning that considers predicted evolutionary responses to potential habitat restoration actions.

In many ecosystems, humans have altered selection regimes either directly through selective mortality (e.g., commercial fisheries, trophy hunting) or indirectly through habitat modification (e.g., habitat fragmentation, habitat alteration) (Palkovacs et al. 2012, Carroll et al. 2014, Smith et al. 2014). For example, fisheries-induced mortality of anadromous sockeye salmon (*Oncorhynchus nerka*) and alewife (*Alosa pseudoharengus*) appear to have driven changes in life history traits and body size (Davis and Schultz 2009, Kendall et al. 2014). Reduced body size translates into a reduction in marine-derived nutrients brought into freshwater ecosystems, potentially impacting the ecology of stream and riparian habitats (Schindler et al. 2003; West et al. 2010; Carlson et al. 2011; Twining et al. 2016). In such scenarios, evolutionary restoration via reduced harvest rates and reduced size-selectivity could help restore both trait values and ecological functions (Dunlop et al. 2009; Dunlop et al. 2015). A specific scenario where traits have been altered due to human habitat disturbance is dam construction. Dams fragment rivers and change upstream and downstream habitat, driving changes in selection that can reshape migratory behavior and morphology for impacted fish populations (Palkovacs et al. 2008; Haas et al. 2010). Such trait changes can alter important ecological processes such as food web interactions and nutrient transport (Post et al. 2008; Palkovacs and Post 2009; Jones et al. 2013).

Here we apply an evolutionary restoration framework to inform the recovery of coastal California steelhead trout (*Oncorhynchus mykiss*) (Walbaum). Steelhead trout display variability in migratory behavior. Both within and among populations, some individuals are anadromous, spawning in freshwater and migrating to the ocean, whereas others are residents, completing their entire life cycle in freshwater (Sogard et al. 2012, Kendall et al. 2015). Populations can rapidly evolve freshwater residency when dams or other barriers impede migratory corridors (Pearse et al. 2014). Across a broad suite of species, the loss of anadromy has important implications for ecosystems. Anadromous fishes play a critical role in coastal watersheds by connecting ecosystems, driving nutrient dynamics, impacting food web interactions, shaping local species diversity (Willson and Halupka 1995, Naiman et al. 2002, Schindler et al. 2003, Flecker et al. 2010, Hocking and Reynolds 2011). This ecological role is fundamentally altered when human disturbance, often in the form of dam construction, causes populations to evolve freshwater residency (Post et al. 2008, Palkovacs and Post 2009).

Anadromous populations of many species have declined substantially over recent decades (Limburg and Waldman 2009, Rand et al. 2012, Chaput et al. 2013). In California, anadromous steelhead populations are at risk of disappearing (Katz et al. 2013). Extirpation threatens some populations; however, the evolutionary loss of the anadromous life history is a more widespread phenomenon where populations persist but as non-anadromous freshwater residents. Currently, some anadromous steelhead populations in California are listed as either threatened (north of Point Conception, California, USA to the Klamath River basin) or endangered (south of Point

Conception) under the US Endangered Species Act. In contrast, freshwater resident populations, commonly referred to as rainbow trout, are not protected, even though many populations are native and have lost anadromy due to human habitat alteration (Clemento et al. 2009). In a somewhat ironic twist of fate, freshwater resident rainbow trout has become the most widely distributed freshwater fish in the world due to human introductions, and these invasive rainbow trout originate largely from California hatchery stocks (Crawford and Muir 2008; Halverson 2008; Stanković et al. 2015).

Across a wide variety of fish species, anadromy and freshwater residency evolve rapidly, although individual decisions to migrate or remain resident depend on interactions among genetic, individual condition, and environmental factors (Hendry et al. 2004, Dodson et al. 2013). Anadromy may benefit some individuals by allowing them to escape stressful conditions in freshwater (i.e., reduced food supply, harmful flows, etc.) and providing opportunities for increased growth in the ocean and ultimately higher fecundity (Hendry et al. 2004). In California, females comprise a larger proportion of anadromous individuals in some populations, presumably because of the fitness benefits of greater fecundity for females (Satterthwaite et al. 2010, Rundio et al. 2012, Ohms et al. 2014). But anadromy is costly during the migratory period and may subject individuals to increased energy expenditures and elevated risks of mortality through physiological stress and predation. Theory therefore predicts that anadromy should become less favored as freshwater growth rate increases (or marine productivity decreases), and if the risk of migrating to the ocean increases mortality (Hendry et al. 2004).

Because of widespread variation in migratory behavior within and among populations of steelhead trout, the determinants of anadromy and residency in this species have received much attention (Satterthwaite et al. 2009; Satterthwaite et al. 2010; Hayes et al. 2012; Hale et al. 2013; Berejikian et al. 2014; Pearse et al. 2014; Sloat and Reeves 2014; Kendall et al. 2015; Phillis et al. 2016). Quantifying the proportion of anadromous steelhead *vs*. resident rainbow trout in a population typically requires directly observing the behavior of a large number of individuals. However, the distribution of adaptive genomic variation associated with specific traits has the potential to provide inference about the selective environments and adaptive difference among populations.

In coastal California watersheds, a region of *O. mykiss* chromosome 5 (*Omy5*) has been recently identified, the Omy5 Migration Associated Region (MAR), with alternate alleles being tightly associated with the population prevalence of either migration or freshwater residency (Pearse et al. 2014; Leitwein et al. 2017). Many loci in the MAR are in strong linkage disequilibrium, suggesting the presence of a chromosomal inversion with loci associated with anadromous migratory traits (Pearse et al. 2014; Leitwein et al. 2017). Some of these traits include smoltification, growth rate, survival in sea water, and observed out-migration of juveniles (Doctor et al.

2014, Pearse et al. 2014, Hecht et al. 2015, Phillis et al. 2016). In one example, a population recently translocated from below to above a waterfall has undergone a 49% reduction in the frequency of anadromy-associated alleles, a 19% reduction in smoltification, a 37% decrease in survival when exposed to sea water, and a 25% reduction in observed juvenile out-migration (Pearse et al. 2014, Phillis et al. 2016). Thus, although a single genomic locus should not be considered representative of all the adaptive genomic variation associated with this complex phenotype, variation in MAR allele frequencies does provide substantial utility for evaluating evolutionary restoration as a conservation tool (Pearse 2016). Here we evaluated the effects of natural and anthropogenic environmental variables on the observed frequency of MAR alleles across 39 steelhead trout populations and modeled the potential for evolutionary restoration of anadromy at sites that have been impacted by anthropogenic barriers.

Materials & Methods

Modeling Overview

The overall goal of our modeling exercise was to link environmental variables such as climate, geomorphology, and migratory barriers to the frequency of MAR alleles associated with anadromy in steelhead populations across California. We then used model predictions to inform conservation strategies aimed at restoring anadromous migratory behavior to populations that have lost anadromy due to human habitat modification.

Sample collection and genotyping

Genetic samples were collected from coastal California steelhead populations as part of earlier studies to assess population genetic structure within and among distinct population segments (DPSs) (Clemento et al. 2009, Garza et al. 2014, Pearse et al. 2014). We examined 1332 samples from 39 populations collected in 2001. Populations sampled belong to four DPSs: Southern California (SC), South-Central California Coast (SCCC), Central California Coast (CCC), and Northern California (NC) (Fig. 1.1.). Single nucleotide polymorphisms were genotyped following Pearse & Garza (2015), including two loci linked to the chromosome Omy5 MAR (Pearse et al. 2014; Abadía-Cardoso et al. 2016; Leitwein et al. 2017). The alternative alleles at loci in this region show strong differences in frequency between predominantly anadromous vs. predominately resident populations (Pearse et al. 2014; Pearse and Garza 2015; Abadía-Cardoso et al. 2016; Leitwein et al. 2017). For convenience, we hereafter refer to these as "anadromous" and "resident" alleles. The frequency of haplotypes associated with anadromy, ***f*(A),** was calculated as the sum of the anadromy-associated alleles over the total number of alleles in the population at the locus Omy114448 (Abadía-Cardoso et al. 2011; Pearse et al. 2014).

Environmental variables

A range of environmental variables shape the contemporary evolution of anadromous migratory behavior in fishes (Table 1.1.) (Hendry et al. 2004, Quinn 2005, Quinn and

Myers 2005). Climatological variables associated with anadromy include rainfall, runoff, streamflow, and baseflow. Geomorphological variables include streambed geology, stream order, stream gradient, riparian vegetation, elevation, stream temperature, maximum air temperature, and migration distance. Natural and anthropogenic barriers to instream migration fall into two broad categories. Partial barriers impede but do not entirely prevent riverine migration. These barriers are surmountable under most flow condition; however, they do impart an energetic cost to migration (Jonsson et al. 2010). Complete barriers block upstream migration entirely, but opportunities for downstream migration are possible if a fish can survive passage over a waterfall or dam, and in some cases through hydroelectric turbines. Both partial and complete barriers may be either natural features (e.g., waterfalls, rapids, sandbars, log jams) or anthropogenic disturbances (e.g., road crossing, culverts, water diversions, dams). While all anthropogenic disturbances are relatively recent, natural landscape features may isolate populations for long periods of time (e.g., large waterfalls), while others may only be temporary (e.g., log jams).

Using ArcGIS 10.2 (ESRI 2019), we created point shapefiles for each georeferenced sampling location. We then constructed polyline shapefiles from each respective sampling point to the ocean to represent the stream-path, which was used to calculate migration distance for the freshwater portion of the migration. GIS layers for climatological and geomorphological variables were downloaded on December 13, 2013 via the OSU Prism (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu), Geospatial Gateway (USDA, https://gdg.sc.egov.usda.gov/), and CalAtlas (CNRA, http://www.atlas.ca.gov/download.html) databases. The California Fish Passage Assessment Database (CFPAD; www.calfish.org/tabid/420/Default.aspx) was used to identify all the potential barriers to migratory fish along each stream-path. Based on barriers cataloged in this database, we calculated the number of barriers within each category occurring along each migratory pathway that were present prior to genetic sampling in 2001 (see Supplementary Methods 1). We classified barriers as partial or complete and natural or anthropogenic (Table 1.1.). Partial barriers are those in-stream barriers that are considered passable in an upstream direction by anadromous fishes under at least some flow conditions. Complete barriers are insurmountable in an upstream direction under all flow conditions. The effects of partial barriers were considered to be additive, as they can consecutively impart an energetic cost along the migration path (Jonsson et al. 2010). In contrast, the effects of complete barriers were considered to be binary (present/absent), as they function to block all upstream movement.

Statistical framework

In order to determine which environmental variables contributed significantly to variation in the frequency of anadromy-associated alleles, we conducted backward stepwise regressions for model selection to establish Akaike's Information Criterion (AIC) for each combination of variables. The minimum AIC value was used to select a best-fit model. The frequency of the anadromous allele ***f*(A)**, at each sampling location was used as the dependent variable. Relative effect contributions for each factor were estimated as the amount of change in the population's haplotype frequency when a given factor was included or excluded from the model. Model validation was conducted in two ways. First, observed ***f*(A)** was plotted against predicted ***f*(A)** using a simple liner regression. Predicted ***f*(A)** values were calculated using the best-fit model. We used an R^2 value and 95% prediction interval to evaluate model accuracy. The 95% prediction interval takes into the account the uncertainty of predicting a single observation in the model when compared to the 95% confidence interval, which is used to evaluate the mean values of the dataset. Second, bootstrap values were generated by taking 10,000 iterations of subsamples of the independent variables and using a p-value of <0.05. We then quantified the proportions of times the term was below the p-value significance threshold and reported it as frequency of when the term was included in the model. Analyses were performed in JMP Pro 12 (SAS 2015).

Evolutionary restoration

Using the relative effect contributions determined by the best-fit model, we calculated the expected evolutionary responses (predicted ***f*(A)**) for each population in a scenario where all anthropogenic barriers were removed from the downstream watershed. We then considered the change in the frequency of the anadromous allele **ΔA** under current versus restored scenarios as our measure of potential for evolutionary restoration. Then we assessed the potential for evolutionary restoration for each DPS, as these are the primary regional management units for coastal California.

When accurate cost estimates are available, our evolutionary restoration framework can be used to inform management of which watersheds to restore and which specific barriers to remove. This approach allowed us to compare the theoretical effectiveness of various barrier removal scenarios and to determine what types of barriers and which watersheds can yield the greatest evolutionary restoration at the lowest dollar cost. We obtained cost estimates for specific barrier types and watersheds within our study range from the Pacific States Marine Fisheries Commission (PSMFC). The PSMFC has been compiling cost estimates in hopes to incorporate them into their Passage Assessment Database, which contains all the potential barriers to anadromy along the Pacific coast. We were able to use exact cost estimates or approximate removal costs based on barrier type for Lion Canyon Creek, South Fork Bear Creek, Santa Paula Creek, Los Trancos Creek, Boulder Creek, and the Nacimiento River (PSMFC, *unpublished data*).

Results

The AIC best-fit model contained five terms explaining significant variation in $\boldsymbol{f}(\mathbf{A})$ (Table 1.2.). Migration distance was the sole climatological or geomorphological variable selected in the model. The largest effect contributions were due to the presence of complete anthropogenic or natural barriers. Complete natural barriers had the highest effects contribution at ±30.66% with a bootstrap frequency of 0.95. Complete anthropogenic barriers had an effect contribution of ±18.47% with a bootstrap value of 0.93. The remaining three terms had an additive effect in the model and thus are all negative effect contributions. Partial anthropogenic barriers had an effect contribution of -1.82% per barrier and a bootstrap value of 0.55. Migration distance had a -6.79% per 100 km and a bootstrap value of 0.53. Finally, partial natural barrier effect contribution was calculated to be -0.51% per barrier along the migration path with a bootstrap value of 0.08. Even though this term was not significant, its presence did help increase the overall accuracy of the model.

Model validation through linear regression of observed versus predicted ***f*(A)** had all but two data points falling within the 95% prediction interval (R^2=0.745; Fig. 1.2.). The two sampling sites falling outside of the prediction interval were both within the Salinas River watershed, which is a large river system with diverse habitats. Historical or contemporary factors may be present in this drainage that caused our model to perform poorly. The model performed well for all other sampling sites.

Frequency of anadromy ***f*(A)** generally decreased north to south, while restoration potential **ΔA** generally increased from north to south (Fig. 1.3., Table 1.3.). However, considerable variation among sampling locations was found in every DPS (Table 1.4.). The *Southern California* (SC) DPS is within a highly urbanized and anthropogenically impacted region (Fig. S1.1.). The average ***f*(A)** in SC was 41.02%, the lowest of any DPS. It also had the highest average number of partial anthropogenic barriers per watershed (n=4.7, range 1-9) and the highest total number of complete anthropogenic barriers (n = 8). The SC also had a relatively long average potential migration distance at 80.46 km. Rugged coastal mountains and agricultural land dominate the *South-Central California Coast* (SCCC) DPS (Fig. S1.2.). The average ***f*(A)** in SCCC was 71.37%. The average number of partial anthropogenic barriers was 1.6 per watershed (range 0-4) and there was only one complete anthropogenic barrier affecting our sampled populations in this DPS. The SCCC had the longest average migration distance at 112.26 km due to the inclusion of the Salinas River. The *Central California Coast* (CCC) DPS is a mix of rugged coast and urbanized areas (San Francisco Bay Area) (Fig. S1.3.). The average ***f*(A)** was 75.84% which was the highest of any DPS evaluated. The average number of partial anthropogenic barriers was 3.8 per watershed (range 0-12) and there were no complete anthropogenic barriers present but one complete natural barrier affecting our sampled populations. The average migration distance was shortest of all the DPS's at just 12.91 km. The *Northern California* (NC) DPS is the least urbanized section of coastal California, although impacts from forestry and illegal marijuana cultivation (Bauer et al. 2015) are widespread (Fig. S1.4.). The average ***f*(A)** was 72.35%, which was the second highest of all the DPS's. The average number of partial anthropogenic barriers was 0.5 per watershed (range 0-2), the lowest of any DPS considered. There were no complete anthropogenic barriers in this DPS but two complete natural barriers affecting our sampled populations. The average migration distance of NC was 103.31km, the second highest of any DPS considered.

Based on the model output, when complete anthropogenic barriers were present, populations had a difference of ±18.47% in anadromy-associated alleles. However, partial anthropogenic barriers (-1.82% per barrier) can have an additive effect that can equal that of complete barriers (e.g., Los Trancos Creek). Highly urbanized areas have the highest densities of partial and complete anthropogenic barriers, thus their restoration potential is higher.

Using the subset of watersheds where there is reliable cost information, we evaluated a few case studies (Table 1.5.). Los Trancos Creek (CCC, Fig. S1.3.) has 12 partial anthropogenic barriers. We estimated the cost to remove all 12 barriers as $2,036,000. The estimated evolutionary response is a 21.84% increase in anadromy for this watershed, representing $93,223 per one percent increase in anadromy. In contrast, some watersheds have large complete anthropogenic barriers such as the 64m earthen dam on the Nacimiento River (SCCC, Fig. S1.2.). It would cost an estimated $75,000,000 to remove this dam (PSMFC, *unpublished data*). The estimated evolutionary response in this case is a 18.47% increase in anadromy, which represents a substantially more costly $4,060,638 per one percent increase in anadromy. However, there are some highly urbanized watersheds that have complete anthropogenic barriers that are not large dams but improperly designed culverts or grade structures. These types of barriers prevent upstream movement just as large dams but are considerably less expensive to remove. For example, our model estimated that a 20.29% increase in anadromy-associated alleles would result from removing a partial barrier and a diversion dam in Lion Canyon Creek (SC, Fig. S1.1.), for only \$320,000. This restoration project is estimated to cost \$17,551 per one percent increase in anadromy, the highest return on investment for any of the watersheds considered.

Discussion

Ecologists and evolutionary biologists have become increasingly aware that human-driven evolution can shape key traits of ecologically important species (Hendry et al. 2008; Allendorf and Hard 2009; Palkovacs et al. 2012). Returning traits and their associated ecological functions to historical conditions has led to an increasing interest in evolutionary restoration (Hendry et al. 2011; Carroll et al. 2014; Smith et al. 2014). In this study, we examined the impact of anthropogenic disturbance on the loss of genetic variation associated with anadromous migratory behavior in coastal California steelhead trout. We estimated the impacts of various anthropogenic factors on adaptive genomic variation in a migration-associated region (MAR) of the *O. mykiss* chromosome 5. Based on the anthropogenic factors associated with the loss of anadromy-associated alleles, we evaluated the potential for evolutionary restoration at sites across California, USA. Finally, we estimated the financial cost of implementing various proposed restoration efforts across our study watersheds, with the goal of promoting evolutionary restoration of anadromy for the lowest economic cost.

We examined the impacts of climate, geomorphology, and migratory barriers on the frequency of anadromy-associated alleles. Migratory barriers were found to have the greatest association with anadromous allele frequencies. Natural barriers (e.g., waterfalls, cascades) represent long-term migratory barriers and had the largest effect, the anadromous allele frequency being on average 31% lower when present. Complete anthropogenic barriers (mostly dams) also had a relatively large effect, with the anadromous allele frequency being an average of 18% lower when complete barriers were present. Most California dams have been operating for less than 100 years (Hanak et al. 2011); the large effect of complete anthropogenic barriers supports the idea that freshwater residency evolves rapidly following dam construction (Pearse et al. 2014).

While we do not have temporal information from most sites to estimate the rate of allele frequency change following barrier introduction, we can draw some inferences from below-above barrier population comparisons. There are three cases where we have estimates of neutral genetic divergence and variation at the MAR for above- and below-barrier populations (one from Scott Creek and two from the Santa Ynez). In these cases, changes in allele frequencies at the MAR (49-76%) are large relative to the extent of genetic divergence at neutral SNP loci (pairwise F_{ST} values all < 0.01;

Clemento et al. 2009; Pearse et al. 2009). Particularly informative is a documented translocation that occurred within the Scott Creek watershed. Here, the frequency of anadromy-associated MAR alleles is 83% below a barrier waterfall and is reduced to 34% in a population translocated above the waterfall about 100 years ago ($F_{ST} > 0.3$, Martinez et al. 2011). These same populations display a pairwise F_{ST} of 0.018 at neutral SNP loci (Pearse et al. 2009), clearly demonstrating that drift is not solely responsible for the large-magnitude directional changes in allele frequencies detected at the MAR. The translocated Scott Creek population above the waterfall currently shows an anadromous allele frequency similar to populations above dams, which were probably isolated for a similar amount of time. Assuming that the below-barrier population on Scott Creek has not changed dramatically in its allele frequency over the past 100 years, we can infer that the reduction of anadromy-associated alleles occurred at a rate of approximately 0.05% per year. We anticipate that this rate of change was likely much greater in the years immediately following the translocation and has slowed markedly since then (Kinnison & Hendry 2001).

Waterfalls, dams, and other impassable barriers are not the only types of migratory barriers found to impact the frequency of anadromy. Partial barriers impart an energetic cost to migration (Kinnison et al. 2003; Hendry et al. 2004; Kendall et al. 2015). When anthropogenic partial barriers were present, anadromous allele frequencies were on average about 2% lower per barrier. While individual partial barriers had a relatively small effect, they occur at very high densities in some watersheds. For example, Boulder Creek (a tributary of the San Lorenzo River in Santa Cruz County) (CCC, Fig. S1.3.) has 11 partial anthropogenic barriers, three partial natural barriers, no complete barriers, and an anadromous allele frequency of just 54% (compared to an expected allele frequency of 74% based on its migration distance and number of natural barriers). Thus, the accumulated effects of many partial barriers can have an impact equivalent to that of an impassable dam. Importantly, removal of small partial barriers is less expensive and presents fewer engineering, social, and regulatory challenges compared to large dam removal (Graff 1999, Doyle et al. 2005).

We found a significant effect of migration distance on the frequency of anadromy-associated alleles. Migration distance has previously been found to affect anadromy in a wide variety of species, with spawning sites further from the ocean generally displaying lower rates of anadromy (Hendry et al. 2004, Ohms et al. 2014, Kendall et al. 2015). The longer the migration, the more energy must be expended to reach the spawning grounds and the higher the chance of encountering barriers, predators, and other mortality sources. Thus, our results are consistent with prior studies showing that longer migrations select for increased rates of freshwater residency.

In California, steelhead trout are managed in Distinct Population Segments (DPSs) under the US Endangered Species Act. The Southern California DPS had the lowest average anadromous allele frequency measured (Table 1.3., Fig. S1.1.), most likely due to the high level of human disturbance in Southern California watersheds. A plethora of instream impediments have likely contributed to the overall reduction in the average frequency of anadromy-associated alleles within its sampled watersheds to just 41%, compared to an expected allele frequency of 62% based on the average migration distance and number of natural barriers. In contrast, the Northern California DPS has the lowest human population, the fewest anthropogenic barriers, and an average frequency of anadromy-associated alleles of 72% (compared to an expected allele frequency of 73%) (Fig S1.4.). The Central California Coast DPS contains streams that range between highly altered (11-12 partial anthropogenic barriers) to relatively undisturbed (0-2 partial anthropogenic barriers) (Fig. S1.3.). While there are no complete anthropogenic barriers in our study populations for the Central California Coast DPS, the accumulation of partial barriers is associated with the reduction in anadromy-associated alleles in parts of this DPS. The South-Central California Coast contains the two populations that are outliers in the model (Fig. S1.3.). Both of these populations are in the highly altered Salinas River watershed, which may function differently than other coastal streams due to major anthropogenic disturbances, particularly in the form of intensive agriculture. For example, Tassajera Creek (SCCC, Fig. S1.2.) shows a lower than expected frequency of anadromy-associated alleles, perhaps due to the agricultural withdrawals that may seasonally dry the Salinas River along much of it main stem channel, creating a low-flow barrier to migration. In contrast, the Nacimiento River (SCCC, Fig. S1.2.) shows a higher than expected frequency of alleles associated with anadromy. This river flows into the

Lake Nacimiento, which may represent the destination for an adfluvial migration, where fish migrate to the lake instead of the ocean (Pearse et al. 2014). Similar adfluvial patterns were found in above reservoir populations around the San Francisco Bay Area (CCC, Fig. S1.3.), where there is a strong association between reservoir size and the frequency of anadromy-associated alleles (Leitwein et al. 2017).

Each of our study populations were sampled at a single time point, yet we anticipate that allele frequencies at any given site may fluctuate somewhat through time due to drift and dynamic local selective drivers such as stream flow conditions. We do not have the data from repeated sampling events to address within-site changes in allele frequencies for this study. Nonetheless, our results show that major variation in allele frequencies are predictably related to migration distance and the presence of natural and anthropogenic barriers. These strong and consistent signals would not be expected to emerge in a scenario with high temporal variability in allele frequencies due to random or site-specific factors. Thus, our overall results are likely robust to fine scale temporal shifts in allele frequencies within sites.

Our study shows that partial and complete anthropogenic barriers are strongly associated with variation in the frequencies of anadromy-associated alleles. We therefore calculated the expected evolutionary responses for each population in a scenario where all anthropogenic barriers were removed from the downstream watershed. While simulating the removal of large impassable dams yields the biggest predicted evolutionary responses, there are many social, engineering, and legal challenges for projects of this scale (Graff 1999, Doyle et al. 2005). Smaller dams yield smaller returns, however there are many more of them, which can add up to similar effect contributions to that of a large complete barrier. Smaller scale projects can also be conducted with relative ease by local agencies or watershed stewardship groups. This strategy should be considered as an important complement to large-scale dam removal when considering the evolutionary restoration of anadromy.

In the subset of watersheds where we evaluated restoration costs, the economic potential of different barrier removal scenarios varied greatly (Table 1.5.). The removal of many smaller partial barriers was substantially cheaper than removing a large impassable dam, yet still achieved a similar evolutionary response. Large dam removals can cost tens of millions of dollars and take decades of planning to complete. For example, the San Clemente Dam Removal Project on the Carmel River in Monterey County, CA cost approximately $83,000,000 and took 20 years of planning and execution (CalAm 2015). The cost to remediate or remove a small partial barrier on the other hand averaged around $160,000 and some projects can be completed in just under a month (PSMFC, *unpublished data*). In some locations, complete barriers were poorly designed culverts or flow-control structures. Removal of these smaller complete barriers could also achieve large gains in anadromy at relatively low costs.

An alternative approach to barrier removal is barrier remediation, which can be conducted on partial and complete barriers. Not all barriers were originally constructed in ways that would allow them to be modified. Nonetheless, some partial barriers such as culverts can be modified to reduce flow velocity and increase water depth, allowing unimpeded passage for anadromous fish. Some dams can have fishways installed, converting them from complete barriers into partial barriers, reducing their impacts substantially. However, fishway construction can be difficult and expensive on some larger dams and many fishways perform poorly, making dam removal the preferred restoration strategy whenever possible (Brown et al. 2013).

Ecologists have called for the use of dam removals as large-scale experiments to examine ecological processes in rivers and streams (Hart et al. 2002). Our study extends this framework to include evolution. Here we provide predicted evolutionary responses to various restoration scenarios. The next step is to monitor evolutionary change following large- and small-scale barrier removals as management experiments to test these predictions. Evolutionary experiments at this scale are rarely undertaken. Thus, barrier removal provides an important opportunity to achieve restoration objectives while testing basic hypotheses about the factors driving natural selection and evolution in wild populations.

Conclusions

Human-induced trait change has been observed in species and ecosystems around the world, and recent efforts have been made to identify and manages these changes (Allendorf and Hard 2009, Palkovacs et al. 2012). Most evolutionary restoration approaches have focused on manipulating gene flow (Hendry et al. 2011, Carroll et al. 2014, Smith et al. 2014). However, manipulating the environment in ways that shift selection is another method that can effectively restore historical trait values and associated ecological functions (Ashley et al. 2003; Smith et al. 2014). Our study shows that habitat modification in the form of migratory barriers such as dams and culverts are associated with the loss of anadromy-associated alleles in coastal California steelhead trout populations. While complete barriers such as dams are associated with a dramatic loss of anadromy, the accumulation of large numbers of smaller partial barriers can add up to similarly large impacts. Removing large dams is expected to result in the greatest evolutionary restoration of anadromy, however such projects can be expensive and present many social, engineering, and legal challenges (Graff 1999, Doyle et al. 2005). Our results suggest that removal of partial barriers can be effective at restoring anadromy at a fraction of the cost. Projects involving small barrier removal present fewer technical and socio-political challenges. Thus, restoration projects involving the removal of small partial barriers could be considered alongside large dam removals and fishway construction projects as effective tools to restore anadromy to populations that have evolved increased freshwater residency.

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Tables and Figures

Table 1.1. Environmental variables included in the model based on possible effects on anadromy.

Environmental Conditions Affecting Migration			
Climatological	**In-stream Barriers**	**Geomorphology**	
Runoff	Partial Anthropogenic Barriers	Streambed Geology	Migration Distance
Rainfall	Complete Anthropogenic Barriers	Stream Order	Elevation
Streamflow	Partial Natural Barriers	Stream Gradient	Stream Temp
Baseflow	Complete Natural Barriers	Riparian Vegetation	Max Air Temp

Table 1.2. Model output representing relative effect contributions and bootstrapping results for population haplotype frequencies. Complete natural and anthropogenic barriers are presence (-) absence (+) terms, while partial natural and anthropogenic barriers and migration distance have additive effects.

Effect Contribution Results				**Bootstrapping Results**	
Environmental Variable	**Effect Contribution**	**Standard Error**	**Units**	**N(10,000) p<0.05**	**Frequency in Model**
Complete Natural Barriers	±30.66%	.0540	Yes=negative, No=positive	9488	0.95
Complete Anthropogenic Barriers	±18.47%	.0400	Yes=negative, No=positive	9343	0.93
Partial Anthropogenic Barriers	-1.82%	.0079	* number of barriers	5523	0.55
Migration Distance	-6.79%	.0329	per 100km	5288	0.53
Partial Natural Barriers	-0.51%	.0319	* number of barriers	797	0.08

Table 1.3. Summary of anadromous allele frequency $f(\text{A})$ by Distinct Population Segment (DPS). The Southern California DPS contains the greatest amount of anthropogenic disturbance across all our sampling locations in the form of partial and complete anthropogenic barriers. This is reflected in the average restoration potential ΔA, which is much higher than the other DPSs.

DPS	**Southern California (SC)**	**South-Central California Coast (SCCC)**	**Central California Coast (CCC)**	**Northern California (NC)**
Average f(A)	41.02	71.37	75.84	72.35
Average ΔA	21.77	6.40	6.28	1.02
Status	Endangered	Threatened	Threatened	Threatened
Average Partial Anthro Bar No.	4.7	1.6	3.8	0.5
Average Partial Natural Bar No.	0	0	0.64	0.81
Total Complete Anthro Bar No.	8	1	0	0
Total Complete Natural Bar No.	0	0	1	3
Average Migration Distance	80.46	112.26	12.91	103.31

Table 1.4. Individual sampling locations and their corresponding data sorted from south to north and organized by watershed.

Sampling Location	Location Codes	Latitude	Longitude	Major Watershed	DPS	Status	*f*(A)	Restored *f*(A)	ΔA	Partial Natural Bar No.	Complete Natural Bar PA	Partial Anthro Bar No.	Complete Anthro Bar PA	Migration Distance (km)
Santa Paula Creek (a,b)	SPC	34.444837	-119.068914	Santa Clara River	SC	Endangered	**28.26**	**54.01**	**25.75**	0	No	4	Yes	39.42
Lion Canyon Creek (a,b)	LCC	34.549924	-119.16586	Santa Clara River	SC	Endangered	**35.42**	**55.71**	**20.29**	0	No	1	Yes	91.9
Piru Creek (a,b)	PC1	34.635302	-118.756754	Santa Clara River	SC	Endangered	**45.65**	**76.86**	**31.21**	0	No	7	Yes	96.91
Piru Creek (a,b)	PC2	34.703043	-118.937168	Santa Clara River	SC	Endangered	**12.5**	**47.35**	**34.85**	0	No	9	Yes	124.33
Hilton Creek (a,b)	HC	34.586241	-119.986434	Santa Ynez River	SC	Endangered	**72.92**	**82.02**	**9.1**	0	No	5	No	76.85
Salsipuedes Creek (a,b)	SC-SYR	34.633739	-120.412621	Santa Ynez River	SC	Endangered	**84.09**	**85.91**	**1.82**	0	No	1	No	24
West Fork Santa Cruz Creek (a,b)	WFSCC	34.657939	-119.759101	Santa Ynez River	SC	Endangered	**8.33**	**37.72**	**29.39**	0	No	6	Yes	109.81
Willow Creek (b)	WLLC	35.893746	-121.460507	Willow Creek	SCCC	Threatened	**72.58**	**72.58**	**0**	0	No	0	No	0.13
Big Sur River (b)	BSR	36.245949	-121.773275	Big Sur River	SCCC	Threatened	**88.71**	**90.53**	**1.82**	0	No	1	No	12.11
Carmel River* (a,b)	CR	36.409742	-121.674336	Carmel River	SCCC	Threatened	**95.57**	**100**	**4.43**	0	No	3	No	37.55
Tassajera Creek (a)	TC	35.38441	-120.682174	Salinas River	SCCC	Threatened	**25**	**32.28**	**7.28**	0	No	4	No	243.73
Nacimiento River (a)	NR	36.00643	-121.398949	Salinas River	SCCC	Threatened	**75**	**93.47**	**18.47**	0	No	0	Yes	267.82
San Lorenzo River (a)	SLR	37.029971	-122.057524	San Lorenzo River	CCC	Threatened	**88.18**	**91.82**	**3.64**	2	No	2	No	12.29
Boulder Creek (d)	BC-SLR	37.126409	-122.123467	San Lorenzo River	CCC	Threatened	**54.69**	**74.71**	**20.02**	3	No	11	No	29.77
Scott Creek (a)	SC	37.050498	-122.226909	Scott Creek	CCC	Threatened	**82.78**	**82.78**	**0**	0	No	0	No	1.45
Big Creek (a)	BC-SC	37.083094	-122.217591	Scott Creek	CCC	Threatened	**33.7**	**33.7**	**0**	0	Yes	0	No	5.89
Waddell Creek (b)	WDC	37.116208	-122.268818	Waddell Creek	CCC	Threatened	**93.55**	**95.37**	**1.82**	0	No	1	No	3.65
Peters Creek* (d)	PC-PC	37.251634	-122.218089	Pescadero Creek	CCC	Threatened	**85.48**	**100**	**14.52**	1	No	12	No	30.46
Los Trancos Creek (b)	LTC	37.405982	-122.193483	San Francisquito Creek	CCC	Threatened	**75**	**96.84**	**21.84**	0	No	12	No	14.33
Redwood Creek (c)	RC	37.866403	-122.578553	Redwood Creek	CCC	Threatened	**85.48**	**85.48**	**0**	0	No	0	No	1.23
Miller Creek (c)	MC	38.025405	-122.567561	Miller Creek	CCC	Threatened	**70.88**	**72.7**	**1.82**	0	No	1	No	7.82
Lagunitas Creek (d)	LC	38.034194	-122.743381	Lagunitas Creek	CCC	Threatened	**94.26**	**96.08**	**1.82**	0	No	1	No	16.28
Willow Creek (d)	WC-RR	38.42017	-123.036371	Russian River	CCC	Threatened	**70.31**	**73.95**	**3.64**	1	No	2	No	11.02
Fuller Creek (b)	FC	38.699424	-123.327231	Gualala River	NC	Threatened	**75.33**	**75.33**	**0**	0	No	0	No	33.12
North Fork Big River (d)	NFBR	39.333469	-123.560718	Big River	NC	Threatened	**95.16**	**95.16**	**0**	0	No	0	No	49.52
Kass Creek (c)	KC	39.417581	-123.719985	Noyo River	NC	Threatened	**91.94**	**93.76**	**1.82**	0	No	1	No	12.01
Pudding Creek (d)	PC	39.472249	-123.716991	Pudding Creek	NC	Threatened	**90.32**	**92.14**	**1.82**	0	No	1	No	13.25
Smith Creek (d)	SC-TMR	39.527682	-123.728451	Tenmile River	NC	Threatened	**91.94**	**91.94**	**0**	2	No	0	No	6.23
Wages Creek (d)	WC	39.647917	-123.770039	Wages Creek	NC	Threatened	**87.1**	**87.1**	**0**	0	No	0	No	1.88
Big Creek (d)	BC	40.157456	-124.210424	Big Creek	NC	Threatened	**69.35**	**69.35**	**0**	0	No	0	No	0.14
South Fork Bear Creek (b)	SFBC	40.035764	-124.025037	Mattole River	NC	Threatened	**61.29**	**64.93**	**3.64**	0	No	2	No	101.14
Bear River (d)	BR	40.399481	-124.137965	Bear River	NC	Threatened	**79.69**	**79.69**	**0**	0	No	0	No	32.11
Eel River (a)	ER	39.38652	-123.116409	Eel River	NC	Threatened	**75**	**76.82**	**1.82**	0	No	1	No	252.19
Hollow Tree Creek (c)	HTC	39.817585	-123.757815	Eel River	NC	Threatened	**84.38**	**88.02**	**3.64**	1	No	2	No	189.28
Middle Fork Eel River (a)	MFER	39.984042	-123.090546	Eel River	NC	Threatened	**63.72**	**63.72**	**0**	3	No	0	No	272.87
North Fork Middle Fork Eel R. (a)	NFMFER	40.072531	-123.13593	Eel River	NC	Threatened	**2.08**	**2.08**	**0**	3	Yes	0	No	286.28
Cutfinger Creek (a)	CC	40.106932	-123.028493	Eel River	NC	Threatened	**0**	**0**	**0**	3	Yes	0	No	296.85
Lawrence Creek (c)	LWC	40.616988	-123.990458	Eel River	NC	Threatened	**95.16**	**95.16**	**0**	0	No	0	No	52.1
Blue Slide Creek (c)	BSC	40.737754	-123.885432	Mad River	NC	Threatened	**95.16**	**98.8**	**3.64**	1	No	2	No	53.99

* Locations with predicted restored *f*(A) values >1.0 and capped at 100%.

(a) Genetic data from Pearse and Garza (2015)

(b) Genetic data from Abadía-Cardoso et al. (2016)

(c) Genetic data from Pearse et al. (2014)

(d) New data

Table 1.5. Sampling locations with reliable cost information were used to create a ranking function to generate best return on investment for potential restoration projects. Restored f(A) values and remediation costs represent a scenario where all anthropogenic barriers are removed from the migration path.

Sampling Location	**Location Code**	**DPS**	**Status**	**f(A)**	**Restored f (A)**	**ΔA**	**Remediation Cost**	**Cost per 1% f(A)**	**Number of Barriers Removed**	**Complete Anthro Bar Removed?**
Lion Canyon Creek	LCC	SC	Endangered	35.42	55.71	20.29	$320,000	$15,771	2	**Yes**
South Fork Bear Creek	SFBC	NC	Threatened	61.29	64.93	3.64	$380,000	$104,395	2	No
Santa Paula Creek	SPC	SC	Endangered	28.26	54.01	25.75	$640,000	$24,854	4	**Yes**
Los Trancos Creek	LTC	CCC	Threatened	75.00	96.84	21.84	$2,036,000	$93,223	12	No
Boulder Creek	BC-SLR	CCC	Threatened	54.69	74.71	20.02	$2,046,400	$102,217	11	No
Nacimiento River	NR	SCCC	Threatened	75.00	93.47	18.47	$75,000,000	$4,060,638	1	**Yes**

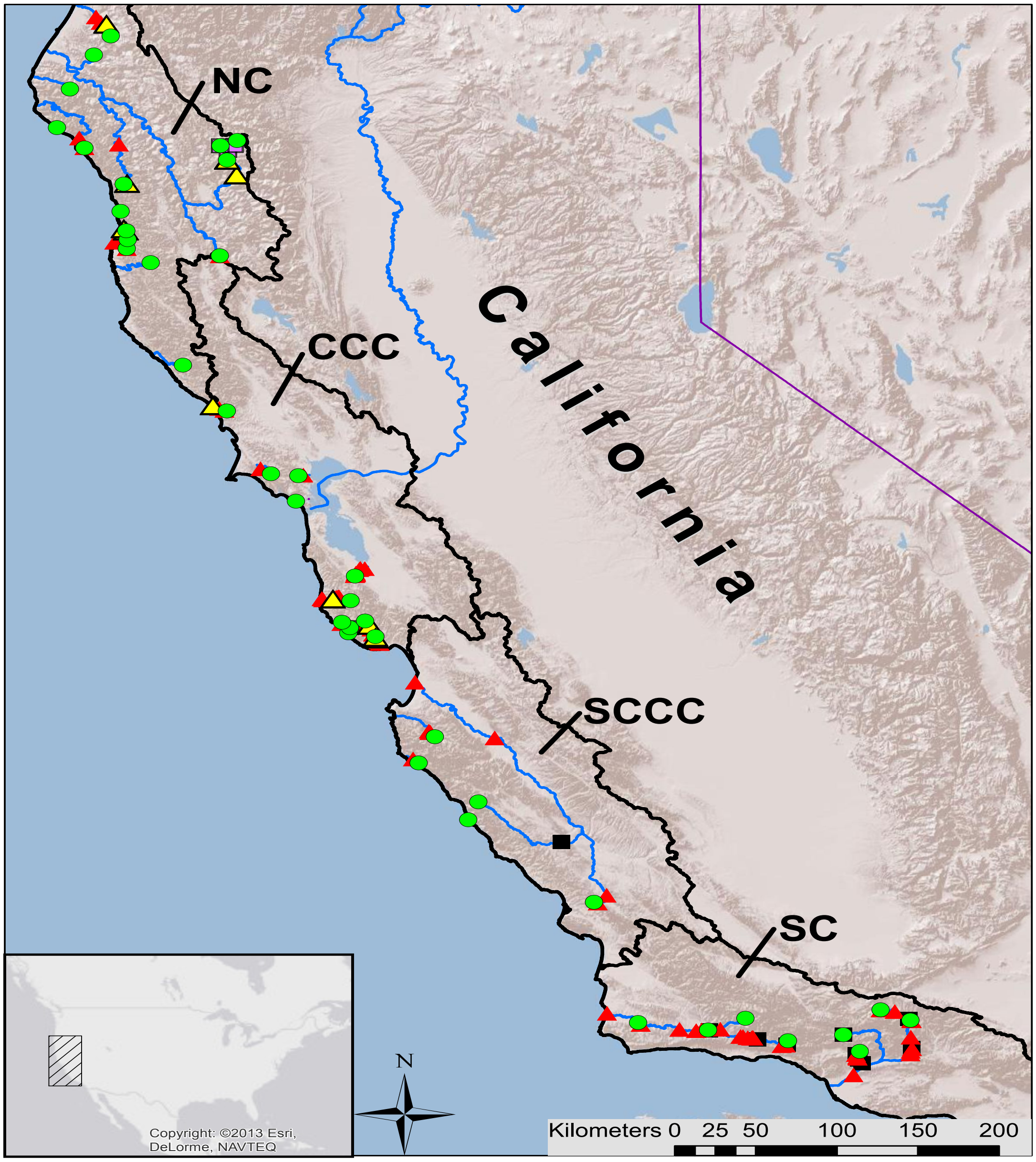

Figure 1.1. California O. mykiss sampling locations with different barrier types georeferenced along the migration path. The Distinct Population Segments from North to South are as follows: Northern California (NC), Central California Coast (CCC), South-Central California Coast (SCCC), and Southern California (SC). *Sampling Locations* are represented by hollow/green circles and their corresponding *Sampling Streams* are solid/blue lines. *Partial Natural Barriers* are represented by yellow/hollow triangles, while *Partial Anthropogenic Barriers* are solid/red triangles. *Complete Natural Barriers* are hollow/purple squares and *Complete Anthropogenic Barriers* are solid/black squares.

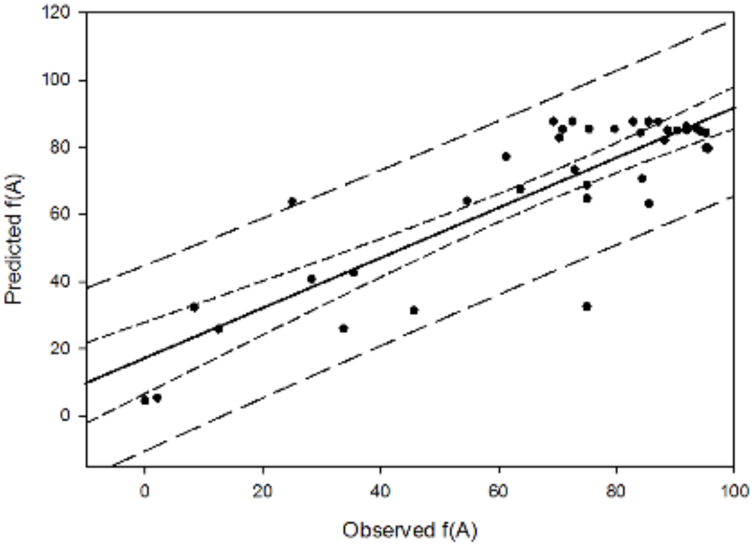

Figure 1.2. Observed vs. predicted anadromous allele frequency f(A) for each sampling location using the best-fit model predictions. Short-dashed line represents 95% confidence interval, long-dashed line represents 95% prediction interval. Two outlier points are Tassajera Creek and Nacimiento River from the Salinas River watershed. Tassajera Creek is at the head of a highly agricultural watershed that experiences main stem seasonal drying from agricultural withdrawals. The Nacimiento River population may exhibit adfluvial migrations downstream into Nacimiento Lake.

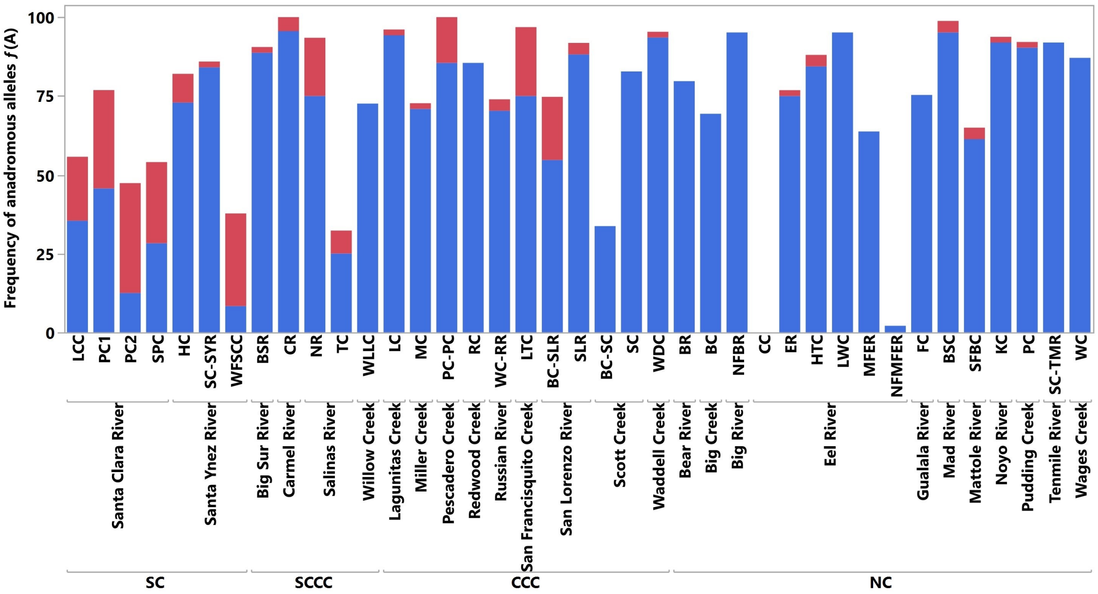

Figure 1.3. Observed vs. restored anadromous allele frequency *f*(A) for each sampling location grouped by watershed and DPS. Blue bars represent measured *f*(A), red bars represent Restored *f*(A). Restored f(A) is the calculated increase in anadromy-associated alleles if all anthropogenic barriers were removed, thus showing overall restoration potential for each location. Site abbreviations follow those given in Table 1.4.

Chapter 2: Alternative migratory strategies are widespread in subyearling Chinook Salmon

Abstract

Variation in life-history traits within and across species are known to reflect adaptations to different environmental drivers through a diversity of mechanisms. Trait variation can also help buffer species and populations against extinction in fluctuating environments and against anthropogenic disturbances. Here we examine the distribution and drivers of Ocean-type Chinook salmon *(Oncorhynchus tschawytscha)* juvenile migratory life-histories. We defined alternative migratory strategies according to whether individuals reared in the stream (*natal rearing*) or left shortly after hatching to rear elsewhere (*non-natal rearing*). We then evaluated the frequency of migratory strategies across 16 populations with time-series extending up to 25 years, and evaluated the environmental variables that influenced variation in migration strategy. We found bimodal migration patterns and abrupt transitions in migrant sizes across all populations, supporting the widespread nature of alternative migratory strategies. Additionally, we found that the amount of freshwater rearing habitat available to juveniles, relative juvenile density, and spring flow patterns significantly influenced the overall migration pattern for populations. Smaller streams and higher conspecific densities generally produced more *non-natal rearing* migrants and larger streams and lower conspecific densities producing more *natal rearing* migrants. Our results shed light on previously unexplored patterns of juvenile

migratory strategies and encourage broader consideration for how current conservation actions perform at protecting juvenile migratory diversity.

Introduction

The expression of multiple life-history traits within and across species is known to reflect adaptations to varying environmental drivers and displays their ability to respond plastically to fluctuating environmental constraints (Stearns 1992, Suryan et al. 2009). These environmental drivers can range in scale from seasonal variations in resource availability to region-wide multi-decade climate cycles, each affecting species differentially depending on generation time and geographic distribution (Bradshaw 1965, Stearns 1989, Taylor et al. 2019). Understanding how these environmental drivers shape the life-history evolution of different species and populations is critically important, as varying life-history traits can have fundamentally different effects on community interactions, ecosystem functions, and population persistence (Woodward et al. 1991, Fussmann et al. 2007, Flecker et al. 2010, De Meester et al. 2019). Another important consideration is how widespread a particular set of life-history traits might be, as their frequency and distribution might also strongly influence population, community, ecosystem dynamics (Stearns 1992, Fussmann et al. 2007, Apgar et al. 2017). Also, the loss of life-history variation is becoming more common due to climate change, habitat loss and fragmentation, and overharvest (Beechie et al. 2006, Sharpe and Hendry 2009, Palkovacs et al. 2012, Apgar et al. 2017). This has left many economically and ecologically important species in vulnerable states, because populations that express reduced ranges of phenotypes for a given life-history trait are often less resilient to fluctuating environmental conditions (Schindler et al. 2010, Carlson and Satterthwaite 2011). The ability to access different forage and habitats, and migrate at different times buffers populations and species against extinction when conditions are not favorable (Dingle and Drake 2007). Without the critical knowledge of where certain life-history traits are found and what drives their frequency, we have a reduced ability to managed imperiled populations. Loss of life-history diversity may lead populations to extirpation when faced with anthropogenic disturbances and extreme climate shifts (Firth and Fisher 1992, Harley 2011, Alberti et al. 2016).

Migratory species are particularly susceptible to habitat disturbances and shifting climates, as they rely on migratory corridors, consistent environmental cues, and reliable resources along their routes and destinations (Alerstam et al. 2003, Dingle and Drake 2007, Liedvogel et al. 2011). As a result, many species have evolved alternative migratory life-history phenotypes as a way to maximize fitness (Liedvogel et al. 2011). These alternative life-histories can result in differences in survival, fecundity, and growth depending on the range of environmental conditions they may be exposed to (Alerstam et al. 2003). The maintenance of multiple life-history traits within and across populations is known as the ‘portfolio effect’ (Bolnick et al. 2011, Schindler et al. 2015). This ‘portfolio’ of traits can act as a form of bet-hedging against adverse environmental conditions and buffers a population from extinction

(Carlson and Satterthwaite 2011, Schindler et al. 2015). Many migratory stream fish typically face strong selective pressures because of narrow and highly variable migratory corridors and express a variety of different life-history strategies to cope with these conditions (McDowall 1988). One well-known group that has evolved a range of alternative migratory life-histories are the salmonids (Hendry et al. 2004, Dodson et al. 2013).

While we have greatly expanded our understanding of migratory life-histories in salmonids, important information is still lacking on what determines these traits and the degree of within- and among-population variation (Waples et al. 2004, Bourret et al. 2016, Apgar et al. 2017). A majority of this work has been conducted for adult traits (Quinn and Myers 2005, Dodson et al. 2013). Examples of variation in adult migratory life-histories include anadromous vs. residents in steelhead (*Oncorhynchus mykiss*), dominant vs. precocious male spawners in coho (*Oncorhynchus kisutch*) and Atlantic salmon (*Salmo salar*), lake vs. stream spawners in sockeye salmon (*Oncorhynchus nerka*), and spring vs. fall migrants in Chinook salmon (*Oncorhynchus tshawytscha*) (Hendry et al. 2004, Dodson et al. 2013). However, far less is known about the variation in juvenile migratory life histories across these species (Beckman et al. 1998, Nichols et al. 2008, Sykes et al. 2009, Jonsson et al. 2016, 2017). Chinook Salmon in particular are highly prized economically, provide important ecosystem functions in the form of marine-derived nutrient transportation, and have one of the greatest longitudinal ranges in the salmonid family (Behnke, 2002; Gustafson et al., 2007; Merz & Moyle, 2006; Quinn & Myers, 2005). However, populations have been struggling across their range due to climate change and anthropogenic disturbances so widespread monitoring and restorations efforts are being conducted to help these populations recover. This makes Chinook a prime study species because we can take advantage of these monitoring efforts to evaluate the effects of varying environmental drivers on the frequency of juvenile migratory strategies across broad spatial and temporal ranges.

The most prevalent life-history difference in Chinook salmon is Ocean- (fall) vs. Stream-type (spring) individuals. Adults express major distinctions in freshwater entry timing and maturity while juveniles have different rearing duration and outmigration patterns. In this study, we focus exclusively on Ocean-type populations, which are presently more common at the southern extent of their range (Healey 1991). Adult Ocean-type fish typically return at a mature state from July through November to spawn in lower elevations of gravel streams. Their offspring characteristically hatch between December and March (Moyle et al. 1995), and once emerged from gravel redds, most are believed to rear in natal streams for 1-6 months before migrating to the marine environment as subyearling migrants (Beechie et al. 2006) However, recent studies have begun to explore the variation within these juvenile outmigration patterns, showing that some populations display substantial variation in the timing and size of juvenile outmigration (Miller et al. 2010, Bourret et al. 2016).

In some populations, subyearling migrants have been observed out-migrating from their natal streams at roughly two stages (Healey 1991). The typical migrants associated with subyearling Chinook are what were historically called fingerlings, but now are classified as parr and smolts depending on their visual differences (Healey 1991). Parr still express dark lateral bands (parr marks) that help them be more cryptic in freshwater habitats while smolts become bright silver, which helps them be more cryptic while schooling in an ocean environment (Healey 1991). These fish spend an extended period rearing in natal streams (1-6 months) feed and grow before migrating downstream. Thus, we refer to these fish collectively as *natal rearing* migrants or simply *natal*. A less understood group is fry. These small, weak swimmers emigrate from January to March, after spending only a few days to weeks in their natal stream. Because fry do not spend any significant amount of time rearing in natal streams, we refer to them as *non-natal rearing* migrants or simply *non-natal*. Fry have traditionally been viewed as surplus, or those that cannot be supported by watershed's carrying capacity, and therefore unimportant to population productivity (Lister and Genoe 1970, Healey 1991, Williams 2006). Factors contributing to this viewpoint include territorial aggression from *natal* migrants that force some fish downstream and poor swimming ability which can lead to smaller, weaker fish getting washed out during freshets (Puckett and Dill 1985, Healey 1991, Landergren 2004). Combing the previous two factors with their poor ability to ionoregulate leads to the traditional idea that non-natal migrants experience extremely poor survival to adulthood (McDowall 1988).

There has been a long-held belief that the later *natal rearing* migrants are the most important outmigrants due to their larger size. Studies have previously shown these fish have higher survivorship during outmigration and ocean entry due to size-selective mortality (Claiborne et al. 2011, Sabal et al. 2016). However, more recent work has demonstrated that this rule may not be universal (Miller et al. 2010). Sturrock et al. (2015, 2019a) found that in some years, Stanislaus River (California), intermediate-size Chinook outmigrants had the highest proportion of survivorship to returning adults. Additionally, they found that in several years the largest outmigrant proportion was comprised of non-natal 'fry,' sometimes making up >90% of the total migrants (Sturrock et al. 2015, 2019a). In some years, these ‘fry’ and ‘smolt’ migrants also had almost equal survival rates to become returning spawners (Sturrock et al. 2015, 2019a). The “fry” left the natal stream weeks to months before the “smolts” and even with a longer exposure period to predators still had similar overall fitness. This suggests that migratory diversity of juveniles may play a critical role in buffering the population against climatic and hydrologic variation.

Prior studies have explored the frequency and environmental drivers of early Chinook salmon life-histories on one river across a range of years (Anderson & Topping, 2018; Merz, Workman, Threloff, & Cavallo, 2013; Sturrock, Carlson, et al., 2019;

Sturrock et al., 2015; Zeug, Sellheim, Watry, Wikert, & Merz, 2014). Additionally, these rivers have anthropogenically modified flows and may not represent the conditions under which these life-histories evolved. Our study evaluated how widespread these migratory strategies are and what drives their frequency by evaluating patterns across 16 different populations, 5 distinct populations segments (DPSs), and time series of 7 – 25 years (Figure 2.1.). Our research goals were to ask: (1) what is the relative frequency of the *natal rearing* and *non-natal rearing* strategies within- and across populations and (2) what environmental drivers influence the frequency of each of the two migratory strategies across different years and streams.

Materials & Methods

Salmon Data Collection and Standardization

Rotary screw traps (RST) are the most common tool used to monitor out-migrating juvenile salmonids along the Pacific Coast (Volkhardt et al. 2007). Because of this, we exclusively used RST datasets to standardize estimates of CPUE and migration rates. In an effort to cover the largest geographic range possible, we contacted 30 different state and local agencies from California to British Columbia to request access to their monitoring datasets. We chose this geographic distribution as Ocean-type Chinook don't typically occur above 56°N, and are currently the most common life-history from Washington to California (Healey 1991). We prioritized monitoring efforts that had seven or more total sampling years, had primarily naturally reproducing populations, were conducted at the same site across the time-series, and near the mouth of the natal stream. These criteria have been used in previous juvenile migrant studies and allow for sampling across multiple interannual climate cycles such as El Nino/La Nina and to prevent complications with differing numbers of migrants if traps were relocated (Anderson and Topping 2018, Sturrock et al. 2019a). Trap location near the mouth of the natal stream allows us to identify the timing and size when fish out-migrate from their natal habitat. This gives us the ability to identify which migration/rearing strategy they are utilizing. Additionally, we selected for populations with naturally reproducing stocks to focus on natural migratory strategy variations. Datasets with hatchery juveniles released upstream of the RST (<90% of individuals released were marked), irregular trap efficiency tests (Volkhardt et al. 2007) or individual or daily mean fork length (FL) data not recorded, were excluded. Because sampling protocols and RST deployment periods can vary across organizations and years, we made an effort to select years and monitoring programs that encompassed the entire range of juvenile outmigration for each population.

Weekly passage $\hat{n}$ of migrating juvenile Chinook salmon for each trap was estimated as

$$\hat{n} = \frac{c}{\hat{q}}$$

Where c is the number of fish captured each day and $\hat{q}$ is the trap efficiency. During some years, there were periods when RSTs were not fished. If this period extended beyond seven days at the beginning of the season or ten days at the end when migrants are more sparse, then that sampling year was excluded from the analysis. To estimate missing values, we use the method of Zeug et al. (2014), where the weighted average of all observed counts for the five days before and five days after the missing value was used to estimate a missing value of count (c) within a sampling period. The weights were equal to 1 through 5, where daily values that were one day before and after the missing day were weighted as 5, values that were two days before and after the missing day were weighted as 4, and so on. We therefore compiled data on a total of 16 populations over the period from 1993-2018 (Figure 2.1., Supplemental Figure S2.1.). Previous studies have shown many of these populations genetically distinct and represent a broad geographic and genetic diversity of Ocean-type Chinook Salmon (Clemento et al. 2014). However, gene flow has occurred between some populations due to past hatchery practices and straying of returning adults (Sturrock et al. 2019b).

Quantifying migratory strategies

Because differences in subyearling migratory groups are distinguished both by outmigration timing and size, we used two statistical tests that would assign outmigrants to one of two outmigration classes. Most classification of juvenile migratory strategies is currently done by visual observation (size, yolk sac presence, color, parr mark, etc.) in the field, which can lead to subjectivity. Using standardized methods creates a more objective way to classify these migratory strategies. We therefore conducted a suite of modality and piecewise linear regression (breakpoint) tests to determine if these patterns were consistent across streams and how they aligned with previous literature reports. The goal of these tests were threefold, first was to evaluate if there were two distinct migratory pulses. The modality test works by identifying the two separate distributions and the divide between them. The second was to identify if there was a clear size threshold that represented a transition between the two migratory groups, and this was tested by using piecewise linear regressions. Finally, to evaluate the effectiveness of the modality and breakpoint models to correctly identify the transition week between migrant groups for each individual year, we assigned a transition week to each year using the calculated average transition size (mm) from the breakpoint model conducted across all populations and years. This allowed us to compare the yearly model results of both models with one based on an overall average size. These three tests were run at a yearly time step across all the populations with available data (total population years = 260).

We used modality tests to identify discrete migratory "pulses" between the strategies, as has been shown in other species of out-migrating salmonids (McKinnell 2019). We used the 'multimode' package for R, which uses nonparametric approaches for estimating the number of modes and their estimated locations (Ameijeiras-Alonso et al. 2018). The function we chose uses a kernel density test to identify the number and location of modes and provides a critical bandwidth value to describe the model fit. We selected parameters that would identify the two modes and give a corresponding critical bandwidth value. Our goal was to exclude "mini" pulses within a migratory strategy and segregate based on major outmigration events. We defined a mini-pulse as when <20% of a particular migratory strategy moved in a given week, while the program assigned the major pulses as the divide between the two most significant modes. By doing this, we could segregate discrete migratory pulses and identify the anti-mode locations which would be their divide; in our data this represented the transitional week between strategies. All populations had two clear migratory pulses across ~95% of the years.

Piecewise regression tests were used to evaluate two separate metrics of juvenile migratory strategies. First was the transitional fork length between the two groups, and second, was the transitional week, just as in the modality tests. We used the 'segmented' package in R as it was used previously in Zeug et al. (2014) to divide pre-smolt and smolt migrants on the Stanislaus River (Muggeo 2008). This package fits piecewise linear regressions with different slopes to the data and identifies the 'breakpoint' between them. This is a common method of identifying different patterns in temporal data and critical transition points. For the comparison of the modality and piecewise regression test results with the literature values, we used simple linear regressions between the predicted transition lengths of the different methods to evaluate how well these different metrics aligned.

Environmental drivers of migration strategies

To test what factors influence the frequency of juvenile migratory strategies, we referred to the literature and found that a suite of environmental variables have been shown to shape the migratory behavior in anadromous fish (Hendry et al. 2004, Quinn and Myers 2005). Variables included different metrics of flow, water temperature, available rearing habitat, adult escapement, and watershed characteristics (Quinn and Myers 2005, Apgar et al. 2017). We were unable to get quality temperature data across all the populations but it is well known to strongly correlate with flow (Zeug et al. 2014). Based on the life stage timing of Ocean-type Chinook, we broke many of these variables into four different biologically relevant time periods (Healey 1991, Anderson and Topping 2018). These time periods are *Spawning* (Sept-Oct)*, Incubation* (Oct-Dec), *Non-natal Migration* (Jan-Mar), *and Spring Migration* (Jan-June). In this way, we could evaluate which time periods might be most critical within and across rivers. *Spawning* represents the time when adults are building redds and depositing eggs, *Incubation* is when embryos and fry are still developing in the gravel, *Non-natal Migration* is the time when fry emerge from the gravel and only this migrant type is typically present, and *Spring Migration* is the entire migratory period for a cohort. Flow metrics are one of the most important predictors of migratory behavior and timing (Zeug et al. 2014, Sturrock et al. 2015, Anderson and Topping 2018). We acquired most of our flow data from the USGS Surface Water database (https://waterdata.usgs.gov/nwis), while others were provided to us by the monitoring agency themselves. We broke up flow into these relevant time periods and also partitioned the data into *cumulative flow*, which represents the type of hydrologic year a cohort experiences, and *flow variance*, which provides a mechanism for habitat creation and activation (e.g. bar formation, floodplain inundation) and has been identified as a trigger for fish migration and overall metabolism changes (Zeug et al. 2014). *Cumulative flow* was calculated as the total daily flow summed for the entire period of life stage of interest each year, while *flow variance* was calculated as the sample variance of the total daily flow ($m^3 \cdot day^{-1}$) across the period of interest. This gave a total of 8 different flow metrics for our analyses. If a stream did not have a flow gauge available, we chose a nearby stream with similar watershed characteristics to act as a proxy (Archfield and Vogel 2010). Since considerable variation exists across streams in flow conditions, we z-scored these values to make them comparable for this analysis.

In order to account for correlations in predictor variables, we conducted principal component analysis (PCA) on our 8 flow metrics. We used a factor analysis approach with varimax rotation and an eigenvalue threshold of 2.0. This resulted in the grouping of strongly correlated variables into two rotated factors, which also happened to group with their respective seasons, so we named them accordingly (Table 2.1., Figure 2.2.). PC1 included the 4 springtime flow metrics (Non-Natal Cumulative Flow, and Spring Cumulative Flow, Non-Natal Flow Variance, and Spring Flow Variance) while PC2 included the 4 fall flow metrics (Spawning Cumulative Flow, and Incubation Cumulative Flow, Spawning Flow Variance and Incubation Flow Variance).

Additional environmental and demographic variables include the number of stream kilometers (StreamKm) upstream of the RST, which represents the amount of available natal rearing habitat for juveniles. StreamKm was also used to create a *Density* metric, which was the total number of outmigrants for a given river and year divided by the length of stream available to rearing salmonids. Watershed size (Km^2) was included as it can be another metric available rearing habitat and flow dynamics. These values were either taken from reported values or calculated based using ArcGIS 10.6 (ESRI 2019). We acquired an estimated Spawner Abundance for most populations through reported values in the literature and created a Spawner/Km value using the StreamKm term we previously calculated.

Environmental Driver Modeling

To determine which environmental variables contributed significantly to variation in the frequency of different migratory strategies, we used best subset regressions for model selection utilizing the R 'dredge' function to establish Akaike's Information Criterion (AIC) for each combination of variables across all years in 13 of the 16 rivers (flow data was not available for 3 rivers) (R-Core Team 2019). The minimum AIC value was used to select the best fit model unless strong collinearity was found between predictor variables. We used a threshold of >2 AIC points to confer significant model difference and VIF values of >5 to show that model terms were strongly collinear. We logit transformed the proportion of *non-natal* migrants (**%Non-Natal)** for a given stream and year and used this as our dependent variable.

The result of the best fit model selection are the combination of variables that drive the average proportion of migratory strategies **within and across populations**. We chose to use a linear mixed regression model as repeated samples of the same population are not independent of one another. Our full model included Populations as a random effect and log-transformed Density, log-transformed StreamKm, log-transformed Spawners/Km, Watershed Area, and the two PC-Flow Metrics as fixed effects. All statistical analyses were conducted in R 3.6.1 (R-Core Team 2019).

Results

Migratory Strategy Quantification and Frequency

Our analyses of migration timing and size in subyearling juvenile Chinook salmon displayed a clear pattern of modality between the two groups and a clear shift in migrant size. The modality test showed there was multimodality present in all populations. Additionally, the piecewise regression model showed that across all populations, the average transitional size of migrants from *non-natal* to *natal rearing* occurred at 45.7mm FL (SE=0.42mm) (Figure 2.3a). This value aligns with a 45mm value previously reported in the literature, but this is the first time it has been evaluated across this many populations and years (Healey 1991). Both of these model results would suggest that the first migratory pulse represents the *non-natal* migrants while the later pulse would be *natal rearing* fish. When evaluating the effectiveness of the modality and breakpoint models to correctly identify transitions between migrant groups, both models predicted a similar transition week for each year that aligned with the 45.7mm transitional size from our previous test. The modality tests had an R^2 of 0.88, while the piecewise test had an R^2 of 0.95. Given these results, we are confident that ~45mm is a significant transition value across all populations and use it to divide the proportion of *non-natal* and *natal* migrants for the subsequent analyses.

The average proportion of *non-natal* migrants was 60% across all populations while the average proportion of *natal rearing* was 40% (Table 2.2.). However, the proportion of *non-natal* versus *natal rearing* migrants varied considerably across populations (Figure 2.3b,c,d). Some populations consistently had a large proportion of *non-natal* migrants (Clear Creek =98%, Mill Creek, Yaquina River=93%), while others were predominantly *natal rearing* migrants (Nooksack River =93%, Stillaguamish River and Bear Creek = 72%).

Environmental drivers of migration strategies

The proportion of *non-natal* and *natal rearing* migrants that out-migrated in a given year varied considerably across populations and years (Table 2.2). Some years there were >98% *non-natal* migrants while others there were >90% *natal rearing* (Table 2.2.). Model selection indicated the best fit model included Population as a random effect and log-transformed Density, log-transformed StreamKm, and PC-Spring Flow as fixed effects (Table 2.3., Figure 2.4a). The marginal R^2 of the resulting model is 0.70 and represents the percentage of variation explained by the fixed effects. The conditional R^2 is 0.82 and represents the variation explained by both fixed and random effects. The log-transformed StreamKm variable had a negative coefficient and an effect size value of -1.25 (SE=0.21) (Figure 2.4b). Log-transformed Density and PC-Spring Flow had positive coefficients and an effect sizes of 0.65 (SE=0.06) for Density and 0.28 (SE=0.08) for PC1 (Spring Flow) (Figure 2.4c,d). Both StreamKm and Density were strong predictors of migrant frequency while Spring Flow had relatively less predictive capability.

Discussion

Overview

Intraspecific trait variation of migratory life-histories has been observed across a variety of different species, including salmonids (Hendry et al. 2004, Dingle and Drake 2007, Liedvogel et al. 2011). However, the frequency and geographic extent at which juvenile Ocean-type Chinook salmon expressed alternative migratory strategies has in general been poorly understood (Healey 1991, Sturrock et al. 2015). Our study shows that these strategies are widespread and predictable based on juvenile salmon density, the size of the stream network, and spring flow. Modality models clearly demonstrated two distinct migrant groups across all years and populations, and breakpoint models showed that the transitional size between migrants occurs at 45.7mm. This result confirmed anecdotal suggestions that the transition between these strategies is roughly 45mm. Using this 45mm cutoff, we assigned migrants into two classes, *non-natal* and *natal* migrants, in order to quantify their frequency across populations and evaluate what environmental factors drive their relative frequency. Results of our model selection showed that our best fit model was one with Population as a random effect and log-transformed StreamKm, log-transformed Density, and PC1 (Spring Flow) as fixed effects.

Migratory Strategy Quantification and Frequency

Our results show that there are indeed two unique migratory life-histories in juvenile Ocean-type Chinook and they are found across every population and DPS that we examined. The evaluation of the distribution and consistency of strategies across such a large number of populations has not previously been conducted. The size of the *non-natal* strategy consistently ranged from 35-45mm while the *natal rearing* strategy usually began at 50-55mm and extended up to 120mm. However, a majority of the *natal rearing* migrants were between 55-80mm. There was a clear gap between 45 and 55mm with little to no migrants in this range, showing there is a critical transition period between immediately out-migrating and *natal rearing* migrants. This was also evident by the regression line slopes in the breakpoint model. The *non-natal* slope tended to be 0 or slightly positive, suggesting little to no instream growth, while the *natal rearing* slope was always strongly positive but varied depending on population and year. The slight positive slope in the *non-natal* regression may indicate that as the season progress and the water warms, fry may hatch or emerge from the gravel at a slightly larger size or that fry stayed in the gravel longer before finally emerging (Combs and Burrows 1957).

Environmental drivers of migration strategies

Across all the populations in our study, the prevailing pattern associated with the frequency of *non-natal* and *natal rearing* migrants was driven by the number of stream kilometers upstream of the screw trap available for rearing, the relative density of juveniles in a given year, and the spring flow regime. The significance of available rearing habitat as a major driver suggests a density-dependent mechanism might exist (Figure 2.4b). Smaller streams tended to have a higher frequency of *non-natal* migrants than larger ones, suggesting that less available rearing habitat in the stream may prompt individuals to leave their natal streams in search of new rearing areas downstream. To further support this idea, relative density of juveniles had the second-largest effect size (Figure 2.4c). As the density of migrants increases, so does the number of *non-natal* migrants, showing that regardless of stream size, individuals may use density as a cue to migrate early. Finally, spring flow had the smallest effect size, suggesting that while flow is influential, flow variations and hydrologic differences across watersheds might make it difficult to compare them (Figure 2.4d).

The presence of an apparent density-dependent mechanism, as evident by the importance of available rearing habitat and juvenile density, seems to suggest migrants have a potential ability to choose whether to stay and rear or out-migrate shortly after hatching. While the *non-natal* life-history type may have higher individual mortality due to emigration at a small size, this strategy may have evolved to take advantage of a more productive habitat downstream when densities are high (Bond et al. 2008, Phillis et al. 2018). Growth potential is typically much higher in downstream floodplains and estuaries than in natal streams, so fish that rear there have 3-4 times the growth potential of those that rear in the natal streams (Sommer et al. 2001, Williams 2006, Jeffres et al. 2008, Katz et al. 2017). This means if they both rear for the same period of time, the downstream rearing fish may be larger and have higher survival potential when entering the ocean than the *natal rearing* fish (Neilson and Glen 1986, Claiborne et al. 2011, Sabal et al. 2016). A recent modeling study based on Atlantic salmon (Chaparro-Pedraza and de Roos 2020), demonstrated that under high-density high-predation conditions, early migration at smaller sizes improved survival and growth rates. This suggests that *non-natal* migrants may have evolved to follow this pattern as well, risking higher predation to use estuary habitat at smaller sizes. However, as a consequence of anthropogenic activities, many estuaries have been degraded such as the Sacramento San Joaquin Delta, and may actually put *non-natal rearing* migrants at a disadvantage (Williams, 2006).

Besides resource utilization, other studies have found that individuals that rear in natal streams can establish foraging territories and can be aggressive to other individuals (Puckett and Dill 1985, Landergren 2004). This could be another potential mechanism to force migrants out of their natal streams in search of available habitat. However, since *non-natal* migrants occur in years with low densities as well, it suggests that this behavior might be at least partially predisposed (Healey 1991). Also during the spring, higher flows can help expedite downstream migrants to the estuary or ocean (Nislow and Armstrong 2012, Zeug et al. 2014). It can also help them avoid potential predators and keep them from straying in heavily modified watersheds (Nislow and Armstrong 2012, Zeug et al. 2019). Anthropogenic modification of flow regimes due to dam building may actually inhibit *non-natal* migrant survival, as these changes can reduce or delay early flow pulses which would historically cue and help these migrants downstream (Sturrock et al. 2019a).

Density-dependent migratory patterns and survival

Based on the two dominant patterns we identified across a wide range of populations, the expression of alternative migratory strategies appears ubiquitous in subyearling juvenile Ocean-type Chinook salmon. Most populations show a density-dependent mechanism that drives the frequency of each of the two strategies. The traditional view was that 'fry' or our *non-natal* migrants are believed to represent a population ‘surplus’, and their overall survival considered negligible because they exceeded the natal streams carrying capacity (Healey 1991). These ‘surplus’ fish were believed to be unable to establish foraging territories and forced out of the stream (Puckett and Dill 1985, Healey 1991). However, recent work has shown that *non-natal* migrants do survive and contribute to the spawning population, contradicting that these fish are just ‘surplus’ (Sturrock, Carlson, et al., 2019; Sturrock et al., 2015; Miller et al. 2010). It might be true that *non-natal* migrants can be forced out of the natal rearing areas due to limited habitat, and while they individually have low survival during migration, their sheer numbers may offset this high mortality and still lead to a significant number surviving to reach the estuary where there is higher overall growth potential (Williams 2006, Jonsson et al. 2017, Chaparro-Pedraza and de Roos 2020). While it is true that we see more *non-natal* migrants in years with greater overall densities supporting a density-dependent mechanism, we still see pulses of *non-natal* migrants in most populations even in low-density years. Many of these pulses are also independent of high flow events suggesting that they choose to leave the stream. This might be explained if carrying capacity, or available rearing habitat, is dynamic and varies with flow conditions. However, even in the lowest density years with only a few hundred migrants, we still see *non-natal* migrants moving downstream. This is suggestive evidence that there might be an alternative mechanism such as genetic and/or plastic behaviors playing a role in individual decision making where fish choose to leave the natal stream just after hatching. This may have evolved as a form of diversified bet-hedging, where the evolution of more than one strategy leads to increased overall geometric mean fitness for an organism exposed to a fluctuating environment (Philippi and Seger 1989). This may have been particularly advantageous in places such as California and Oregon where large interannual climate fluctuations can lead to periods of prolonged drought or flood (Hanak et al. 2011, Sturrock et al. 2015, 2019b). Drought years (low rainfall/snow-pack) may have benefited early *non-natal* migrants that were able to reach the estuary sooner, as reduced flows in the natal streams could have created less habitable conditions for *natal rearing* migrants that stayed longer (Sturrock, et al., 2019). In extreme drought conditions, it has been observed that *natal rearing* migrants can become stranded due to stream dewatering and may die due to lack of resources, disease, or high water temperatures (Schindler et al. 2008, Mantua et al. 2010, Sturrock et al. 2019b, Zeug et al. 2019). In these scenarios, more diverse life-history strategies would buffer populations from local extinction even in periods of prolonged drought. We unfortunately don't have good measurements of river by year carrying capacity or genetic samples from these populations so we can't entirely rule out either hypothesis, but the driving force could potentially be a combination of both of these scenarios (density-dependence and bet-hedging).

Management Implications

Ocean-type Chinook salmon are one of the many anadromous species that have declined substantially over recent decades (Limburg and Waldman 2009). Many populations now rely on extensive monitoring and hatchery supplementation to keep population sizes large enough for sustainable harvest (Ricker 1981, Huber and Carlson 2015, Satterthwaite and Carlson 2015, Sturrock et al. 2019b). Our findings suggest multiple implications for managers of imperiled Chinook populations. Increased conservation efforts to protect *non-natal* migrants might ultimately lead to greater stability in spawning adults. Another consideration is altering current hatchery practices. Historically in California, hatcheries stocked all the different life-stages of juvenile Chinook across a wide range of habitats (1970-1999 Fry=38%, 2000-2017 Fry=4%) (Sturrock et al. 2019b). However, changes in policy now results in surplus fry being culled instead of released (Sturrock et al. 2019b). While careful monitoring for increased competition with in-river produced juveniles would be advised, returning to historic hatchery practices that included releasing multiple life-stages might bolster population stability by increasing overall life history diversity.

Our study has shed light on the widespread nature of alternative migratory strategies in subyearling Chinook salmon. However, to better understand the evolutionary history and fitness consequences of these different strategies, it is important to not only explore environmental drivers but potential genetic ones as well. Little is known about the genetic underpinnings of these behaviors except for one study conducted on the Nanaimo River by Carl and Healey (1984), which found differences in the frequency of allozymes at four polymorphic loci among different life-history types. Large-scale genetic sampling across populations, years, and life-history types would provide a better understanding of the genetic underpinnings of juvenile migratory diversity, as has recently been uncovered for adult migratory diversity (Prince et al. 2017, Narum et al. 2018, Thompson et al. 2019). Additionally, genetics differences between ESUs can influence spawning and migration timing, however within a population interannual variation can cause these peak dates to vary by weeks (>4) depending on the environmental conditions which would cause overlap with typical dates of other ESUs. Flexibility in deployment dates of monitoring programs are important is to make sure to capture all migrants in a particular year.

Gaining a better understanding of how environmental drivers shape the life-histories of imperiled species along with how wide-spread they are allows ecologist and managers to make more informed decisions about conservation efforts to aid in their restoration (Suryan et al. 2009). Additionally, the maintenance of alternative life-history strategies within a population can act as a buffer to stressors imparted from climate change and anthropogenic disturbances, thus bolstering population resilience (Stearns 1992, Dingle and Drake 2007). Migrating species in particular face a wide range of issues along their migratory corridors, and traits that maximize fitness under varying environmental conditions are a key factor in population persistence (Dingle and Drake 2007, Liedvogel et al. 2011). Our findings shed light on the drivers of life-history variation in subyearling Chinook salmon and the potential mechanisms that may influence other migratory species as well. Our findings show that rearing habitat, conspecific density, and flow play a major role in determining the frequency of different migratory strategies and that management actions could be taken to improve survival of *non-natal* migrants which might lead to overall greater adult return and more stable populations.

Acknowledgments

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Tables and figures

Table 2.1. Orthogonal data transformation with PCA and Rotational Factor Loading using the Varimax method. Loadings of flow parameters on the first two principal components (PCs) using an Eigenvalue threshold of ≥2.0 explains 67.7% of the total variance (percentage of variance explained per PC shown in table). Bold values indicate a high importance of that parameter on the principal component (loadings > 0.4).

PC Factor	**Eigenvalue**	**Percent**	**Cum Percent**
Factor 1- Spring Flow	3.3684	42.105	42.105
Factor 2- Fall Flow	2.0514	25.643	67.747
Rotated Factor Loadings			
Variables	Factor 1	Factor 2	
Spawning Cumulative Flow	-0.072864133	**0.7717367852**	
Spawning Flow Variance	-0.091550788	**0.7772704457**	
Incubation Cumulative Flow	0.349718792	**0.7666549096**	
Incubation Flow Variance	**0.4706472847**	**0.4489702537**	
Non-Natal Cumulative Flow	**0.8804542287**	0.1609363809	
Non-Natal Flow Variance	**0.8760023176**	-0.104061655	
Spring Cumulative Flow	**0.7886488247**	0.1470887257	
Spring Flow Variance	**0.9199615873**	-0.063168871	

Table 2.2. Summary of the frequency of *non-natal* and *natal rearing* migratory strategies across 16 populations ranging from California to Washington. Populations range from almost entirely *non-natal* (>99%) to entirely *natal rearing* migrants (>91%). Years with † represent populations where years were excluded to prolonged trap malfunction or lack of monitoring data.

Population	DPS	Year	Avg. %Non-Natal Rearing (SD) [Min-Max]	Avg. %Natal Rearing (SD) [Min-Max]	Avg. N Migrants (SD)	Avg. Density (SD)	StreamKm	Watershed Area (Km^2)	Avg. Spawner/Km (SD)	Latitude	Longitude
Bear Creek	Puget	2001-2018	28% (22%) [4-78%]	72% (22%) [22-96%]	28918 (18030)	180 (112)	160.00	129.90	1.36 (0.48)	47.667879	-122.11659
Blue Creek	Klamath	1999-2018†	58% (27%) [0-86%]	42% (27%) [14-100%]	388102 (386447)	15840 (15773)	24.50	134.80	NA	41.440161	-123.90946
Cascade Creek	Oregon Coast	2000-2017†	86% (19%) [31-100%]	14% (19%) [0-69%]	4326 (5800)	288 (386)	15.00	14.50	1.38	44.319765	-123.84743
Cedar River	Puget	1999-2018	82% (18%) [34-98%]	18% (18%) [34-98%]	377744 (402249)	6905 (7353)	54.70	480.00	15.87 (8.82)	47.480486	-122.19831
Clear Creek	CACV	1999-2014	98% (4%) [82-100%]	2% (4%) [0-18%]	7542204 (5102007)	374861 (253578)	29.12	644.00	285.52 (130.31)	40.50599	-122.39584
Duckabush River	Puget	2011-2017	76% (10%) [62-90%]	24% (10%) [10-38%]	2317 (1908)	178 (146)	13.00	194.00	0.72 (0.53)	47.649571	-122.93556
Green River	Puget	2000-2017	61% (22%) [10-97%]	39% (22%) [3-90%]	423802 (451922)	4179 (4457)	101.39	1100.00	45.97 (25.81)	47.292048	-122.16375
Mokelumne River	CACV	1993-2018†	30% (27%) [3-91%]	70% (27%) [9-97%]	218031 (321556)	2116 (3121)	103.00	1500.00	28.98 (22.36)	38.157976	-121.29878
Nooksack River	Puget	2005-2017	7% (6%) [1-17%]	93% (6%) [83-99%]	292912 (228361)	573 (446)	511.00	2070.00	17.2 (6.79)	48.876089	-122.33159
Scott River	Klamath	2000-2018†	44% (27%) [6-99%]	56% (27%) [1-94%]	436793 (332067)	4696 (3570)	93.00	2103.00	51.16 (38.24)	41.72541	-123.0095
Shasta River	Klamath	2000-2018	58% (26%) [12-96%]	42% (26%) [4-88%]	1787766 (1589116)	22347 (19863)	80.00	2100.00	107.42 (93.87)	41.829422	-122.59382
Mill Creek, Siletz River	Oregon Coast	1997-2016†	88% (4%) [84-92%]	12% (4%) [7-15%]	14985 (12300)	624 (512)	24.00	33.80	40 (23)	44.7458038	-123.79326
Stanislaus River	CACV	1996-2018†	45% (33%) [6-96%]	55% (33%) [4-94%]	500925 (853104)	5366 (9139)	93.34	1392.00	27 (29.29)	37.696285	-121.18183
Stillaguamish River	Puget	2003-2017†	28% (19%) [8-67%]	72% (19%) [33-92%]	191986 (118195)	468 (288)	410.00	1813.00	41.5 (8.45)	48.203044	-122.13107
Tenmile Creek	Oregon Coast	2013-2018	74% (18%) [40-92%]	26% (18%) [8-60%]	29263 (26612)	1219 (1109)	24.00	60.00	NA	44.2233298	-124.10742
Mill Creek, Yaquina River	Oregon Coast	1997-2018†	93% (8%) [78-99%]	7% (8%) [1-22%]	4063 (4551)	967 (1083)	5.00	4.20	7.02 (5.03)	44.574068	-123.90967

Table 2.3. Model selection results for best-fit global model explaining variation in juvenile Chinook migratory strategies. The top model included three fixed effects and one random effect term, and the next best model was >2 ΔAICc away showing strong support for this set of predictors. Log(Density) and log(StreamKm) were present in all top 5 models and are the terms with the greatest influence.

Global Model-Linear Mixed Effect Regression							
Fixed Effect Predictors	**Random Effect**	**df**	**R^2m**	**R^2c**	**AICc**	**ΔAICc**	**Weight**
log(Density) + log(StreamKm) +Spring Flow	Population	6	0.7022	0.8233	697.7	0.00	0.798
Log(Density) + log(StreamKm) + Spring Flow + log(Spawners/Km)	Population	7	0.7010	0.8167	701.9	4.20	0.099
log(Density) + log(StreamKm) + Spring Flow + Fall Flow	Population	7	0.7023	0.8230	702.8	5.10	0.064
log(Density)+log(StreamKm)	Population	5	0.6928	0.8156	705.5	7.80	0.016
log(Density) + log(StreamKm) + Spring Flow + Fall Flow + log(Spawners/Km)	Population	8	0.7012	0.8158	706.9	9.20	0.008

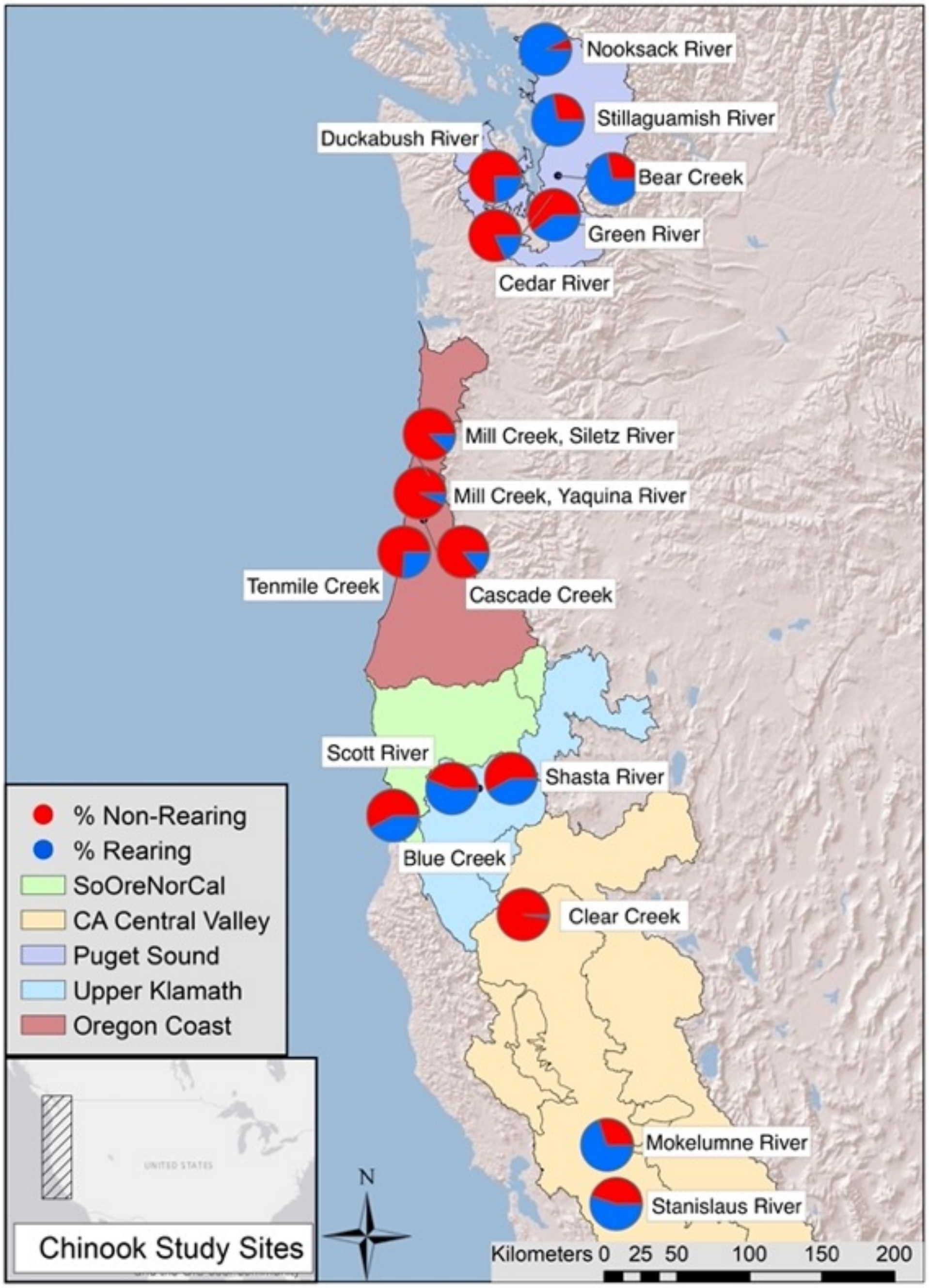

Figure 2.1. Ocean-type Chinook populations sampling locations ranging from California to Washington. Study sites are denoted by pie charts where the red section represents the proportion of *non-natal* migrants and blue represent the proportion of *rearing* migrants. Their corresponding Distinct population segment are represented by shaded polygons. The Distinct Population Segments from North to South are as follows: Puget Sound, Oregon Coast, Southern Oregon Northern California Coast, Upper Klamath, and California Central Valley.

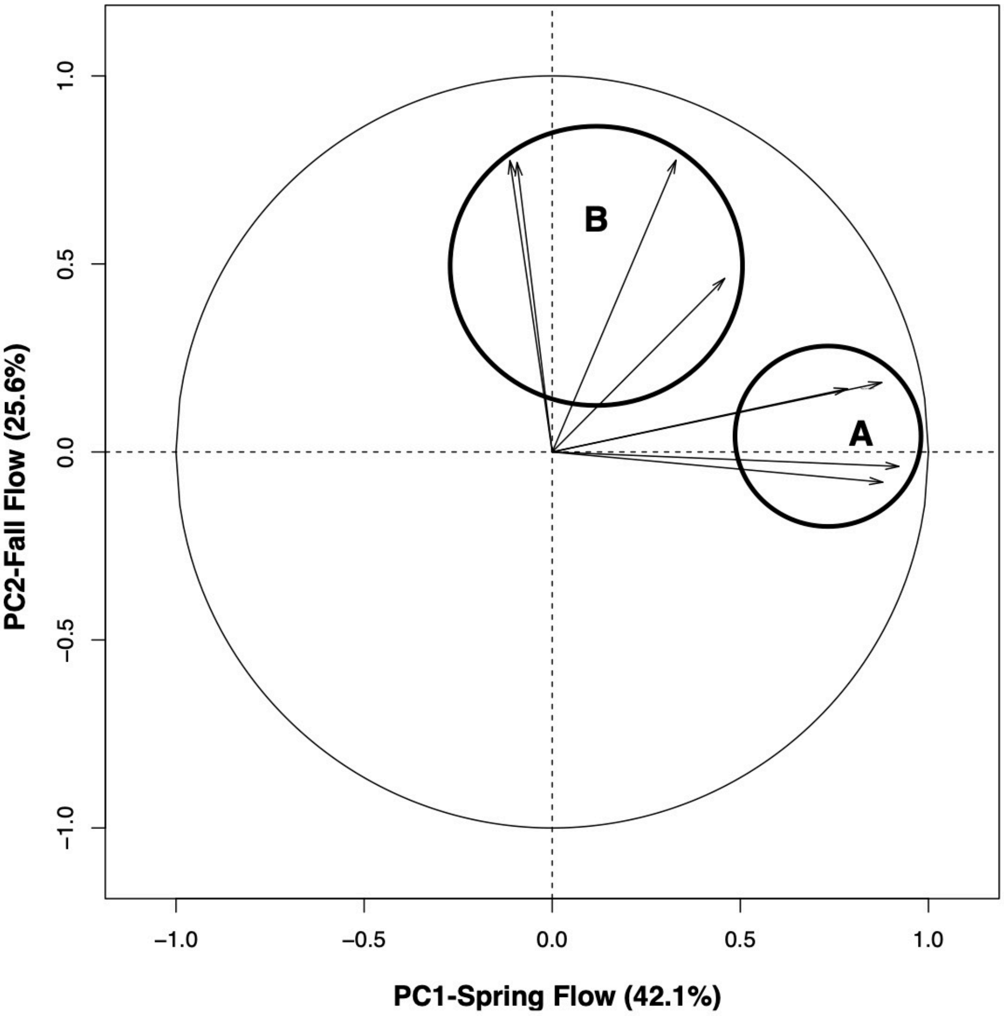

Figure 2.2. Principal component scores for all flow variables across the 13 populations included in the global model. Directions for every flow parameter are indicated (e.g. variables with a positive score on the x-axis tend to be associated with Spring Flow periods). Parameters pointing in similar directions are positively correlated, while those pointing in opposing directions are negatively correlated. Variables in circle A are those representing Spring Flow while those in circle B represent Fall Flow.

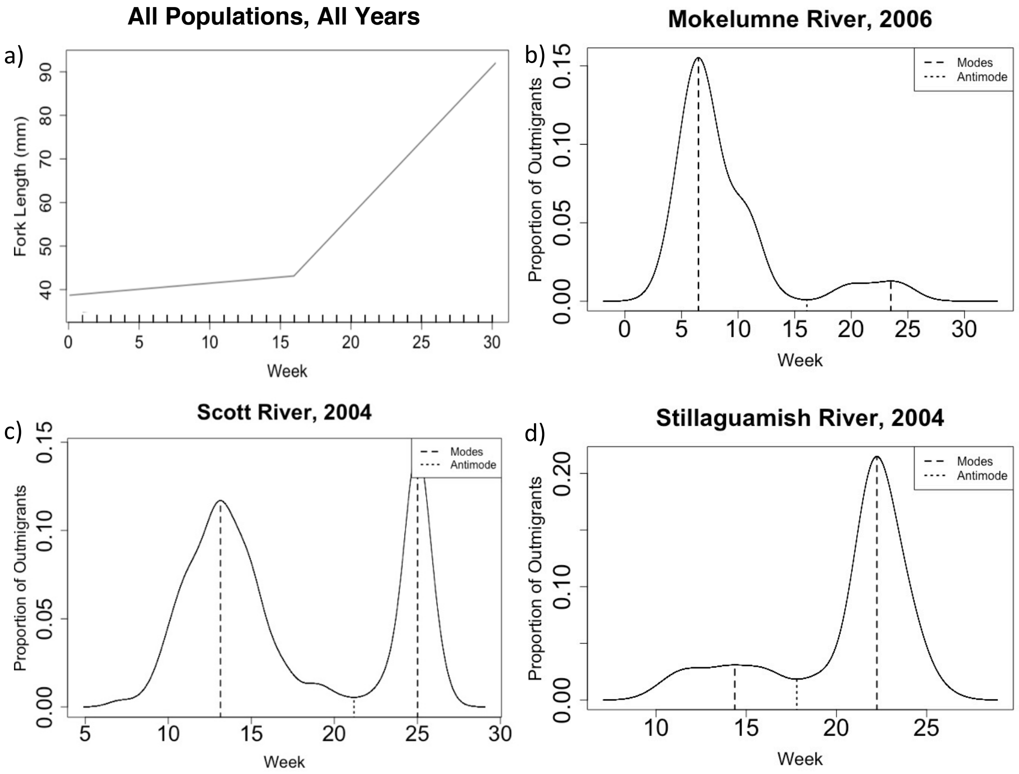

Figure2.3. a) Piecewise regression results for evaluation of fork length transition size between the two migratory strategies across all populations and years b) An example of high proportions of *non-natal rearing* migrants under a high-density scenario c) An example of strong bimodality between the two migratory strategies d) An example of high proportions of *natal rearing* migrants under low-density scenario.

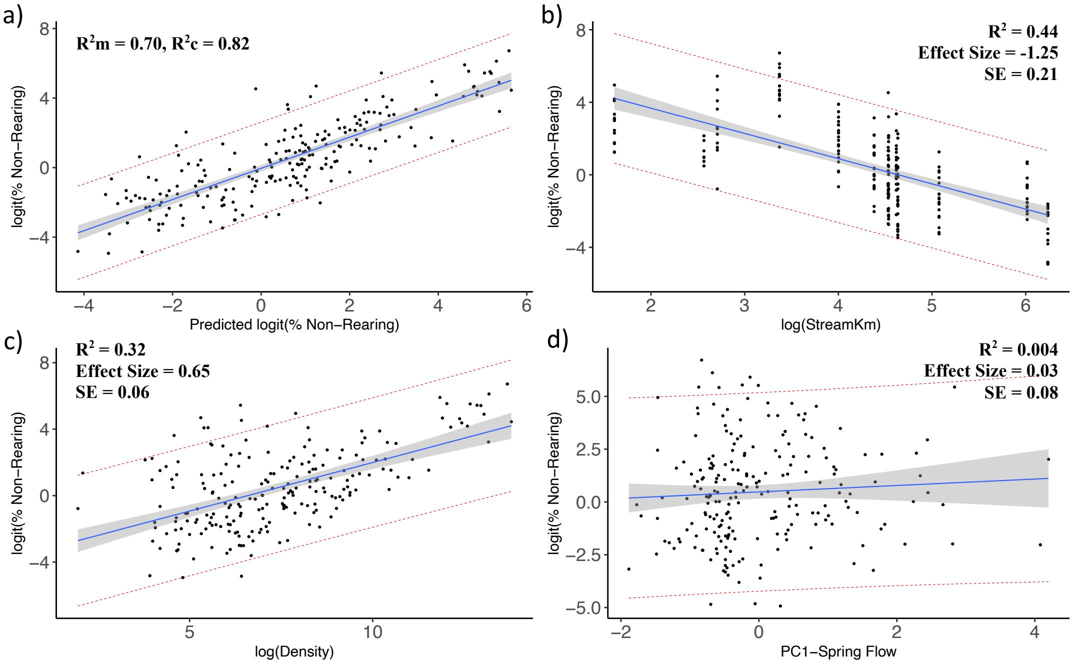

Figure 2.4. Regression models showing the relationship of logit-transformed *non-natal* migrant against the predicted values of best-fit global model and the three fixed effect terms with river included as a random effect. Individually all of these terms are not very explanatory, but when combined they create a highly predictive model. The term effect size in the model is represented by the Partial Eta Squared (η_p^2) value. Shaded grey area represent the 95% confidence intervals while dashed lines represent the 95% prediction interval a) The regression results of the logit-transformed *non-natal* migrant frequency against the predicted values from the global linear mixed effect model. The R^2c value = 0.82 b) The relationship between transformed *non-natal* migrants and log-transformed Density c) The relationship between transformed *non-natal* migrants and PC1-Spring Flow. d) The relationship between transformed *non-natal* migrants and log-transformed StreamKm.

Chapter 3: Exploring spring migratory diversity in juvenile coho salmon at the southern extent of their range

Abstract

The expression of alternative life-history strategies can be beneficial for populations and species that experience fluctuating environmental conditions. A suite of traits can buffer against extinction under different environmental scenarios, including anthropogenic disturbances. Here we examined the distribution and drivers of coho salmon *(Oncorhynchus kisutch)* spring juvenile migratory life-histories. We defined alternative migratory strategies according to whether individuals reared in the natal stream for a full year (Smolt) or left shortly after hatching to rear elsewhere (Young of Year). We then evaluated the frequency of migratory strategies across 18 populations at the southern end of the coho salmon distribution, with time-series extending up to 30 years, and evaluated the environmental variables that influenced migration strategy variation. We found that juvenile density, latitude, and flow regime can influence the frequency of alternative migratory strategies in juvenile coho salmon. These results show consistency with studies of other salmon species, which also suggest that density-dependence could contribute to the expression of alternative juvenile migratory life histories. Our results shed light on drivers and migratory patterns of juvenile salmonids and encourage broader consideration for how conservation strategies can be used to protect important juvenile migratory diversity.

Introduction

The expression of alternative life-history strategies can be advantageous to species that experience fluctuating environmental conditions (Stearns 1992, Suryan et al. 2009, Audzijonyte et al. 2014). A suite of strategies can protect against unfavorable environmental conditions and buffer populations from extinction (Satterthwaite and Carlson 2015, Schindler et al. 2015, Yamane et al. 2018). One approach to better understand these alternative life-histories is to study the frequency and distribution of these traits across a range of populations (Stearns 1992, Fussmann et al. 2007, Schaefer 2012, Apgar et al. 2017). Many migratory species have also evolved alternative migratory life-history behaviors as a way to maximize fitness while traversing across variable landscapes and climate regimes (Liedvogel et al. 2011). Environmental factors such as precipitation, temperature, habitat type, population density, and barriers can influence expression of alternative migratory strategies and ultimately lead to differences in timing, destinations, and migratory vs. non-migratory populations (Vøllestad et al. 2009, Dodson et al. 2013, Apgar et al. 2017). Understanding what factors influence the frequency of these migratory behaviors becomes increasingly more important for threatened species with broad ecosystem-level effects (Hellmair and Kinziger 2014, Taylor et al. 2019).

Salmonids (Salmonidae) have considerable life-history variation within and across populations (Dodson, Aubin-Horth, Thériault, & Páez, 2013; Hendry, Bohlin, Jonsson, & Berg, 2004). Adult life-histories are well described, including differences in migration timing (Fall- vs. Spring-run) in Chinook salmon (*Oncorhynchus tschawytscha)*, anadromous vs. resident migratory behaviors in Arctic char (*Salvelinus alpinus*) and rainbow trout *(Oncorhynchus mykiss*), and different breeding locations (lake vs. stream) in sockeye salmon (*Oncorhynchus nerka*)(Quinn and Myers 2005, Carlson et al. 2011, Finstad and Hein 2012, Dodson et al. 2013, Apgar et al. 2017). The expression of these traits results from genetic polymorphisms, phenotypic plasticity, or a combination of both (Quinn and Myers 2005, Finstad and Hein 2012, Pearse et al. 2019, Thompson et al. 2020). While juvenile life-history variation in salmonids has received less attention (Dodson et al., 2013; Quinn & Myers, 2005), recent work has demonstrated important variation in juvenile migration and freshwater rearing duration (Sturrock et al. 2015, Apgar et al. 2020). The frequency of two distinct migratory strategies in subyearling Chinook salmon is associated with flow regime, rearing habitat availability, and juvenile density (Zeug et al. 2014, Sturrock et al. 2019a, Apgar et al. 2020). These alternative migratory strategies are likely a form of diversified bet-hedging against fluctuating freshwater conditions and ocean-entry timing (Seger and Brockmann 1987, Apgar et al. 2020). Ill-timed juvenile migration can cause an entire cohort to perish, but a diversified migration portfolio offers some protection again environmental unpredictability (Woodson et al. 2013, Sabal et al. 2016).

Coho salmon range from Central California to Alaska and the Kamchatka Peninsula, and are both ecologically and economically important to coastal ecosystems and communities (Sandercock 1991, Behnke and Tomelleri 2002). The most well-known life-history variation in coho salmon occurs at the adult stage, where males exhibit one of two distinct migration and breeding strategies: fighter vs. sneaker (Aubin-Horth et al. 2005, Watters 2005). Fighter males rear longer in the ocean and return to spawn at a larger size, exhibiting strong sexual dimorphism from females, and actively defend spawning territories (Aubin-Horth et al. 2005, Koseki and Fleming 2006). Conversely, sneaker males tend to return at a smaller size with less pronounced secondary sexual characteristics, enabling them to avoid territorial male aggression to gain mating opportunities. The frequency of these male strategies has been linked to juvenile size at outmigration (Gross 1991, Vøllestad et al. 2004, Koseki and Fleming 2006). Smaller emigrants tend to spend greater time in the marine environment and return as fighter males, while those that emigrate at larger sizes return sooner as sneaker males (Gross 1991, Vøllestad et al. 2004, Koseki and Fleming 2006).

Since decisions made during the juvenile life stage can set the trajectory for adult outcomes, this highlights the importance of understanding what factors might influence the frequency of juvenile migratory strategies across a range of populations. In contrast to adult migratory behavior, we know much less about juvenile migratory strategies. The 'typical' coho migrant has long been considered those that rear in the natal stream and out-migrate during the spring of their second year after undergoing smoltification (Sandercock 1991, Koski 2009). Another strategy termed "nomad" has been described as juveniles that do not follow this 'typical' pattern (Koski 2009). Nomads emigrate from the natal stream at smaller sizes and without undergoing smoltification before their second spring, spending a prolonged period rearing in estuaries (Koski 2009). The most widespread of these alternative migratory strategies identified were Young of Year (YOY) that left the natal stream shortly after hatching in their first year (Chapman 1962, Crone, R.A., Bond 1976). These migrants were long believed to be 'surplus' to the natal stream's carrying capacity, experiencing increased outmigration mortality, thus leading them to be overlooked for many years. However, there is emerging evidence of the contrary, as recent studies have found that these alternative migratory strategies do survive and contribute to spawning (Koski, 2009; Roni et al., 2012; Nordholm, 2014).

Here, we ask what factors influence the frequency and distribution of juvenile coho salmon strategies. While previous studies have focused on a single watershed or group of neighboring streams, a broader look across watersheds is still lacking. We take advantage of an array of monitoring programs along the southern extent of coho salmon in North America, that provide reliable long-term data sets across various stream types and over large geographic ranges, facilitating analysis on a region-wide scale. Our research goals are twofold: first, to describe the relative frequency of each migratory life-history in juvenile coho salmon across coastal streams in California and Oregon. Second, to examine what environmental and demographic drivers are associated with their frequency.

Materials & Methods

Salmon Data Collection

This study explores the migratory diversity in coastal coho salmon (*Oncorhynchus kisutch*) at the southern extent of their range, where they experience larger environmental fluctuations compared to their northern counterparts (Moyle et al. 2013, Herbold et al. 2018). These populations are all ESA listed threatened or endangered, exemplifying the need to gain greater understanding to aid in conservation planning. Additionally, due to their listed status, these populations have extensive monitoring and long-term data on juvenile migration, affording us an opportunity to expand our understanding of their migratory diversity.

We acquired data from several agencies with intensive monitoring programs in Oregon and California (Figure 3.1.). Monitoring of juvenile salmonid outmigration is conducted using several different techniques depending on stream size and flow dynamics (Volkhardt et al. 2007). Because coho salmon commonly reproduce in streams ranging from small tributaries to larger mainstem rivers, the most common downstream migrant traps employed are Fyke/Pipe and Rotary Screw Traps (RST) (Volkhardt et al. 2007). We selected data from traps located at the mouth of streams allowing us to estimate juvenile timing and size when emigrating from natal habitat. Rotary screw traps are the most common traps used for monitoring out-migrating juvenile salmonids. However, RSTs require a minimum water depth of ~0.75 meters (Volkhardt et al. 2007, Merz et al. 2013a). Conversely, in smaller coastal streams where water can be as shallow as a few centimeters, Fyke/Pipe traps are commonly deployed. These traps use Fyke nets that block the entire stream channel to funnel fish into a large-diameter pipe connected to a holding pen. In this study, we selected data from monitoring programs that performed regular trap efficiencies using a mark-recapture model. This validated proper trap function and generated an estimate of daily outmigrants. Trap calibrations were done for YOY (fry and parr size ~35-80mm) and age 1+ smolts (~80-120mm) size class coho as these are the most common sizes in this region (Nordholm 2014). Larger juveniles (age 2+ & 3+ smolts) do infrequently occur in these populations. Therefore, they may be underrepresented in trap data due to their low numbers hindering size-specific trap calibration and their increased swimming ability to avoid the trap (Volkhardt et al. 2007). To focus on naturally reproducing populations, we prioritized populations with no hatchery inputs or where >90% of hatchery production is marked, facilitating their exclusion from datasets. To ensure datasets reliability, we followed data quality protocols from Apgar et al. (2020). Weekly passage of migrating juvenile coho salmon for each trap was estimated as $\hat{n} = c/q\hat{}$, where c is the number of fish captured each day and $\hat{q}$ is the trap efficiency. To estimate missing values, we used the weighted average of all observed counts for the five days before and five days after the missing value was used to estimate a missing value of count (c) within a sampling period (Zeug et al., 2014). We therefore compiled data on a total of 18 populations over a period of 1987 to 2017 (Figure 3.1. and S3.1.).

Defining migratory strategies

Recent work has highlighted that some coho populations can express a wide range of juvenile migratory strategies (Koski 2009, Roni et al. 2012, Bennett et al. 2015). The most widespread and frequently observed migratory strategies are age 1+ smolt and Young of Year that out-migrate from the natal stream during spring. Another recognized group is demonstrated by juveniles that rear in natal streams over summer and emigrate during the fall. These fish typically do not occur in southern populations with the exception of Freshwater Creek, CA, where they are sometimes present in small numbers (Nordholm 2014, Rebenack et al. 2015, Suring et al. 2015, Faukner et al. 2019). Some coho also rear longer than one year in freshwater (age 2+ & 3+ smolts), but these fish are more common in northern populations (Alaska & British Columbia) and may represent ~2% of smolts along the Oregon coast (Nordholm 2014, Suring et al. 2015). To estimate relative density of juvenile coho from a particular cohort, we used a metric of juvenile potential (Eggs/KM), where the estimated number of eggs deposited for a given stream in a given year was divided by the amount of rearing habitat available upstream of the migrant trap. This term provides an analog for juvenile density and allows us to standardize the data across populations and years. Since interannual variability exists from out-of-basin conditions and some fish might be missed before and after the trapping period, we used this scaled term as it has been shown that adult abundance and productivity can influence juvenile salmon densities (Suring et al. 2015, Sellheim et al. 2016).

This study focuses on the two most well-defined and present groups along the Oregon and California coast, spring migrating YOY and age 1+ smolts. Young of Year represent those fish that leave the natal stream in the first spring and rear elsewhere, and are what some call the nomads (Koski 2009, Shaul et al. 2013, Bennett et al. 2015). Age 1+ smolts are those that rear in the natal stream for one full year and leave the following spring after undergoing smoltification and will be abbreviated to Smolts going forward. Measurements and visual characterizations have typically been used to categorized juvenile coho migrants that out-migrate during spring (Sandercock 1991, Suring et al. 2015). Our data providers pre-classified each individual into one of these groups, YOY and Smolt. However, to ensure these classifications were consistent across monitoring programs, we compiled timing and size data across a number of populations to test if YOY and Smolt sizes were significantly different each week. We used ANOVA to evaluate the mean migrant sizes across all years and weeks to test if these groups significantly differed.

Environmental drivers of migration strategies

A suite of environmental variables shapes the migratory behavior in anadromous salmonids (Hendry et al. 2004, Quinn and Myers 2005, Apgar et al. 2020). This study included metrics of flow, available rearing habitat, juvenile density, and latitude (Quinn and Myers 2005, Apgar et al. 2017, 2020). Based on juvenile coho life stage timing and work in previous studies, we divided the flow variables into two different biologically relevant time-periods (Healey 1991, Anderson and Topping 2018). These time-periods are *Fall Flow (Sept-Dec) and Spring Flow* (Jan-June). *Fall Flow* represents the period of redd construction, gamete deposition, and embryo and fry incubation within the redd. Pulse flow events during the fall can also attract adults into smaller spawning tributaries and during extremely events, can scour established redds. *Spring Flow* represents the period when fry emerge from the gravel and freshets can trigger juvenile emigration from nata habitats. Flow metrics are among the most important predictors of juvenile salmon migratory behavior and timing (Zeug et al. 2014, Sturrock et al. 2015, Anderson and Topping 2018). In this way, we could evaluate which time-periods might have the greatest influence on migration strategies within and across rivers. In addition to breaking flow into relevant time-periods, we also partitioned the data into *cumulative flow* and flow variance. Cumulative flow represents the type of hydrologic year a cohort experiences, and *flow variance* provides a mechanism for habitat creation and activation (e.g. bar formation, floodplain inundation), and has also been identified as a trigger for juvenile salmon migration and overall metabolism changes (Zeug et al. 2014). *Cumulative flow* was calculated as the total daily flow summed for the entire Fall or Spring time period each year, while *flow variance* was calculated as the sample variance of the total daily flow ($m^3 \cdot day^{-1}$) across the period of interest. This gave a total of four different flow metrics for our analyses. When a stream did not have measured flow data available, we selected a nearby stream with similar watershed characteristics to act as a proxy (Archfield and Vogel 2010). To account for the considerable variation that exists across streams in flow conditions, we z-scored these values to make them comparable for this analysis. Most flow data were accessed from the USGS Surface Water database (https://waterdata.usgs.gov/nwis), while a small number were provided by local water agencies.

We used principal component analysis (PCA) on our four flow metrics to address correlation issues in predictor variables. We selected a factor analysis approach with varimax rotation and an eigenvalue threshold of 1.5. This generated groupings of strongly correlated variables into two rotated factors, which cluster with their respective seasons, so they were named accordingly (Table 3.1., Figure 3.2.). PC1 included the two fall flow metrics (Fall Cumulative Flow and Fall Flow Variance), while PC2 included the two spring flow metrics (Spring Cumulative Flow and Spring Flow Variance).

We also included additional variables that are related to influencing salmonid emigration from natal streams (Zeug et al. 2014, Anderson and Topping 2018, Apgar et al. 2020). Latitude can represent differences in genetic backgrounds or local adaption, potentially translating to behavioral differences. The number of stream kilometers upstream of the migrant trap (StreamKm) represents the amount of available natal rearing habitat for juveniles. Finally, juvenile density (Eggs/KM) was calculated as the estimate number of eggs deposited in a given population and year divided by the length of stream available to rearing salmonids. Where egg estimates were not available, we took the female spawner number and multiplied it by 2500 as this was the average number of eggs per female for this region (Sandercock 1991, Suring et al. 2015). We also did not have egg-to-fry survival numbers for each year, which might potentially allow for overestimations. Data for these predictor variables were acquired either from reported values or calculated them using ArcGIS 10.6 (ESRI 2019).

Environmental Driver Modeling

Our modeling approach to evaluate which demographic and environmental variables contributed significantly to variation in migratory strategies utilized best subset regressions for model selection. We chose to use the R 'dredge' function to establish Akaike's Information Criterion (AIC) for all possible combinations of variables across all years in the 18 populations (R Core Team, 2019). The minimum AIC value was used to select the best fit model unless strong collinearity was found between predictor variables. We used a threshold of >2 AIC points to confer significant model difference and VIF values of >5 to show that model terms were strongly collinear. We logit transformed the proportion of YOY migrants (**%YOY)** for a given stream and year and used this as our dependent variable. The result of the best fit model selection is the combination of variables that drive the average proportion of migratory strategies within and across populations. We chose to use a linear mixed regression model as repeated samples of the same population are not independent of one another. Our full model included Population and Trap Type as a random effect and log-transformed Eggs/KM, log-transformed StreamKm, Latitude, and the two

PC-Flow Metrics as fixed effects. All statistical analyses were conducted in R 3.6.1 (R-Core Team 2019).

Results

Migratory Strategy Quantification and Frequency

When evaluating size differences in all migrants across all weeks and populations, we found that coho expressed two clear outmigration strategies from the natal stream ($p < 0.001$) (Figure 3.3.). When we split the analysis across individual weeks, the two migrant groups' sizes continued to differ significantly (p-value range = 0.023 to <0.001). We found that the average size difference between migrant types at the beginning of the migration period was ~60mm, while at the end, decreased to ~40mm. The average YOY migrant size across all populations was 43.6mm, while Smolt was 99.2mm. The overall proportion of migrants was 84% YOY and 16% Smolt; and Smolt frequency increased as latitude decreased (Figure 3.1.). The average proportion of each migrant type also varied highly between population and year, where Freshwater Creek in California had almost exclusively Smolt migrants (Avg. 99%). In comparison, East Fork Lobster Creek in Oregon had predominantly YOY (Avg. 91%)(Figure S3.1.). The Smolt strategy also had a relatively short migration period (16 weeks), while YOY had an overall longer migration period (24 weeks) (Figure 3.3.).

Environmental drivers of migration strategies

The proportion of annual emigrants that left as YOY or Smolts varied considerably across populations and years (Table 3.2.). Model selection indicated the best fit model explained 52% of the variation in migratory strategy and included Population as a random effect and log-transformed Eggs/KM, Latitude, and Fall Flow as fixed effects (marginal $R^2 = 0.52$)(Table 3.3.,3.4., Figure 3.4a). The conditional R^2 is 0.80 and represents the variation explained by both fixed and random effects. Together with the random effect of population, juvenile density, stream km, and fall flow regime explained 80% of migration strategy variation. One other possible model combination with less than 2 ΔAIC points from zero included Spring Flow as a non-significant model term. In the best-fit model, log-transformed Eggs/KM and Latitude were strongly positively related with %YOY, while Fall Flow had a negative relationship (Table 3.4, Figure 3.4b,c,d). Trap type was also removed during model selection due to its strong collinearity with Latitude. Latitudinal variations in precipitation creates higher rainfall and more consistent rainfall further north, leading to deeper and more consistent flows in natal tributaries, allowing for more frequent utilization of Rotary Screw Traps.

Discussion

Gaining a more comprehensive understanding of what factors influence the frequencies of alternative life-histories in ecologically important species has become increasingly important as those species become more imperiled (Hendry et al. 2004, Dingle and Drake 2007, Liedvogel et al. 2011). Our study demonstrates that spring alternative migratory strategies in coho salmon occur predictably across populations in California and Oregon and are driven by juvenile density, latitude, and fall stream flow. Across all populations and years, migrant size significantly differed between the two strategies. The average size of YOY migrants across all populations was 43.6mm, compared to 99.2mm for Smolts. These results highlight that juvenile coho, within the southern extent of their range, express at least two consistent migratory behaviors across streams and years which are predictably influenced by both environmental and demographic factors.

Migratory Strategy Quantification and Frequency

The YOY strategy size ranged from 35-80mm, but most migrants were in the 40-50mm range. The Smolt strategy usually began at ~80mm and extended up to 145mm. This large size range is consistent with fish of an older age class. One interesting pattern we observed was that Smolts also had a shorter average migration duration (16 weeks) compared to YOY migrants (24 weeks) (Figure 3.3.). Juvenile salmon tend to migrate together as protection from predators, so this may be a schooling behavior expressed by the older fish (Sandercock 1991, Jonsson et al. 2017). We also see large numbers of YOY, especially in the northernmost populations where they make up a majority of the migrants leaving in spring. This result could show that smaller coastal tributaries have limited rearing habitat, and smaller fish move downstream sooner to rear in estuaries (Koski 2009, Shaul et al. 2013, Nordholm 2014).

Environmental drivers of migration strategies

Our results show a clear pattern associated with the frequency of YOY and Smolt migrants as being driven by juvenile density (measured as juvenile potential; Eggs/KM), latitude, and the fall flow regime. The strong, positive relationship between juvenile density and YOY frequency shows that a carrying capacity might be lower in these smaller streams. This result again supports that a density-depended mechanism can influence juvenile salmonid migratory behavior. It is clear, though, that across all populations, as juvenile density increases, so does the number of YOY migrants, showing that regardless of stream size, individuals may use density as a cue to migrate early. Another factor that supports this density-dependent mechanism is that juvenile coho can be extremely territorial (Puckett and Dill 1985, Landergren 2004). This territorial behavior, especially by larger fish that set up territory first, might force smaller or later hatching fish out of the natal streams due to increased harassment (Puckett and Dill 1985). Fall flow had a negative relationship with the frequency of YOY migrants, suggesting that hydrologic differences during the adult migration and spawning period may strongly influence egg-fry survival (Figure 3.4c). One potential explanation is that since coho prefer smaller coastal streams that are more susceptible to strong pulse flows, increased flow variance might translate to greater redd scouring. Redd scouring can lower egg-fry survival and in turn reduced juvenile density leading to more fish rearing as Smolts (Sandercock 1991). There was also a strong positive relationship between the frequency of YOY and latitude (Figure 3.4d). Overall population size decreased with latitude, as southern populations were consistently much smaller, and expressed a consistent higher frequency of Smolt migrants than northern ones.

Sister Taxa Comparison

One relevant outcome of this study is its ability to compare the environmental and demographic drivers that influenced juvenile coho salmon migratory strategies with their closest relatives Chinook salmon. Previous studies have evaluated juvenile migratory patterns of Chinook salmon across the same geographic range and with a similar set of environmental drives (Zeug et al. 2014, Sturrock et al. 2015, 2019a, Anderson and Topping 2018, Apgar et al. 2020). We found a density-dependent mechanism in coho salmon, similar to that found previously in juvenile Chinook salmon. One surprising difference was that Chinook salmon were more strongly influenced by the amount of habitat available for rearing (Apgar et al. 2020). In contrast, coho were influenced more strongly by juvenile density of a particular cohort. These differences may result from differences in stream preferences between the two species and/or an evolved behavioral response. Young of Year coho also tend to utilize estuary habitat as much or more than their Chinook counterparts (Koski 2009, Shaul et al. 2013). This behavior may have evolved in response to the smaller carrying capacity of coastal streams. Larger inland steams that Chinook prefer also have more floodplain and side-channel habitat compared to coastal streams. These side channel habitats can also dramatically increase the carrying capacity when made available during high flows of these areas allowing more fish to rear outside the estuary (Jeffres et al. 2008, Sellheim et al. 2016). Since coho do not have these areas available to them, estuary rearing may afford them their highest growth potential. Although this study did not measure estuary growth, other studies suggest that coho salmon can grow rapidly in estuaries (Koski 2009, Nordholm 2014, Osterback et al. 2018). These overall density-dependence patterns may suggest a model of diversified bet-hedging as the availability of these alternative phenotypes may increase fitness depending on the conditions.

Management Considerations

Our results suggest several management steps that can be taken to promote migratory diversity. Habitat quality both in-stream and in adjacent riparian zones can influence flow and density through a number of different mechanisms such as deforestation and flow modifications (Gasith and Resh 1999, Naiman et al. 2002). Deforestation from logging is common among the coastal watersheds can fundamental alter flow regimes, leading to an increased frequency of extreme pulse flows (Stouder et al. 1997, Perry and Jones 2017). These pulse flow events can cause redd scouring and sediment deposition reducing egg-fry survival and potentially overall juvenile density (Mantua et al. 2010). Watershed management practice that prevent deforestation will promote the maintenance of more natural flow regimes. Shifting precipitation regimes, especially along a latitudinal gradient, can lead to more extreme flood and drought cycles (Mantua et al. 2010, Recsetar and Bonar 2013, Crozier 2016). Prolonged droughts, especially at the southern extent of the range, can prevent juveniles from leaving estuaries if the sand bars of bar-built estuaries do not breach (Behrens et al. 2013, Osterback et al. 2018). Smaller tributaries can also be inaccessible during low-flow conditions preventing adults from reaching preferred spawning habitats or keep juveniles from out-migrating later in spring (Meixler et al. 2009). Reduced flows may also curtail the overall spring migration period and reduce available rearing habitat influencing juvenile densities. An issues associated with flow in these coastal watersheds is water diversions or agricultural or cannabis productions, which can severely modify the flow regimes (Bauer et al. 2015). Watershed manager should attempt to curtail these action to help provided ample water for rearing and migration for juvenile salmon.

With a large number of YOY coho moving out of the natal stream after only a few months, especially in the more northern populations, the quality of alternative rearing sites becomes increasingly important. Coastal streams tend to have limited side-channel habitat so previous studies have found that many fish spend a prolonged time rearing in estuaries (Koski 2009, Shaul et al. 2013, Nordholm 2014). Estuary health across much of the US Pacific Coast has also been degraded to anthropogenic modifications, so estuary restoration practices can be an effective tool to increase survival of these YOY migrants. Studies have shown that coho that rear in healthy estuaries can become as large or larger than their siblings upstream in as little as 60 days and enter the ocean at similar sizes (Koski 2009, Nordholm 2014). This effectively eliminates the risk of increased mortality due to smaller sizes at ocean entry for these migrants. However, they can still suffer increased mortality while migrating and rearing in the estuary. This risk could also be offset by the higher numbers of individuals that express this migratory strategy, especially in the northern populations of our study.

Since density-dependence influences the migratory behavior of juveniles, hatchery practices may also influence the density cues that trigger movement. The stocking large hatchery juveniles can increase overall instream densities. This stocking may cause younger fish to out-migrate more frequently due to a reduced carrying capacity. Additionally, there is evidence that hatchery juveniles may induce a "pied-piper effect," which can cause wild fish to school with hatchery fish and emigrate at higher rates (Weber and Fausch 2003). Hatcheries also tend to stock the largest fish they can grow in an attempt to increase survival from size-selective mortality (Sturrock et al. 2019b). However, stocking a wide range of juvenile sizes may represent a more natural diversity and allow for individual decision making in relation to migration strategies. Most populations in this study have little to no hatchery input, but this is an important consideration for all juvenile salmonid species. Managers should consider these factors when designing restoration plans for coastal coho salmon, especially since juvenile life-histories can directly influence adult migratory strategies and life-histories. Since the number of returning adult spawners is used as a metric for overall population success, protecting juvenile migratory diversity can allow for greater survival potential under fluctuating environmental conditions.

Improving our understanding of how alternative life-history strategies vary across different populations and what environmental factors influence their frequency is becoming increasingly important. The maintenance of alternative strategies within a population can act as a buffer to stressors imparted from climate change and anthropogenic disturbances, potentially leading to greater population resilience (Dingle & Drake, 2007; Stearns, 1992). We have highlighted that density-dependent factors along with flow and latitude can influence the migratory life-histories of juvenile coho salmon, and may in turn influence adult migration and life-histories as well. These results provide insight for management actions that could be taken to improve the survival of juvenile migrants, which might lead to overall greater adult returns and more stable populations.

Acknowledgements

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Tables and figures

Table 3.1. Orthogonal data transformation with PCA and Rotational Factor Loading using the Varimax method. Loadings of flow parameters on the first two principal components (PCs) using an Eigenvalue threshold of ≥1.5 explains 90% of the total variance (percentage of variance explained per PC shown in table). Bold values indicate a high importance of that parameter on the principal component (loadings > 0.4).

PC Factor	**Eigenvalue**	**Percent**	**Cum Percent**
Factor 1- Fall Flow	1.8373	45.933	45.933
Factor 2- Spring Flow	1.7646	44.114	90.047
Rotated Factor Loadings			
Variables	Factor 1	Factor 2	
Fall Cumulative Flow	0.1470431	**0.9260312**	
Fall Flow Variance	0.0833502	**0.9374362**	
Spring Cumulative Flow	**0.9547045**	0.0968828	
Spring Flow Variance	**0.9472549**	0.1372827	

Table 3.2. Summary of the frequency of YOY and Smolt migratory strategies across 18 populations in Oregon and California

Population	**State**	**DPS**	**Years Sampled**	**Total Years**	**Latitude**	**Longitude**	**Avg. %YOY**	**Avg% Smolt**	**StreamKm**	**Avg. Density**
North Fork Nehalem River (East)	Oregon	Oregon Coast	1999-2013	15	45.81463167	-123.6920415	59%	41%	38.5	1908.333
North Fork Nehalem River (West)	Oregon	Oregon Coast	1998-2015	18	45.80824381	-123.7555538	67%	33%	38.6	4573.166
North Fork Scappoose Creek	Oregon	Lower Columbia	2000-2012	9	45.80196259	-122.9360743	89%	11%	21.3	1027.888
East Fork Trask River	Oregon	Oregon Coast	2004-2014	11	45.41553702	-123.6020283	90%	10%	46	1445.909
Mill Creek, Siletz River	Oregon	Oregon Coast	1997-2016	18	44.74580382	-123.7932556	51%	49%	24	1900.444
Mill Creek, Yaquina River	Oregon	Oregon Coast	1999-2016	18	44.574068	-123.909667	83%	17%	5	14779.888
Cascade Creek	Oregon	Oregon Coast	2002-2016	15	44.31976496	-123.8474269	55%	45%	15	1920.00
East Fork Lobster Creek	Oregon	Oregon Coast	1987-2010	24	44.24918228	-123.6329303	91%	9%	4.7	15558.916
Upper Main Lobster Creek	Oregon	Oregon Coast	1987-2010	20	44.24535016	-123.6412166	79%	21%	4.7	11296.75
West Fork Smith Creek	Oregon	Oregon Coast	1998-2015	16	43.8150301	-123.7701378	44%	56%	55	1159.75
Winchester Creek	Oregon	Oregon Coast	2001-2014	8	43.267413	-124.321007	75%	25%	19.1	1679.375
Shasta River	California	SONCC	2000-2018†	15	41.829422	-122.59382	61%	39%	80	13.292
West Branch Mill Creek, Smith River	California	SONCC	1993-2007	15	41.73368	-124.100126	43%	57%	8.2	393.13666
East Fork Mill Creek, Smith River	California	SONCC	1993-2007	15	41.73276	-124.096978	33%	67%	9.6	119.5893
Scott River	California	SONCC	2000-2018†	13	41.72541	-123.0095	51%	49%	93	29.89769
Freshwater Creek	California	SONCC	2011-2016	6	40.785667	-124.090684	3%	97%	29.5	110.2433
Olema Creek	California	Central California	2003-2017	15	38.04275	-122.792429	13%	87%	15.9	35.6933
Redwood Creek	California	Central California	2004-2017	14	37.866741	-122.579398	6%	94%	7.6	72.63285

Table 3.3: Model selection results for best-fit global model explaining variation in juvenile coho migratory strategies

Global Model-Linear Mixed Effect Regression							
Fixed Effect Predictors	**Random Effect**	**df**	**R^2m**	**R^2c**	**AICc**	**ΔAICc**	**Weight**
log(Eggs/KM) + Fall Flow + Latitude	River	6	0.5165	0.7974	905.2	0.00	0.441
log(Eggs/KM)+ Fall Flow + Latitude + Spring Flow	River	7	0.5174	0.7990	906.7	1.48	0.211
log(Eggs/KM) + Fall Flow + Latitude + log(StreamKm)	River	7	0.5206	0.7984	907.3	2.07	0.157
log(Eggs/KM) + Fall Flow + Latitude + Spring Flow + log(StreamKm)	River	8	0.5212	0.8000	908.8	3.54	0.074
log(Eggs/KM) + Latitude	River	5	0.5068	0.7949	910.1	4.94	0.037

Table 3.4. Best fit model results for factors influencing the frequency of migratory strategies in juvenile coho salmon in coastal streams of Oregon and California.

Best Fit Model Summary						
Random Effect:	**Variance**	**Std. Dev**				
Populations	2.523	1.588				
Fixed Effects:	**Estimates**	**Std. Error**	**df**	**t-value**	**VIF**	**p-value**
Intercept	-29.1378	6.9752	15.50	-4.179	N/A	0.0007
Fall Flow	-0.2452	0.0917	227.94	-2.674	1.014	0.0080
Latitude	0.5378	0.163	16.06	3.299	1.020	0.0045
log(Eggs/KM)	0.6434	0.0798	244.29	8.06	1.034	<0.0001

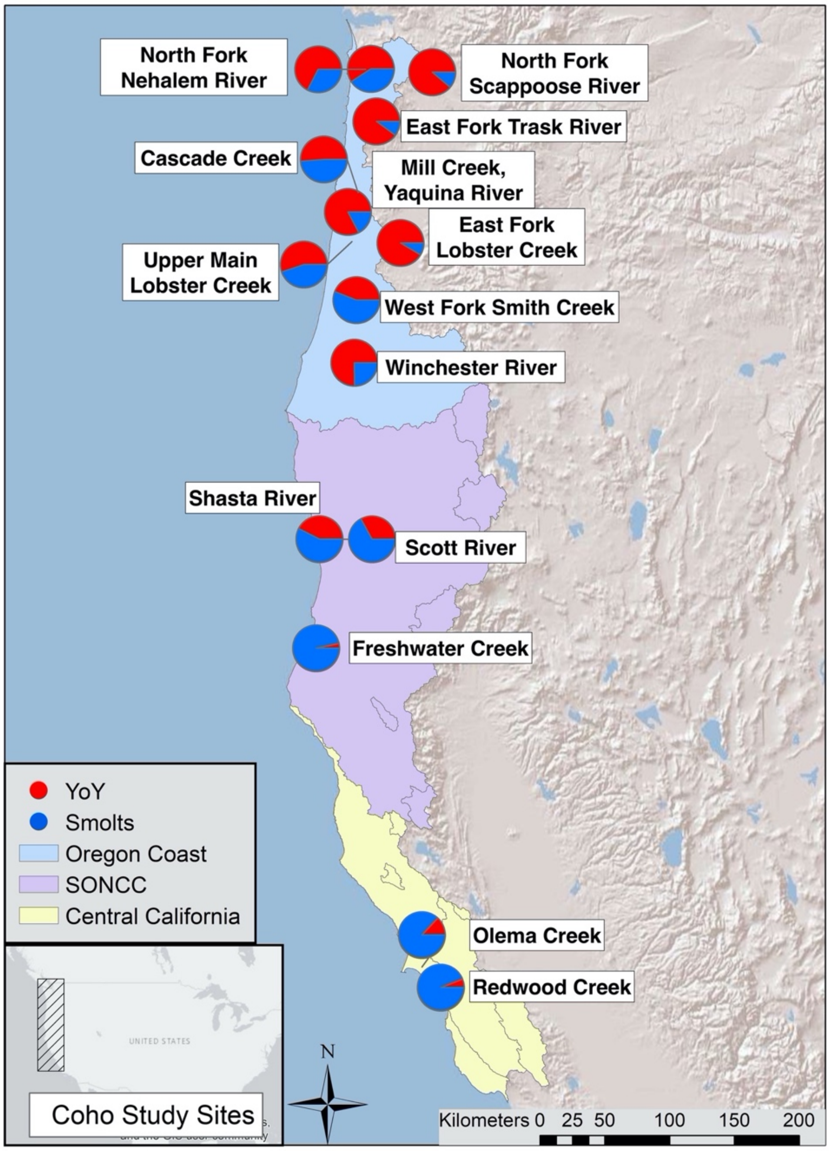


Figure 3.1. Distribution of coho population sampling across California and Oregon. Study sites are denoted by pie charts where the red section represents the proportion of Young of Year (YOY) migrants and blue represent the proportion of Smolt migrants. Shaded polygons represent their corresponding Distinct Population Segment. The Distinct Population Segments from North to South are as follows: Oregon Coast, Southern Oregon Northern California Coast, Central California.

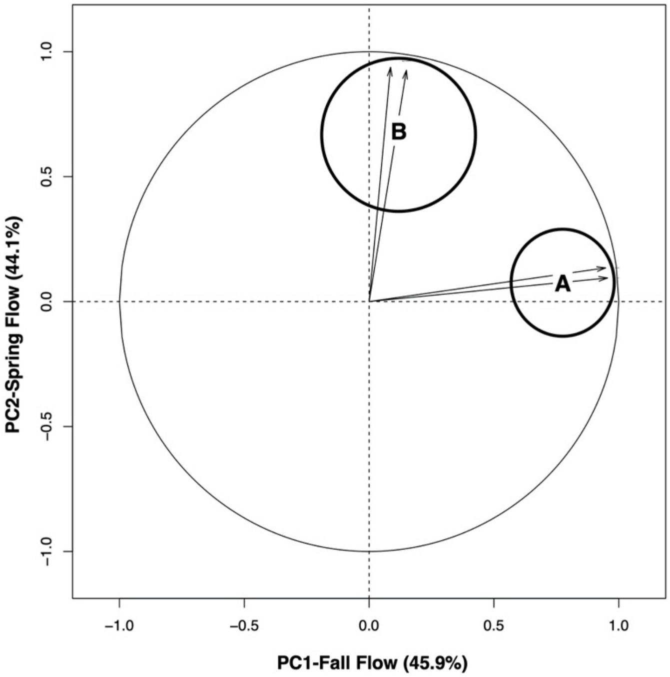


Figure 3.2. Principal component scores for all flow variables across the 18 populations included in the global model. Directions for every flow parameter are indicated (e.g., variables with a positive score on the x-axis tend to be associated with Fall Flow periods). Parameters pointing in similar directions are positively correlated, while those pointing in opposing directions are negatively correlated. Variables in circle A are those representing Fall Flow, while those in circle B represent Spring Flow.

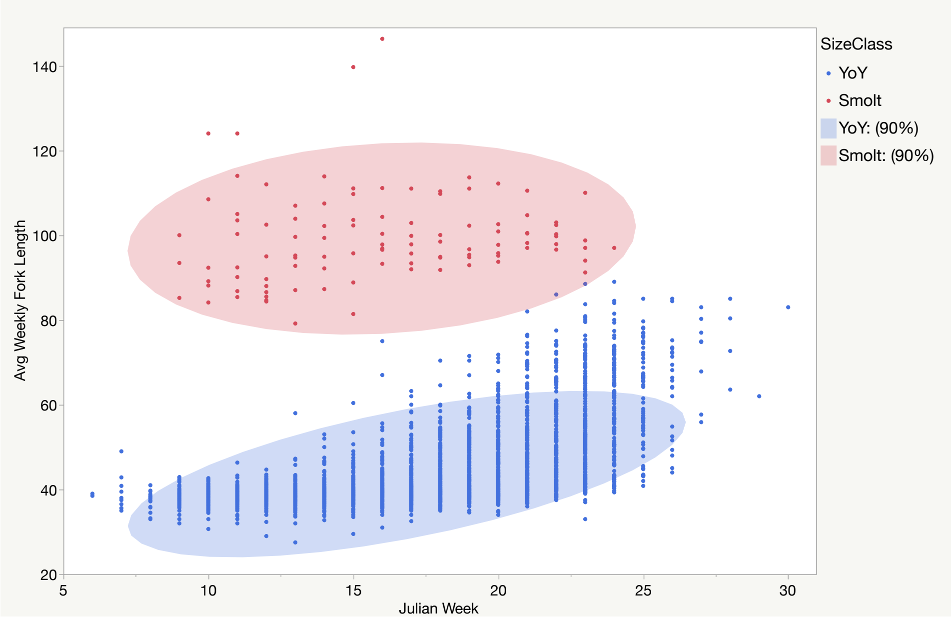


Figure 3.3. Juvenile coho migrant size distribution across populations. Data points in blue represent YOY migrants, while red represents Smolts. Shaded circles represent 90% coverage of the data distribution.

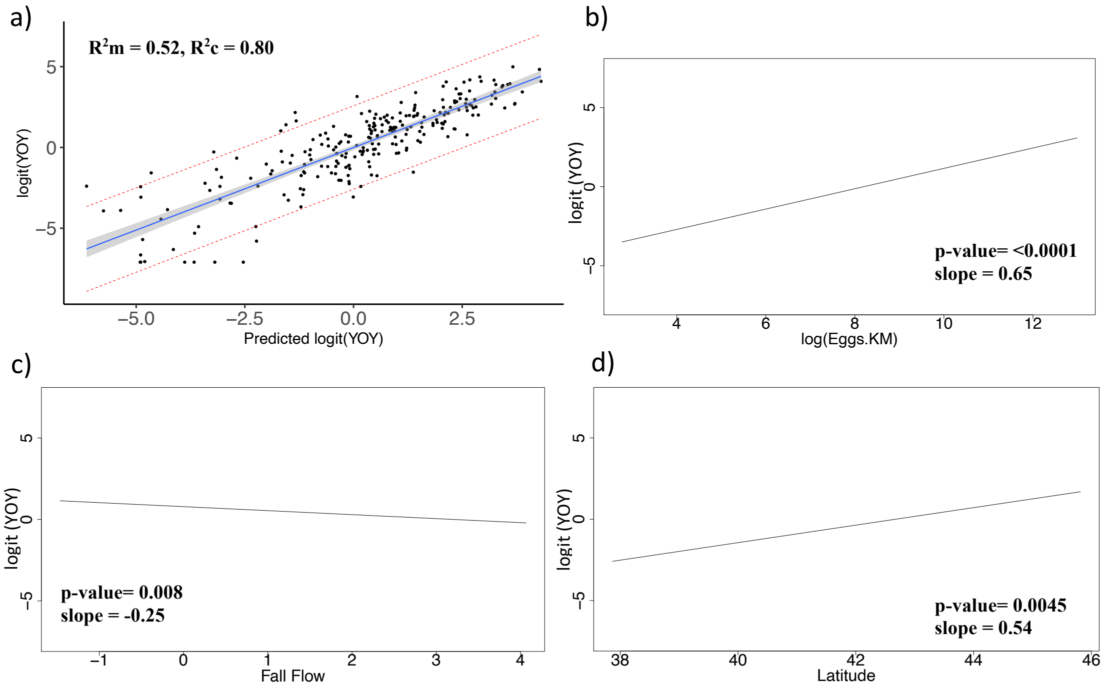


Figure 3.4. Regression models showing the relationship of actual vs predicted values of best fit models and the partial residuals vs model terms. A Shaded grey area represents the 95% confidence intervals, while dashed lines represent the 95% prediction interval. a) The regression results of the logit(%YOY) migrant frequency against the inverse logit predicted values (Predicted logit(%YOY)) from the global linear mixed effect model. The R^2c value = 0.80 b) Partial effects plot of the best fit model and juvenile density [log(Eggs/KM)] c) Partial effects plot of the best fit model and PC1-Fall Flow d) Partial effects plot of the best fit model and Latitude

Synthesis

My dissertation advanced the study of the how alternative life-history strategies can vary across populations and what environmental factors drive their frequency. I found significant variation and complexity in three separate species of Pacific salmonids, all of which had alternative migratory strategies. In steelhead, I found that anthropogenic modifications to streams have led to a significant reduction in anadromy across much of the southern extent of their range. In Chinook, I quantified two distinct migratory strategies that are widespread across their range and whose frequencies are driven by density-dependent mechanisms. And finally in coho, I found once again a density-dependent mechanism influenced the migratory strategies of juvenile salmon. My work now paves the way for more studies to explore the potential genetic basis for these behavior and how potential restorations efforts can more restore imperiled populations.

In Chapter 1, I found that the frequency of anadromy is directly linked to the selective pressures of migrations, specifically in the form of instream impediments and distance from the ocean. I modeled the relative effect of each of these selective agents and use it to develop an evolutionary restoration framework to aid in the recovery of the anadromous life-history through the modification of the instream selection regime. This framework can also be utilized for other species where genetic-liked traits play an important roll in survival and ecological processes, making it a way to develop targeted restoration scenarios.

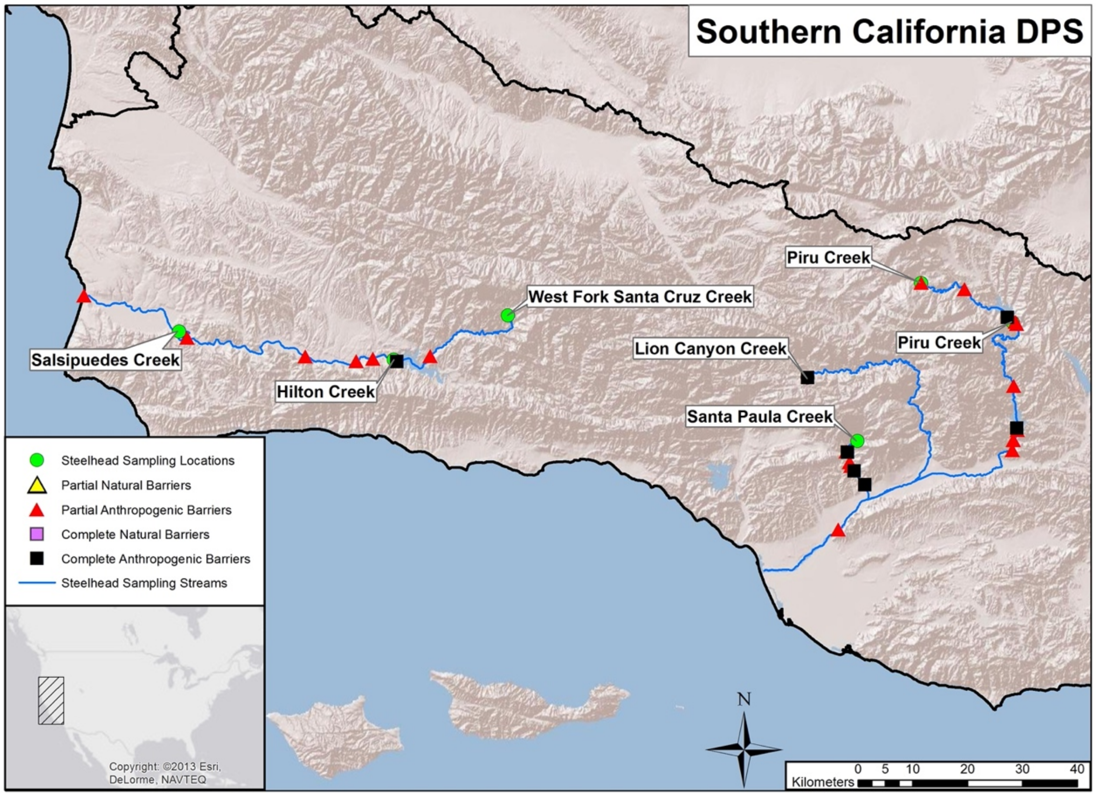
In Chapter 2, I examined if there was more than one migratory strategy in juvenile Chinook salmon. I found that across their range from California to Washington, two unique migratory life-histories exist in every populations and are driven by juvenile density, available rearing habitat, and flow regime. These environmental factors suggest that a strong density-dependent mechanism is in place that drive the frequency of these alternative migratory strategies. Additionally, this life-history variation can act as a potential bet-hedging strategy when environmental conditions become unfavorable.

In Chapter 3, I revisited what environmental factors may influence the migratory strategies of juvenile salmon, but this time in spring migration of coastal coho in Oregon and California. I found that once again that density-dependent factors along with flow and latitude can influence the migratory life-histories of juvenile coho salmon, and may in turn influence adult migration and life-histories as well. This suggest that there could be an overarching trend across Pacific salmonid species, and provide insight for management actions that could be taken to improve the survival of juvenile migrants, which might lead to overall greater adult returns and more stable populations.

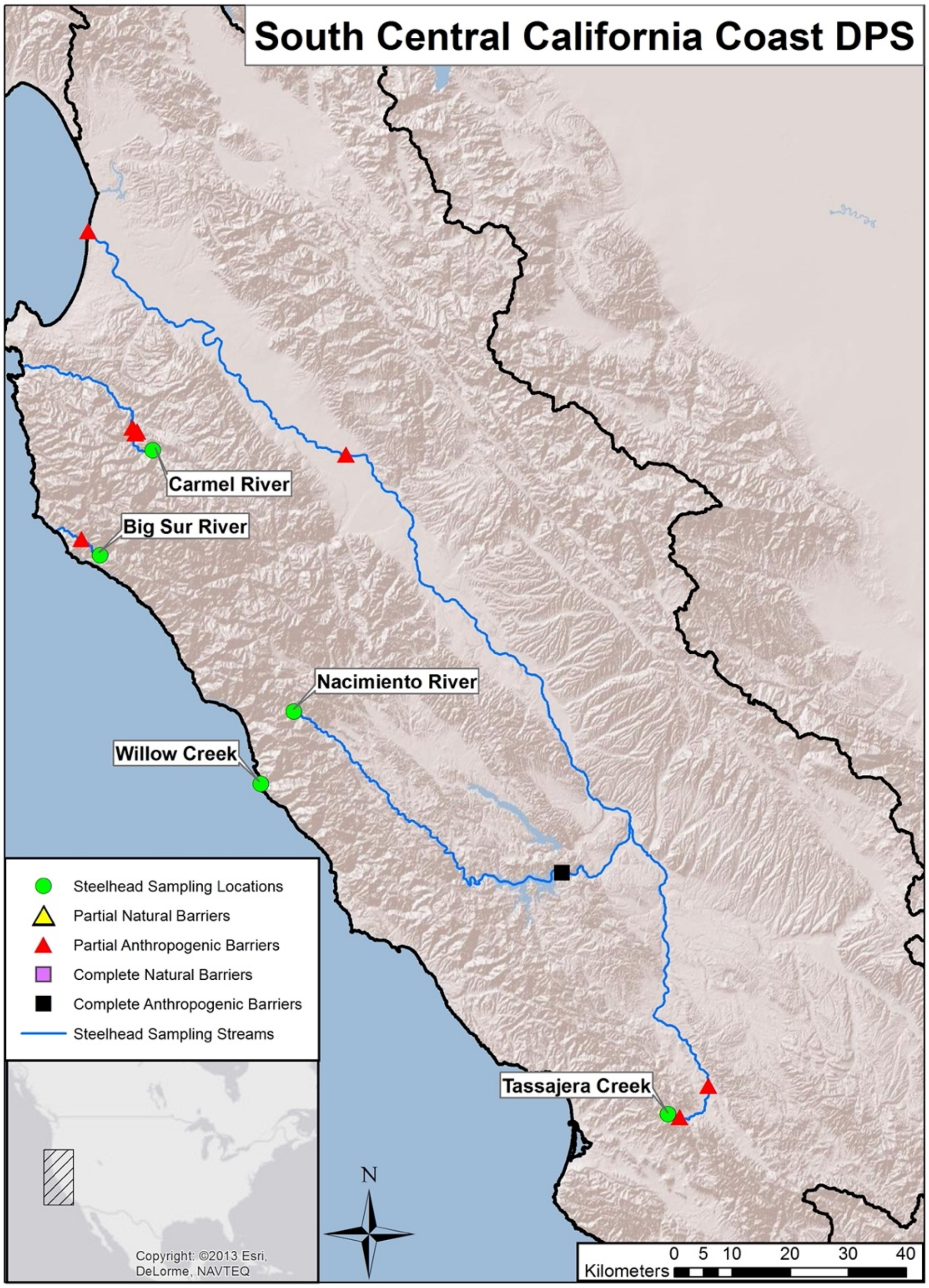
Anadromous fish, especially salmonids, are extremely important economically and ecologically around the world (Quinn and Myers 2005). Declines in their populations have led to the loss of thousands of jobs and millions in revenue for local economies (Ficke et al. 2007). Ecologically, they are an extremely important nutrient subsidy for freshwater and riparian ecosystem, and their loss can lead to cascading consequences (Willson and Halupka 1995, Flecker et al. 2010). Understanding how anthropogenic disturbances and climate change affect their ecosystems, and the feedbacks on their populations and life histories, is an extremely important endeavor. If managers hope to protect remaining populations or attempt to restore them to historic levels, then understanding the drivers of change are critical. My work aimed to uncover these drivers and provide managers with resources they can use to aid in restoration and conservation.

Appendices

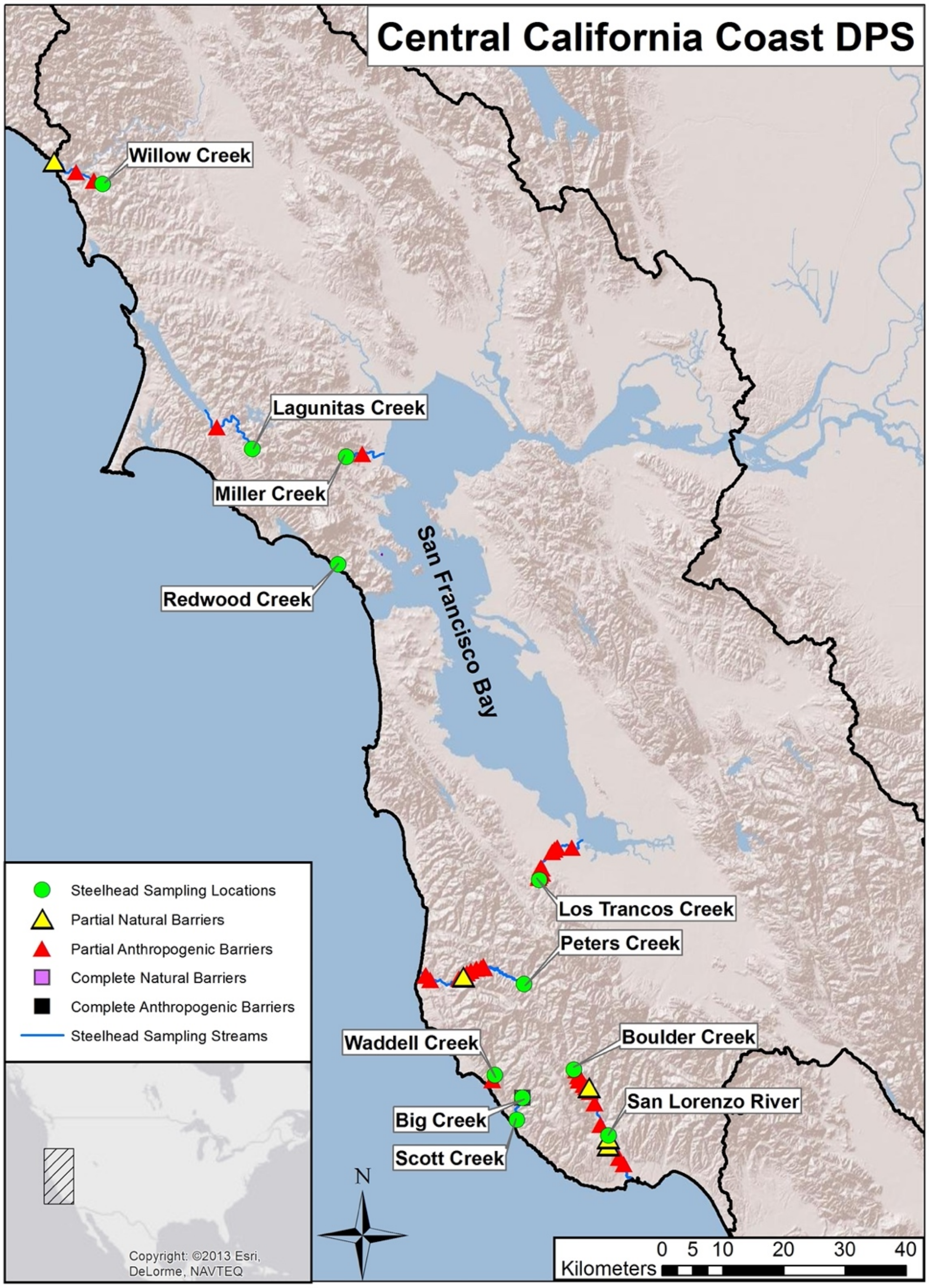
S1: Supplemental Material for Chapter 1



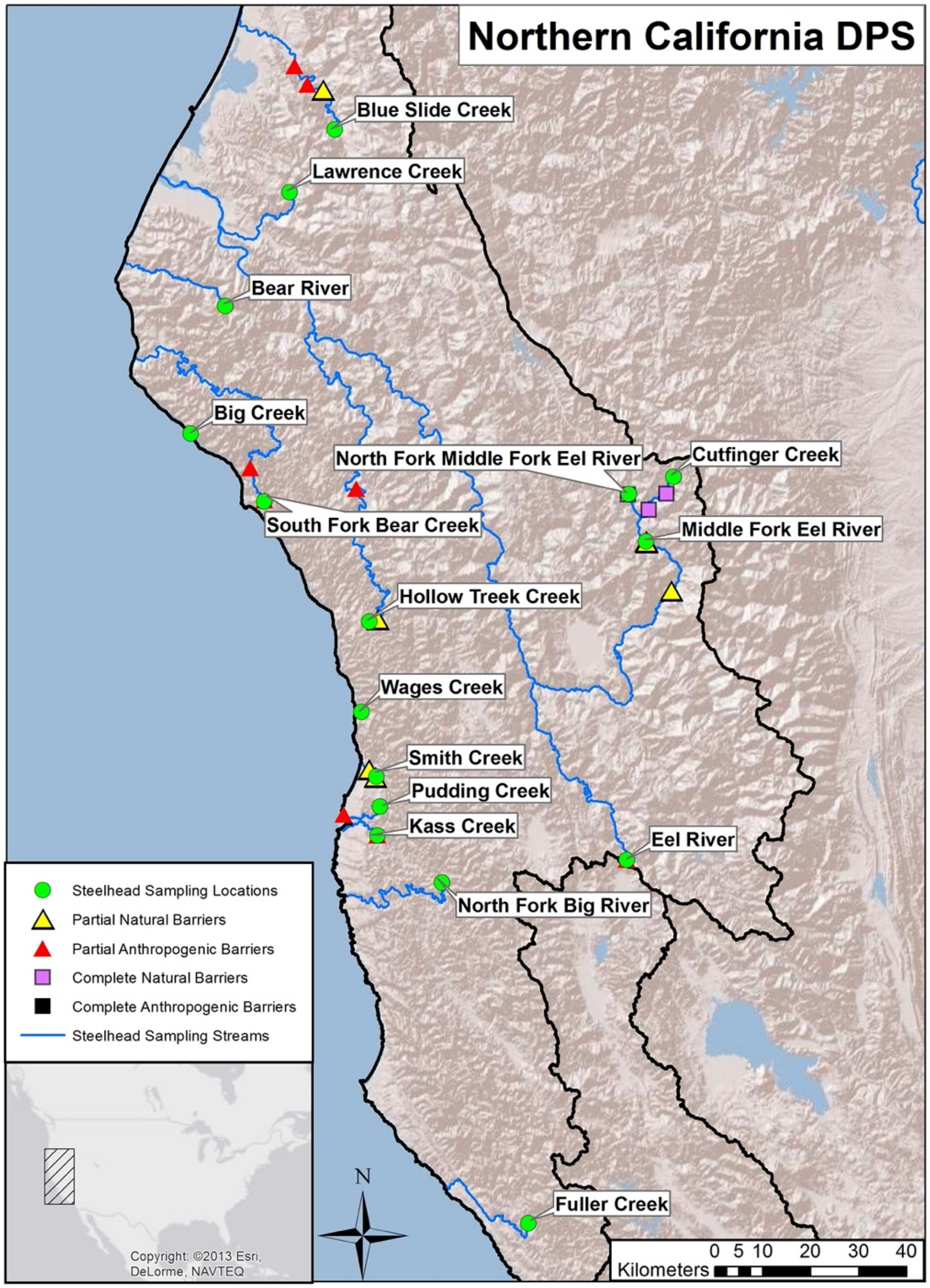
Supplemental Figure S1.1. The Southern California DPS contains the highest number of complete anthropogenic barriers and the lowest average **f(A)** = 41.02.



Supplemental Figure S1.2. The South Central California Coast DPS has an average **f(A)** = 71.37. It contains the Salinas River watershed, which has the two outlier populations in our model (Nacimiento River and Tassajera Creek) perhaps due to main stem seasonally drying from agricultural withdrawals.



Supplemental Figure S1.3. The Central California Coast DPS has the highest average **f(A)** = 75.84. While there are no complete anthropogenic barriers among our sites within this DPS, there are many partial anthropogenic barriers.



Supplemental Figure S1.4. The Northern California DPS sampling sites have an average **f(A)** = 72.35.This DPS has no complete anthropogenic barriers and relatively few partial anthropogenic barriers.

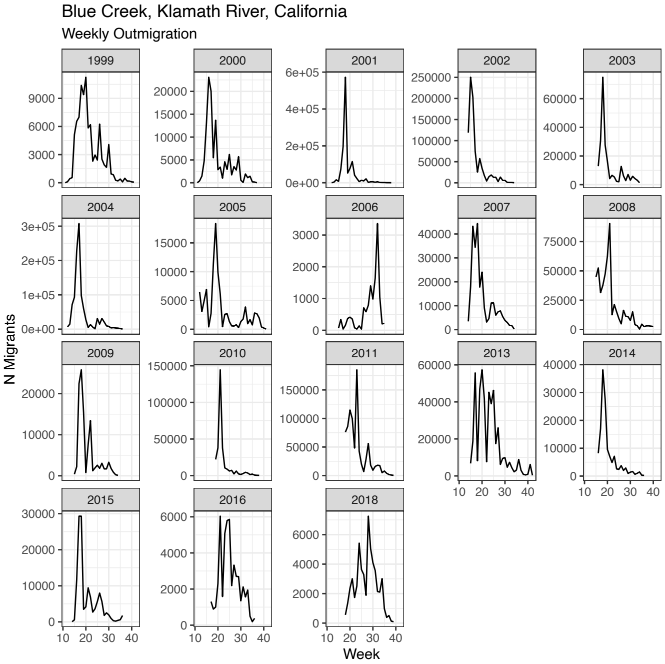
Supplemental Methods 1: GIS analytical methods for extracting environmental variables for each sampling location.

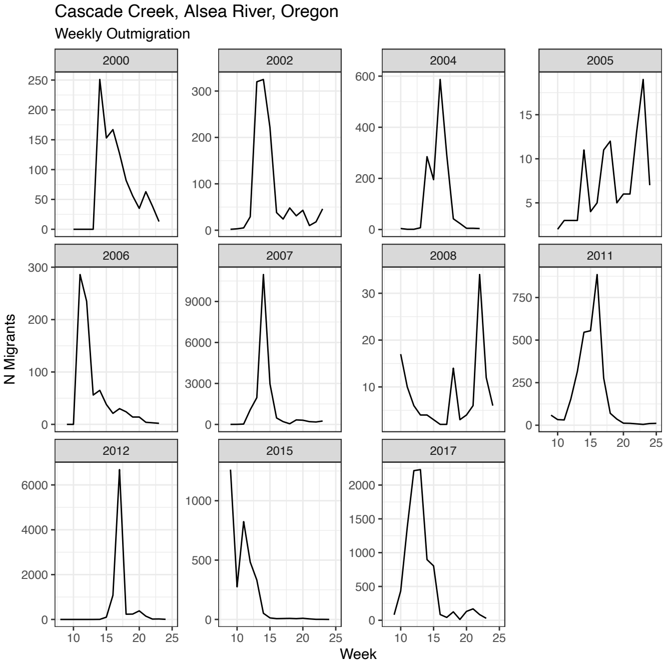
Using ArcGIS 10.2 (ESRI 2014), we created a point shapefile for each georeferenced sampling location. We then constructed polyline shapefiles from each respective sampling point to the ocean to represent the stream-path. This was used to calculate Migration Distance because it represents a returning adults migration path. GIS layers for Climatological and Geomorphological variables were found in the OSU Prism, Geospatial Gateway, and CalAtlas databases. We then accessed the *California Fish Passage Assessment Database*, (available at: www.calfish.org/tabid/420/Default.aspx) to identify all the potential barriers to migratory fish along the stream-path present prior to when genetic sampling was performed in 2001. Their classifications are divided up into 'Complete', 'Partial', 'Temporal', and 'Not a Barrier'. We joined 'Temporal' barriers with 'Partial' and renamed them *partial* because while they might not be permanent they do impart selective pressure on the populations through time. We further divide them into *natural* and *anthropogenic* to discern between their origins. Examples of temporal barriers are sandbars blocking migration at the mouth of streams as well as flow condition barriers like an impassable cascade at <40 cfs. Partial natural barriers were log jams, small waterfalls, shallow riffles, and temporal barriers. The partial anthropogenic barriers make up the majority of the barriers in this dataset. They consist of diversion dams, fish ladders, flashboard dams, concrete drop structures, weirs, road crossings, and poorly designed culverts. *Complete* barriers represent locations where upstream gene flow was impossible and we further classified both sets of barriers into *natural* and *anthropogenic*. Complete natural barriers consist of waterfalls and inaccessible, steep gradient cascades. Complete anthropogenic barriers were poorly designed culverts and road crossings, grade structures, and dams without fish ladders.

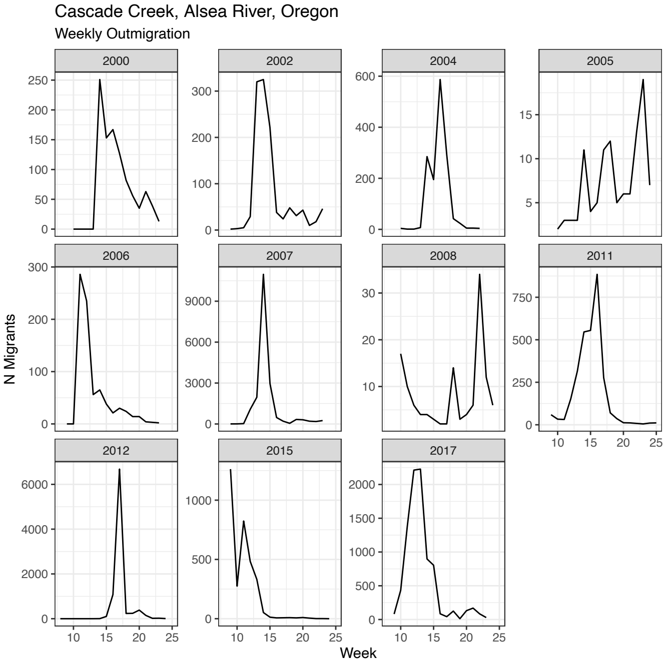
Using the Analysis Toolkit in ArcGIS we conducted a Spatial Join with our Steelhead Sampling Stream polyline layer as the target feature and the four barrier layers as the join features. We used a match option of "WITHIN_A_DISTANCE" to create a buffer of 300ft to capture any barriers whose GPS coordinates were slightly off. Then we removed any extra barriers that were selected at the mouths of tributaries fish did not enter, as they do not block the migration path of the individuals sampled. Conducting this function gave us a count of the number of partial natural and anthropogenic barriers the fish would encounter while migrating to their spawning habitat (or sampling location). It also gave us a count of complete barriers as well, but since they are non-passable, we chose to give them a metric of presence/absence since fish would not be able to encounter more than one. To extract information for Climatological and Geomorphological data we conducted a Spatial Join with the Steelhead Sampling Locations as the target feature and each individual variable as the join features. The match option of "WITHIN_A_DISTANCE" was used to create a 1km buffer to generate a weighted average of the surrounding area. Climatological variables such as rainfall, streamflow, maximum air temperature, etc. were averaged over a five-year period prior to the 2001 sampling year. In this way we could create an average climatological effect that may have affected the sampled populations for the last 1-2 adult generations. The reason we decided not to use a finer resolution climactic data was that the sheer number of monthly and yearly combinations would have presented logistical difficulties in interpreting the model results. We did attempt a number of combinations however they provided no discernable patterns so we decided to use the large-scale averages.

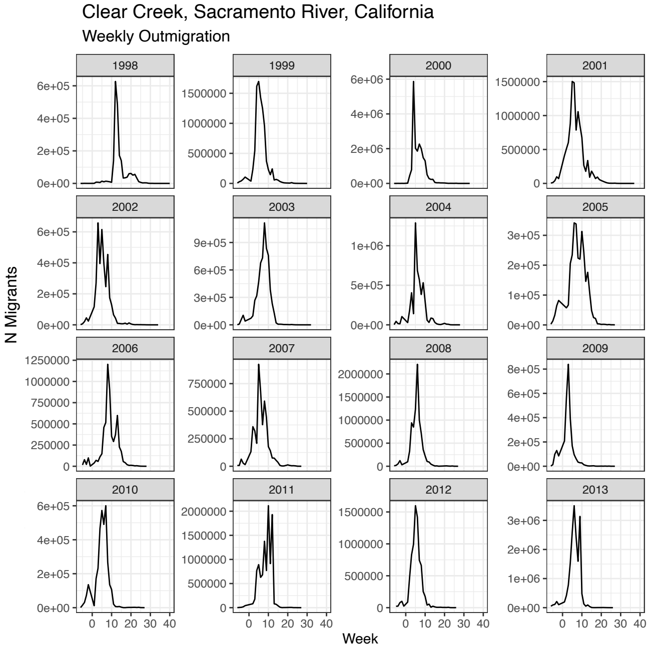
S2: Supplemental Material for Chapter 2

Supplemental Figure S2.1. Weekly outmigration data from populations where weekly measurements were available. Other populations had yearly proportions of fry, parr, and smolts already quantified by data providers.



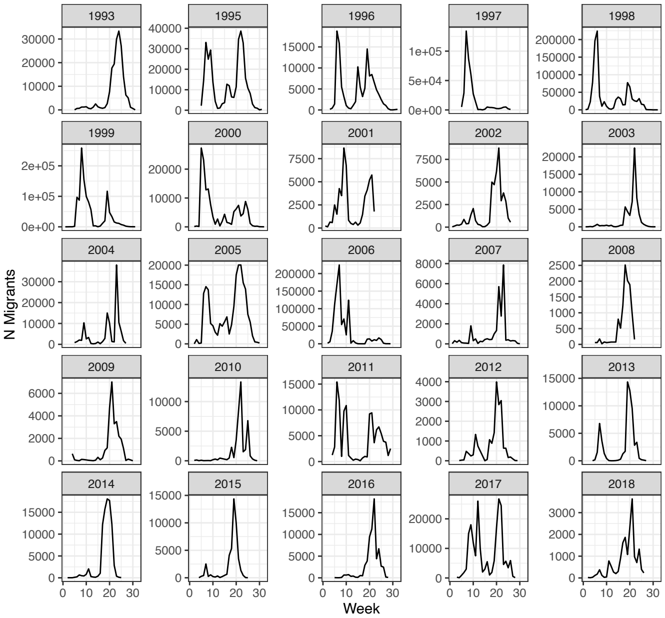



Cascade Creek, Alsea River, Oregon
Weekly Outmigration
2000
2002
2004
2005
2006
2007
2008
2011
2012
2015
2017
N Migrants
Week
10
15
20
25


Clear Creek, Sacramento River, California
Weekly Outmigration
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
N Migrants
Week
0
10
20
30
40

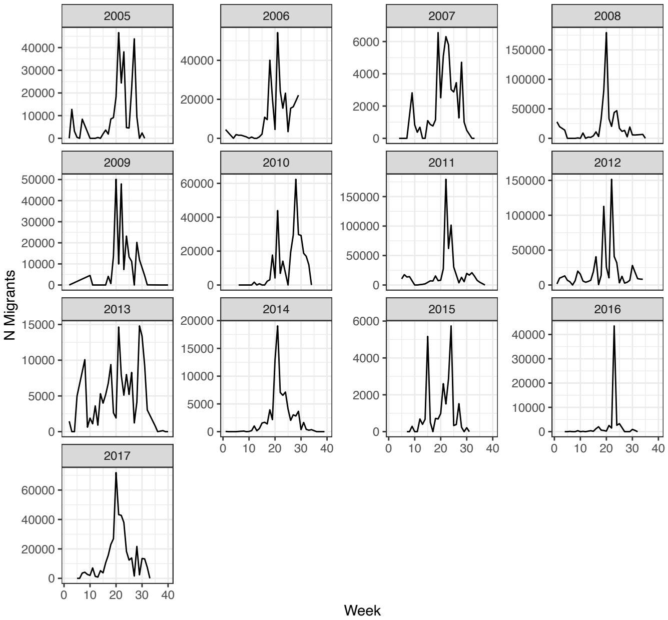
Mokelumne River, San Joaquin River, California

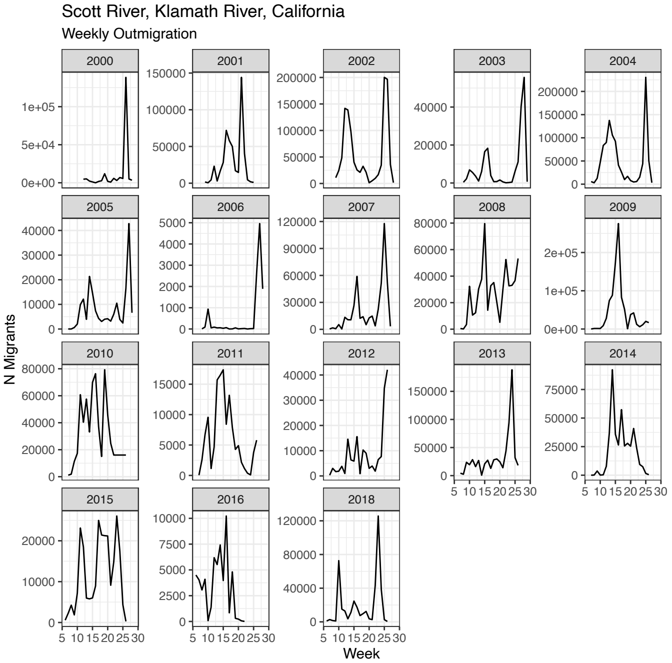
Weekly Outmigration



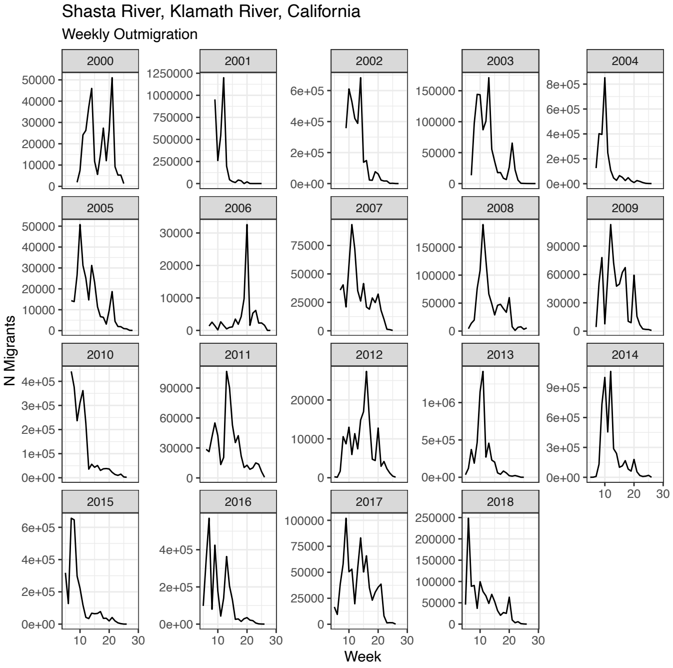
Nooksack River, Washington

Weekly Outmigration

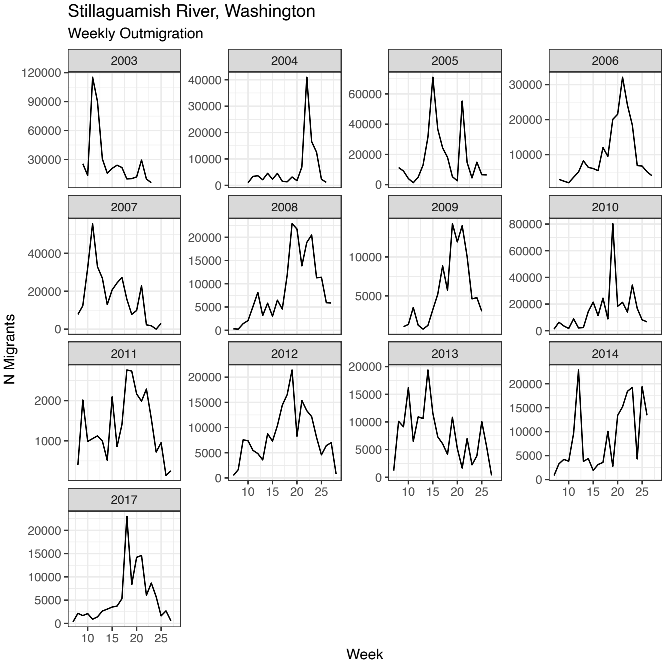



Scott River, Klamath River, California

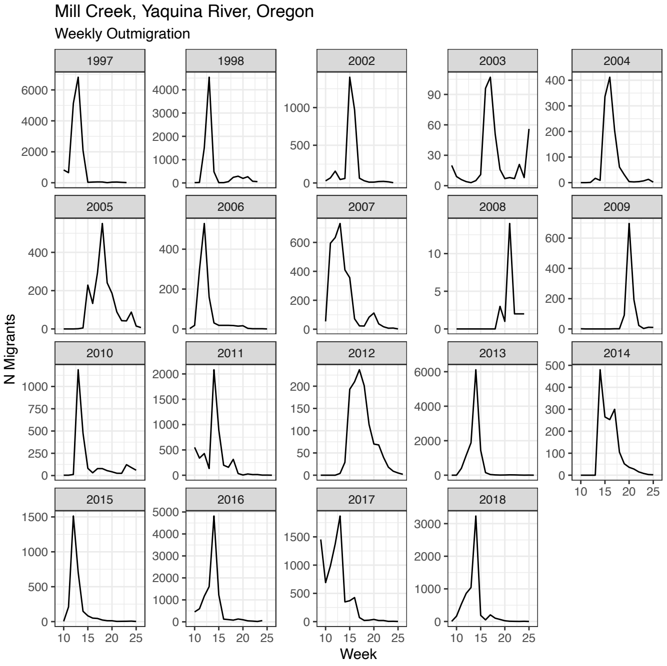
Weekly Outmigration


Shasta River, Klamath River, California

Weekly Outmigration


Stillaguamish River, Washington

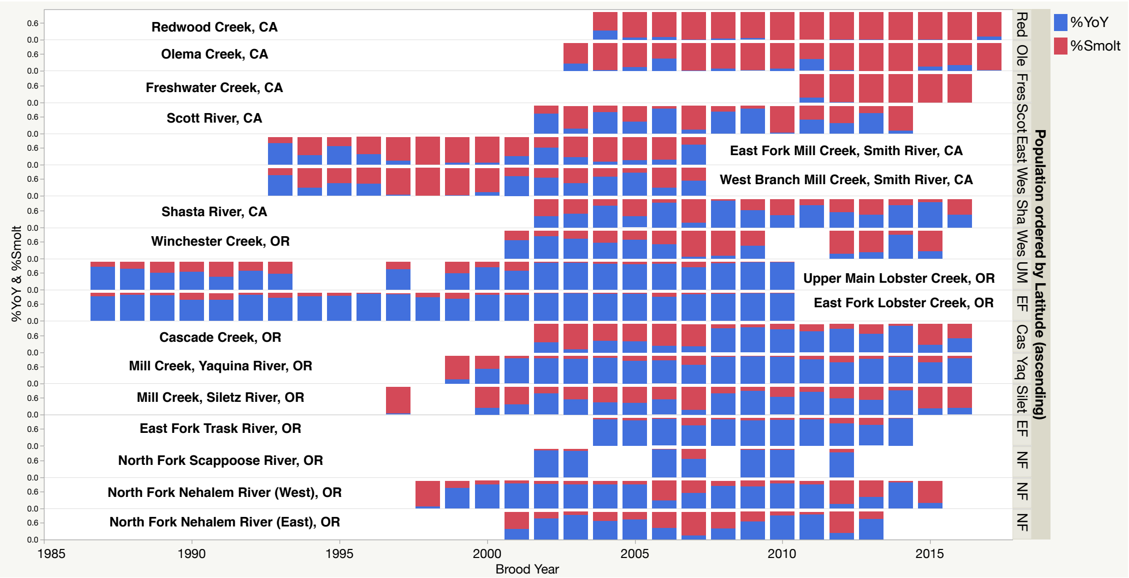
Weekly Outmigration


Mill Creek, Yaquina River, Oregon

Weekly Outmigration

S3: Supplemental Material for Chapter 3

Supplemental Figure S3.1. Proportion of YoY and Smolt migrants across populations and years in Oregon and California.



Bibliography

Abadía-Cardoso, A., A. J. Clemento, and J. C. Garza. 2011. Discovery and characterization of single-nucleotide polymorphisms in steelhead/rainbow trout, *Oncorhynchus mykiss*. Molecular Ecology Resources 11:31–49.

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

Aitken, S. N., and M. C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics 44:367–388.

Alberti, M. 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology & Evolution 30:114–126.

Alberti, M., C. Correa, J. M. Marzluff, A. P. Hendry, E. P. Palkovacs, K. M. Gotanda, V. M. Hunt, T. M. Apgar, and Y. Zhou. 2016. Global urban signatures of phenotypic change in animal and plant populations. Proceedings of the National Academy of Sciences:1–6.

Alerstam, T., A. Hedenstrom, and S. Akesson. 2003. Long-Distance Migration : Evolution and Determinants. Oikos 103:247–260.

Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences of the United States of America 106:9987–9994.

Ameijeiras-Alonso, J., R. M. Crujeiras, and A. Rodríguez-Casal. 2018. Multimode: An R Package for Mode Assessment. bioRxiv.

Anderson, J. H., and P. C. Topping. 2018. Juvenile Life History Diversity and Freshwater Productivity of Chinook Salmon in the Green River, Washington. North American Journal of Fisheries Management 38:180–193.

Andreska, J., and L. Hanel. 2015. Historical occurrence and extinction of Atlantic salmon in the River Elbe from the fourteenth to the twentieth centuries. Archives of Polish Fisheries 23:3–16.

Apgar, T. M., J. E. Merz, B. T. Martin, and E. P. Palkovacs. 2020. Alternative migratory strategies are widespread in subyearling Chinook salmon. Ecology of Freshwater Fish:1–15.

Apgar, T. M., D. E. Pearse, and E. P. Palkovacs. 2017. Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker. Evolutionary Applications 10:485–497.

Archfield, S. A., and R. M. Vogel. 2010. Map correlation method: Selection of a reference streamgage to estimate daily streamflow at ungaged catchments. Water Resources Research 46:1–15.

Aubin-Horth, N., C. R. Landry, B. H. Letcher, and H. a Hofmann. 2005. Alternative life histories shape brain gene expression profiles in males of the same population. Proceedings. Biological sciences / The Royal Society 272:1655–1662.

Audzijonyte, A., A. Kuparinen, and E. Fulton. 2014. Ecosystem effects of contemporary life-history changes are comparable to those of fishing. Marine Ecology Progress Series 495:219–231.

Audzijonyte, A., A. Kuparinen, R. Gorton, and E. Fulton. 2013. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. Biology Letters 9:20121103.

Bauer, S., J. Olson, A. Cockrill, M. van Hattem, L. Miller, M. Tauzer, and G. Leppig. 2015. Impacts of Surface Water Diversions for Marijuana Cultivation on Aquatic Habitat in Four Northwestern California Watersheds. Plos One 10:e0120016.

Beckman, B. R., D. A. Larsen, B. Lee-Pawlak, and W. W. Dickhoff. 1998. Relation of Fish Size and Growth Rate to Migration of Spring Chinook Salmon Smolts. North American Journal of Fisheries Management 18:537–546.

Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. Biological Conservation 130:560–572.

Behnke, R. J., and J. R. Tomelleri. 2002. Trout and salmon of North America. Free Press, New York.

Behrens, D. K., F. A. Bombardelli, J. L. Largier, and E. Twohy. 2013. Episodic closure of the tidal inlet at the mouth of the Russian River — A small bar-built estuary in California. Geomorphology 189:66–80.

Bennett, T. R., P. Roni, K. Denton, M. Mchenry, and R. Moses. 2015. Nomads no more: Early juvenile coho salmon migrants contribute to the adult return. Ecology of Freshwater Fish 24:264–275.

Berejikian, B. A., R. A. Bush, and L. A. Campbell. 2014. Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. Transactions of the American Fisheries Society 143:369–379.

Bisson, P. A., and G. E. Davis. 1976. Production of Juvenile Chinook Salmon, Oncorhynchus tshawytcha, in a Heated Model Stream. Fisheries Bulletin 74:763–774.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (<i>Oncorhynchus mykiss<i/>) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon life history pathways. Springer International Publishing.

Bradshaw, A. D. 1965. Evolutionary Significance of Phenotypic Plasticity in Plants. Advances in Genetics 13:115–155.

Brown, J. J., K. E. Limburg, J. R. Waldman, K. Stephenson, E. P. Glenn, F. Juanes, and A. Jordaan. 2013. Fish and hydropower on the U.S. Atlantic coast: failed fisheries policies from half-way technologies. Conservation Letters 6:280–286.

California American Water, California Coastal Conservancy, and National Oceanographic & Atmospheric Administration (CalAm). 2015. http://www.sanclementedamremoval.org.

Carlson, S. M., T. P. Quinn, and A. P. Hendry. 2011. Eco-evolutionary dynamics in Pacific salmon. Heredity 106:438–447.

Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. 68:1579–1589.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393.

Carroll, S. P., P. S. Jorgensen, M. T. Kinnison, C. T. Bergstrom, R. F. Denison, P. Gluckman, T. B. Smith, S. Y. Strauss, and B. E. Tabashnik. 2014. Applying evolutionary biology to address global challenges. Science 346:1245993.

Caudill, C. C., W. R. Daigle, M. L. Keefer, C. T. Boggs, M. A. Jepson, B. J. Burke, R. W. Zabel, T. C. Bjornn, and C. A. Peery. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? Canadian Journal of Fisheries and Aquatic Sciences 64:979–995.

Chaparro-Pedraza, P. C., and A. M. de Roos. 2020. Density-dependent effects of mortality on the optimal body size to shift habitat: Why smaller is better despite increased mortality risk. Short. Evolution:1–37.

Chapman, D. W. 1962. Aggressive Behavior in Juvenile Coho Salmon as a Cause of Emigration. Can. J. Fish. Aquat. Sci. 19:1047–1080.

Chaput, G., A. Cass, S. Grant, A. M. Huang, and G. Veinott. 2013. Considerations for defining reference points for semelparous species, with emphasis on anadromous salmonid species including iteroparous salmonids. DFO Can. Sci. Advis. Sec. Res. Doc. 146:1–53.

Claiborne, A. M., J. P. Fisher, S. A. Hayes, and R. L. Emmett. 2011. Size at Release, size-selective mortality, and age of maturity of Willamette River hatchery yearling chinook salmon. Transactions of the American Fisheries Society 140:1135–1144.

Clemento, A. J., E. C. Anderson, D. Boughton, D. Girman, and J. C. Garza. 2009. Population genetic structure and ancestry of *Oncorhynchus mykiss* populations above and below dams in south-central California. Conservation Genetics 10:1321–1336.

Clemento, A. J., E. D. Crandall, J. C. Garza, and E. C. Anderson. 2014. Evaluation of a single nucleotide polymorphism baseline for genetic stock identification of Chinook salmon (Oncorhynchus tshawytscha) in the California current large marine ecosystem. Fishery Bulletin 112:112–130.

Combs, B. D., and R. E. Burrows. 1957. Threshold temperature for the normal development of chinook salmon eggs. The Progressive Fish-Culturist 19:3–6.

Crawford, S. S., and A. M. Muir. 2008. Global introductions of salmon and trout in the genus *Oncorhynchus*: 1870–2007. Reviews in Fish Biology and Fisheries

18:313–344.

Crone, R.A., Bond, C. E. 1976. Life history of coho salmon, Oncorhynchus kisutch, in Sashin Creek, Southeastern Alaska. Fisheries Bulletin 74:897–923.

Crozier, L. 2016. Impacts of Climate Change on Salmon of the Pacific Northwest Highlights Physical Processes of Climate Change. Page NOAA.

Davis, J. P., and E. T. Schultz. 2009. Temporal shifts in demography and life history of an anadromous alewife population in Connecticut. Marine and Coastal Fisheries 1:90–106.

Dingle, H., and V. A. Drake. 2007. What Is Migration? BioScience 57:113–121.

Doctor, K., B. Berejikian, J. J. Hard, and D. Vandoornik. 2014. Growth-mediated life history traits of steelhead reveal phenotypic divergence and plastic response to temperature. Transactions of the American Fisheries Society 143:317–333.

Dodson, J. J., N. Aubin-Horth, V. Thériault, and D. J. Páez. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biological Reviews 88:602–625.

Doyle, M. W., E. H. Stanley, C. H. Orr, A. R. Selle, S. A. Sethi, and J. M. Harbor. 2005. Stream ecosystem response to small dam removal: Lessons from the Heartland. Geomorphology 71:227–244.

Dunlop, E. S., A. M. Eikeset, and N. C. Stenseth. 2015. From genes to populations: How fisheries-induced evolution alters stock productivity. Ecological Applications 25:1860–1868.

Dunlop, E. S., K. Enberg, C. Jorgensen, and M. Heino. 2009. Toward Darwinian fisheries management. Evolutionary Applications 2:245–259.

ESRI. 2019. ArcGIS 10.6. ESRI, Redlands, CA.

Faukner, J., S. Silloway, A. Antonetti, T. Soto, A. Corum, E. Tripp, and L. Lestelle. 2019. The role of the Klamath River mainstem corridor in the life history and performance of juvenile coho salmon (Oncorhynchus kisutch).

Ficke, A., C. Myrick, and L. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries.

Finstad, A. G., and C. L. Hein. 2012. Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. Global Change Biology 18:2487–2497.

Firth, P., and S. G. Fisher. 1992. Global climate change and freshwater ecosystems. Springer-Verlag, New York, NY.

Flecker, A. S., J. W. Moore, J. T. Anderson, B. W. Taylor, R. O. Hall Jr., and P. B. McIntyre. 2010. Migratory fishes as material and process subsidies in riverine ecosystems. American Fisheries Society Symposium 73:559–592.

Frankham, R. 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Molecular Ecology 24:2610–18.

Fussmann, G. F., M. Loreau, and P. a. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. Functional Ecology 21:465–477.

Garza, J. C., E. A. Gilbert-Horvath, B. C. Spence, T. H. Williams, H. Fish, S. A. Gough, J. H. Anderson, D. Hamm, and E. C. Anderson. 2014. Population structure of steelhead in coastal California. Transactions of the American

Fisheries Society 143:134–152.

Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean Climate Regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events.

Graff, W. 1999. Dam Nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research 35:1305–1311.

Gross, M. R. 1991. Salmon Breeding Behavior and Life History Evolution in Changing Environments. Ecology 72:1180–1186.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: Quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Haas, T. C., M. J. Blum, and D. C. Heins. 2010. Morphological responses of a stream fish to water impoundment. Biology Letters 6:803–806.

Hale, M. C., F. P. Thrower, E. A. Berntson, M. R. Miller, and K. M. Nichols. 2013. Evaluating adaptive divergence between migratory and nonmigratory ecotypes of a salmonid fish, *Oncorhynchus mykiss*. G3 3:1273–1285.

Halverson, M. A. 2008. A quantitative review of governmental fish stocking in the United States, 1931 to 2004. Fisheries 33:69–75.

Hanak, E., J. Lund, A. Dinar, B. Gray, R. Howitt, J. Mount, P. Moyle, and B. Thompson. 2011. Floods, Droughts, and Lawsuits: A Brief History of California Water Policy. Pages 19–71 Managing California's Water From Conflict to Resolution. Public Policy Institute of California.

Harley, C. D. G. 2011. Climate Change, Keystone Predation, and Biodiversity Loss.

Science 334:1124–1127.

Hayes, S. A., C. V. Hanson, D. E. Pearse, M. H. Bond, J. C. Garza, and R. B. MacFarlane. 2012. Should I stay or should I go? The influence of genetic origin on emigration behavior and physiology of resident and anadromous juvenile *Oncorhynchus mykiss*. North American Journal of Fisheries Management 32:772–780.

Healey, M. . 1991. Pacific Salmon Life Histories: Life History of Chinook Salmon.

Hecht, B. C., J. J. Hard, F. P. Thrower, and K. M. Nichols. 2015. Quantitative genetics of migration-related traits in rainbow and steelhead trout. G3 (Bethesda, Md.) 5:873–89.

Hellmair, M., and A. P. Kinziger. 2014. Increased extinction potential of insular fish populations with reduced life history variation and low genetic diversity. PloS One 9:e113139.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. Pages 92–125 Evolution Illuminated: Salmon and Their Relatives. Oxford University Press.

Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. Molecular Ecology 17:20–29.

Hendry, A. P., M. T. Kinnison, M. Heino, T. Day, T. B. Smith, G. Fitt, C. T. Bergstrom, J. Oakeshott, P. S. Jørgensen, M. P. Zalucki, G. Gilchrist, S. Southerton, A. Sih, S. Strauss, R. F. Denison, and S. P. Carroll. 2011. Evolutionary principles and their practical application. Evolutionary

Applications 4:159–183.

Herbold, B., S. M. Carlson, R. Henery, R. C. Johnson, N. Mantua, M. Mcclure, P. Moyle, and T. Sommer. 2018. Managing for Salmon Resilience in California ' s Variable and Changing Climate. San Francisco Estuary and Watershed Science 16:1–23.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609–1612.

Huber, E. R., and S. M. Carlson. 2015. Temporal trends in hatchery releases of Fall-run Chinook salmon in California's Central Valley. San Francisco Estuary and Watershed Science 13:1–23.

Jeffres, C. A., J. J. Opperman, and P. B. Moyle. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. Environmental Biology of Fishes 83:449–458.

Jones, A. W., E. P. Palkovacs, and D. M. Post. 2013. Recent parallel divergence in body shape and diet source of alewife life history forms. Evolutionary Ecology 27:1175–1187.

Jonsson, B., T. Castro-Santos, and B. H. Letcher. 2010. Modeling migratory energetics of Connecticut River American shad (Alosa sapidissima): implications for the conservation of an iteroparous anadromous fish. Canadian Journal of Fisheries and Aquatic Sciences 67:806–830.

Jonsson, B., M. Jonsson, and N. Jonsson. 2017. Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (Salmo salar). Canadian

Journal of Zoology 95:581–587.

Jonsson, B., N. Jonsson, and J. Albretsen. 2016. Environmental change influences the life history of salmon Salmo salar in the North Atlantic Ocean. Journal of Fish Biology 88:618–637.

Katz, J., P. B. Moyle, R. M. Quiñones, J. Israel, and S. Purdy. 2013. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes 96:1169–1186.

Katz, J. V. E., C. Jeffres, J. L. Conrad, T. R. Sommer, J. Martinez, S. Brumbaugh, N. Corline, and P. B. Moyle. 2017. Floodplain farm fields provide novel rearing habitat for Chinook salmon. PLoS ONE 12.

Kendall, N. W., U. Dieckmann, M. Heino, A. E. Punt, and T. P. Quinn. 2014. Evolution of age and length at maturation of Alaskan salmon under size-selective harvest. Evolutionary Applications 7:313–322.

Kendall, N. W., J. R. Mcmillan, M. R. Sloat, T. W. Buehrens, T. P. Quinn, G. R. Pess, K. V Kuzishchin, M. M. Mcclure, and R. W. Zabel. 2015. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 342:319–342.

Kinnison, M. T., M. J. Unwin, and T. P. Quinn. 2003. Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. Journal of Evolutionary Biology 16:1257–1269.

Koseki, Y., and I. A. Fleming. 2006. Spatio-temporal dynamics of alternative male phenotypes in coho salmon populations in response to ocean environment. Journal of Animal Ecology 75:445–455.

Koski, K. V. 2009. The Fate of Coho Salmon Nomads: The Story of an Estuarine-Rearing Strategy Promoting Resilience. Ecology and Society 14.

Landergren, P. 2004. Factors affecting early migration of sea trout Salmo trutta parr to brackish water. Fisheries Research 67:283–294.

Ledger, M. E., L. E. Brown, F. K. Edwards, A. M. Milner, and G. Woodward. 2012. Drought alters the structure and functioning of complex food webs. Nature Climate Change 3:223–227.

Leger, E. A. 2013. The adaptive value of remnant native plants in invaded communities: An example from the Great Basin. Ecological Applications 18:1226–1235.

Leitwein, M., J. C. Garza, and D. E. Pearse. (n.d.). Evolutionary ancestry and migratory adaptation of andromous, 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. Evolutonary Applicaitons.

Liedvogel, M., S. Åkesson, and S. Bensch. 2011. The genetics of migration on the move. Trends in Ecology and Evolution 26:561–569.

Limburg, K. E., and J. R. Waldman. 2009. Dramatic Declines in North Atlantic Diadromous Fishes. BioScience 59:955–965.

Lister, D. B., and H. S. Genoe. 1970. Stream Habitat Utilization by Cohabiting

Underyearlings of Chinook (<i>Oncorhynchus tshawytscha<i/>) and Coho (<i>O. kisutch<i/>) Salmon in the Big Qualicum River, British Columbia. Journal of the Fisheries Research Board of Canada 27:1215–1224.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102:187–223.

McDowall, R. M. 1988. Diadromy in fishes: migrations between freshwater and marine environments. Croom Helm, London.

McKinnell, S. 2019. Modelling salmon migration as a mixture problem. Canadian Journal of Fisheries and Aquatic Sciences 76:856–870.

De Meester, L., K. I. Brans, L. Govaert, C. Souffreau, S. Mukherjee, H. Vanvelk, K. Korzeniowski, L. Kilsdonk, E. Decaestecker, R. Stoks, and M. C. Urban. 2019. Analysing eco-evolutionary dynamics—The challenging complexity of the real world. Functional Ecology 33:43–59.

Meixler, M. S., M. B. Bain, and M. Todd Walter. 2009. Predicting barrier passage and habitat suitability for migratory fish species. Ecological Modelling 220:2782–2791.

Merz, J. E., and P. B. Moyle. 2006. Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of Central California. Ecological Applications 16:999–1009.

Merz, J. E., M. Workman, and D. Threloff. 2013a. Salmon Life Cycle Considerations to Guide Stream Management : Examples from California’s Central Valley. San Francisco Estuary & Watershed Science June:1–26.

Merz, J., M. Workman, D. Threloff, and B. Cavallo. 2013b. Salmon Life Cycle Considerations to Guide Stream Management: Examples from California’s Central Valley. San Francisco Estuary & Watershed Science 11:1–26.

Miller, J. A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon <i>Oncorhynchus tshawytscha<i/>. Marine Ecology Progress Series 408:227–240.

Moyle, P. B., J. D. Kiernan, P. K. Crain, and R. M. Quiñones. 2013. Climate Change Vulnerability of Native and Alien Freshwater Fishes of California: A Systematic Assessment Approach. PLoS ONE 8.

Moyle, P. B., R. M. Yoshiyama, J. E. Williams, and E. D. Wikramanayake. 1995. Fish Species of Special Concern in California. Page Department of Wildlife & Fisheries Biology University of California.

Muggeo, V. M. R. 2008. segmented: An R Package to Fit Regression Models with Broken-Line Relationships. R News 8:20–25.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Narum, S. R., A. Di Genova, S. J. Micheletti, and A. Maass. 2018. Genomic variation underlying complex life-history traits revealed by genome sequencing in Chinook salmon. Proceedings of the Royal Society B: Biological Sciences 285.

Neilson, J. D., and H. G. Glen. 1986. Inferred from Otoliths: Effects on Mortality and Age at Maturity. Transactions of the American Fisheries Society 115:28–33.

Nichols, K. M., A. F. Edo, P. a. Wheeler, and G. H. Thorgaard. 2008. The genetic basis of smoltification-related traits in Oncorhynchus mykiss. Genetics 179:1559–1575.

Nicola, G. G., B. Elvira, B. Jonsson, D. Ayllón, and A. Almodóvar. 2018. Local and global climatic drivers of Atlantic salmon decline in southern Europe. Fisheries Research 198:78–85.

Nislow, K. H., and J. D. Armstrong. 2012. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management and Ecology 19:451–463.

Nordholm, K. E. 2014. Contribution of Subyearling Estuarine Migrant Coho Salmon (Oncorhynchus kisutch) to Spawning Populations on the Southern Oregon Coast.

O'Neal, K. 2002. Effects of Global Warming on Trout and Salmon in U. S. Streams. Page Defenders of Wildlife-Natural Resources Defense Council.

Ohms, H. A., M. R. Sloat, G. H. Reeves, C. E. Jordan, J. B. Dunham, and I. Fleming. 2014. Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 71:70–80.

Osterback, A.-M. K., C. H. Kern, E. A. Kanawi, J. M. Perez, and J. D. Kiernan. 2018. The effects of early sandbar formation on the abundance and ecology of coho salmon (Oncorhynchus kisutch) and steelhead trout (Oncorhynchus mykiss) in a central California coastal lagoon. Canadian Journal of Fisheries and Aquatic Sciences 75:2184–2197.

Palkovacs, E. P., K. B. Dion, D. M. Post, and A. Caccone. 2008. Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. Molecular Ecology 17:582–597.

Palkovacs, E. P., M. T. Kinnison, C. Correa, C. M. Dalton, and A. P. Hendry. 2012. Fates beyond traits: Ecological consequences of human-induced trait change. Evolutionary Applications 5:183–191.

Palkovacs, E. P., and D. M. Post. 2009. Experimental evidence that phenotypic divergence in predator foraging traits drives ecological divergence in prey communities. Ecology 90:300–305.

Palkovacs, E. P., B. A. Wasserman, and M. T. Kinnison. 2011. Eco-evolutionary trophic dynamics: Loss of top predators drives trophic evolution and ecology of prey. PLoS ONE 6:1–8.

Palumbi, S. R. 2001. Humans as the World's Greatest Evolutionary Force. Science 293:1786–1790.

Pearse, D. E., N. J. Barson, T. Nome, G. Gao, M. A. Campbell, A. Abadía-Cardoso, E. C. Anderson, D. E. Rundio, T. H. Williams, K. A. Naish, T. Moen, S. Liu, M. Kent, M. Moser, D. R. Minkley, E. B. Rondeau, M. S. O. Brieuc, S. R. Sandve, M. R. Miller, L. Cedillo, K. Baruch, A. G. Hernandez, G. Ben-Zvi, D. Shem-Tov, O. Barad, K. Kuzishchin, J. C. Garza, S. T. Lindley, B. F. Koop, G. H. Thorgaard, Y. Palti, and S. Lien. 2019. Sex-dependent dominance maintains migration supergene in rainbow trout. Nature Ecology & Evolution 3:1–12.

Pearse, D. E., and J. C. Garza. 2015. You can't unscramble an egg: Population genetic structure of *Oncorhynchus mykiss* in the California Central Valley inferred from combined microsatellite and single nucleotide polymorphism data. San Francisco Estuary & Watershed Science 13:1–17.

Pearse, D. E., M. R. Miller, A. Abadía-Cardoso, and J. C. Garza. 2014. Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. Proceedings of the Royal Society B: Biological Sciences 281:1–9.

Perry, T. D., and J. A. Jones. 2017. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. Ecohydrology 10:1–13.

Philippi, T., and J. Seger. 1989. Hedging One's Evolutionary Bets, Revisited. Trends in Ecology and Evolution 4:41–44.

Phillis, C. C., J. W. Moore, M. Buoro, S. a. Hayes, J. C. Garza, and D. E. Pearse. 2016. Shifting thresholds: rapid evolution of migratory histories in steelhead/rainbow trout, Oncorhynchus mykiss. Journal of Heredity 106:1–10.

Phillis, C. C., A. M. Sturrock, R. C. Johnson, and P. K. Weber. 2018. Endangered winter-run Chinook salmon rely on diverse rearing habitats in a highly altered landscape. Biological Conservation 217:358–362.

Poff, L. N., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implicatations. Proceedings of the National Academy of Sciences 104:5732–5737.

Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology 89:2019–2032.

Prince, D. J., S. M. O'Rourke, T. Q. Thompson, O. A. Ali, H. S. Lyman, I. K. Saglam, T. J. Hotaling, A. P. Spidle, and M. R. Miller. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Science Advances 3.

Puckett, K. J., and L. M. Dill. 1985. The Energetics of Feeding Territoriality in Juvenile Coho Salmon (Oncorhynchus kisutch). Behaviour 92:97–111.

Quinn, T. P. 2005. Upstream Migration and Energetics. Pages 67–84 The Behavior and Ecology of Pacific Salmon & Trout. University of Washington Press.

Quinn, T. P., and K. W. Myers. 2005. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries 14:421–442.

R-Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rand, P. S., B. a. Berejikian, T. N. Pearsons, and D. L. G. Noakes. 2012. Ecological interactions between wild and hatchery salmonids: An introduction to the special issue. Environmental Biology of Fishes 94:1–6.

Rebenack, J. J., S. Ricker, C. Anderson, M. Wallace, and D. M. Ward. 2015. Early Emigration of Juvenile Coho Salmon: Implications for Population Monitoring. Transactions of the American Fisheries Society 144:163–172.

Recsetar, M. S., and S. a Bonar. 2013. Survival of Apache Trout Eggs and Alevins under Static and Fluctuating Temperature Regimes. Transactions of the American Fisheries Society 142:373–379.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636–1656.

Roni, P., T. Bennett, R. Holland, G. Pess, K. Hanson, R. Moses, M. McHenry, W. Ehinger, and J. Walter. 2012. Factors affecting migration timing, growth, and survival of juvenile coho salmon in two coastal Washington watersheds. Transactions of the American Fisheries Society 141:890–906.

Rundio, D. E., T. H. Williams, D. E. Pearse, and S. T. Lindley. 2012. Male-biased sex ratio of nonanadromous *Oncorhynchus mykiss* in a partially migratory population in California. Ecology of Freshwater Fish 21:293–299.

Sabal, M. C., D. D. Huff, M. J. Henderson, J. Fiechter, J. A. Harding, and S. A. Hayes. 2016. Contrasting patterns in growth and survival of Central Valley fall run Chinook salmon related to hatchery and ocean conditions. Environmental Biology of Fishes 99:949–967.

Sandercock, F. K. 1991. Life history of coho salmon (Oncorhynchus kisutch). Pages 395–446 Pacific Salmon Life Histories.

SAS. 2015. JMP Pro 12. SAS Institute Inc., Cary, NC.

Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2009. Steelhead life history on California's Central Coast: Insights from a state-dependent model. Transactions of the

American Fisheries Society 138:532–548.

Satterthwaite, W. H., M. P. Beakes, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. State-dependent life history models in a changing (and regulated) environment: Steelhead in the California Central Valley. Evolutionary Applications 3:221–243.

Satterthwaite, W. H., and S. M. Carlson. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. Can. J. Fish. Aquat. Sci. 72:1860–1875.

Scavia, D., J. Field, and D. Boesch. 2002. Climate change impacts on US coastal and marine ecosystems. Estuaries.

Schaefer, J. 2012. Hatch success and temperature-dependent development time in two broadly distributed topminnows (Fundulidae). Naturwissenschaften 99:591–595.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13:257–263.

Schindler, D. E., X. Augerot, E. Fleishman, N. J. Mantua, B. Riddell, M. Ruckelshaus, J. Seeb, and B. M. Foundation. 2008. Climate Change, Ecosystem Impacts, and Management for Pacific Salmon. Fisheries 33:502–506.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–612.

Schindler, D. E., M. D. Scheuerell, J. W. Moore, S. M. Gende, T. B. Francis, and W. J. Palen. 2003. Pacific salmon and the ecology of coastal ecosystems. Frontiers in Ecology and the Environment 1:31–37.

Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Oxford Surveys in Evoluntionary Biology 4:182–211.

Selle, A. 2014. Dam Removal – A Primer. http://www.epa.gov/osp/tribes/NatForum10/ntsf10_1m_Selle.pdf.

Sellheim, K. L., C. B. Watry, B. Rook, S. C. Zeug, J. Hannon, J. Zimmerman, K. Dove, and J. E. Merz. 2016. Juvenile Salmonid Utilization of Floodplain Rearing Habitat after Gravel Augementation in a Regulated River. RIVER RESEARCH AND APPLICATIONS 32:610–621.

Sharpe, D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish stocks: An analysis of trends across studies. Evolutionary Applications 2:260–275.

Shaul, L. D., R. Ericksen, K. Crabtree, and J. Lum. 2013. Beyond the Estuary : An Extension of the Nomad Life History Strategy in Coho Salmon. North Pacific Anadromous Fish Commission Technical Report 9:174–178.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Sloat, M. R., and G. H. Reeves. 2014. Individual condition, standard metabolic rate, and rearing temperature influence steelhead and rainbow trout (*Oncorhynchus mykiss*) life histories. Canadian Journal of Fisheries and Aquatic Sciences 71:491–501.

Smith, T. B., M. T. Kinnison, S. Y. Strauss, T. L. Fuller, and S. P. Carroll. 2014. Prescriptive evolution to conserve and manage biodiversity. Annual Review of Ecology, Evolution, and Systematics 45:1–22.

Sogard, S. M., J. E. Merz, W. H. Satterthwaite, M. P. Beakes, D. R. Swank, E. M. Collins, R. G. Titus, and M. Mangel. 2012. Contrasts in habitat characteristics and life history patterns of *Oncorhynchus mykiss* in California's Central Coast and Central Valley. Transactions of the American Fisheries Society 141:747–760.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325–333.

Stanković, D., A. J. Crivelli, and A. Snoj. 2015. Rainbow trout in Europe: Introduction, naturalization, and impacts. Reviews in Fisheries Science & Aquaculture 23:39–71.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology 3:259–268.

Stearns, S. C. 1992. The Evoluton of Life Histories. Oxford University Press, Oxford.

Stockwell, C. a., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution 18:94–101.

Stouder, D. J., P. A. Bisson, and R. J. Naiman. 1997. Pacific salmon & their ecosystems. Page (D. J. Stouder, P. A. Bisson, and R. J. Naiman, Eds.) Journal of Chemical Information and Modeling. 1st edition. Chapman & Hall.

Sturrock, A. M., S. M. Carlson, J. D. Wikert, T. Heyne, S. Nusslé, J. E. Merz, H. J. W. Sturrock, and R. C. Johnson. 2019a. Unnatural selection of salmon life histories in a modified riverscape. Global Change Biology 00:1–13.

Sturrock, A. M., W. H. Satterthwaite, K. M. Cervantes-Yoshida, E. R. Huber, H. J. W. Sturrock, S. Nusslé, and S. M. Carlson. 2019b. Eight Decades of Hatchery Salmon Releases in the California Central Valley: Factors Influencing Straying and Resilience. Fisheries:433–444.

Sturrock, A. M., J. D. Wikert, T. Heyne, C. Mesick, A. E. Hubbard, T. M. Hinkelman, P. K. Weber, G. E. Whitman, J. J. Glessner, and R. C. Johnson. 2015. Reconstructing the Migratory Behavior and Long-Term Survivorship of Juvenile Chinook Salmon under Contrasting Hydrologic Regimes. PLoS ONE 10:1–23.

Suring, E., P. Burns, R. J. Constable, Jr., C. M. Lorion, and D. J. Wiley. 2015. Salmon Life-Cycle Monitoring in Western Oregon Streams, 2012-2014.

Suryan, R. M., V. S. Saba, B. P. Wallace, S. A. Hatch, M. Frederiksen, and S. Wanless. 2009. Environmental forcing on life history strategies: Evidence for multi-trophic level responses at ocean basin scales. Progress in Oceanography 81:214–222.

Sykes, G. E., C. J. Johnson, and J. M. Shrimpton. 2009. Temperature and Flow Effects on Migration Timing of Chinook Salmon Smolts. Transactions of the American Fisheries Society 138:1252–1265.

Taylor, B. M., J. H. Choat, E. E. DeMartini, A. S. Hoey, A. Marshell, M. A. Priest, K. L. Rhodes, and M. G. Meekan. 2019. Demographic plasticity facilitates ecological and economic resilience in a commercially important reef fish. Journal of Animal Ecology:1888–1900.

The Heinz Center. 2002. Dam Removal: Science and decision making.

Thompson, N. F., E. C. Anderson, A. J. Clemento, M. A. Campbell, D. E. Pearse, J. W. Hearsey, A. P. Kinziger, and J. C. Garza. 2020. A complex phenotype in salmon controlled by a simple change in migratory timing. Science (New York, N.Y.) 370:609–613.

Thompson, T. Q., M. Renee Bellinger, S. M. O'Rourke, D. J. Prince, A. E. Stevenson, A. T. Rodrigues, M. R. Sloat, C. F. Speller, D. Y. Yang, V. L. Butler, M. A. Banks, and M. R. Miller. 2019. Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. Proceedings of the National Academy of Sciences of the United States of America 116:177–186.

Twining, C. W., E. P. Palkovacs, M. A. Friedman, D. J. Hasselman, and D. M. Post. (n.d.). Nutrient loading by anadromous fishes: species-specific contributions and the effect of diversity. Canadian Journal of Fisheries and Aquatic Sciences.

Twining, C. W., E. P. Palkovacs, M. A. Friedman, D. J. Hasselman, and D. M. Post. 2016. Nutrient loading by anadromous fishes: species-specific contributions and the effects of diversity. Can. J. Fish. Aquat. Sci. 619:609–619.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human

Domination of Earth’s Ecosystems. Science 277:494–499.

Volkhardt, G. C., S. L. Johnson, B. A. Miller, T. E. Nickelson, and D. E. Seiler. 2007. Rotary Screw Traps and Inclined Plane Screen Traps. Pages 235–266 Salmonid Field Protocols Handbook: Techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland.

Vøllestad, L. A., D. Hirst, J. H. L’Abée-Lund, J. D. Armstrong, J. C. MacLean, A. F. Youngson, and N. C. Stenseth. 2009. Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers. Proceedings of the Royal Society 276:1021–7.

Vøllestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of Freshwater and Marine Growth Rates on Early Maturity in Male Coho and Chinook Salmon. Transactions of the American Fisheries Society 133:495–503.

Waples, R. S., D. J. Teel, J. M. Myers, and A. R. Marshal. 2004. Life-History Divergence in Chinook Salmon: Historic Contigency and Parallel Evolution. Evolution 58:386–403.

Watters, J. V. 2005. Can the alternative male tactics “fighter” and “sneaker” be considered “coercer” and “cooperator” in coho salmon? Animal Behaviour 70:1055–1062.

Weber, E. D., and K. D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: Differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60:1018–1036.

West, D. C., A. W. Walters, S. Gephard, and D. M. Post. 2010. Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. Canadian Journal of Fisheries and Aquatic Sciences 67:1211–1220.

Whiteley, A. R., S. W. Fitzpatrick, W. C. Funk, and D. A. Tallmon. 2015. Genetic rescue to the rescue. Trends in Ecology & Evolution 30:42–49.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:1361–1364.

Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary & Watershed Science 4:1–393.

Willson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology 9:489–497.

Woodson, L. E., B. K. Wells, P. K. Weber, R. B. MacFarlane, G. E. Whitman, and R. C. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon Oncorhynchus tshawytscha during early ocean residence. Marine Ecology Progress Series 487:163–175.

Woodward, F. I., G. B. Thompson, and I. F. McKee. 1991. The Effects of Elevated Concentrations of Carbon Dioxide on Individual Plants, Populations, Communities and Ecosystems. Annals of Botany 67:23–38.

Woodward, G. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Proceedings of the Royal Society B Biological Sciences.

WWF/ZSL. 2020. Living Planet Report. Page (and P. T. Almond, R.E.A, Grooten M, Ed.) Zoological Society of London. Gland, Switzerland.

Yamane, L., L. W. Botsford, and D. P. Kilduff. 2018. Tracking restoration of population diversity via the portfolio effect. Journal of Applied Ecology 44:472–481.

Zeug, S. C., K. Sellheim, J. Melgo, and J. E. Merz. 2019. Spatial variation of juvenile Chinook Salmon (Oncorhynchus tshawytscha) survival in a modified California River. Environmental Biology of Fishes September:1–15.

Zeug, S. C., K. Sellheim, C. Watry, J. D. Wikert, and J. Merz. 2014. Response of juvenile Chinook salmon to managed flow: Lessons learned from a population at the southern extent of their range in North America. Fisheries Management and Ecology 21:155–168.