

CONTRIBUTION OF JUVENILE ESTUARINE RESIDENCY IN A BAR-BUILT
ESTUARY TO RECRUITMENT OF CHINOOK SALMON (*ONCORHYNCHUS*
TSHAWYTSCHA)

By

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ABSTRACT

CONTRIBUTION OF JUVENILE ESTUARINE RESIDENCY IN A BAR-BUILT ESTUARY TO RECRUITMENT OF CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)

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Estuaries are commonly touted as nurseries for outmigrating salmonids, providing higher prey availability than streams, a physiological transition zone, and refugia from marine predators. Yet the diversity of estuaries makes it difficult to generalize the effect they have on salmonid recruitment. In bar-built estuaries, sandbars form at the mouth of rivers during periods of low flow, closing access to the ocean and disrupting outmigration. In this thesis, I evaluated how residency in a bar-built estuary affects the growth, survival, and ultimately recruitment of Chinook salmon (*Oncorhynchus tshawytscha*) in Redwood Creek, California. I conducted a mark-recapture experiment on outmigrating juveniles during the summer of 2018 to determine estuary abundance, growth, and survival. I used scales and sagittal otoliths collected from spawning adult carcasses to quantify the contribution of different juvenile life histories to the adult population. I then integrated these data and monitoring data collected from spawning ground surveys, rotary screw traps, and estuary seines to create a stage-structured matrix model.

Juveniles that remained in the estuary after the mouth closed were larger at ocean entry than ocean rearing juveniles that entered the ocean earlier in the spring. However, estuary rearing juveniles grew less and ultimately were smaller than ocean rearing juveniles prior to winter. Despite having a larger ocean entry size, estuary rearing juveniles had lower survival from river outmigration to adult return than ocean rearing juveniles and contributed disproportionately less to the spawning population. Lack of marine influence and low river flow are common attributes of bar-built estuaries that may lower food availability and deteriorate conditions in these estuaries. Levees constructed in lower Redwood Creek prevent flooding and establishment of marsh and floodplain habitat, potentially majorly limiting the productivity of the estuary and salmonid growth. Restoration efforts designed to address limitations to growth in the estuary such as low food availability and high temperatures are needed to increase the ocean survival and ultimately contribution of estuary juveniles to the population.

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INTRODUCTION

Variation in size, habitat use, and maturity among individuals within a population can produce a diverse array of life history strategies (Goertler 2016; Kilduff 2015). This diversity is a critical element to the resilience of a population. Individuals that do not grow and mature at the same time or in the same location distribute risk and lower the impact of a single, possibly catastrophic, event (Schindler et al. 2010). Diversity in life history can stabilize a population's response to annual variation in environmental conditions (Carlson and Satterthwaite 2011). For example, different ocean entry times of smolts in a population produce a mixture of matches and mismatches to the onset of ocean upwelling (Satterthwaite et al. 2014). While not all individuals enter the ocean during the ideal time, this variation reduces the probability of a collapse from a complete mismatch to ocean phenology.

Initial ocean entry and the first winter at sea account for a majority of salmon mortality in the ocean (Beamish and Mahnken 2001; Duffy and Beauchamp 2011). Survival during both periods is size-dependent, placing importance on size at ocean entry and growth rate during the first summer and fall at sea (Healey 1980; Moss et al. 2005). The optimal time to enter the ocean balances the trade-off between the higher predation risk at sea and the higher ocean productivity. Delaying ocean entry allows juveniles to continue rearing in a habitat of relatively low predation and enter the ocean at a larger size, but results in less time to forage at sea prior to the first winter (Weitkamp et al.

2015). Annual variation in the phenology of upwelling shifts the optimum ocean entry date; furthermore, magnitude of El Niño and Pacific Decadal Oscillation changes intensity of size-selective mortality each year (Woodson et al. 2013; Satterthwaite et al. 2014). Diversity in the size and timing of ocean entry theoretically increases stability in a population during this critical, but unpredictable period.

Coastal habitats such as estuaries, deltas, and floodplains support diversity in juvenile life history by providing alternative rearing habitats prior to ocean entry. Estuaries serve as nurseries for outmigrating salmonids, providing higher prey availability than streams, a physiological transition zone, and refugia from marine predators (Simenstad et al. 1982; Craig et al. 2014). Juvenile Chinook salmon reside in estuaries as early as April, still as fry, to as late as October (Reimers 1975, Simenstad et al. 1982). Juveniles enter the ocean after reaching a certain size threshold, about 70 mm in Chinook salmon (Healey 1980). Differences in size and timing of juveniles exiting the stream produce varying degrees of estuarine residency within the population. The number of juvenile life history types differs among watersheds, and not all types are present in each system. The broad range of estuary characteristics produces a broad range of effects on salmonid recruitment. Individuals with life history types including some period of estuarine rearing composed a majority of returning spawners in some watersheds (Reimers 1973; Schluchter and Lichatowich 1977; Bottom et al. 2005), but were virtually non-existent in others (MacFarlane and Norton 2002).

Pacific coast estuaries include fjords, drowned river valleys, lagoons, and bar-built estuaries (Emmett et al. 2000). Most previous studies on estuarine residency were conducted in drowned river valleys because of their prominence (e.g. Reimers 1973; Bottom et al. 2005; Craig et al. 2014). Bar-built estuaries are the least common type of estuary, but their unique geology may provide insight into the efficacy of estuaries as salmonid nurseries. In bar-built estuaries, waves create sandbars at the mouth of rivers during periods of low flow, closing access to the ocean (Bond et al. 2008). When closed, bar-built estuaries can remain closed for months and have very limited marine influences. Juveniles are unable to exit into the ocean until the mouth breaches, typically as the result of heavy precipitation or a large wave event (Heady et al. 2015). Juvenile life histories in these estuaries are divided into two distinct types, those that exit the watershed prior to mouth closure in the spring and those that exit after its reopening in the fall. The prevalence of bar-built estuaries may rise throughout California with the increasing frequency of drought conditions (Bedsworth et al. 2018). Low estuary levels induced by low rainfall cause the mouth of rivers to close in estuaries typically open year-round (Vivier et al. 2010). Understanding how this phenomenon affects juvenile salmonid rearing would help predict how populations that typically do not have closed estuaries may be affected by changes in precipitation.

While estuaries are an important intermediate between freshwater and marine systems, they are often the most heavily modified (Simenstad et al. 1982). Alterations to estuaries include filling marsh and swamp habitats, construction on coastal wetlands, and

installing levees to confine estuaries and reduce flooding. These alterations remove previous habitat or alter them to be less suitable for juvenile rearing, contributing the decline of some populations along the coast (Katz et al. 2013). Like streams, estuaries are relatively manageable compared to the ocean and restoring them can be an effective avenue of improving population abundance and productivity if they disproportionately contribute to survivorship (Simenstad and Cordell 2000; Roni et al. 2004).

Redwood Creek's estuary is a bar-built estuary that has been significantly altered by the construction of levees in the lower river. The Redwood Creek Watershed Group identified the estuary as the most degraded portion of the watershed and concluded that estuary restoration could have the greatest impact on salmonid abundance (Cannata et al. 2006). The purpose of this thesis was to evaluate this bar-built estuary in its current state as juvenile rearing habitat and assess its effect on the recruitment of Chinook salmon. I broke this goal into four objectives: 1) Identify factors contributing to individuals remaining in the estuary after mouth closure, 2) Estimate abundance, growth and survival of juveniles in the estuary, 3) Compare smolt-to-adult survival between life histories and determine contribution of estuarine residency to recruitment through a life cycle model, 4) Assess how shifts in the environment due to restoration or anticipated changes in the climate could affect contribution and performance of different life histories.

Understanding the dynamics of this bar-built estuary and its effects on juvenile salmonids directly informs management of systems with bar-built estuaries and provides insight into factors contributing to the efficacy of estuaries as salmonid nurseries.

MATERIALS AND METHODS

Study Site

Redwood Creek is a 108 km long river with a 720 km² watershed within Humboldt County, California (Figure 1) (Anderson 2015). The headwaters begin in the California Coast Ranges and flow northwest into the Pacific Ocean near Orick, California (41.292, -124.092). Logging during the 1960s and 1970s heavily altered the basin and increased water temperature and sediment input (Cannata et al. 2006). Currently Redwood Creek is listed as impaired in the federal Clean Water Act Section 303(d) due to temperature and sedimentation.

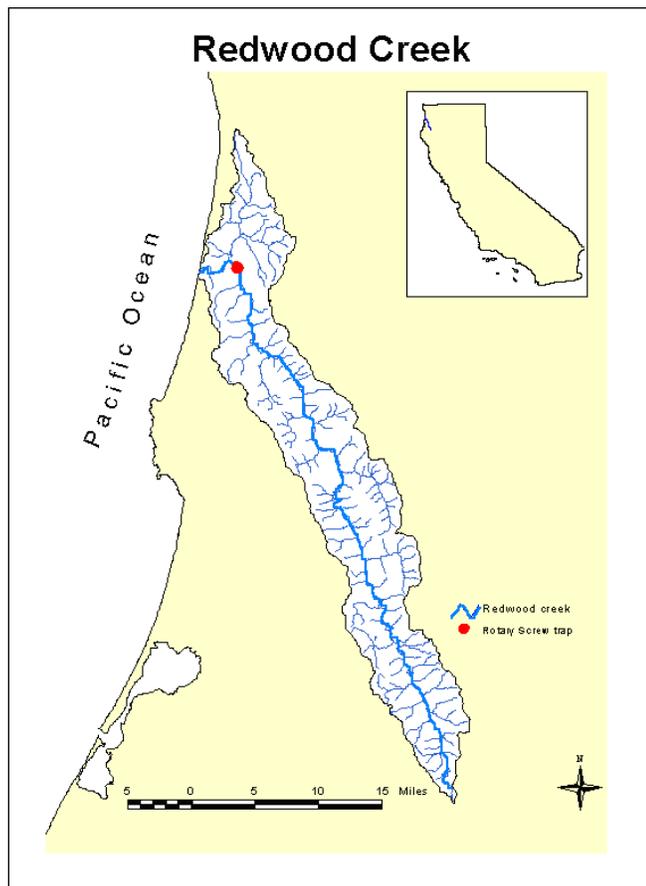


Figure 1. Redwood Creek Basin, Humboldt County, California (Cannata et al. 2006)

The mouth of Redwood Creek closes during the summer when low flow results in a sandbar formation, turning the estuary into a lagoon. The estuary is closed for approximately four months until the river mouth breaches during the first large precipitation event in the late fall (generally November). In 1968, the US Army Corps of Engineers installed 5.1km of levees in the lower river to reduce flooding to neighboring farm and grazing land (Figure 2) (Ricks 1995). Confining the estuary has dramatically reduced the size of the estuary and altered its ecology, likely reducing the productivity and capacity for juvenile salmonids (Anderson 2015).



Figure 2. Redwood Creek estuary, Humboldt County, California (Google Earth November 12, 2017).

Study Population

The Redwood Creek population is the northernmost population of the California Coastal Chinook Evolutionary Significant Unit (ESU) (Good et al. 2005). The Endangered Species Act and the California Endangered Species Act currently classify this ESU as “threatened” because of its declining abundance and reduced distribution (Adams et al. 2011).

Most Chinook salmon in Redwood Creek outmigrate during their first year. For this study, I divided the population into two juvenile life histories. “Ocean type” juveniles outmigrate prior to mouth closure and are at sea during the summer, while “estuary type” juveniles outmigrate after the mouth reopens in the fall. A negligible number of juveniles remain upstream and outmigrate the following spring (stream-type). These smolts composed a small proportion (0.0004) of captured outmigrants from 2004-2016 and were excluded from our model.

Estuarine Rearing

I used passive integrated transponder (PIT) tags to identify the subset of juveniles that remain in the estuary during the summer and to estimate their growth and survival. I injected PIT tags (n= 2,994) into a subset of outmigrants captured at the rotary screw trap from May to July of 2018 (IACUC protocol no. 17/18.F.79-A *approved* May 2, 2018). A maximum of three hundred PIT tags (9 mm or 12 mm) were injected via scalpel each

week into a random subset of individuals larger than 60 mm for individual identification. Additionally, I injected PIT tags into juveniles (n= 599) in the estuary during seining to increase the sample size of recaptured fish for a more precise growth estimate.

The National Park Service and I seined the estuary from June to October 2018 to estimate juvenile abundance in the estuary and to recapture tagged juveniles. Each month, the estuary was seined for two consecutive days. We marked all fish captured using Alcian Blue Dye and then seined to recapture fish following one day of mixing to allow for tagged individuals to redistribute among the population (Seber 1982). Fish were counted and up to 200 individuals were measured and weighed each month. I scanned fish for PIT tags to determine which individuals remained in the estuary and their estuarine growth and survival rate. As with previous years (1980-2017), the National Park Service calculated a Petersen estimate of estuary abundance during each monthly seining event (Seber 1982; Anderson 2015).

Life History Reconstruction Using Scale Morphometrics and Otolith Microstructure

Overview

The age composition and proportion of each juvenile life history type in returning spawners were determined by examining adult scales collected from 2011-2015 spawning seasons and scales and sagittal otoliths collected during the 2017 spawning season. Scales were collected from juveniles in the estuary throughout the summer of 2018 to reference freshwater and estuarine scale patterns. Scale morphometrics and otolith microstructure

have sufficient resolution to detect variation in juvenile life history (Reimers 1973; Campbell et al. 2015). Scales grow isometrically with body length, and spacings between circuli increase when smolts enter the ocean, allowing me to determine ocean entry and duration in each system (Ricker 1992; Bond et al. 2008). Otoliths also grow isometrically to body length and increments are laid daily, making it possible to approximate growth and size-at-age (Neilson and Geen 1982; Campana and Neilson 1985; Whitman and Johnson 2016).

Age composition

To determine the age composition and thereby the maturation rate of Chinook salmon in Redwood Creek, I aged spawners by counting annuli present in scales. Because scales grow isometrically to somatic growth and winter growth is largely lower than summer growth, it is possible to age spawners based on changes in spacings between circuli (Gilbert 1912). Each set of scales from an adult was read by two readers, and age and degree of confidence (rank 1 to 4) were assigned. A third reader reviewed and finalized assessments, discarding samples with a high degree of uncertainty among readers (rank 3 and 4).

Juvenile life history

To identify adults that remained in the estuary as juveniles, I counted the number of circuli laid prior to the ocean entry check and compared it to the total number of circuli laid prior to the first annuli. I assumed the lengths of freshwater/estuarine residency of the two different life histories are sufficiently different to be apparent in the scale pattern,

despite potential individual variation in the rate of circuli deposition (Walker and Sutton 2016). I chose this metric over absolute estimates such as fork length of ocean entry, which is back-calculated from scale radius (Ricker 1992; Bond et al. 2008), for two reasons: 1) Previous studies support the hypothesis that circuli patterns possess a delay in response to environmental conditions, which would result in an overestimate in fork length of ocean entry (Campbell et al. 2015), and 2) I found different measures of radii of ocean entry among scales from the same individual because of the different shapes of scales. Scales collected from juveniles in the estuary throughout the summer of 2018 (n=13) were used as reference for scale patterns of estuarine growth and estuary type life history. I counted the total number of circuli and measured the width of each spacing to estimate the number of circuli laid throughout the summer and the growth pattern in the estuary (Craig et al. 2014).

I bolstered our assessments of juvenile life history from scale morphometrics by comparing scale morphometrics and otolith microstructure of spawning adults from 2017. I evaluated juvenile life history using otolith microstructure by back-calculating fork length at late fall and if possible, ocean entry. I mounted the adult otoliths on microscope slides and polished them until daily increments became visible and could be measured (n= 28) (Whitman and Roddam 2014). Otoliths were imaged and measured using Image-Pro Plus®. I measured the radius of the otolith starting from the dorsal-posterior primordia to the increment of interest, directly 90° from the tip of the rostrum towards the dorsal side (Whitman and Johnson 2016). Otolith radius at 210 daily increments from the

exogenous feeding check was measured to estimate size during the late fall. If ocean entry could be confidently identified through the presence of ocean checks or an abrupt change in the spacings between increments, I measured the radius to back-calculate size at ocean entry and recorded its approximate age. Fork lengths were back-calculated from otolith radii using the known otolith-fork length relationship from Central Valley fall-run Chinook salmon (Sturrock and Johnson 2014). I ensured Redwood Creek's population had a comparable relationship by measuring the otolith radius on incidental mortality juveniles collected from estuary seines in 2018 (n= 13) and comparing the otolith-fork length relationship to Central Valley's.

Once samples from individuals were aged and categorized by life history, I back-calculated the brood year of each individual and estimated the proportion (τ) of each life history in the adult spawning population for brood years 2009-2015.

$$n_{i\gamma} \sim \text{Binomial}(n_{\gamma}, \tau_{i,\gamma})$$

n is the number of individuals assessed for each brood year (γ) and the number of individuals identified for each life history (i).

Estuarine Growth Model

I evaluated growth in the estuary by comparing the observed growth of recaptured PIT-tagged individuals in the estuary to their expected growth under ad libitum feeding using the Ratkowsky growth equation (Ratkowsky et al. 1983). Expected mass (M_{exp}) after t days was calculated using:

$$M_{exp} = \left(M_0^b + \frac{\Omega bt}{100} \right)^{\frac{1}{b}}$$

Where M_0 is the initial measured weight, b is an allometric growth parameter, and Ω is the mass-standardized growth rate. Mass-standardized growth rate (Ω) at temperature T is expressed as a function of upper and lower thermal limits, T_U and T_L , and shape parameters d and g , obtained from Perry et al. (2015) (Appendix A),

$$\Omega = d(T - T_L)[1 - e^{g(T - T_U)}]$$

I assumed differences between the expected mass (M_{exp}) and the observed mass (M_{obs}) are due to differences in growth rate (Ω). I added the variable r to evaluate the ratio of actual growth rate to the optimal growth rate (Ω).

$$M_{obs} = \left(M_0^b + \frac{r\Omega bt}{100} \right)^{\frac{1}{b}}$$

I evaluated for r , the ratio of the actual growth rate to the expected growth rate, and calculated the mean r for each monthly seining occasion.

Life Cycle Model

Statistical analysis

The parameters of statistical models were estimated using Bayesian methods in order to assess parameter uncertainty. For conducting the Bayesian analysis, I used the JAGS sampler software (Plummer 2017) called from the R Statistical Environment (R Development Core Team 2018). I used the R statistical packages rjags (Plummer et al.

2018) and jagsUI (Kellner 2018). I ran three chains with 15,000 iterations after a burn-in of 5,000 iterations for each sub-model. I assessed convergence of MCMC chains both visually and with \hat{r} , a metric that evaluates convergence by comparing variance among chains versus within chains (Gelman and Rubin 1992; Hobbes and Hooten 2015). Each sub-model was tested for goodness-of-fit using a Bayesian p-value of the deviance.

Fecundity (spawner to smolt)

Fecundity (F) was measured as the number of smolts per spawner.

$$F = \frac{R}{S}$$

This parameter F was applied as fecundity to all spawning age-classes. The density-dependent parameter combines actual fecundity (spawner to egg) and freshwater survival (egg to smolt). I fit a Beverton-Holt stock-recruitment curve to predict F each year given the number of spawning adults.

Statistical Distribution

$$R \sim dlnorm(\hat{R}, \sigma^2)$$

Process Model

$$\hat{R} = \frac{aS}{1+S/K}$$

The productivity parameter (a) and the carrying capacity (K) were estimated using the number of spawners (S), calculated from spawning ground surveys (Appendix B), and the subsequent number of outmigrants (R) using a rotary screw trap (Appendix C) for the 2011-2015, 2017 spawner seasons.

Juvenile life history

At outmigration, the population is separated into juveniles that enter the ocean prior to mouth closure and those that remain in the estuary after closure. I evaluated the migration timing and size of juveniles outmigrating from the stream and their apparent survival in the estuary to determine how they may affect the number of juveniles in each life history. Outmigrant count and size data collected from a rotary screw trap during the 2004-2016 and 2018 outmigrant seasons were used to inform the migration timing and size of juveniles outmigrating from the stream.

To predict the migration timing of juveniles, I modeled the probability of outmigration each week dependent on environmental covariates using a binomial count model. I chose a binomial distribution of outmigrants over a beta or normal distribution to predict a discrete number of outmigrants conditional on total abundance. I hypothesized temperature, flow, and density of outmigrants influence the outmigration behavior of juveniles given the well documented effect of these variables on the ecology of juvenile salmonids (Quinn 2005). Because I expected outmigration to not only depend on the temperature and flow of a specific week, but also earlier in the year when eggs and fry are developing, I expressed temperature and flow as the sum of temperature (degree days) and river discharge (cumulative flow) from January 1 each year. Air temperature and river discharge were collected at the gauging station located on Redwood Creek in Orick, CA by the US Geological Survey and Department of Water Resources.

I used non-informed Gaussian priors of mean = 0, variance = 1000 for estimating parameters. The count of outmigrants each week (i) varies as a function of the number of remaining outmigrants (N) and the unobserved probability of outmigrating (\hat{p}):

Statistical Distribution $C_i \sim \text{Binomial}(N_i, \hat{p}_i)$

\hat{p}_i was estimated with potential covariates:

Process Model
$$\text{logit}(\hat{p}_i) = \alpha + \beta_1 * \text{Degree Week}_i + \beta_2 * \text{Cumulative Flow}_i + \beta_3 * \text{Total Outmigrants}_\gamma + \varepsilon_\gamma + \delta_i$$

where *Degree Week* is the cumulative degree days C° for week i , *Cumulative Flow* is the sum of mean daily river discharge (ft³/sec) since the beginning of each year. *Total Outmigrants* is the estimated number of outmigrants for year γ based on the rotary screw trap catch. ε_γ is a random effect of year, and δ is an overdispersion correction for observations.

I selected the most parsimonious model among the global model and nested models that I chose based on results of the global model. I used posterior predictive loss (PPL) as the model selection criterion, which predicts new data and compares it to observed data to calculate a goodness-of-fit G and a variance term P that are then combined to produce a PPL score (Hooten and Hobbes 2015).

I modeled the size of outmigrants using a general linear model and the same possible covariates and prior distributions as the binomial count model. Additionally, I predicted *Degree Week* to have a quadratic relationship given the rate of increase for fork

length declines through the outmigration season. *Mean Fork Length* (mm) for week i varied normally around its mean with variance σ ,

Statistical Distribution $Mean\ Fork\ Length_i \sim dnorm(\widehat{Mean\ Fork\ Length}_i, \sigma^2)$

Process Model $Mean\ \widehat{Fork}\ Length_{i_i} = \alpha + \beta_1 * Degree\ Week_i + \beta_2 * Degree\ Week_i^2 + \beta_3 * Cumulative\ Flow_i + \beta_4 * Total\ Outmigrants_{i_i}$

To select the most parsimonious model, I used the same model selection procedure as outmigration timing.

To estimate the probability of emigration from the estuary prior to closure, as well as survival in the estuary, I fit data from 2018's marked outmigrants and estuary recaptures to a Cormack-Jolly-Seber model (CJS) (Cormack 1964; Jolly 1965; Seber 1965). Occasions were defined by week, with tags that were applied daily grouped by week. Capture probability (p) was fixed to zero during non-seining weeks. I estimated apparent weekly survival (Φ), defined as the rate of both surviving and remaining in the estuary. Apparent survival differs from true survival because it excludes those that survive and emigrate from the sampling area as survivors. I evaluated temporal constraints on weekly survival (Φ) by grouping weeks into months or by the status of the estuary mouth (open or closed) (Figure 3). After calculating Bayesian p-values to determine goodness-of-fits, I selected the temporal constraint by calculating the residual variance (σ^2) of each CJS model. Bayesian p-value was calculated by summarizing the data in the m-array format and fitting the array to a multinomial likelihood (Burnham 1987; Kery and Schaub 2012). After selecting a temporal constraint, I tested for an effect

of fish size on apparent survival by adding individual fork length as a covariate in the model. I added a size effect to the appropriate groupings of Φ if the 95% confidence interval of the posterior distribution of the size parameter did not overlap with zero. To estimate emigration when the estuary was open, I borrowed mortality from the first Φ value after mouth closure and subtracted it from apparent mortality.

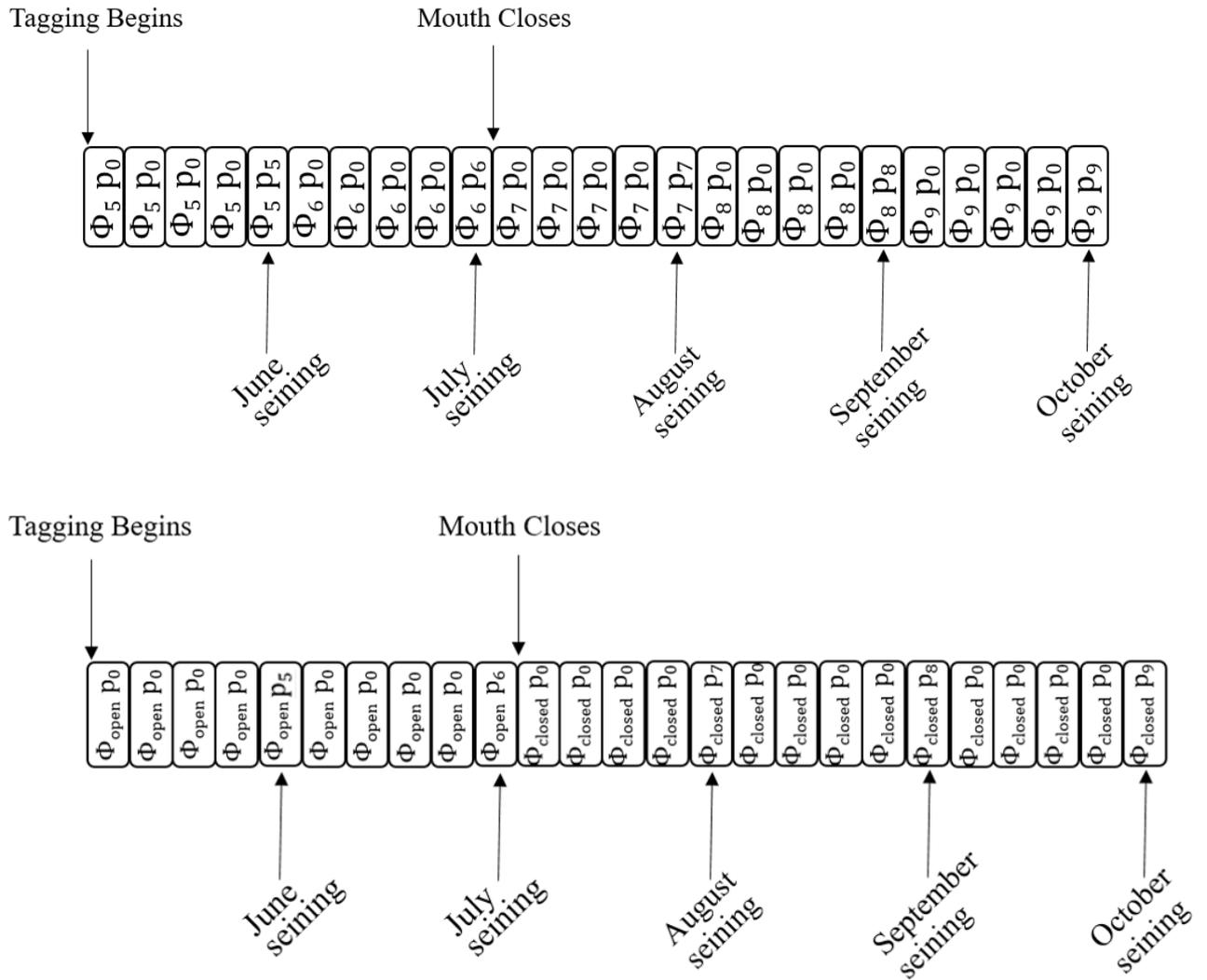


Figure 3. Conceptual diagrams of mark-recapture PIT tag data fit to a Comack-Jolly-Seber model with weekly apparent survival Φ_i grouped by monthly seining occasions i (top) and estuary status (bottom). Capture probability p is estimated for each estuary seining occasion with p equaling zero during non-seining weeks (p_0).

I applied survival and emigration calculated from the CJS model during 2018 to outmigration data from 2004-2016 to estimate abundance and survival of each life history type during those years. The number of estuary type juveniles is the estimated number of fish remaining immediately following mouth closure. The number of ocean type juveniles is the sum of juveniles that emigrated from the estuary prior to mouth closure. To estimate the number of estuary type juveniles that survive until the mouth reopens, I used the last estuary abundance calculated from seine catches and applied the weekly mortality rate calculated from our model until the mouth reopened.

Juvenile ocean survival

Ocean survival during the first year at sea (S_o) was separately calculated for each of the life histories. Ocean survival for ocean type juveniles ($S_{o.oc}$) includes the initial ocean entry during spring through the first winter. Ocean survival for estuary type ($S_{o.est}$) includes initial ocean entry in the late fall through the first winter. I calculated juvenile ocean survival for each life history type (i) for 2009-2015 brood years (γ) using the estimated number of two-year-olds (N_2) and the estimated number of juveniles entering the ocean (N_1) for each life history type,

$$S_{o.i,\gamma} = \frac{N_{2,\gamma} \times \tau_{i,\gamma}}{N_{1,i,\gamma}}$$

Proportion of each life history in the adult spawning population (τ) was estimated through scale morphometrics and otolith microstructure. I back-calculated the total number of two-year-olds for each brood year using known estimates of spawners (N_{sp}) for

each age-class (i) and survival for sub-adults (S_i). For cohorts with partial reconstructions, I used the reported maturation rate of fall-run Klamath Chinook to estimate the number of spawners for unknown $N_{sp.i}$ (Klamath River Technical Team 1986).

$$N_2 = \frac{N_{sp.2} + (N_{sp.3} + (N_{sp.4} + (N_{sp.5}/S_5)/S_4)/S_3)}{S_2}$$

Sub-adult survival

Survival after the first time-step (S_2, S_3, S_4, S_5) includes surviving harvest (I) and natural mortality (A) for the time-step. Harvest and natural mortality for these older age classes were borrowed from the estimated natural mortality and ocean harvest for fall-run Chinook salmon in the Klamath River basin (Klamath River Technical Team 1986; Prager and Mohr 2001). Sub-adult survival for the two populations is likely comparable given the high overlap in ocean distribution of California Coastal Chinook ESU and Upper Klamath-Trinity River ESU. Harvest rate equaled 0.106 for three-year olds, 0.151 for four-year olds, and 0.150 for five-year-olds (Prager and Mohr 2001; O'Farrell et al. 2012). Natural mortality was applied after harvest and equaled 0.5 for two-year-olds and 0.2 for three-, four-, and five-year-olds.

Maturation

I calculated maturation (m) for age-class (i) using the number of spawners and the estimated total number of individuals at each age for each cohort,

$$m_i = \frac{N_{sp.i}}{N_i}$$

The number of spawners (N_{sp}) for age (i) is the product of their proportion of contribution to the spawning run and the estimated total number of spawners that year. The total number of individuals in that age class was determined by reconstructing the cohort from the final year the cohort was observed. The total number of individuals (N) for each age class (i) was determined by,

$$N_i = I_i + \left(\frac{N_{sp.i} + N_{i+1}}{1 - A_i} \right)$$

where I is the estimated number of harvested individuals and A is the natural mortality rate for age class i .

Leslie matrix model

To assess the contribution of estuarine rearing to the population, I integrated parameters estimated in the life cycle model into a Leslie matrix model (Table 1). Ocean type and estuary type juvenile life histories were divided in the Leslie matrix to track their contribution. Proportion of each life history was calculated based on the weekly emigration rate from the estuary. I assumed equal fecundity, maturation, and sub-adult (Age 2 through maturity) ocean survival for the two life history types. The Leslie matrix included five annual time steps. The first year begins at outmigration from the stream and ends after the first winter (Figure 4). For ocean type individuals (oc), survival during the first year ($S_{l.oc}$) equals ocean survival from entry in the spring to the first winter ($S_{o.oc}$). First year survival for estuary type juveniles ($S_{l.est}$) includes survival in the estuary each

week once the mouth closes (Φ_{closed}) until it reopens and their ocean survival through the first winter ($S_{\text{o,est}}$). The second, third, fourth, and fifth time steps compose survival in the ocean as sub-adults. Starting at age 2, a proportion of the population spawns at maturation rate m for age i and are removed from the surviving population. Spawning adults produce smolts at a rate of F and can produce smolts of both life histories.

Table 1. Vital rate parameters in Leslie matrix model for Chinook salmon in Redwood Creek. Derivations are described in referenced portion of the text or borrowed from Klamath River fall-run Chinook.

| Leslie matrix Parameter | Equation or Value | Reference |
|-------------------------|-------------------------------------|--|
| Survival | | |
| $S_{1.oc}$ | $S_{o.oc}$ | Juvenile Ocean Survival |
| $S_{1.est}$ | $\Phi_{closed}^{weeks} * S_{o.ost}$ | Juvenile Life History; Juvenile Ocean Survival |
| S_2 | .5 | (Klamath River Technical Team 1986) |
| S_3 | .8 | (Klamath River Technical Team 1986) |
| S_4 | .8 | (Klamath River Technical Team 1986) |
| S_5 | .8 | (Klamath River Technical Team 1986) |
| Harvest | | |
| I_3 | .106 | (Prager and Mohr 2001) |
| I_4 | .151 | (Prager and Mohr 2001) |
| I_5 | .150 | (Prager and Mohr 2001) |
| Maturity | | |
| m_2 | 0.036 | Maturation |
| m_3 | 0.196 | Maturation |
| m_4 | 0.912 | Maturation |
| m_5 | 1.0 | Maturation |
| Fecundity | | |
| F | $\frac{a}{1 + \frac{S}{K}}$ | Fecundity (Spawner to Smolt) |
| Life History | | |
| p_{est} | $\frac{N_{est}}{R}$ | Fecundity (Spawner to Smolt); Juvenile Life History |
| p_{oc} | $\frac{N_{oc}}{R}$ | Fecundity (Spawner to Smolt); Juvenile Life History |

$$\begin{bmatrix}
 0 & 0 & S_2 m_2 F p_{oc} & S_2 m_2 F p_{oc} & S_3 m_3 F p_{oc} & S_3 m_3 F p_{oc} & S_4 m_4 F p_{oc} & S_4 m_4 F p_{oc} & S_5 m_5 F p_{oc} & S_5 m_5 F p_{oc} \\
 0 & 0 & S_2 m_2 F p_{est} & S_2 m_2 F p_{est} & S_3 m_3 F p_{est} & S_3 m_3 F p_{est} & S_4 m_4 F p_{est} & S_4 m_4 F p_{est} & S_5 m_5 F p_{est} & S_5 m_5 F p_{est} \\
 S_{1.oc} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & S_{1.est} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & S_2(1 - m_2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_2(1 - m_2) & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & S_3(1 - m_3) & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_3(1 - m_3) & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & S_4(1 - m_4) & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_4(1 - m_4) & 0 & 0
 \end{bmatrix}$$

Figure 4. Leslie matrix model for Chinook salmon in Redwood Creek, partitioned by juvenile life history. S_i = survival in time step i for ocean type (oc) and estuary type (est) juveniles, m_i = age specific maturation rate, F = smolt per spawner rate, and p = proportion oc and est juveniles.

To evaluate the current population trajectory, I projected the population's demographics for ten years. For the initial abundance of juveniles (Age 1), I used the mean estimated number of estuary type and ocean type juveniles from 2004-2016 cohorts. Initial abundance of Age 2 to Age 5 individuals for each life history was the mean number of individuals for each age class based on reconstructions of 2009-2015 cohorts, partitioned into life histories using the mean proportion of estuary- and ocean-type life histories in the spawning population.

Parameters within the Leslie matrix remained fixed during each time step except for fecundity (F) and the juvenile proportion (p) of each life history (i), which was calculated during each time step. Density-dependent fecundity (smolts-per-spawner) was calculated each time using the estimated number of returning adults and the Beverton-Holt function for the population. The expected number of juveniles and mean environmental conditions from 2004-2016 were used to predict the outmigration timing and size of juveniles. As juveniles outmigrated from the stream into the estuary, I applied the 2018 weekly apparent survival to the estuary population. For mouth closure and breach dates, I used the mean dates of closure and breaching from 2004-2016 and assumed all estuary fish transition to the juvenile ocean stage once the mouth breaches.

Sensitivity analysis

I assessed how future anticipated changes in the environment may affect the distribution of life histories and spawner recruitment through a sensitivity analysis. Anticipated changes in the environment include changes in the region's climate and

restoration in the estuary. On the North Coast of California, temperatures are expected to increase 0.6-1.0°C in the summer season and 1.0-1.4°C in the winter season by the mid-century (2040-2069) (Grantham 2018). I evaluated this increase in temperature on the outmigration timing and size of juveniles. I propagated the changes to outmigration timing and size on estuary abundance and contribution of each life history to determine how estuary residency may change with warmer temperatures upstream.

Although restoration in the watershed has primarily been focused on reducing sediment input upstream (Madej and Ozaki 2009), the value of restoring the estuary is recognized among managers in the watershed. Removing dikes and levees confining estuaries have expanded floodplains and salt marshes and increased estuarine use in other watersheds (Sommer et al. 2001; Bottom et al. 2005). These habitats provide higher growth for juveniles than mainstem freshwater habitats, but whether they also provide higher survival while rearing is less apparent (Sommer et al. 2001; Hayes et al. 2008; Johnston et al. 2018). To assess the effects of estuary restoration in the sensitivity analysis, I raised the growth rate of estuary juveniles throughout the entire summer to the growth rate during months when the growth ratio (r) was highest. I calculated the potential size of juveniles by late fall using the estuarine growth model. Potential and actual weights were converted to fork lengths using the weight-length relationship reported for Trinity River Chinook salmon in Perry et al. 2018. To approximate how a larger ocean entry size may increase juvenile ocean survival, I increased juvenile ocean

survival of estuary fish using estimates of size-selectivity for ocean survival of Chinook salmon with similar sizes (Claiborne et al. 2011).

RESULTS

Life History Reconstruction Using Scale Morphometrics and Otolith Microstructure

Juvenile life history

The majority of adult spawning salmon returning to Redwood Creek between 2011 and 2017 were ocean type fish. Using scale samples from 2006-2015 brood years, I categorized individuals as estuary type if the ratio of circuli at ocean entry to circuli at first winter exceeded 0.8 (Figure 5 Histogram of ratio of number of circuli at ocean entry to number of circuli at first winter Figure 5). Of the 214 adult scale samples, I identified only seven individuals (3%) that had circuli patterns representative of the estuary type life history (Table 2). The mean estimated proportion of estuary type individuals in the spawning population was 0.109 ($\sigma^2 = 0.100$). The mean number of circuli on scales from juvenile fish in the estuary in October 2018 was 20.6. The mean number of circuli at ocean entry for ocean type juveniles was 15.0, while the mean for estuary type juveniles was 26.6 (

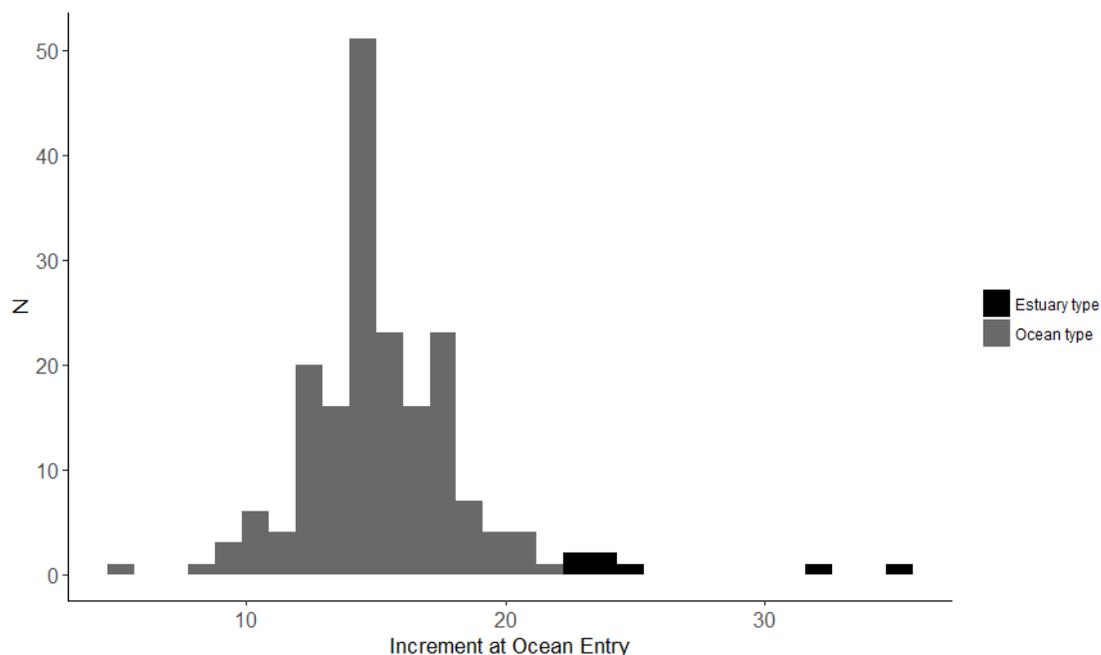


Figure 6).

Table 2. Juvenile life history assessments from adult scale samples from 2011-2016, 2017 spawning seasons. τ_{est} is the estimated proportion of estuary type life history in the adult population.

| Brood Year | Samples Estuary Life History | τ_{est} | Sample Size n |
|------------|------------------------------|---------------------|-----------------|
| 2006* | 0 | | 1 |
| 2007* | 0 | | 1 |
| 2008* | 0 | | 3 |
| 2009 | 3 | 0.268 | 13 |
| 2010 | 0 | 0.016 | 60 |
| 2011 | 1 | 0.036 | 54 |
| 2012 | 0 | 0.038 | 25 |
| 2013 | 1 | 0.182 | 9 |
| 2014 | 2 | 0.186 | 14 |
| 2015 | 0 | 0.039 | 24 |

* denotes too small sample size to incorporate in later calculations

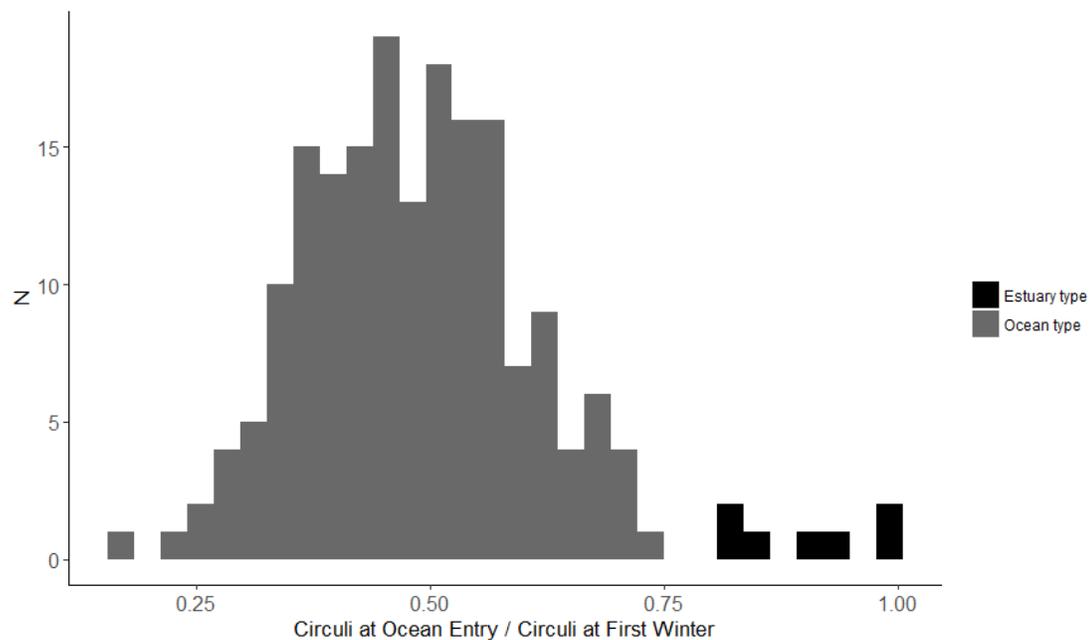


Figure 5 Histogram of ratio of number of circuli at ocean entry to number of circuli at first winter.

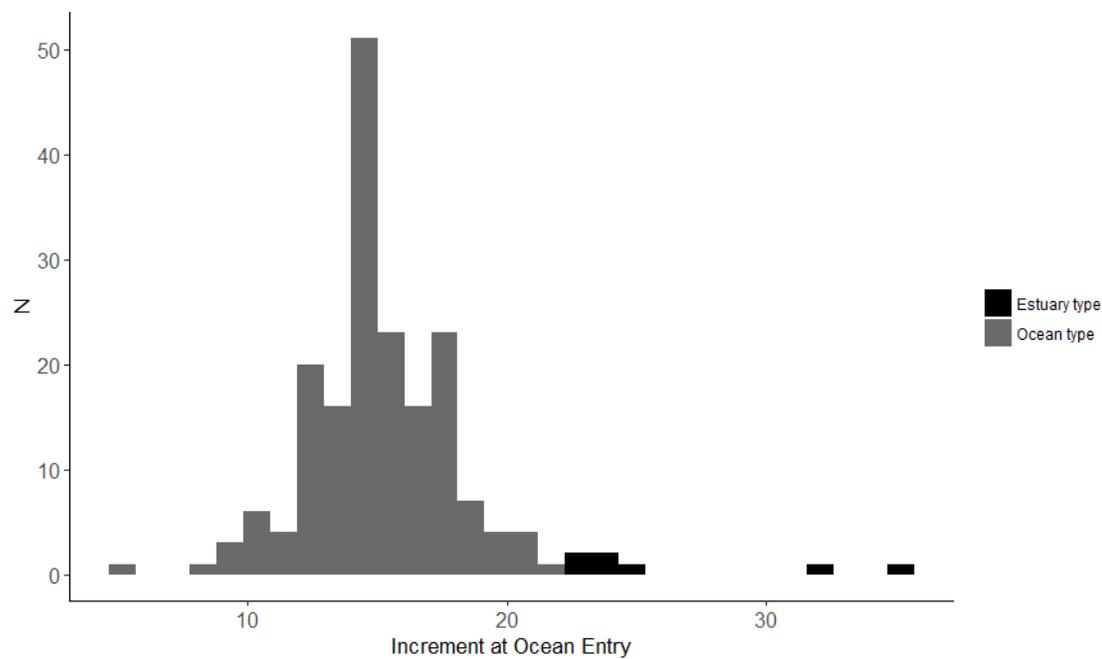


Figure 6. Histogram of increment of ocean entry for adult scales collected from 2011-2015, 2017.

There were twenty-eight scale samples from the 2017 spawning season that had a corresponding otolith sample that could be analyzed (Appendix D). Of the twenty-eight otoliths analyzed from the 2017 spawning season, twenty-three had back-calculated fork lengths by fall greater than the maximum observed fork length in the estuary from 2013-2016 (maximum = 144 mm) and were automatically categorized as ocean type juveniles (Anderson 2013, 2014, 2015, 2016). Of the five samples that were within range of estuary size in the late fall, one sample (ID 19137 in Appendix D) had a spring ocean entry check and was also categorized as ocean type. Another sample (ID 18041) had a clear, late ocean entry check and was identified as an estuary type. The remaining three otolith samples had uncertainty regarding ocean entry and could not be categorized into a juvenile life history type based on otolith sample. One sample (ID 19514) was ultimately categorized as estuary type based on scale pattern and two were ultimately categorized as ocean type (ID 28917, ID 18362).

Age composition

I identified two-, three-, four-, and five-year old spawners through scale analysis. Four-year old spawners were most common in all years, except for 2017, when three-year olds were most prevalent (Figure 7). Across years, 10.3 percent of spawners were age two, 22.1 percent were age three, 58.7 percent were age four, and 8.9 percent of spawners were age five.

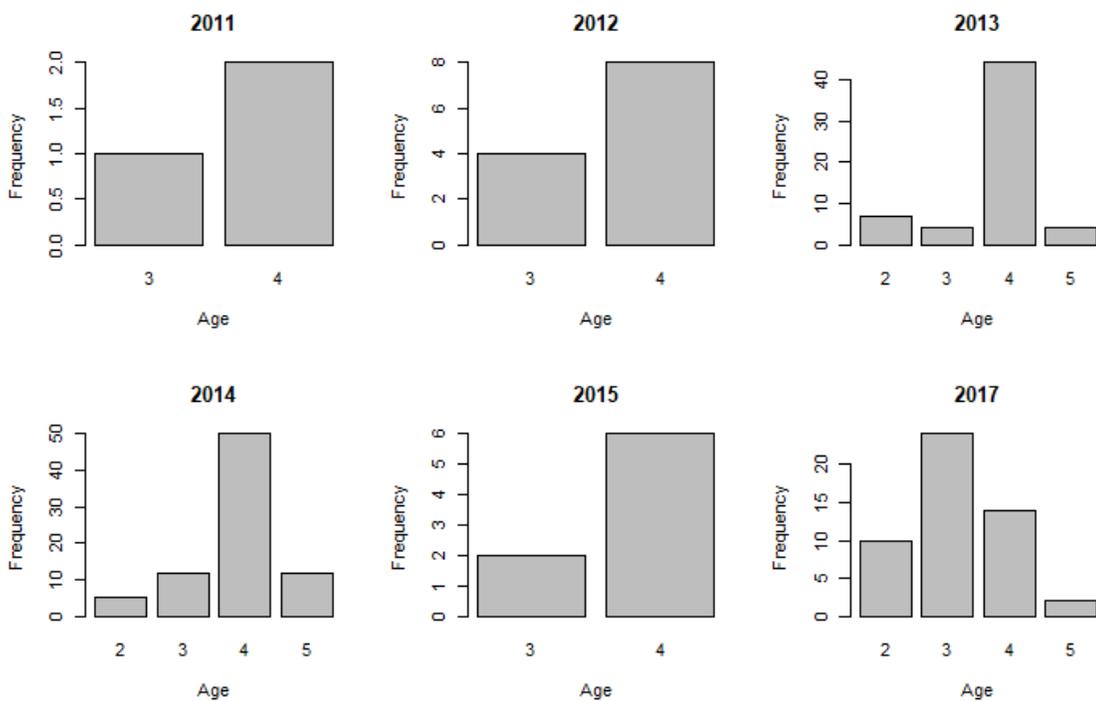


Figure 7. Histogram age-classes present in sampled scales for each fall spawning year in Redwood Creek

Estuarine Growth Model

Estuarine growth in recaptured individuals was lower when the mouth was closed versus open according to both absolute growth measurements and the Ratkowsky growth equation. Absolute growth rates for recaptured fish each month are reported in Table 3. The mean estuary temperature between capture and recapture (T), an input for the Ratkowsky growth equation, was highest for individuals captured during July, August, and September seining events (Figure 8. Mean temperature ($^{\circ}\text{C}$) experienced by recaptured fish from the date fish were initially tagged to their recapture. Mean temperature was inputted into the Ratkowsky growth equation to calculate optimum growth. Figure 8). The mean growth ratio (r) in June was $.81$ ($\sigma^2 = .34$, $n = 4$) and $.60$ ($\sigma^2 = .18$, $n = 5$) in July. In August, mean r equaled $.26$ ($\sigma^2 = .18$, $n = 7$). In September and October, mean r equaled $.23$ ($\sigma^2 = .17$, $n = 5$) and $.37$ ($n = 1$), respectively (Figure 9).

Table 3. Absolute growth rate since capture of juveniles recaptured in the estuary each month in 2018.

| Month of Recapture | ΔFL (mm)/day | %FL increase/day | ΔWt (g)/day | %Wt increase /day | Sample size (n) |
|--------------------|-------------------------------|---------------------|------------------------------|----------------------|--------------------|
| June | .26 | .41 | .073 | 2.4 | 5 |
| July | .39 | .67 | .070 | 2.4 | 6 |
| August | .11 | .18 | .031 | .94 | 10 |
| September | .17 | .21 | .043 | .75 | 8 |
| October | .31 | .33 | .096 | 1.0 | 1 |

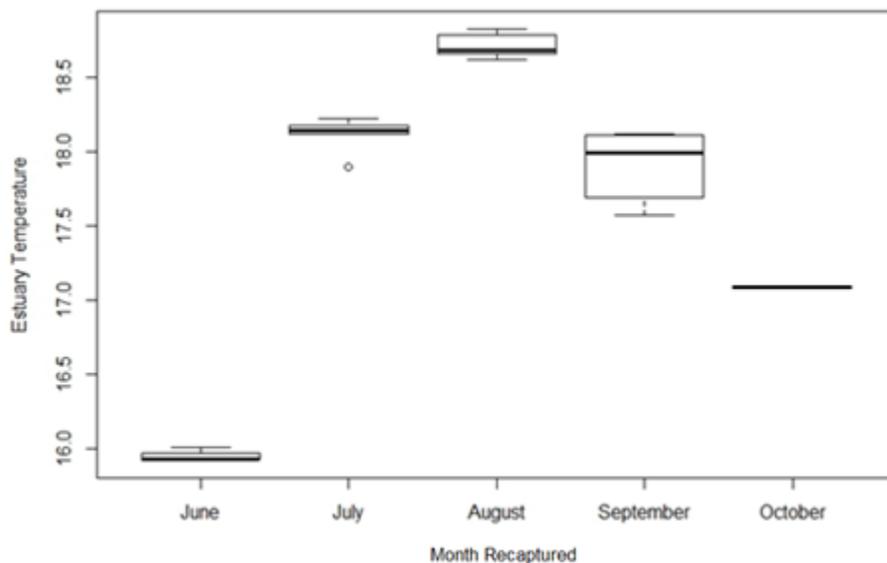


Figure 8. Mean temperature ($^{\circ}\text{C}$) experienced by recaptured fish from the date fish were initially tagged to their recapture. Mean temperature was inputted into the Ratkowsky growth equation to calculate optimum growth.

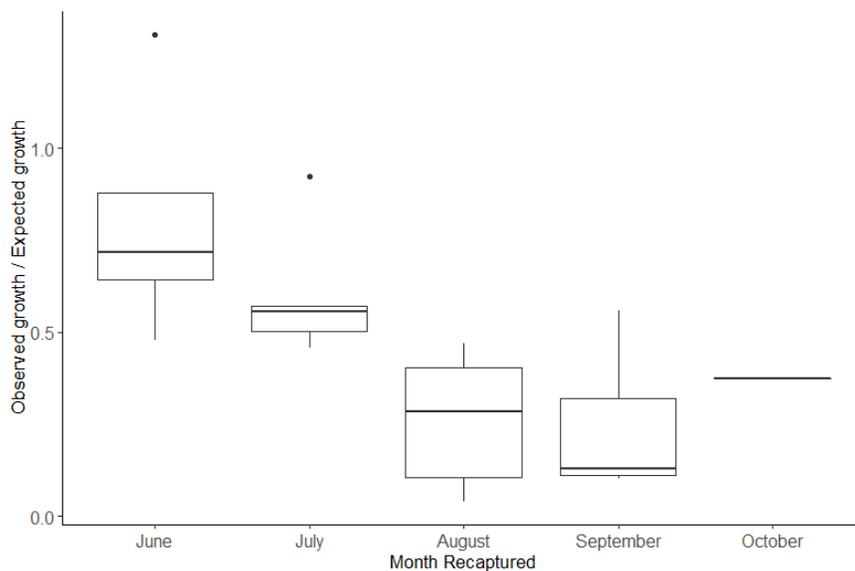


Figure 9. Ratio of observed growth rate to expected growth rate (r) of recaptured fish in the estuary through the summer. Expected growth was calculated using the Ratkowsky growth equation.

Life Cycle Model

Fecundity (spawner to smolt)

Using a Beverton-Holt function, I evaluated density dependence on the number of smolts produced per spawner (Figure 10). The carrying capacity (K) of spawners was estimated to be 3452 ($\sigma = 1071$) and the smolt productivity parameter (a) equaled 255.2 ($\sigma = 30.72$). In years with low spawner abundance ($n= 500$), I estimated a smolt-per-spawner rate of 222.9. At carrying capacity, the estimated smolt-per-spawner rate was 127.6.

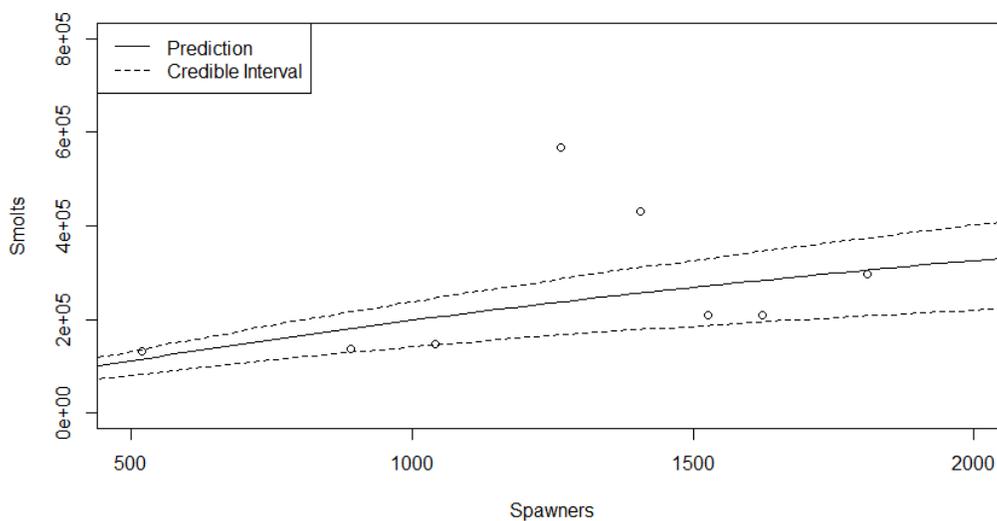


Figure 10. Beverton-Holt spawner-smolt curve for Chinook salmon in Redwood Creek. Points indicate estimated spawner and subsequent outmigrant abundances from 2010–2015, 2017 spawning seasons.

Juvenile life history

I fit outmigrant data to a binomial count model to predict the number of weekly outmigrants. The top-ranked model estimated the number of outmigrants each week using degree week ($\beta_1 = 2.251$, 95% confidence interval = 2.076 – 2.432) and total outmigrants ($\beta_4 = 0.472$, 95% confidence interval = 0.240 – 0.708) (Appendix E.1; Goodness-of-fit: Appendix E.2). Cumulative river discharge, which was evaluated in the global model and in other nested models, did not improve predictions of weekly outmigration probability (Table 4). In the top-ranked model, both degree week and cohort size had a positive relationship with probability of outmigration in a given week (Figure 11. Proportion of remaining Chinook salmon juveniles outmigrating each week in Redwood Creek, CA. Points indicate observed proportion from 2004-2016, and 2018 outmigration seasons. Lines indicate the predicted probability of outmigrating for a given week across degree weeks for different juvenile densities using the top-ranked model. **Figure 11 Error!**

Reference source not found.)

Table 4. Model comparison for the binomial outmigration model, ranked by Δ PPL. α = intercept, β_1 = Degree week, β_2 = Cumulative river discharge, β_3 = Total outmigration count. The optimum model was selected using posterior predictive loss.

| | Bayesian P-value | Fit (G) | Prediction Variance (P) | Posterior Predictive Loss D_∞ | Δ PPL |
|--|---------------------|---------|-------------------------------|--|--------------|
| $\alpha + \beta_1 + \beta_3$ | .577 | 1056 | 4148203 | 4149259 | 0 |
| $\alpha + \beta_1 + \beta_2 + \beta_3$ | .572 | 1079 | 4157946 | 4157962 | 8703 |
| $\alpha + \beta_1$ | .588 | 941 | 4157020 | 4159025 | 9766 |

| Bayesian P-value | Fit (G) | Prediction Variance (P) | Posterior Predictive Loss D_∞ | ΔPPL |
|---------------------|---------|-------------------------------|--|--------------|
|---------------------|---------|-------------------------------|--|--------------|

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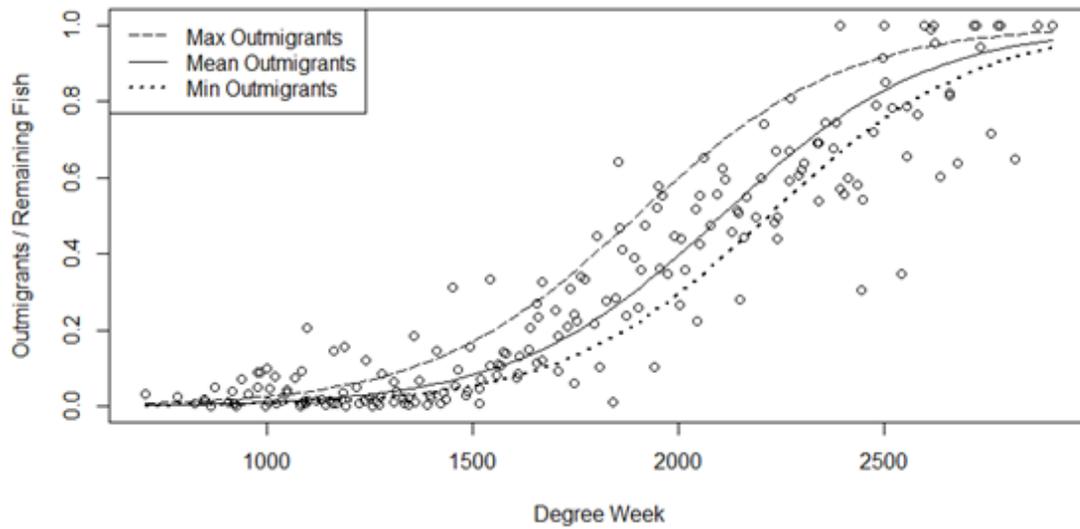


Figure 11. Proportion of remaining Chinook salmon juveniles outmigrating each week in Redwood Creek, CA. Points indicate observed proportion from 2004-2016, and 2018 outmigration seasons. Lines indicate the predicted probability of outmigrating for a given week across degree weeks for different juvenile densities using the top-ranked model.

Mean fork length of outmigrants was modeled using a general linear model with degree week, degree week², cumulative river discharge, and total outmigrants as covariates in the global model. The model selected using posterior predictive loss included degree week ($\beta_1 = 14.588$, 95% confidence interval = 13.838 – 15.329), degree week² ($\beta_2 = -2.388$, 95% confidence interval = -3.151 – -1.638), and total outmigrants ($\beta_3 = -0.837$, 95% confidence interval = -1.547 – -0.708). Total outmigrant had a relatively weak, but significant effect on outmigrant size and was included because of its improvement to model predictions (Table 5; Figure 12). Cumulative river discharge had a weak, non-significant positive effect on fork length and was excluded.

Table 5. Model comparison for the outmigrant size model, ranked by Δ PPL. B_0 = Degree week, B_1 = Degree week², B_2 = Cumulative river discharge, B_3 = Total outmigration count. The optimum model was selected using posterior predictive loss.

| | Bayesian P-value | Fit (G) | Prediction Variance (P) | Posterior Predictive Loss D_∞ | Δ PPL |
|--|---------------------|---------|-------------------------------|--|--------------|
| $\alpha + \beta_0 + \beta_1 + \beta_3$ | .508 | 5009 | 5262 | 10271 | 0 |
| $\alpha + \beta_0 + \beta_1 + \beta_2 + \beta_3$ | .501 | 5019 | 5319 | 10339 | 67 |
| $\alpha + \beta_0 + \beta_1 + \beta_2$ | .504 | 5100 | 5350 | 10449 | 178 |
| $\alpha + \beta_0 + \beta_1$ | .492 | 5123 | 5365 | 10493 | 222 |

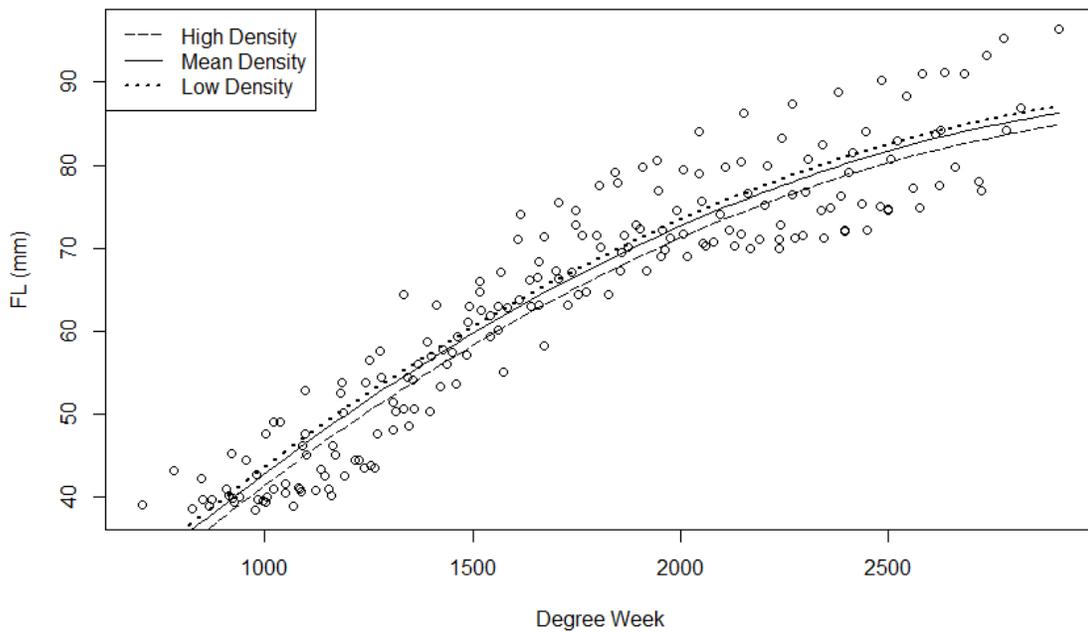


Figure 12. Mean fork length (mm) of outmigrating Chinook salmon each week in Redwood Creek, CA. Points indicate observed mean sizes from 2004-2016, and 2018 outmigration seasons. Lines indicate the predicted mean size of outmigrants for a given week across degree weeks for different juvenile densities using the top-ranked model.

The selected Cormack-Jolly-Seber model constrained Φ by estuary mouth status (open vs closed) and had a size-dependent Φ when the estuary mouth was open (Table 6). Residual variance for CJS models with different temporal constraints were comparable, so I chose the more parsimonious model with the fewer parameters (estuary mouth status). Apparent survival was lower in months when the estuary was open and ocean entry was possible (Table 7) **Error! Reference source not found.** Size had a negative effect on Φ when the estuary mouth was open ($\beta_{\text{open}} = -.613$, $\sigma^2 = .288$). Size only had a weak positive effect on Φ when the mouth was closed ($\beta_{\text{closed}} = .178$, $\sigma^2 = .210$), and β_{closed} was subsequently excluded.

Table 6. Model comparison for Cormack-Jolly-Seber models with different temporal constraints for apparent survival Φ .

| | Bayesian P-value | Residual variance σ^2 |
|-------------------------------------|------------------|---------------------------------|
| model(Φ_{mouth}, p_t) | .88 | 34.260 |
| model(Φ_{month}, p_t) | .89 | 35.226 |

Table 7. Estimated and derived weekly vital rates from the Cormack-Jolly-Seber mark-recapture model in the estuary.

| | Apparent Survival | True Survival | Emigration | Mortality |
|--------|----------------------|---------------|------------|-----------|
| Open | .325 | - | .433* | .242* |
| Closed | .758 | .758 | 0 | .242 |

* denotes rates derived from estimated parameters in the mark-recapture model.

To estimate the abundance of fish remaining in the estuary in 2004-2016, I applied mortality and emigration rates (Table 7) to weekly outmigrant data from those years and estimated an average of 0.109 of the migrants remain in the estuary after mouth closure ($\sigma^2 = 0.108$, range= 0.000980–0.301) (Figure 13**Error! Reference source not found.**; Figure 14). The mean estimate of estuary abundance immediately after mouth closure was 24,971 individuals ($\sigma^2 = 37,305$; range: 190–138,074) (Figure 14). Using a combination of the final seining abundance estimate and the weekly mortality Φ , the mean number of juveniles estimated to enter the ocean after the mouth reopened was 2,377 ($\sigma^2 = 3,084$; range 9-11,061).

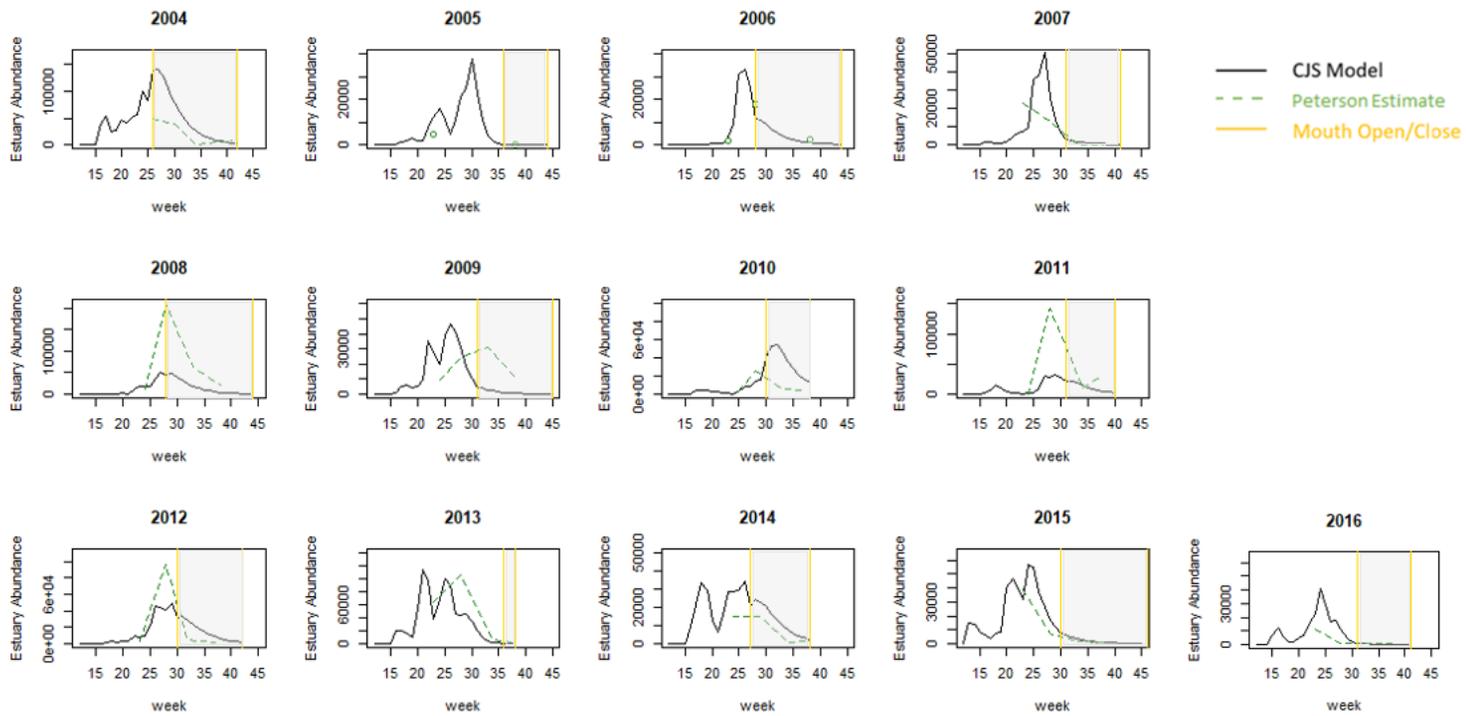


Figure 13. Abundance of juvenile Chinook salmon in Redwood Creek estuary as predicted using parameters from the Cormack Jolly Seber model (black) and Petersen estimate (green).

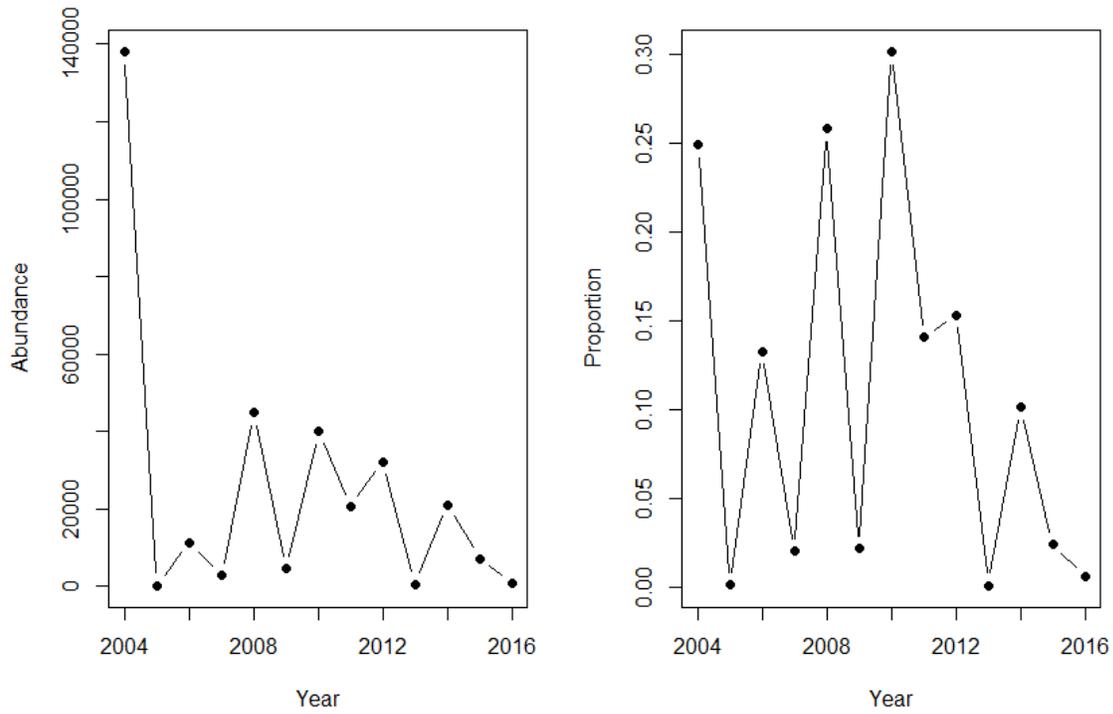


Figure 14. Estuary type abundance (left) and proportion (right) at time of mouth closure from 2004-2016 calculated using the rotary screw trap data from those years and parameters for emigration and survival estimated from the Cormack-Jolly-Seber model.

Juvenile ocean survival

Juvenile ocean survival S_o was variable across years (Figure 15). For 2009-2015 cohorts, the mean ocean survival for ocean type juveniles from ocean entry in the spring through the first winter was 0.038 ($\sigma^2 = 0.052$). The mean survival for estuary type from ocean entry in the late fall through the first winter was 0.22 ($\sigma^2 = 0.23$).

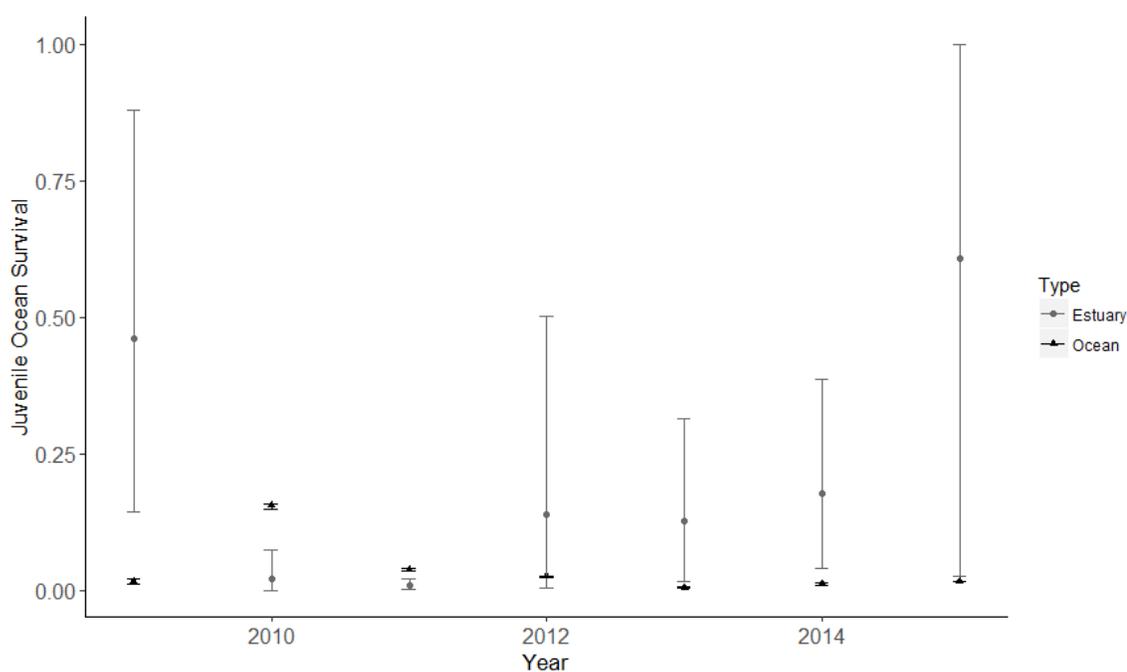


Figure 15. Ocean survival during the first year at sea for estuary and ocean type juveniles for 2009-2015 brood year.

Maturation

Using the proportion of age-classes from each spawning year and the estimated number of spawners, I fully reconstructed cohorts from 2009, 2010, 2011 and partially the cohort from 2008. Maturation for the 2-year-olds was calculated to be 0.032.

Maturation rate for 3- and 4-year-olds was 0.156 and 0.897, respectively. As the oldest age encountered, 5-year-olds had a maturation rate of 1.0.

Leslie matrix model

I fit parameters of the life cycle model into a Leslie matrix model and projected the population abundance for 10 years. I tracked the juvenile proportion and spawning contribution of each life history. The 10-year population growth rate was -0.08 and the estimated population abundance (excluding young-of-year) decreased from 12,451 individuals to 11,438 individuals. The model estimated the projected mean juvenile percentage of estuary type life history to be 9.56 percent and their contribution to be 6.84 percent. Projected spawning adult abundance equaled 1,426 adults.

Sensitivity analysis

I evaluated how climate change and different habitat restoration would influence performance and total population growth through a sensitivity analysis. When I increased the mean daily temperature by 1.0 °C, the predicted temperature change on the North Coast of California (Grantham 2018), juveniles outmigrated sooner and estuarine residency in the population declined by 79.7 percent. With a higher proportion of juveniles entering the ocean before the mouth closes, the 10-year population abundance

increased 13.5 percent due to the current lower smolt-to-adult survival of estuary type fish (Table 8; Figure 16).

Table 8. Projected 10-year population growth rate, spawning adult abundance, and mean prevalence and contribution of life histories under current parameters and future scenarios.

| Scenario | 10-year population growth rate | Spawning adults in 10 years | % Estuary Juvenile | % Estuary Adult | % Ocean Juvenile | % Ocean Adult |
|---------------------|--------------------------------|-----------------------------|--------------------|-----------------|------------------|---------------|
| As is | -0.08 | 1426 | 9.56 | 6.84 | 90.4 | 93.2 |
| Climate Change | 0.04 | 1601 | 1.95 | 1.04 | 98.1 | 99.0 |
| Estuary Restoration | 0.25 | 1932 | 7.86 | 19.2 | 92.1 | 80.8 |

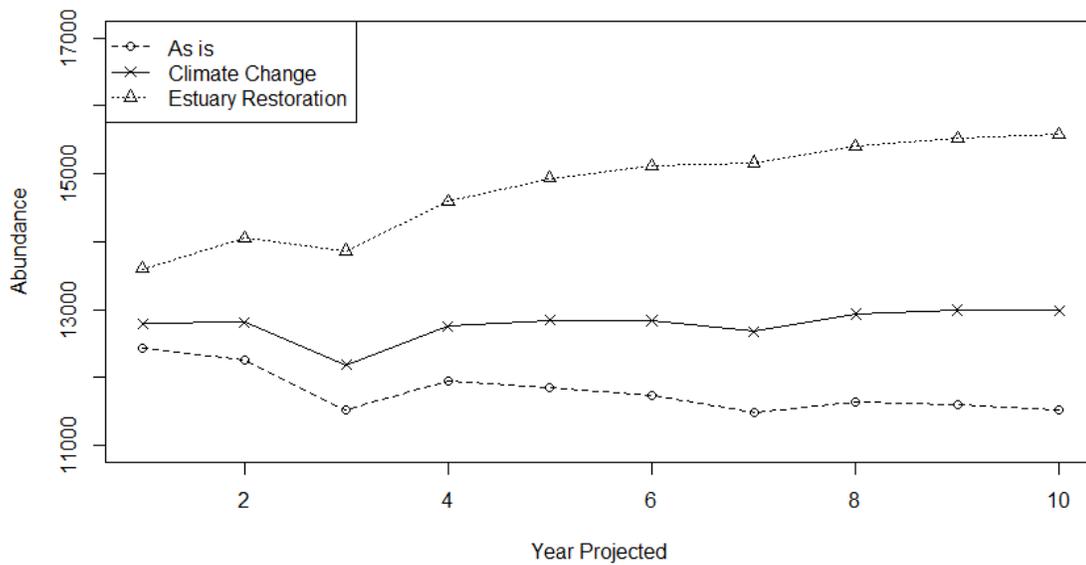


Figure 16. 10-year population projection under anticipated future environmental changes in Redwood Creek. Young of the year are excluded from population abundance.

I tested for potential effects of estuary restoration by increasing growth in the estuary and propagating its effects on ocean survival. I raised the growth ratio (r) throughout the summer of 2018 to 0.705, the mean growth ratio in June and July when the mouth was open and growth was higher. Under higher growth conditions, the estimated mean size of juveniles by late fall increased from 95.5 mm to 141.4 mm. Using reported values of size-selectivity in ocean survival from Claiborne et al. 2011, I estimated ocean survival for estuary juveniles with a mean fork length of 141.4 mm ($\sigma^2 = 9.517$) to be 4.1 times greater than survival of juveniles with a mean fork length of 95.5 mm ($\sigma^2 = 9.517$). Survival for estuary juveniles during their first year increased from 1.7 percent to 7.0 percent. With this higher juvenile survival rate, contribution of the estuary type life history nearly tripled. The 10-year population abundance increased by 36.2 percent and the estimated adult spawning population in ten years increased from 1,350 to 1,932 adults (Table 8).

DISCUSSION

Estuaries are influential juvenile rearing habitats that affect timing and size of ocean entry, primary factors that determine survival during the first year at sea. This thesis assessed Redwood Creek estuary as juvenile rearing habitat and answered how the dynamics of a bar-built estuary affect recruitment of Chinook salmon. I measured and compared vital rates of two life histories that rear in different habitats and enter the ocean during different seasons. I integrated empirical data into a series of statistical and mechanistic models to 1) identify individual and environmental propensities for estuarine rearing 2) measure juvenile abundance, growth, and survival in the estuary 3) compare overall survival and contribution of life history types to the adult spawning population 4) anticipate the response of Chinook salmon in Redwood Creek to future environmental changes and potential restoration actions.

Individual and Environmental Propensities for Estuarine Rearing

To determine if size affected whether juveniles remain in the estuary, I tested for size-dependence on apparent survival. When the mouth was open and both emigration and mortality were possible, apparent survival declined with size. Therefore, larger individuals were more likely to leave the estuary either through death or emigration. Since larger fish are generally considered to have higher survival (Healey 1982; Henderson and Cass 1991), I interpret this relationship as support for larger fish having

higher emigration. Furthermore, if simultaneously smaller individuals had higher mortality, the positive effect of size on emigration is stronger than predicted because emigration and mortality would have opposing effects on size-dependence for apparent survival. Size had a weak positive effect on survival when the mouth was closed (β_{closed} 95% confidence interval = $-.176 - .642$), suggesting size-dependent mortality on apparent survival when the mouth was open is likely minor.

In addition to smaller individuals, later outmigrants were also more likely to become estuary type juveniles. Early migrants are unlikely to both survive and remain in the estuary until the mouth closes (Table 7). Fish recaptured in the estuary were often recently tagged outmigrants. All fish recaptured in the closed estuary from August to October were tagged after the mouth closed in July or the week prior. No fish tagged in May or June were recaptured in the estuary after the mouth closed. Apparent survival in the estuary was low, approximately 33 percent each week (one percent each month) when the estuary was open. Earlier migrants are less likely to be in the estuary after mouth closure either because they perished or emigrated. Because estuarine residency is dependent on the size and migration timing of juveniles, environmental conditions upstream impact the prevalence of rearing in the estuary.

Temperature in the freshwater environment influences juvenile development and subsequently their size and outmigration timing (Bohlin et al. 1993; Whalen et al. 1999; Kovach et al. 2013). Both the probability of outmigration and migrant size increased with degree week. This metric of temperature is the sum of degree days and therefore accounts

for the time of year and temperature relative to other years. Time of year primarily drove the positive relationship as juveniles are more likely to outmigrate and be larger later in the migration season.

Warmer years, however, accumulate degree days more quickly and may alter juvenile migration. From incubation to outmigration, temperature regulates many functions that affect development (Crozier et al. 2010). Temperature affects the incubation time of eggs, and warmer temperatures result in earlier hatch dates (Alderdice and Velsen 1978). Earlier hatch times from warmer temperatures may produce earlier migrations and larger individuals, both of which increase the probability of ocean entry before the mouth closes (Bohlin et al. 1993; Whalen et al. 1999).

Cohort size influenced outmigration timing and size, and estuary abundance may be greater in years of high abundance if juvenile capacity upstream is limited. In years of high outmigrant abundance, juveniles outmigrated from freshwater earlier and at a smaller size. Smolt abundance reflects juvenile density in habitats upstream, and competition for food and territory increases with abundance (Grant and Imre 2005). Earlier migration and smaller outmigrants size suggest the capacity for juvenile rearing in the freshwater system is limited. Redwood Creek is listed in the Clean Water Act because of sedimentation in the river, which reduces habitat for juveniles and the macroinvertebrates they consume and may be largely responsible for decline in stream productivity and capacity for juvenile salmonids. During years of high abundance, more juveniles may be outmigrating to rear in the estuary. The population may rely on the

additional habitats downstream in the estuary during years of the high abundance, especially if juveniles are smaller (Healey 1980; Roegner et al. 2012).

Juvenile Abundance, Growth, and Survival in Redwood Creek Estuary

From 2004-2016, the percentage of juveniles remaining after closure ranged from zero to thirty percent of smolt abundance (Figure 14). The abundance of juvenile Chinook salmon remaining in the estuary after mouth closure depended on both migration timing and time of sandbar formation. As previously discussed, the former is dependent on the environment and number of conspecifics upstream. Timing of sandbar formation is dependent on river flow, tidal forces, and geomorphology of the mouth inlet (Heady et al. 2015). I tested whether river discharge alone predicted the timing of estuary closure and found no relationship. Because the mouth closes as waves deposit more sand than the river can scour, tidal parameters such as wave height and intensity influence timing of bar formation (Behrens et al. 2013). Annual variation in the morphology of the entrance of the river, such as mouth width and degree of channel bending, may determine how soon waves close the mouth (Behrens et al. 2013).

The growth ratio (r) was lower when the mouth was closed versus open, suggesting lack of ocean access, or the processes causing this phenomenon, reduce growth in the estuary. Low flow during summer months, which contributes to mouth closure, influences not only the amount of food flowing from upstream, but also physical conditions in the estuary that affect food productivity and juvenile metabolism within the

estuary (Hayes et al. 2000; Heady et al. 2015). Bar closure reduces mixing and flushing of the estuary and can raise water temperature and lower dissolved oxygen (Behrens et al. 2013).

Redwood Creek estuary has limited marine influx when the mouth is closed, affecting diet and consequently growth (Larson 1987). From scale morphometrics, growth in the estuary appeared comparable to growth upstream. I observed no change in circuli spacings in juvenile scales collected in the estuary, nor intermediate spacings in circuli prior to ocean entry in adult scales. A previous analysis of food habits in Redwood Creek showed similar diet composition upstream and in the estuary prior to the berm breaching (Larson 1987). That study found that Chinook salmon diet in Redwood Creek estuary consisted primarily of Dipterans and is more similar to diets in freshwater habitats than those in brackish estuaries, which is typically comprised of amphipods, isopods, and mysids. Bar-built estuaries may have prey communities more similar to freshwater environments than other types of estuaries because of their limited marine influence.

With limited marine influence when closed, production of food is dependent on the estuary and surrounding habitats (Largier and Taljaard 1991). Despite limited marine input, some bar-built estuaries remain highly productive and have high juvenile salmonid growth rates throughout summer months for more thermally tolerant species (*Oncorhynchus mykiss* in Bond et al. 2008). When closed, bar-built estuaries may inundate surrounding marsh or floodplains, increasing terrestrial input and drift

invertebrates (Sommer et al. 2001; Behrens et al. 2013). While mouth closure may be reducing marine prey, this phenomenon may also increase productivity through flooding of seasonally inundated floodplains. Levees constructed in the lower Redwood Creek prevent flooding and establishment of marsh and floodplain habitat, potentially majorly limiting the productivity of the estuary and salmonid growth. Limited growth in Redwood Creek estuary produces juveniles smaller than their ocean rearing counterparts at the end of summer.

Constraining apparent survival in the CJS model by month versus by status of the estuary's mouth did not improve model fit, suggesting survival in the estuary after mouth closure remained relatively constant during the year of the mark-recapture experiment. True survival in the estuary was only estimated when the mouth was closed and emigration into the ocean was not possible. Although emigration into the ocean was barred, I detected evidence of some juveniles returning upstream or to Prairie Creek tributary in July and August after the mouth closed. Approximately three percent of juveniles ($n = 20$) tagged at the rotary screw trap after or near mouth closure were detected at a PIT tag antenna array in Prairie Creek, a main tributary, near its confluence with Redwood Creek. While some individuals may have been consumed by coastal cutthroat trout and detected within the gut of the predator, detections for several days suggest some proportion are from individuals returning upstream after the mouth closed, possibly because of high temperatures or lack of ocean access. Because of this emigration upstream, I expect the estimate of survival to be biased low.

Smolt-to-Adult Survival and Contribution of Life History Types

Although not the case for all years, juveniles remaining in the estuary after the mouth closed generally had lower survival than their ocean rearing counterparts. I estimated a mean of 19.8 percent of the smolt population remaining after bar closure, but only found 10.9 percent of adult scale samples exhibited this life history. Estuary and ocean type fish experience mortality differently during the early ocean phase due to their different ocean entry sizes and times. Mortality during the first year at sea occurs in two stages: predation during initial ocean entry and starvation during winter (Beamish and Mahnken 2001). Juveniles that enter the ocean in the early summer are more susceptible to the former because of their smaller ocean entry size and longer rearing time in the ocean. Estuary type juveniles have a higher risk of mortality than their counterparts during the winter period.

Mortality for estuary type juveniles is more variable during winter because they may be more sensitive to fluctuations in annual ocean conditions. Estuary type juveniles are smaller than ocean type juveniles at the start of winter; therefore, they are more affected by the favorability of ocean conditions during winter. Ocean type juveniles are also affected by variation in ocean conditions during winter, but additional mortality during initial ocean entry and ocean rearing keep ocean survival for this life history type more consistent. The intensity of size selective mortality changes with ocean productivity (Woodson et al. 2013). There are numerous (up to 31 in Burke et al. [2013]) contributing

factors that influence salmon ocean productivity during winter. Large global processes, such as the Pacific Decadal Oscillation, have the potential to influence survival through multiple physical and biological intermediaries such as sea-surface temperature and ichthyoplankton density (Burke et al. 2013; Malick et al. 2015). Fluctuations in processes influencing mortality complicate the performance of life histories and result in varying success across years.

Predicted Response to Future Environmental Change and Restoration

Future anticipated changes to the environment in Redwood Creek include an increase in mean daily temperature on the North Coast and potentially restoration by the Redwood Creek Management Council. Because temperature was a covariate in the freshwater portion of the life cycle model, an increase in temperature impacted the migration timing and size of outmigrants. Higher temperatures resulted in earlier and larger outmigrants, subsequently affecting the distribution of life history types. Larger smolts and an earlier outmigration predict more juveniles will emigrate to the ocean prior to mouth closure, decreasing the prevalence of estuary type juveniles. Because ocean juveniles had an overall higher survival than estuary juveniles, the population growth rate increased (Table 8). Although increasing temperature increased the abundance of the population by producing more ocean type juveniles, I stress temperature impacts multiple vital rates not incorporated in the model, including ocean phenology and productivity.

Maintaining the higher growth ratio in June and July throughout the entire summer raised the size of ocean entry for estuary fish and increased their contribution nearly three-fold. Their predicted size by late fall under improved conditions is similar to the size of surviving ocean type adults during that stage (Appendix D). A higher growth rate and ocean survival resulted in estuary fish contributing disproportionately more, rather than less, to the spawning population. The outcome of this scenario is similar to what has been observed in other bar-built estuaries (Bond et al. 2008). In highly productive estuaries where juvenile salmonid growth is high, individuals that rear in these habitats have higher smolt-to-adult survival and contribute disproportionately more to the spawning population (Bond et al. 2008; Hayes et al. 2008).

Under the potential restoration scenario, the population growth rate changed from remaining relatively stable to becoming positive. The effects of estuary restoration are conservative as the scenario only considers the impact of higher estuary growth on ocean survival. I did not include potential benefits of restoration on survival within the estuary or for juveniles that briefly rear in the estuary but emigrate prior to mouth closure. If estuary restoration reduces mortality in estuary or increases estuarine use in the population, the impacts of estuary restoration on the population may be greater than predicted.

CONCLUSION

Estuary type juveniles frequently experienced years with little to no survival, but on occasion had higher survival than ocean type juveniles. Poor growing conditions in the estuary cause low survivorship most years for estuary type fish. Due to the poor estuary growing conditions, these estuary rearing juveniles are smaller at the beginning of winter than their counterparts that have reared in the ocean. Variability in ocean conditions may change which strategy is optimal from year to year, as occasionally estuary type fish had higher survival. Years when these juveniles experienced higher survivorship may be attributed to favorable ocean conditions. During these years, estuary juveniles experience improved survivorship during winter and avoid some of the high mortality from predation during initial ocean entry. Variability in ocean conditions that affect juvenile salmonid survival means no single life history is most optimal in all years.

Diversity in life history allows for stability of the population despite fluctuations in environmental conditions. Bar-built estuaries polarize juvenile life history. Rather than multiple, or possibly a gradient of life histories, mouth closure divides juveniles into either exiting the system before the bar closes or after it breaches. Depending on the timing and duration of estuary closure, juveniles may be barred from entering the ocean when ocean conditions are most favorable. Ocean entry timings for these populations are at extremes ends of the spectrum, with possibly neither strategy overlapping with the optimal entry time. Furthermore, bar-built estuaries that remain closed until the late fall

produce a life history with an usually late ocean entry time, which may be unfavorable given this life history does not occur in watersheds with estuaries open year-round.

Increasing contribution of the estuary type life history requires improving growth and survival in the estuary. Expanding floodplain and estuary habitats has notably increased the growth and smolt-to-adult survival of juveniles in other watersheds (Sommer et al. 2001; Bottom et al. 2005). Improving estuarine growth would increase their size towards the thresholds required to survive overwinter. I posit that current limitations to growth in the estuary include reduced food availability in the summer due low food production in the estuary and lack of marine influx. High temperatures in the estuary during the summer also increase metabolism and the foraging required to achieve growth, contributing to lower growth if this level of consumption is not met.

The unique phenomenon of mouth closure in bar-built estuaries has consequences on their efficacy and provides insight into how estuaries function as salmonid nurseries. These estuaries are frequently the result of low flows from upstream, which contributes to low food availability and higher temperatures. Bar-built estuaries have limited marine influence when closed, creating a freshwater lagoon and eliminating many of the benefits attributed to estuaries, such as high food availability and saline water to initiate smolting. Bar-built estuaries vary in timing and duration of estuary closure, along with size, condition, and degree of marine influxes. Bar-built estuaries may influence performance of life histories and contribution to salmonid recruitment differently because of these factors. As climate change may increase the prevalence of bar-built estuaries,

understanding how mouth closure impacts the outmigration and survival of salmonids is vital to managing watersheds in California.

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APPENDIX A

Appendix A. Ratkowsky growth equation parameters obtained from Perry et al. (2015) for Chinook salmon.

| Parameter | Estimate |
|-----------|----------|
| b | 0.338 |
| d | 0.415 |
| g | 0.315 |
| T_u | 24.918 |
| T_l | 1.833 |

APPENDIX B

Appendix B: Methods for calculating adult escapement

The California Department of Fish & Wildlife or the California Cooperative Fish & Wildlife Research Unit surveyed spawning grounds in the Redwood Creek watershed to estimate recruitment from 2010-2015, 2017 (Deibner-Hanson 2019). Spawning ground surveys followed the protocol in Adams et al. (2011). Surveys recorded redds, live fish, and carcasses. Escapement of Chinook salmon was calculated in the Redwood Creek basin and in Prairie Creek tributary. Escapement for Chinook salmon in Redwood Creek each year was estimated by subtracting the estimated recruitment of Chinook salmon in Prairie Creek from recruitment in the entire watershed.

APPENDIX C

Appendix C: Methods for calculating outmigrant abundance

To estimate outmigrant abundance, the California Department of Fish and Wildlife or the California Cooperative Fish & Wildlife Research Unit deployed a rotary screw trap during the 2004-2016, 2018 outmigration seasons. The rotary screw trap operated from approximately March to July of each year. Fish were removed and identified to species from the screw trap daily. They measured fork length and weighed up to 30 random individuals from each age class. Trap efficiency was determined using mark-recapture methods and outmigration estimates were calculated using the methods described in Sparkman et al. (2016).

APPENDIX D

Appendix D: Comparison of assessment of juvenile life history from adult sagittal otoliths and scales. Ocean Entry = otolith radius (μm) at ocean entry check, when identifiable with a certainty greater than 2 (certainty range 1-4). Late Fall = otolith radius (μm) during the late fall (210 increments). Fork Length = back-calculated fork length (mm) at late fall using otolith radius and regression parameters calculated from Sturrock and Johnson (2014). Otolith = juvenile life history type determined using otolith microstructure. Scale = juvenile life history type determined using scale pattern.

| Otolith | Ocean Entry | Late Fall | Fork Length | Otolith | Scale |
|---------|-------------|-----------|-------------|--------------|---------|
| 28917 | | 904.2 | 141.9 | Undetermined | Ocean |
| 28724 | | 949.1 | 149.5 | Ocean | Ocean |
| 27918 | | 1019.2 | 161.5 | Ocean | Ocean |
| 25049 | | 954.5 | 150.4 | Ocean | Ocean |
| 19921 | | 941.19 | 148.2 | Ocean | Ocean |
| 19626 | | 967.3 | 152.6 | Ocean | Ocean |
| 19514 | | 882.42 | 138.1 | Undetermined | Estuary |
| 19137 | 523.3 | 866.9 | 135.5 | Ocean | Ocean |
| 19052 | | 945.1 | 148.8 | Ocean | Ocean |
| 18556 | 460.2 | 1144.7 | 183.0 | Ocean | Ocean |
| 18544 | | 1081.1 | 172.1 | Ocean | Ocean |
| 18438 | 844.6 | 1111.9 | 177.4 | Ocean | Ocean |
| 18362 | | 907.6 | 142.4 | Undetermined | Ocean |
| 18361 | 336.2 | 963.3 | 152.0 | Ocean | Ocean |
| 18273 | | 1026.72 | 162.8 | Ocean | Ocean |
| 18247 | | 962.61 | 151.8 | Ocean | Ocean |
| 18110 | | 956.2 | 150.7 | Ocean | Ocean |
| 18045 | | 1023.2 | 162.2 | Ocean | Ocean |
| 18041 | 788.8 | 888.2 | 139.1 | Estuary | Estuary |
| 18036 | 593.4 | 1004.5 | 159.0 | Ocean | Ocean |
| 18034 | 511.5 | 956 | 150.7 | Ocean | Ocean |
| 17463 | 609.4 | 977.2 | 154.3 | Ocean | Ocean |
| 17372 | | 927.4 | 145.8 | Ocean | Ocean |

| Otolith | Ocean Entry | Late Fall | Fork Length | Otolith | Scale |
|---------|----------------|-----------|-------------|---------|-------|
| 17354 | 499 | 958.3 | 151.1 | Ocean | Ocean |
| 17253 | | 1021.9 | 162.0 | Ocean | Ocean |
| 17009 | | 1027.9 | 163.0 | Ocean | Ocean |
| 15542 | | 1046.1 | 166.1 | Ocean | Ocean |
| 10055 | 547.2 | 1061.2 | 168.7 | Ocean | Ocean |

APPENDIX E

Appendix E: Figures for top-ranked freshwater outmigration model for Chinook salmon in Redwood Creek.

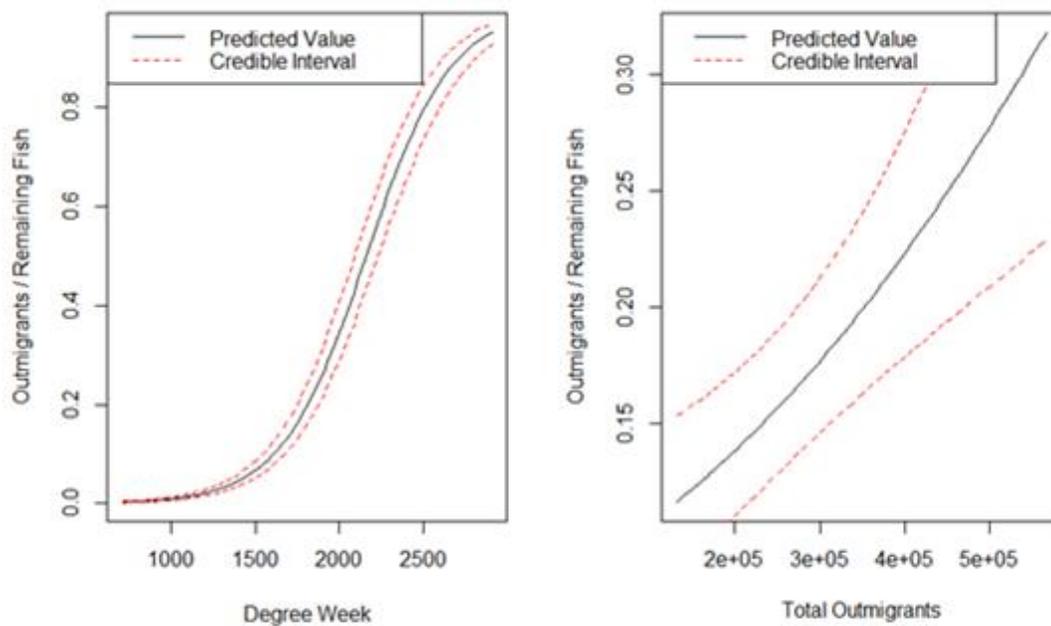


Figure E.1. Left: relationship between temperature (degree week) and proportion of outmigrants in the selected binomial count model. Right: effect of density dependence on the proportion of outmigrants in the selected binomial count model.

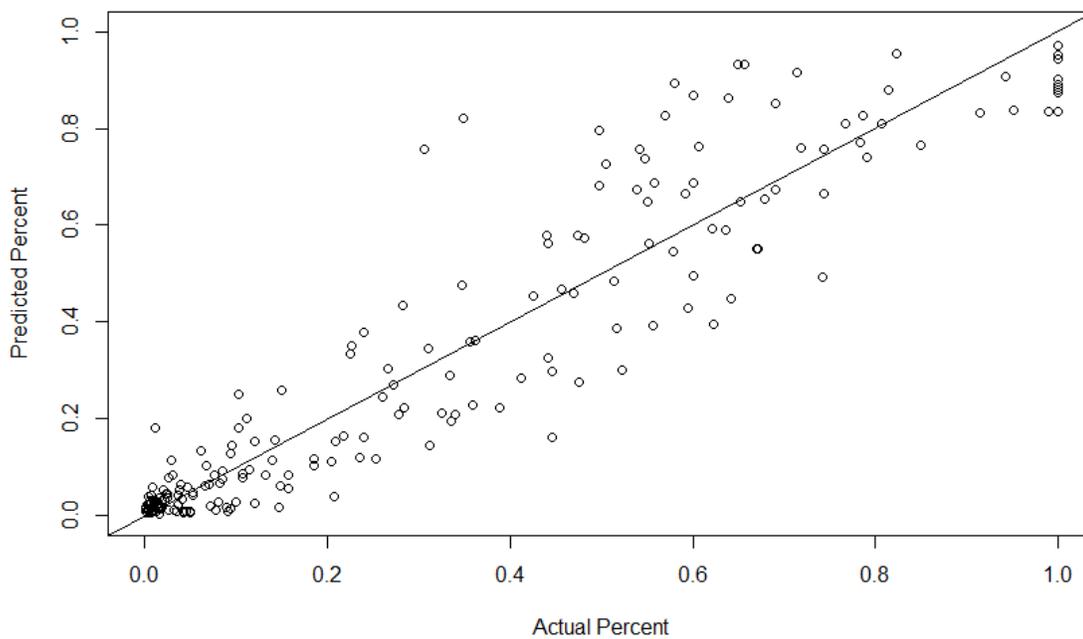


Figure E.2. Observed proportion of juveniles upstream outmigrating each week and predicted proportion using the binomial count model given *Degree Week* and *Total Outmigrants*. The line shows a 1:1 relationship.

APPENDIX F

Appendix F: Figures for the top-ranked linear model for outmigrant size of Chinook salmon in Redwood Creek.

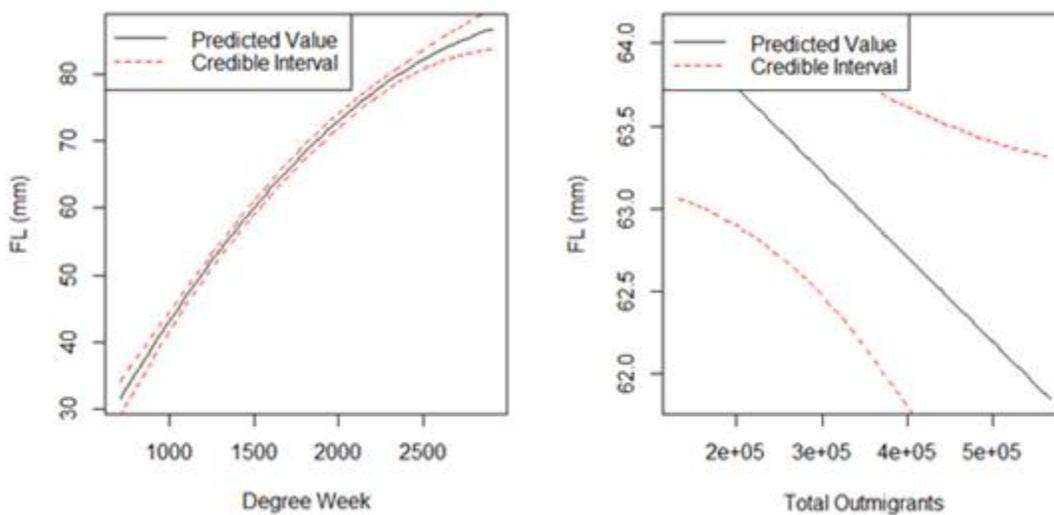


Figure F.1. Left: relationship between temperature (degree week) and mean fork length (mm) of outmigrants in the selected binomial count model. Right: effect of density dependence on the mean fork length of outmigrants in the selected general linear model.

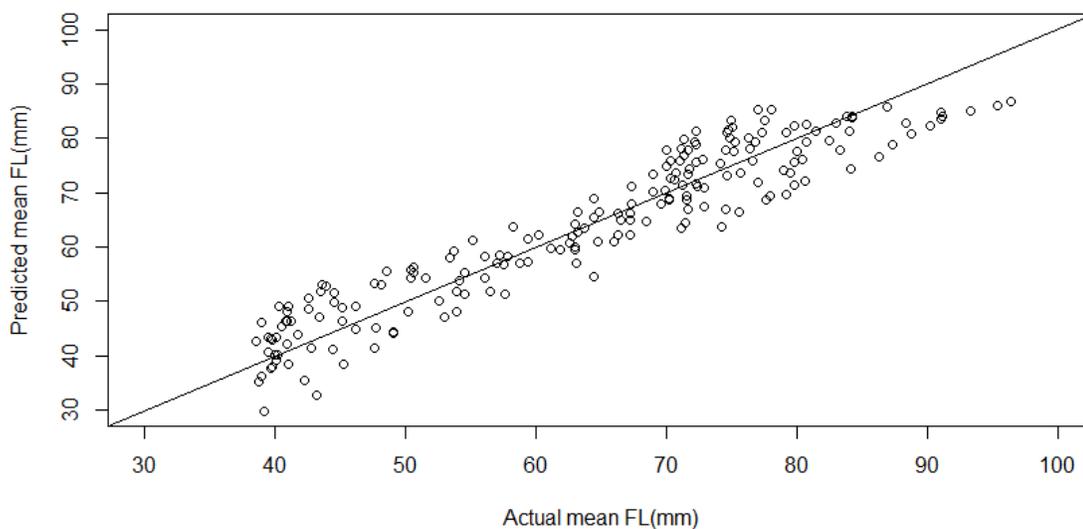


Figure F.2. Observed mean fork length (mm) of juveniles each week and predicted mean fork length using the linear model given *Degree Week* and *Total Outmigrants*. The line shows a 1:1 relationship.