FRESHWATER AND MARINE SURVIVAL OF COHO SALMON (*ONCORHYNCHUS KISUTCH*) AS A FUNCTION OF JUVENILE LIFE HISTORY

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ABSTRACT

FRESHWATER AND MARINE SURVIVAL OF COHO SALMON (*ONCORHYNCHUS KISUTCH*) AS A FUNCTION OF JUVENILE LIFE HISTORY

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Juvenile Coho Salmon (*Oncorhynchus kisutch*) in coastal California streams exhibit various life history strategies during their freshwater development. One strategy of interest to managers and conservationists is the early migrant. Juvenile early migrants emigrate from natal habitat into lower parts of the watershed or estuary during their first fall or winter, where they rear before migration to the ocean. By contrast, the more prevalent spring migrant resides in natal reaches over the winter and migrates directly to the ocean the following spring. Salmon monitoring programs generally estimate juvenile production and demographic rates using only spring migrants, and these estimates are likely biased without the inclusion of early migrants. In Freshwater Creek in Northern California, an ongoing monitoring program PIT-tags juvenile Coho Salmon in the fall and winter, detects their movements throughout the stream and estuary over their first winter, captures spring outmigrants, and then detects adults as they return to spawn. Using six years of this mark-recapture data (2013-2018), I constructed a full life cycle multistate model to estimate (1) over winter survival of both the spring and early migrating juveniles (2) apparent marine survival of spring and early migrating juveniles (3) the probability of fall tagged juveniles migrating early and (4) the probability of each

juvenile life history returning as jacks. Overwinter survival for all three cohorts and all life histories ranged from 25-73%. In cohort one, overwinter survival for spring migrants was greater than the early migrants: overwinter survival was between 38-53% for spring migrants (depending on analysis assumptions) compared to 26% for early migrants; overwinter survival for the two life histories was indistinguishable in the other two cohorts. Apparent marine survival, including all cohorts and life histories ranged from 1.6-4.9%. Marine survival was indistinguishable between juvenile life history strategies likely due to small sample sizes. A power analysis was performed with simulated data, to estimate the sample size of fall tags necessary in order to distinguish between juvenile life histories, this ranged from 3500-6000 tags. The transition probability to the jack state ranged from 1.5-55.8% and was indistinguishable between life history strategies.

Multistate models provide the opportunity to incorporate life history diversity into estimates of population demographic rates. Use of these models and ongoing monitoring effort will continue to add new insights into Coho Salmon life history variation and the consequences for populations

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INTRODUCTION

Coho Salmon (*Oncorhynchus kisutch*) are a widespread species of Pacific Salmon native to the Arctic and Pacific drainages in North America. They are found in coastal streams from Alaska to Central California. Coho Salmon have experienced drastic declines in abundance and local extinctions in the last century, likely the result of stream alterations, urbanization, logging, overharvest, hatchery production and dam construction (Brown et al. 1994). Some populations of the species are currently federally listed on the Endangered Species Act as threatened or endangered. Evolutionary significant units (ESUs) from the Lower Columbia River, the Oregon Coast and the Southern Oregon and Northern California Coast are listed as threatened and the Central California Coast ESU is listed as endangered (NMFS 2016a and NMFS 2016b).

In response to declining populations, extensive research and habitat restoration effort has been dedicated to salmon recovery. In California, the California Coastal Salmonid Monitoring Plan (CMP) (Adams et al. 2011). was established to measure progress toward the recovery of salmon populations. The CMP assesses viability of salmon populations with regards to key population indices. One of these indices is life history diversity. Life history diversity within salmon populations moderates the response to disturbance reduces extinction risk through a mechanism that is referred to as the portfolio effect (Moore et al. 2014, Greene et al. 2010, Schindler et al. 2010). Salmon populations that express more diverse life histories, whether because of genetic differences between subpopulations or phenotypic plasticity within subpopulations,

spread risk across the population and thus are more resilient to fluctuating environments. Populations with higher life history diversity exhibit decreased variability in numerical abundance and biomass, usually measured as a coefficient of variance (Moore et al. 2014, Schindler et al. 2010).

The basic life history pattern for Coho Salmon begins as adults migrate from the ocean to freshwater streams to spawn during the winter. The eggs incubate in gravel redds and the free-swimming fry emerge in the spring. The juveniles typically spend a full year in fresh water before migrating to the ocean in the spring as smolts (the transition to the marine form is often called smolting). Most Coho Salmon spend one and a half years (2 summers) in the ocean before returning to fresh water to spawn, but some males, called jacks, return to spawn after only one summer at sea (Quinn 2011). In addition to age at spawning, individuals within a single population of Coho Salmon may vary in juvenile migration timing and the duration of freshwater habitat use.

In Northern California, the most common juvenile life history for Coho Salmon is to remain in natal streams through the first winter and migrate to the ocean the following spring (Sandercock 1991). Other strategies include migration into lower parts of the watershed or estuaries as newly-hatched young of the year or parr (Koski 2009), moving directly to sea as young of the year (Bennett et al. 2015), or remaining in fresh water for 2 or 3 years before smolting (Bell and Duffy 2007). Bennett et al. (2015) asserts that as many as five juvenile life history types may be expressed in a single basin. For this study, I examined the two most prevalent juvenile life history strategies in my study area in the Freshwater Creek Basin, spring migrants and early migrants. Spring migrants express a

typical life history, migrating from natal streams early in their second year. Early migrants migrate downstream into lower-basin estuary or wetland habitats as young of the year, usually during their first spring or fall. Early migrating juvenile Coho Salmon occur in watersheds throughout their range from Alaska to California (Murphy et al. 1982, Miller and Sadro 2003, Scarlett and Cederholm 1984, Rebenack et al. 2016).

Historically, the early migrant Coho Salmon life history was usually ignored in population studies because little was known about their contribution to adult returns. It was generally assumed that early migrants did not survive, that they were pushed downstream into unsuitable habitat either by territorial aggression or high winter flows (Chapman 1966, Sandercock 1991). Newer studies have challenged this hypothesis, suggesting that early migrants are a distinct, evolved life history strategy that either goes directly to sea (Bennett et al. 2015) or capitalizes on productive habitats in wetlands and tidal sloughs (Koski 2009). Recent reports have verified that some early emigrants survive to adulthood. Bennett et al. (2015) demonstrated that early emigrating Coho Salmon from three streams in Washington accounted for 37% of the adult returns, and Jones et al. (2014) concluded that 20-35% of returning adults from Salmon Creek in Oregon had estuarine-associated life histories based on scale analysis.

In California and other states, monitoring of Coho Salmon smolt production focuses exclusively on spring migrants. The typical procedure for measuring smolt abundance and survival rates depends on the operation of downstream migrant traps during the period when spring-migrating smolts are moving to the ocean (Adams et. al 2011). This practice does not consider early migrants traveling downstream before

trapping begins (Rebenack et al. 2016). Without the inclusion of early migrants, population monitoring efforts are incomplete. This results in juvenile abundance estimates that are biased low and smolt to adult return rate estimates that are biased high (Cochran et al. 2019). There are two general methods for calculating the SAR of Coho Salmon in common use today: the abundance-based method and the tag-based method. The abundance method involves dividing the estimated abundance of returning adult salmon by the estimated abundance of smolts from the same cohort. The tag-based method involves tagging a portion of the migrating smolts and estimating the proportion tagged, returning adults. Both methods only use smolts captured at the downstream migrant trap and are biased in different ways. The abundance-based approach is generally greater than the tag-based approach (Cochran et al. 2019) because it includes not only spring-migrating smolts but all returning adults, which are a combination of spring migrants and early migrants. The tag-based approach on the other hand includes only the number of tagged adults that were tagged as spring smolts, so this estimate represents the marine survival of smolt migrants only. It is unknown whether the tag-based SAR estimate is biased high or low for the entire population, this depends on the true marine survival of the early migrants.

Freshwater Creek, located in Humboldt County California, is a designated salmonid life cycle monitoring station as part of the CMP operated by Humboldt State University. On Freshwater Creek, early migrants have been documented and studied since 2009. Rebenack et al. (2015) determined that there are distinct winter (or early) and spring emigration periods for coho salmon in Freshwater Creek. Over three years, they

estimated that 2-29% of fish tagged in the fall at different locations in the watershed became early migrants (Rebenack et al. 2015). Rebenack et al. (2015) used two Cormack-Jolly-Seber (CJS) models to estimate the proportion of fish tagged in the fall that migrate early and the proportion that migrate in spring as smolts (Cormack 1964, Jolly 1965, Seber 1965). This two-model approach is still used in the ongoing population monitoring effort at Freshwater Creek (Anderson and Ward 2016). However, interpreting these parameter estimates in the context of population demography presents substantial challenges. For example, in Rebenack's CJS models, the first occasion corresponds to the fall tagging of young of year. For the spring migrant model, the second occasion corresponds to downstream smolt trapping in the spring. In past studies, the apparent survival estimate between these two occasions was considered the overwinter survival estimate for the juvenile population. Because early migrants leave the study area during this interval, this apparent survival estimate only represents the proportion of fall-tagged juveniles that survive and remain in the stream for the winter to emigrate in the spring, *not* just overwinter survival, leading to overwinter survival estimates that are biased low. In Rebenack's CJS model for early migrants, the second occasion corresponds to downstream antenna detections during the winter. The apparent survival between these two occasions represents the proportion of fall-tagged juveniles that emigrate early, not overwinter survival of these fish.

Along with including adult early migrants into calculations of SAR, it may prove insightful to understand whether juvenile life history affects the expression of the adult life histories. As described earlier, male Coho Salmon can express two adult life history

strategies, the jack or the three-year-old adult. The physiological mechanism that determines whether a male Coho Salmon becomes a jack versus a three -year -old adult is still unknown. However, it is thought to be a physiological process initiated during the juvenile life stages in fresh water (Gross 1991, Koseki and Fleming 2007). For this reason, juvenile life history and habitat use may affect the expression of the jack life history. With the use of multistate models, it may be possible to evaluate associations between juvenile and life history expression.

Multi-state capture-recapture models are an extension of the standard CJS approach that might be able to address the challenges with overwinter survival and SAR estimates (Hestbeck et al. 1991, Nichols et al. 1992, Brownie et al. 1993, Schwarz et al. 1993). Multi-state models estimate separate survival and detection probabilities from observed, incomplete encounter histories of animals in alternative ecological states (e.g. life histories) while also estimating the probabilities of transitioning between those states. In this way, a multi-state model can potentially estimate the overwinter survival of both the life histories, and the probability of transitioning among life history states. Similarly, using a multi-state model may allow for separate marine survival rates for juvenile life history strategies. In this project, I developed, tested, and implemented a multi-state modeling framework for the Freshwater Creek Coho Salmon population.

The objectives of this study were to (1) examine whether there was a difference in marine survival between early and spring migrants in the Freshwater Creek basin, (2) examine whether there was a difference in overwinter survival between early and spring migrants, (3) examine whether there was a difference in the probability of a fall tagged

young of year (YOY) becoming an early migrant between years, (4) examine whether there was a difference in the probability of returning as a jack between early and spring migrants. To accomplish these objectives, I used a single multi-state mark recapture model which included six years of mark recapture data, representing three full cohorts, from young of the year to adult. I then simulated data to determine the sample sizes necessary to distinguish separate survival rates in this basin. Additionally, I identified a subset of ambiguous individuals in the mark-recapture dataset whose life history strategies cannot be distinguished using the current monitoring framework, requiring further investigation.

STUDY SITE

The study site for this project, located in Humboldt County California, includes Freshwater Creek and the stream-estuary ecotone of Freshwater Slough, Ryan Creek and Wood Creek (Figure1). The Freshwater Creek watershed is located approximately 8 km east of Eureka, California, draining into Humboldt Bay through Freshwater Slough. Freshwater Creek is a fourth-order stream with a drainage area of approximately 80 km^2. There are five major tributaries to upper Freshwater Creek: Cloney Gulch, South Fork, Little Freshwater Creek, McCready Gulch, and Graham Gulch. Elevation in the Freshwater Creek watershed ranges from 823 meters at the headwaters to sea level at the mouth in Humboldt Bay.

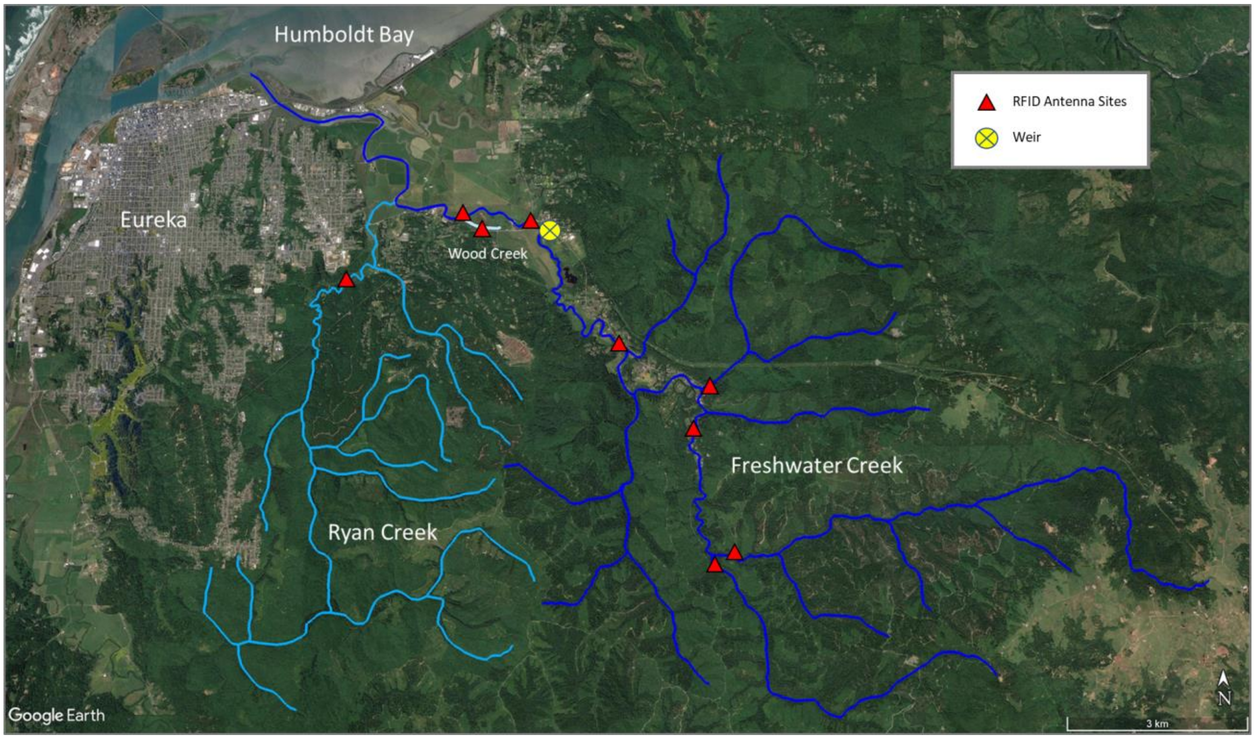

Figure 1. Study Site. Freshwater Creek, Ryan Creek and Wood Creek indicated by color. Freshwater Creek drains into Humboldt Bay just North of the city of Eureka, California. The yellow circle denotes the location of the permanent weir and the red triangles indicate the location of RFID antennas.

The lower 9.7 km of Freshwater Creek is channelized and leveed, and the surrounding land is primarily used for cattle grazing or residential parcels. Upstream land use consists largely of lands actively managed for timber harvest, along with low-density residential areas and riparian woodland. Common tree species in the watershed include redwood *(Sequoia sempervirens*), Douglas-fir (*Psuedotsuga menziesii*), white fir (*Abies concolor*) and Sitka spruce (*Picea sitchensis*), willow (*Salix* spp.), alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) (Barnard 1992). Three species of salmon are native to Freshwater Creek: Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon, and Steelhead Trout (*O. mykiss*). Occasionally, Chum (*O. keta*) and Pink Salmon (*O. gorbuscha)* are observed entering Freshwater Creek. Other species of fish that can be found in the watershed are Pacific Lamprey (*Entosphenus tridentatus*), Pacific Brook Lamprey (*Lampetra pacifica*), Cutthroat Trout (*O. clarki*), Prickly and Coast Range Sculpin (*Cottus asper, Cottus aleuticus*) and Threespine Stickleback (*Gasterosteus aculeatus*) (Barnard 1992).

Within the main stem of Freshwater Creek, 14.5 km are accessible to anadromous fish. Upstream of 14.5 km, a six-meter waterfall prevents access to anadromous fishes (Barnard 1992). Each major tributary to Freshwater Creek adds an additional 2-4 km of anadromous habitat, with exact distance in each tributary depending on flow conditions during migration each year. A permanent weir is installed on the main stem of Freshwater Creek, slightly upstream of tidal influence, which serves as a trap for emigrating smolts and returning adults.

For the purpose of this study, the “estuary” refers to the sampling locations that experience tidal influence; this includes Freshwater Slough, Wood Creek and the last kilometer of Ryan Creek. Freshwater Slough drains into Humboldt Bay just North of Eureka; it is considered tidal freshwater habitat with riparian vegetation. The slough is brackish during the summer and fall (up to 20 ppt) and mostly freshwater in the winter and spring (Wallace et al 2016). Wood Creek and Ryan Creek are tributaries to Freshwater Slough. Wood Creek is a recently restored tidal wetland containing a network of channels and ponds. The restoration of Wood Creek was a two-fold project. Phase 1 was carried out in 2010 and included the removal of a tide gate, the construction of tide channels and the construction of an off-channel pond, called Wood Creek Pond. Phase 2 was carried out in 2016 and included the construction of more tide channels to increase overwinter habitat for salmonids (Wallace et al 2015). Ryan Creek is a large tributary to Freshwater Slough with a total drainage area of 33 km^2. Previous studies (Rebenack et al. 2015, Wallace et al. 2017) have confirmed that the estuary provides seasonal rearing habitat for juvenile fish originating from Freshwater Creek and tributaries.

MATERIALS AND METHODS

Field Methods

In my analysis, I incorporated Freshwater Creek Coho Salmon tagging and recapture data from July 2013 -March 2018, capturing the full life cycle of three cohorts. For each cohort, the first major tagging event occurred in the fall of their first year, when young of year Coho Salmon were tagged with passive integrated transponder (PIT) tags from mid-September to late October. For this fall tagging effort, the basin was divided into six study reaches, encompassing the mainstem and each of the five major tributaries (Figure 2). Other small tributary streams (not depicted in Figure 2) were excluded from sampling either because they were inaccessible or because there was no evidence of Coho Salmon spawning. A systematic random sampling approach was used to select pools within the various reaches, with a goal to tag 1500-2000 juveniles each fall. Each selected pool was seined and 4-8 individuals were tagged. Individuals selected for tagging were first anesthetized with tricaine methanesulfonate (MS-222), and the fork lengths and weight of each fish was measured. In 2013 and 2014, juveniles measuring between 55 and 64 mm were marked with full-duplex PIT tags (Biomark, Inc., Boise, Idaho; full-duplex B, 8.4 mm long, 1.4 mm wide). Juveniles greater than or equal to 65 mm were marked with a larger PIT tag (Oregon RFID, Portland, Oregon; half-duplex, 12.0 mm long, 2.12 mm wide). In 2015, permit requirements changed so that juveniles between 60 and 69mm were marked with full-duplex and those greater or equal to 70 were marked

with half-duplex. A sterile scalpel was used to make a 1-2 mm incision posterior to the pectoral fin, tags were inserted into the body cavity and fish were allowed 10-30 mins of recovery time before being released back into the pools.

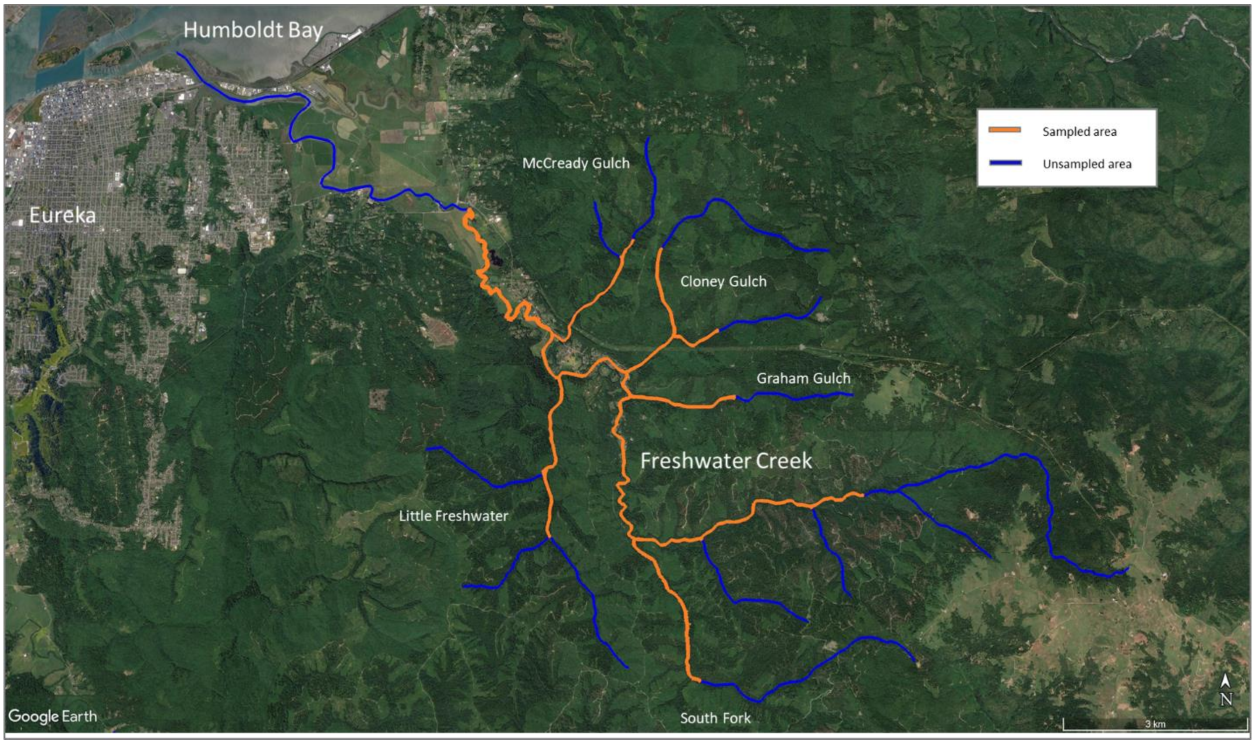

Figure 2. Sampling locations for the Freshwater Creek lifecycle monitoring tagging of young of year. Sampled area shown in orange, unsampled in dark blue.

Additional tagging of YOY Coho Salmon that had moved from natal streams to the estuary was conducted year-round, on a bi-weekly or monthly basis by collaborators from California Department of Fish and Wildlife. For this sampling effort, a seine net was used to sample two sites in Freshwater Slough and one site in Wood Creek pond. Minnow traps baited with frozen salmon roe were used to sample nine sites plus an adjacent wetland in Ryan Creek (Figure 3), 6 sites in Wood Creek (Figure 4), and two sites in Wood Creek Pond. Minnow traps were used in heavily vegetated areas where seining was impossible. Each captured fish was anesthetized with tricaine methanesulfonate (MS-222), and the fork lengths and weights were measured. If the fish was not already marked it was given a PIT tag, following the same size requirement/tag type specifications as the juveniles in Freshwater Creek. The tag numbers of individuals that were already marked were recorded. The life stage was also recorded for each fish based on size and season. During spring, two cohorts of fish occurred in the estuary at the same time (YOY and one-year-old parr or pre-smolts); during this period, juveniles were designated as YOY or one-year-olds based on clear size differences between the cohorts at each sampling event (Wallace et al. 2017). .

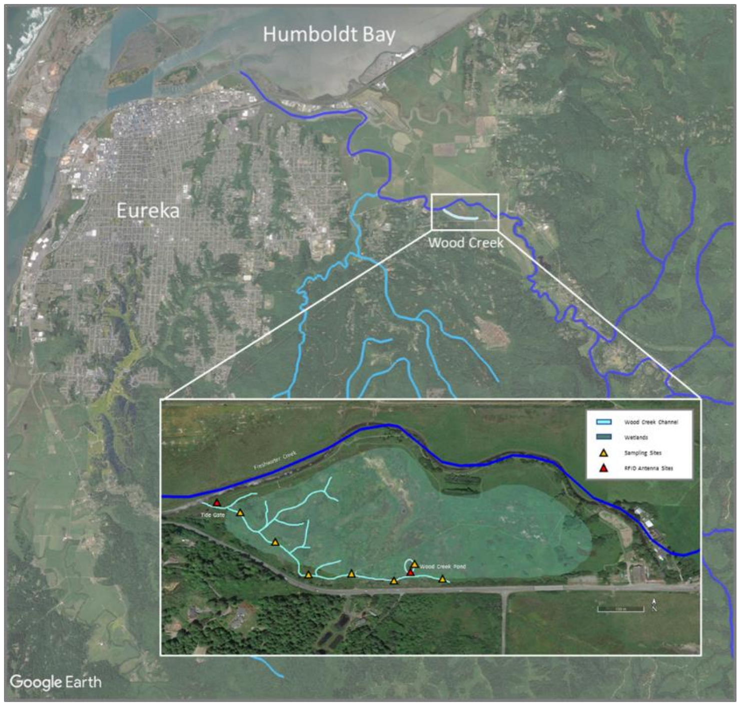

Figure 3. Wood Creek Restoration site. Approximate location of sampling sites and RFID antennas.

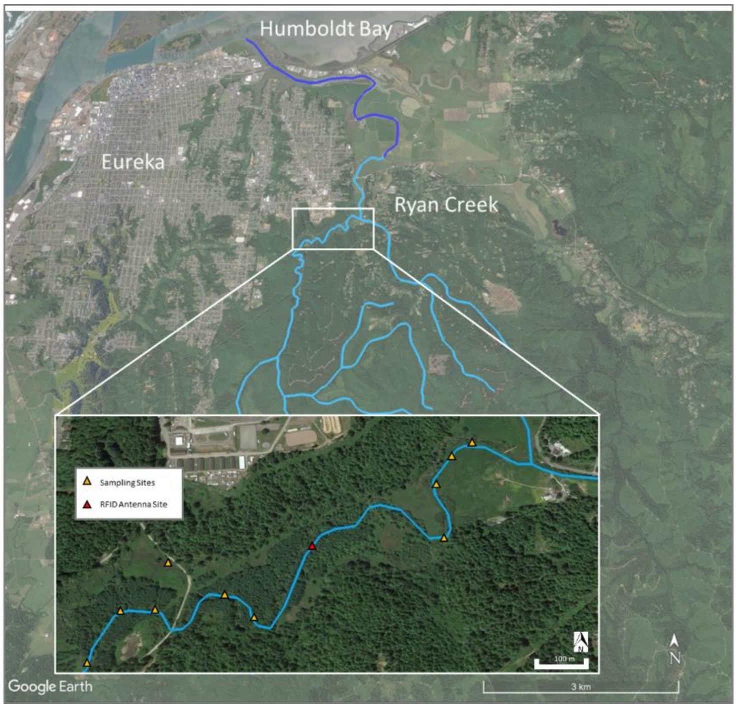

Figure 4. Ryan Creek sampling sites and approximate location of RFID antennas.

Spring migrants leaving stream habitats for the ocean were captured in a downstream migrant trap (DSMT) located at the permanent weir on Freshwater Creek. The trap was operated from March through June. One panel of the permanent weir was fitted with a large PVC pipe leading to the floating trap. The other panels of the weir were boarded off to funnel all water through the trap. The juvenile trap was checked daily, and fish were anesthetized with MS-222 before handling. Individuals were scanned for PIT tags, their weight and fork lengths measured, and a subset were tagged. Fish that were marked on the day of capture were released upstream so that trap efficiency could be measured. Fish caught that already had a tag and fish that were not tagged that day were released below the weir.

Fish returning as either jacks or adults were captured at the weir, which is operated November through June when discharge was between 0.28-14.2 m^3/s. Captured fish were scanned for PIT tags, and the weight, fork length and sex were measured. If they were not already marked, they were injected with a 12 mm PIT tag and given an opercular punch mark. Individuals were released just upstream of the weir, unless there were high flow events, in which case they were allowed to recover in a tank for up to two hours before release. Adult fish carcasses were also detected during spawning ground surveys, conducted frequently throughout the spawning season. All reaches upstream and including the Lower main stem were walked approximately once every 10 days. The carcasses were measured, sexed, and scanned for PIT tags and opercular punches.

Fish were detected after tagging either in-hand (i.e. weir, DSMT, carcass surveys) or using antennas. On Freshwater Creek, 6 RFID antennas were maintained along the

main stem and at the confluence of each of the larger tributaries (Figure 1). They were operated October through July to detect juveniles through fall rearing and spring outmigration and adults on their return migration to spawn. Three RFID antennas were maintained in the estuary; one on Wood Creek at the tide gate, one at Wood Creek Pond and one in between sampling sites on Ryan Creek. All antennas were capable of reading HDX tags, however only the Wood Creek tide gate, Wood Creek Pond, and Ryan Creek Antennas were dual readers, able to read both FDX and HDX tags. Fall tagged YOY were detected over their first winter, if they moved through an antenna site, or if they were captured during estuary sampling. Smolts were detected on antennas or captured in the DSMT. Adults returning to spawn were detected on antennas, captured in hand at the adult weir, or detected as carcasses.

Modeling

Capture history formation

To summarize the marking and detection data into a data set for analysis, the Coho Salmon life cycle was divided into five mark-recapture occasions, corresponding to life stages and tagging efforts of the monitoring program. The first occasion was from May through October, corresponding to the summer and fall tagging of YOY. Summer tagging in the estuary and fall tagging in the stream and estuary. The second occasion was from November through March corresponding to detections on antennas or during estuary sampling during the juvenile’s first winter. The third occasion was from March to June, corresponding to the outmigration of smolts and operation of the smolt trap. The

fourth occasion corresponded to the return of spawning adults to fresh water; this could either be after 6-8 months if the fish returned as a jack, or after 18 months if the fish returned as a three-year-old adult. The fifth occasion corresponded to the upstream detection of the spawners above the weir on antennas or spawning ground surveys. Capture histories were constructed for each tagged fish, representing a sequence of their state at each occasion. A fish could exist in one of three states: the “S” state represented the spring migrant life history, the “E” state represented the early migrant life history, and the “J” state represented the jack life history. Fish not observed at an occasion received a “0” in their capture history.

Occasion 1 May-October: A YOY captured during summer or fall tagging efforts received an S or an E for the first occasion, depending on where it was captured. If the fish was tagged in natal streams (upstream of the weir on Freshwater Creek) during the fall tagging efforts of the Freshwater Creek monitoring program, it received an S for spring migrant life history. If the fish was captured and tagged in the summer or fall by CDFW estuary sampling (downstream of the weir on Freshwater Creek), it was assigned an E for early migrant life history. There is no suitable spawning habitat in the estuary, so any YOY present in the estuary during this occasion must have emigrated early from their natal stream habitat. No individuals that were tagged upstream in the first occasion were documented in the estuary during the first occasion.

Occasion 2 November-February: A YOY captured or detected on an antenna over the winter received an S or an E depending on where it was detected. If the fish was detected on antennas or captured in a seine upstream of the weir, it received an S. If a fish was

detected on estuary antennas or caught in a seine in the estuary it received an E. An individual tagged in the first occasion in the S state was considered to have transitioned to the E state for the second occasion if it was detected on the Freshwater weir antenna (FWW), Wood Creek antennas or the Ryan Creek antenna during this occasion, or if it was captured during winter estuary seining. The interval between occasion 1 and 2 is the only occasion where a fish can transition from an S state to an E state. E state fish were not allowed to transition back to the S state, even if they were detected back upstream (only four individuals were detected that traveled from the estuary back upstream in the duration of the study). Although these individuals traveled back upstream, they still were considered to exist in the E state.

Occasion 3 March-June: Smolts captured and tagged at the DSMT were given an S for this occasion, which assumes that they spent their entire juvenile rearing period in the stream habitat. A smolt captured at the DSMT that was already tagged as an S received another S for the third occasion. Previously tagged E fish received another E in this occasion if they were detected on antennas in the estuary during this time.

Occasion 4 November-March spawning adults return: A tagged adult captured at the weir or detected on the weir antenna less than one year following outmigration received a J for this occasion. A tagged adult captured at the weir or detected on the weir antenna more than one year after outmigration received an S or an E for this occasion depending on which state they were in on occasion 3.

Occasion 5 November-March upstream detection of spawning adults: A tagged adult detected on the Freshwater Creek upstream antennas the winter following outmigration

received a J for this occasion. A tagged adult detected on the upstream antennas 2 winters after outmigration, received an S or an E for this occasion depending on which state that individual was in on occasion 3.

Two-year-old juveniles

Many more jacks were detected on antennas than would be expected given historical data, it was evident that many of these detections were probably two-year-old juveniles, or juvenile fish that remained in fresh water an additional year. The following criteria were constructed in order to determine whether these antenna detections were two-year-old juveniles:

1. If a fish was captured in-hand at the adult weir, it was considered a jack return.
2. If the fish was detected on one of the antennas in the late summer or fall following spring outmigration (indicating that it had not gone to sea), it was considered a two-year-old juvenile.
3. If the fish was detected during the spring of the following year (after the typical return period for spawning fish, when juveniles would be migrating to sea) the fish was determined to be a two-year-old juvenile.
4. If the fish was detected in Wood Creek Pond or at the Wood Creek tide gate the winter following spring outmigration (indicating that it was still alive after the typical spawning period), it was considered a two-year-old juvenile.
5. Fish were considered ambiguous if they were detected during the typical adult return time on the Freshwater Creek or Ryan Creek antennas without being captured at the weir as a documented jack return. These individuals were assumed

to be two-year-old juveniles for one iteration of the capture history formation, and jacks for the other.

The number of two-year-old juveniles and ambiguous fish for each year is presented in Table 1. The number of two-year-old juveniles for the third cohort appears relatively small compared to the previous two years. This is because later years of detection data were not analyzed and many of these juveniles are unknown until they are detected the following year out-migrating with the subsequent cohort. Extraction and organization of detection data is a formidable process, this data was not integral to the life cycle model and thus was not analyzed as part of this project. Fish that were identified as two-year-old juveniles were given zeros for the last two occasions (i.e. they were considered mortalities), this assumption was made because no two-year-old juveniles were detected returning as adults during the study. Two sets of capture histories were constructed in an effort to include ambiguous detections. In the first set, from this point forward referred to as A=2+, ambiguous fish were assumed to be two-year-old juveniles. In the second set, from this point forward referred to as A=J, ambiguous fish were considered jacks. Both sets of capture histories were analyzed using the model construction below.

Table 1. Number of known jacks, assigned two-year-old juveniles, and ambiguous fish per cohort

Cohort	Two-year-old	Jack	Ambiguous
1	93	1	22
2	52	4	20
3	10	2	26

Model construction

For the analysis, I used a general multi-state capture recapture model framework (MSCR) The model included three states: early migrant (E), spring migrant (S) and jack (J), with estimable parameters of survival (*s*), detection probability (*p*) and transition probability (ψ). Initial analysis of the observed data included a model with grouping variables for tag type, however juveniles tagged with FDX were removed from subsequent analysis because very few were detected as adult or jack returns, including them greatly increased the number of parameters, and removing them had little effect on parameter estimates.

All models were constructed in Program Mark (Cooch and White 2005) and fit using the sin link function. The assumptions of the MSCR model are as follows (Calvert et al. 2009):

1. All tagged animals were assigned the correct state.
2. Tags were not lost.
3. Tagging did not affect the survival, detection or movement of the animals.
4. Every individual in a state was subject to the same survival, capture and transition probabilities.
5. The fate of each individual was independent of the fates of others.
6. Sampling was instantaneous.
7. All emigration from the sample area was permanent.

Clearly, the Freshwater Creek sampling program does not meet all of these assumptions (particularly 6). Violation of one or more of these assumptions can result in

overdispersion of the data, thus goodness of foot testing was necessary to determine how well the model fit the data. A median ĉ test was performed on each of the global models using the 'median c-hat test' in Program Mark (Cooch and White 2005). Both global models were slightly overdispersed; the estimated ĉ of A=2+ was 1.5 and the estimated ĉ of A=J was 1.9. The quasi-likelihood adjusted ($QAIC_c$) values were used for model selection instead of AIC. $QAIC_c$ is both corrected for small sample size and adjusted for overdispersion (Burnham and Anderson 2002).

The general model (*general*) included grouping variables for each of the three cohorts. There was temporal variation in survival between cohorts and between each state in a cohort, except that the first 3 occasions of the J state were fixed to zero, because the jack state is not possible until fish return as adults in the 4^{th} and 5^{th} occasions. Additionally, survival for the last interval for each state within each cohort was fixed to 1, representing survival between capture at the weir and detection on antennas upstream. There was temporal variation in detection between states, except for a constraint on the E state so that the detection probabilities for the 3^{rd} and 4^{th} occasions were set equal to those of the S state. This decision represents the assumption that E and S state adults had equal detection probabilities at the weir and on the upstream antennas. The third occasion for the S state of each cohort (representing weir efficiency) was fixed to a specific value obtained from a separate general escapement study. In short, adult fish captured at the weir that are not already tagged were given opercular punches. During carcass surveys, the proportion of opercular punches versus non opercular punches observed represents weir efficiency. These values were 0.59 for the first cohort, 0.41 for the second cohort

and 0.45 for the third cohort. There was temporal variation in detection between cohorts except for a constraint on the J state of cohort 2 and 3, so that the 3rd and 4th occasions were set equal to the 3rd and 4th occasions of the previous cohort's S and E states. This assumption is based on J state fish returning to freshwater in the same year as adult fish of the previous cohort. The detection probability for the 1st and 2nd occasion of the J state were fixed to zero for each cohort since the jack state is not possible until the 4th and 5th occasions. Almost all possible transition probabilities between states were constrained to zero except the first transition from S to E which varied by cohort, the third transition from S to J which varied by cohort, and the third transition from E to J which varied by cohort. A simplified conceptual diagram of the general model, depicting a single cohort is shown in Figure 5. Alternative models included the global model (*global)* which had no constraints, a model with no cohort grouping (*no group*), and 25 additional models, resulting from the multistage analysis I performed. It should be noted that the marine survival parameters represent apparent survival. The model cannot account for individuals that permanently emigrate from the system during that interval.

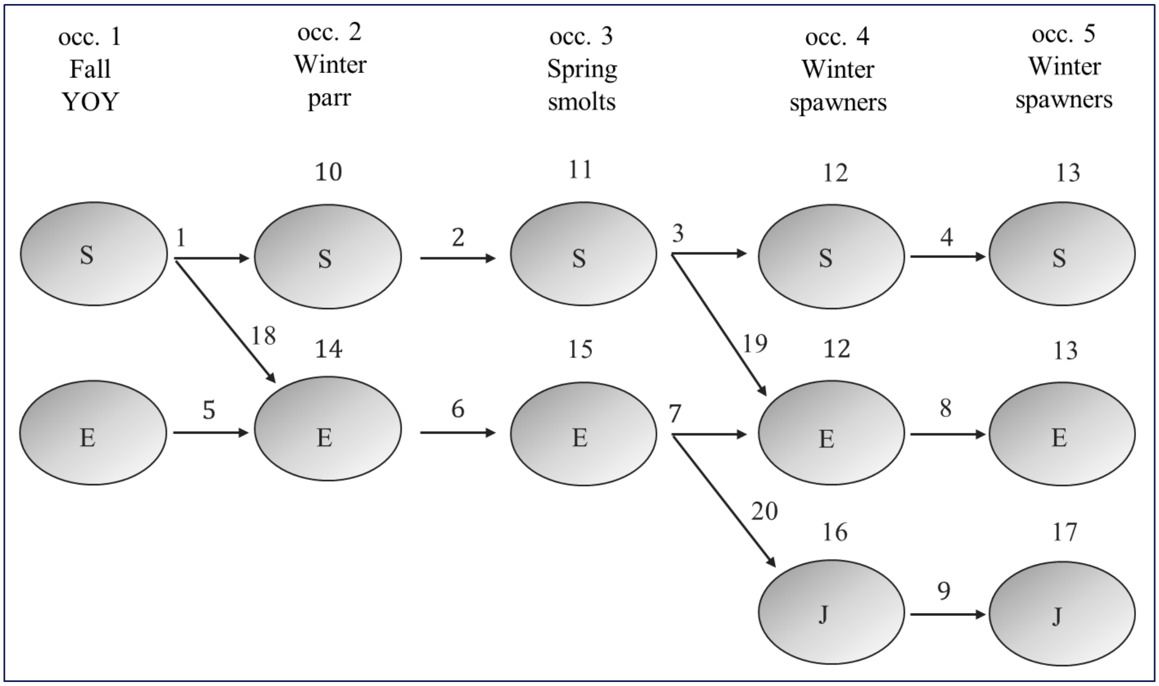

Figure 5. Simplified conceptual diagram of the *general* model, depicting just one cohort. Rows correspond to the five mark-recapture occasions: occasion one is in-hand tagging of YOY in the fall, occasion two is antenna detections and in-hand capture over winter, occasion three is antenna detections and in-hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream. Ovals represent occasions, letters represent states: spring migrant (S), early migrant (E) and jack (J). Parameters 1-9 represent survival (*s*). Parameters 10-17 represent detection probability (*p*). Parameters 18-20 represent transition probability (ψ), where individuals first survive, then transition. All parameters not depicted were fixed to zero. The last survival parameters of each state were fixed to 1.

The purpose of the model selection process was to examine more closely parameters of interest that may differ between juvenile life history strategies. The questions I addressed through this approach were 1. Are there differences in marine survival between the S and E states in each cohort? 2. Are there differences in overwinter survival between S and E states in each cohort? 3. Are there differences in the transition from the S to E state between cohorts? 4. Are there differences in the transition probabilities to the J state between S and E states in each cohort? I decided to employ a multistage approach because constructing combinations of all parameters of interest for each cohort would result in too many models. Using the general model as the base, I set marine survival between S and E states equal one cohort at a time, then two cohorts at a time then in all three cohorts. I chose the top ranked model according to $QAIC_c$ and used this as the base model for testing of my next hypothesis. I did the same with overwinter survival, and then the probability of transitioning from S to E and finally the probability of transitioning to the J state. The S to E step was different from the others in that S to E was manipulated between cohorts and not between states in a particular cohort, see Table 2 for the detailed parameterization of each model in the multistage approach.

Table 2. Multistage model construction. Stage represents the parameter of interest in which the set of models examines. Stage base model denotes the model after which all models in the stage are parameterized, with the exception of specific changes to the base model outlined in the Deviation from Base Model column. The top ranked model (according to $QAIC_c$) from the previous stage was used as the base model for the respective stage.

Stage	**Stage base model**	**Model**	**Deviation from base model**
Marine Survival	*general*	*MS(cohort1)*	marine survival parameter set equal between juvenile states in cohort 1 only
		MS(cohort2)	marine survival parameter set equal between juvenile states in cohort 2 only
		MS(cohort3)	marine survival parameter set equal between juvenile states in cohort 3 only
		MS(cohort1cohort2)	marine survival parameter set equal between juvenile states in cohorts 1 and 2
		MS(cohort1cohort3)	marine survival parameter set equal between juvenile states in cohorts 1 and 3
		MS(cohort2cohort3)	marine survival parameter set equal between juvenile states in cohorts 2 and 3
		MS(COHORT)	marine survival parameter set equal between juvenile states in all cohorts.
Overwinter Survival	*MS(COHORT)*	*OS(cohort1)*	overwinter survival parameter set equal between juvenile states in cohort 1 only
		OS(cohort2)	overwinter survival parameter set equal between juvenile states in cohort 2 only
		OS(cohort3)	overwinter survival parameter set equal between juvenile states in cohort 3 only
		OS(cohort1cohort2)	overwinter survival parameter set equal between juvenile states in cohorts 1 and 2
		OS(cohort1cohort3)	overwinter survival parameter set equal between juvenile states in cohorts 1 and 3

Stage	Stage base model	Model	Deviation from base model
		OS(cohort2cohort3)	overwinter survival parameter set equal between juvenile states in cohorts 2 and 3
		OS(COHORT)	overwinter survival parameter set equal between juvenile states in all cohorts.
Transition to E	*OS(cohort2cohort3)*	*TE(cohort1cohort2)*	transtion to E parameter set equal between cohorts 1 and 2
		TE(cohort1cohort3)	transtion to E parameter set equal between cohorts 1 and 3
		TE(cohort2cohort3)	transtion to E parameter set equal between cohorts 2 and 3
		TE(COHORT)	transtion to E parameter set equal between all cohorts
Transition to J	*TE(COHORT)*	*TJ(cohort1)*	transition to J parameter set equal between juvenile states in cohort 1 only
		TJ(cohort2)	transition to J parameter set equal between juvenile states in cohort 2 only
		TJ(cohort3)	transition to J parameter set equal between juvenile states in cohort 3 only
		TJ(cohort1cohort2)	transition to J parameter set equal between juvenile states in cohorts 1 and 2
		TJ(cohort1cohort3)	transition to J parameter set equal between juvenile states in cohorts 1 and 3
		TJ(cohort2cohort3)	transition to J parameter set equal between juvenile states in cohorts 2 and 3
		TJ(COHORT)	transition to J parameter set equal between juvenile states in all cohorts.

Models were ranked according to $\Delta QAIC_c$ (the distance between the best model and the *ith* model). Model averaging was used to report the final estimated parameters. Model averaging incorporates model uncertainty into parameter estimates and is calculated by averaging each parameter with the respective parameters in all the other models, weighted by $QAIC_c$ (Hoeting et al 1999, Madigan and Raftery 1994, Wasserman 2000). Since winter spanned two capture occasions, overwinter survival was calculated by multiplying the first two survival parameters. Their respective standard error and confidence intervals were estimated using a custom parametric bootstrap algorithm developed in Microsoft Excel. In short, I used the delta method to obtain standard errors for the two intervals, then generated 6000 bootstrap replicates using the cumulative normal distribution function in Excel. The logit-scale bootstrap replicates were transformed, and the two values were multiplied together for each replicate to approximate the distribution of the combined overwinter parameter.

Simulations

The sample size of returning adults was very low for the early migrant life history strategy. Consequently, I wanted to test how much the sample size affected the ability to detect a difference in marine survival between the two juvenile life history strategies S and E. To do this I performed a power analysis using simulated data. In Program Mark, I used a variation of the *general* model structure as the ‘true model’, in which survival varied between states. The model differed from *general* by only including one cohort

grouping. I used the point estimates from cohort 2 as the parameters for the simulations both for the A=2+ and A=J data sets. I chose cohort 2 because there was the largest difference in the point estimates between the marine survival parameters of S and E. This difference was 0.020 in the A=2+ data set and 0.031 in the A=J data set, which may be a large enough difference to be considered biologically important to conservationists and managers.

I simulated data sets where the sample size of fall tagged juveniles was 500, 1000, 2000, 3000, 4000, 5000 and 6000, with 1000 simulations per sample size. I analyzed each data set using model comparison of two models; the 'true model' in which marine survival varied between the S and E states, and a reduced parameter model, in which marine survival was set equal between the S and E states. I then performed a likelihood ratio test (LRT) (Sokal and Rohlf 1995) for each of the 1000 simulations. I calculated the LRT test statistic and assessed whether the difference in model deviances (between the true and reduced parameter models) was significant at the alpha=0.05 level. I also calculated the mean ΔAIC_c, evidence ratios and model likelihoods for each of the simulated sample sizes (Cooch and White 2005).

RESULTS

Capture Histories

Dataset=Ambiguous juveniles (2+)

For the first cohort, a total of 759 juveniles were PIT- tagged upstream during the first occasion and 30 were PIT-tagged in the estuary. Of those fish PIT-tagged upstream in the first occasion, 16 were detected upstream on the second occasion and 153 were detected moving downstream into the estuary on the second occasion. Ten of the fish tagged in the estuary in the first occasion were detected in the estuary during the second occasion. During the second occasion, 123 additional fish were marked in the stream state and 157 additional fish were marked in the estuary state. Of those fish PIT-tagged in the first and second occasions, 273 stream fish were detected moving downstream on the third occasion, and 121 estuary fish were detected again in the estuary. An additional 2442 stream fish were marked during the third occasion at the downstream migrant trap. In summary, by the third occasion there were 3171 juveniles in the stream state and 340 in the estuary state. Of those PIT-tagged in the first three occasions, 41 were detected returning as adults: 38 stream fish, 2 estuary fish and 1 jack (J) that transitioned from the stream state. There were no jacks detected transitioning from the estuary state (Table 3, Figure 6).

Table 3. M-array for cohort 1 of the A=2+ dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2013- Winter 2015/2016. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions															
Occ.	State	Number	Second			Third			Fourth			Fifth			Total recaptured	Never
		released	winter occasion			spring occasion			spawning occasion			spawning occasion			from a given	recaptured
		(R_i)	S	E	J	S	E	J	S	E	J	S	E	J	release batch (r_i)	(R_i- r_i)
1	S	759	16	153	0	237	0	0	0	0	0	0	0	0	406	353
1	E	30	0	10	0	0	10	0	0	0	0	0	0	0	20	10
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	139				36	0	0	0	0	0	0	0	0	36	103
2	E	320				0	111	0	0	0	0	0	0	0	111	209
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	2715							28	0	1	10	0	0	39	2676
3	E	121							0	2	0	0	0	0	2	119
3	J	0							0	0	0	0	0	0	0	0
4	S	28										18	0	0	18	10
4	E	2										0	2	0	2	0
4	J	3										0	0	1	1	2
5	S	28													0	28
5	E	2													0	2
5	J	1													0	1

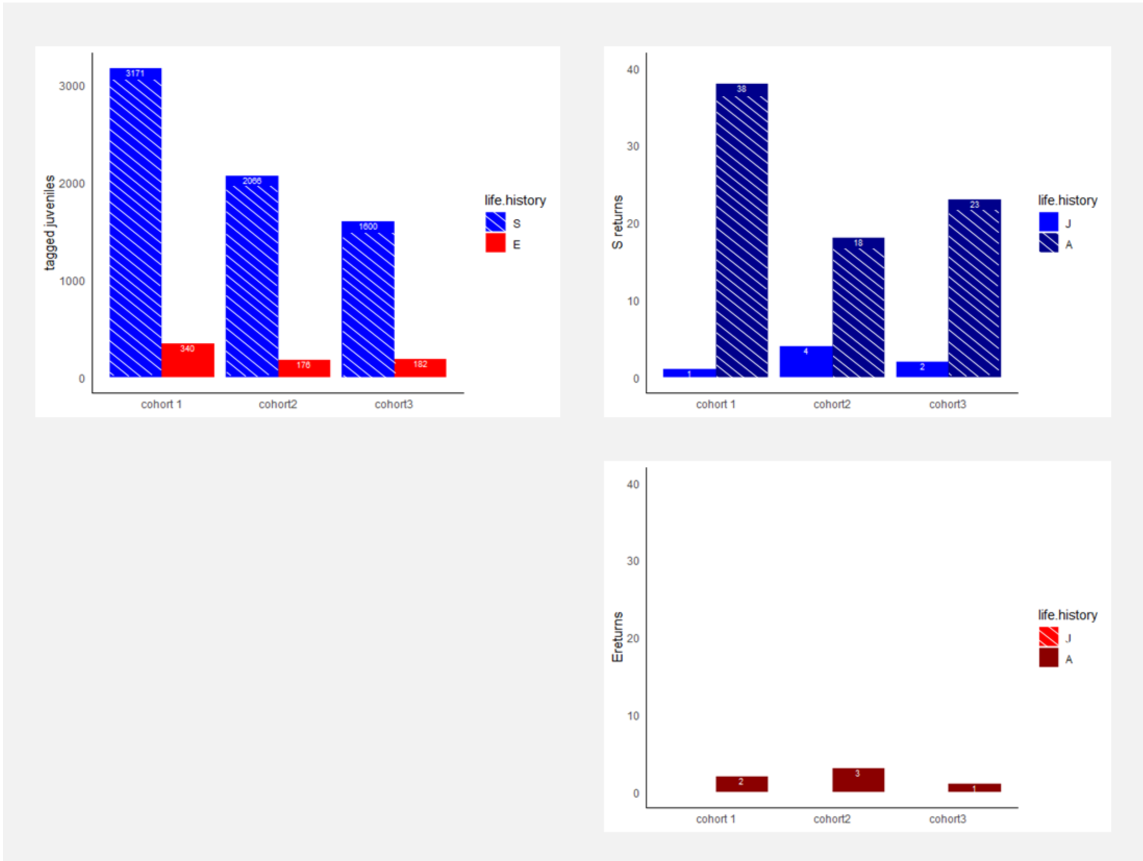

Figure 6. Tagged juveniles and returning adults from data set A=2+. Top left graph: the number of tagged juveniles per cohort. The hashed blue bars represent the number of spring migrating juveniles and the solid red bars represent the number of early migrating juveniles. Top right: the number of spawners detected, originating from the spring migrant juvenile life history. Solid light blue represents the number of those returning as jacks, the hashed dark blue represents the number of those returning as adults. Bottom right: the number of spawners detected, originating from the early migrant juvenile life history. Hashed light red represents the number of those returning as jacks, the solid dark red represents the number of those returning as adults.

For the second cohort, a total of 530 juveniles were PIT- tagged upstream during the first occasion and 17 were PIT-tagged in the estuary. Of those fish PIT-tagged upstream in the first occasion, 69 were detected upstream on the second occasion and 52 were detected moving downstream into the estuary on the second occasion. Eight of the fish tagged in the estuary in the first occasion were detected in the estuary during the second occasion. During the second occasion, 38 additional fish were marked in the stream state and 107 additional fish were marked in the estuary state. Of those fish PIT-tagged in the first and second occasions, 233 stream fish were detected moving downstream on the third occasion, and 108 estuary fish were detected again in the estuary. An additional 1550 stream fish were marked during the third occasion at the downstream migrant trap. In summary, by the third occasion there were 2066 juveniles in the stream state and 176 in the estuary state. Of those PIT-tagged in the first three occasions, 25 were detected returning as adults: 18 stream fish, 2 estuary fish and 4 jacks (J) that transitioned from the stream state. There were no jacks detected transitioning from the estuary state (Table 4).

Table 4. M-array for cohort 2 of the A=2+ dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2014- Winter 2016/2017. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions															
Occ.	State	Number	Second			Third			Fourth			Fifth			Total recaptured	Never
		released	winter occasion			spring occasion			spawning occasion			spawning occasion			from a given	recaptured
		(R_i)	S	E	J	S	E	J	S	E	J	S	E	J	release batch (r_i)	(R_i- r_i)
1	S	530	69	52	0	185	0	0	0	0	0	0	0	0	306	224
1	E	17	0	8	0	0	4	0	0	0	0	0	0	0	12	5
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	107				48	0	0	0	0	0	0	0	1	49	58
2	E	167				0	104	0	0	0	0	0	0	0	104	63
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	1783							8	0	3	10	0	0	21	1762
3	E	108							0	0	0	0	3	0	3	105
3	J	0							0	0	0	0	0	0	0	0
4	S	8										4	0	0	4	4
4	E	0										0	0	0	0	0
4	J	12										0	0	8	8	4
5	S	14													0	14
5	E	3													0	3
5	J	9													0	9

For the third cohort, a total of 437 juveniles were PIT- tagged upstream during the first occasion and 24 were PIT-tagged in the estuary. Of those fish PIT-tagged upstream in the first occasion, 19 were detected upstream on the second occasion and 116 were detected moving downstream into the estuary on the second occasion. Twelve of the fish tagged in the estuary in the first occasion were detected in the estuary during the second occasion. During the second occasion, 15 additional fish were marked in the stream state and 42 additional fish were marked in the estuary state. Of those fish PIT-tagged in the first and second occasions,95stream fish were detected moving downstream on the third occasion, and 91 estuary fish were detected again in the estuary. An additional 1263 stream fish were marked during the third occasion at the downstream migrant trap. In summary, by the third occasion there were 1600 juveniles in the stream state and 182 in the estuary state. Of those PIT-tagged in the first three occasions, 26 were detected returning as adults: 23 stream fish, 1 estuary fish and 2 jacks (J) that transitioned from the stream state. There were no jacks detected transitioning from the estuary state (Table 5).

Table 5. M-array for cohort 3 of the A=2+ dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2015- Winter 2017/2018. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions														
Occ.	State	Number released (R_i)	Second winter occasion			Third spring occasion			Fourth spawning occasion			Fifth spawning occasion			Total recaptured from a given release batch (r_i)	Never recaptured (R_i- r_i)
			S	E	J	S	E	J	S	E	J	S	E	J		
1	S	437	19	116	0	83	0	0	0	0	0	0	0	0	218	219
1	E	24	0	12	0	0	7	0	0	0	0	0	0	0	19	5
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	34				12	0	0	0	0	0	0	0	0	12	22
2	E	170				0	84	0	0	0	0	0	0	0	84	86
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	1358							18	0	0	5	0	2	25	1333
3	E	91							0	1	0	0	0	0	1	90
3	J	0							0	0	0	0	0	0	0	0
4	S	18										7	0	0	7	11
4	E	1										0	0	0	0	1
4	J	4										0	0	3	3	1
5	S	12													0	12
5	E	0													0	0
5	J	5													0	5

Dataset=Ambiguous jacks

The number of tagged juveniles is the same as the A=2+ data set; only the number of jacks differs between the two data sets. For the first cohort, 56 fish were detected returning as adults; 38 S fish, 2 E fish and 16 jacks that transitioned from the S state. There were no jacks detected transitioning from the E state (Table 6, Figure 7). For the second cohort, 46 fish were detected returning as adults; 18 S fish, 3 E fish, 22 jacks that transitioned from the S state and 3 jacks that transitioned from the E state (Table 7). For the third cohort, 50 fish were detected returning as adults; 23 S fish, 1 E fish, 23 jacks that transitioned from the S state and 3 jacks transitioning from the E state (Table 8).

Table 6 M-array for cohort 1 of the A=J dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2013- Winter 2015/2016. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions														
Occ.	State	Number released (R_i)	Second winter occasion			Third spring occasion			Fourth spawning occasion			Fifth spawning occasion			Total recaptured from a given release batch (r_i)	Never recaptured (R_i- r_i)
			S	E	J	S	E	J	S	E	J	S	E	J		
1	S	759	16	153	0	237	0	0	0	0	1	0	0	1	408	351
1	E	30	0	10	0	0	10	0	0	0	0	0	0	0	20	10
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	139				36	0	0	0	0	0	0	0	0	36	103
2	E	320				0	111	0	0	0	0	0	0	0	111	209
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	2715							28	0	7	10	0	7	52	2663
3	E	121							0	2	0	0	0	0	2	119
3	J	0							0	0	0	0	0	0	0	0
4	S	28										18	0	0	18	10
4	E	2										0	2	0	2	0
4	J	10										0	0	5	5	5
5	S	28													0	28
5	E	2													0	2
5	J	13													0	13

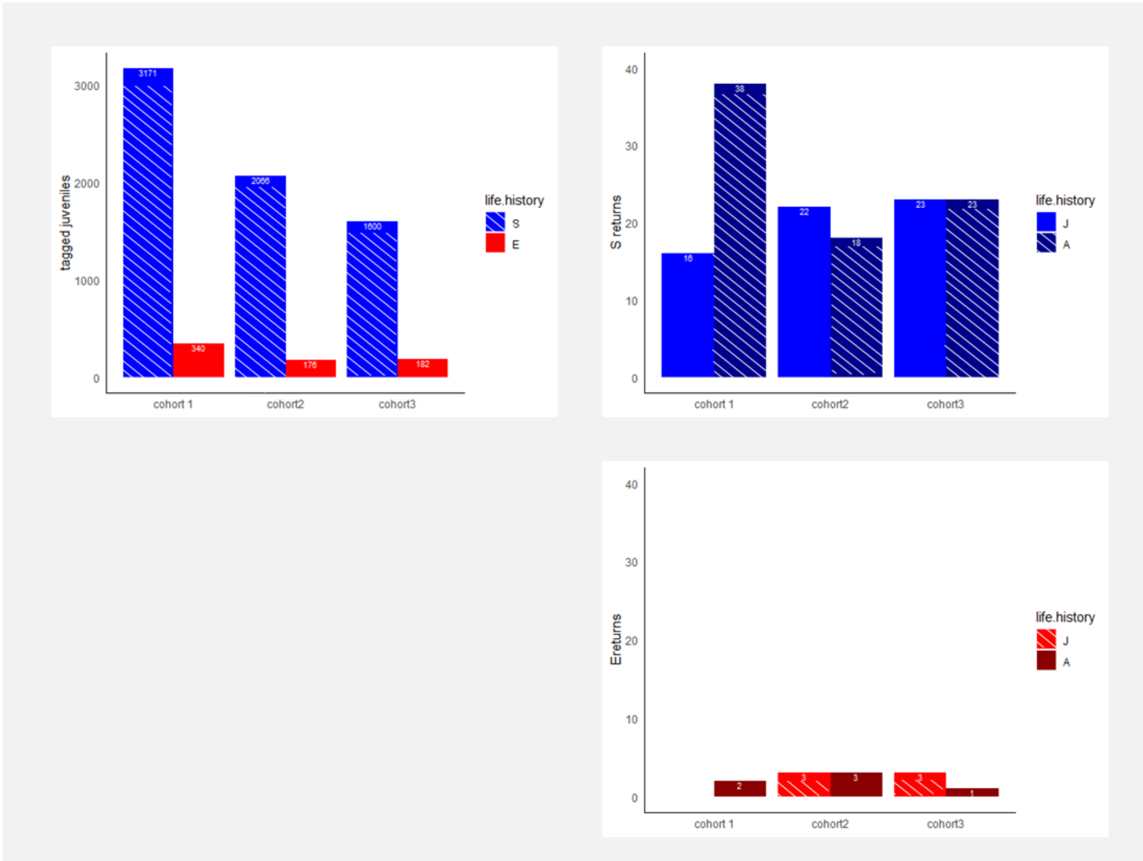

Figure 7. Tagged juveniles and returning adults from data set A=J. Top left graph: the number of tagged juveniles per cohort. The hashed blue bars represent the number of spring migrating juveniles and the solid red bars represent the number of early migrating juveniles. Top right: the number of spawners detected, originating from the spring migrant juvenile life history. Solid light blue represents the number of those returning as jacks, the hashed dark blue represents the number of those returning as adults. Bottom right: the number of spawners detected, originating from the early migrant juvenile life history. The hashed light red represents the number of those returning as jacks, the solid dark red represents the number of those returning as adults.

Table 7. M-array for cohort 2 of the A=J dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2014- Winter 2016/2017. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions														
Occ.	State	Number released (R_i)	Second winter occasion			Third spring occasion			Fourth spawning occasion			Fifth spawning occasion			Total recaptured from a given release batch (r_i)	Never recaptured (R_i- r_i)
			S	E	J	S	E	J	S	E	J	S	E	J		
1	S	530	69	52	0	185	0	0	0	0	0	0	0	1	307	223
1	E	17	0	8	0	0	4	0	0	0	0	0	0	0	12	5
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	107				48	0	0	0	0	0	0	0	2	50	57
2	E	167				0	104	0	0	0	0	0	0	1	105	62
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	1783							8	0	10	10	0	9	37	1746
3	E	108							0	0	1	0	3	1	5	103
3	J	0							0	0	0	0	0	0	0	0
4	S	8										4	0	0	4	4
4	E	0										0	0	0	0	0
4	J	20										0	0	12	12	8
5	S	14													0	14
5	E	3													0	3
5	J	26													0	26

Table 8. M-array for cohort 3 of the A=J dataset. Table for recaptured Coho Salmon in Freshwater Creek Fall 2015- Winter 2017/2018. The total number of released fish on a given occasion and in which state (R_i), total number of individuals captured from a given batch release (r_i), and the total number never recaptured (R_i-r_i). Occasion represents in hand tagging of YOY in the fall, occasion two is antenna detections and in hand capture over winter, occasion three is antenna detections and in hand capture of smolts outmigrating in the spring, occasion four is detections of adults at the weir and weir antenna and occasion five is detection of adults upstream.

		Recapture Occasions														
Occ.	State	Number	Second			Third			Fourth			Fifth			Total recaptured	Never
		released	winter occasion			spring occasion			spawning occasion			spawning occasion			from a given	recaptured
		(R_i)	S	E	J	S	E	J	S	E	J	S	E	J	release batch (r_i)	(R_i- r_i)
1	S	437	19	116	0	83	0	0	0	0	0	0	0	1	219	218
1	E	24	0	12	0	0	7	0	0	0	0	0	0	0	19	5
1	J	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	S	34				12	0	0	0	0	0	0	0	0	12	22
2	E	170				0	84	0	0	0	0	0	0	0	84	86
2	J	0				0	0	0	0	0	0	0	0	0	0	0
3	S	1358							18	0	11	5	0	11	45	1313
3	E	91							0	1	2	0	0	1	4	87
3	J	0							0	0	0	0	0	0	0	0
4	S	18										7	0	0	7	11
4	E	1										0	0	0	0	1
4	J	17										0	0	9	9	8
5	S	12													0	12
5	E	0													0	0
5	J	22													0	22

Model Selection

For both data sets (A=2+ and A=J) the best supported models were those in which marine survival between juvenile states S and E were equal in all three cohorts. The top models allowed overwinter survival to vary between S and E in the first cohort only, while keeping them equal in cohorts 2 and 3. In the top models, the transition probability from S to E was allowed to vary between cohorts, while the transition probabilities of S to J and E to J were equal to each other for each cohort (Table 9 and 10).

Table 9. A=2+ Model results using a Multi-state Capture Recapture model in Program MARK to estimate marine survival, overwinter survival, probability of a fall tagged fish migrating early and probability of transitioning to a jack for both spring and early migrating Coho Salmon in Freshwater Creek, 2013-2018. Models are in order from best supported to least supported. The variance inflation factor ($\hat{c}$) was estimated from the global model at 1.50 and the adjustment is reflected in the $QAIC_c$.

Model	ΔQAICc	QAICc Weight	No. of parameters
TJ(COHORT)	0	0.32816	34
TJ(cohort1cohort3)	1.2876	0.17238	35
TJ(cohort1cohort2)	1.8916	0.12745	35
TJ(cohort2cohort3)	1.9495	0.12381	35
TJ(cohort1)	3.1796	0.06693	36
TJ(cohort3)	3.2375	0.06502	36
TJ(cohort2)	3.8415	0.04807	36
OS(cohort2cohort3)	5.1299	0.02524	37
OS(cohort3)	6.301	0.01406	39
OS(COHORT)	7.94	0.00619	35
OS(cohort2)	8.4139	0.00489	39
MS(COHORT)	8.7219	0.00419	41
OS(cohort1cohort3)	9.1092	0.00345	37
TE(cohort1cohort3)	9.844	0.00239	36
MS(cohort1cohort3)	10.5272	0.0017	42
OS(cohort1cohort2)	11.2222	0.0012	37
MS(cohort1cohort2)	11.4176	0.00109	42
MS(cohort2cohort3)	11.58	0.001	42
MS(cohort1)	12.3584	0.00068	43
OS(cohort1)	12.3932	0.00067	39
MS(cohort3)	12.5208	0.00063	43
MS(cohort2)	13.4112	0.0004	43
general	14.3525	0.00025	44
TE(cohort1cohort2)	15.5229	0.00014	36
global	28.0568	0	54
TE(COHORT)	29.162	0	35
TE(cohort2cohort3)	30.9707	0	36
no group	86.5582	0	17

Table 10. A=J Model results using a Multi-state Capture Recapture model in Program MARK to estimate marine survival, overwinter survival, probability of a fall tagged fish migrating early and probability of transitioning to a jack for both spring and early migrating Coho Salmon in Freshwater Creek, 2013-2018. Models are in order from best supported to least supported. The variance inflation factor ($\hat{c}$) was estimated from the global model at 1.90 and the adjustment is reflected in the $QAIC_c$.

Model	ΔQAICc	QAICc Weight	No. of parameters
TJ(COHORT)	0	0.31266	34
TJ(cohort2cohort3)	1.3266	0.16107	35
TJ(cohort1cohort2)	1.458	0.15083	35
TJ(cohort1cohort3)	2.0046	0.11476	35
TJ(cohort2)	2.785	0.07768	36
TJ(cohort3)	3.3315	0.05911	36
TJ(cohort1)	3.4629	0.05535	36
OS(cohort2cohort3)	4.7903	0.0285	37
OS(cohort3)	6.7576	0.01066	39
OS(COHORT)	7.2251	0.00844	35
TE(cohort1cohort3)	7.8651	0.00613	36
OS(cohort2)	8.7916	0.00385	39
OS(cohort1cohort3)	9.1906	0.00316	37
MS(COHORT)	9.9503	0.00216	41
MS(cohort1cohort3)	11.1023	0.00121	42
OS(cohort1cohort2)	11.2247	0.00114	37
TE(cohort1cohort2)	12.2934	0.00067	36
MS(cohort1cohort2)	12.6799	0.00055	42
MS(cohort2cohort3)	12.7213	0.00054	42
OS(cohort1)	13.192	0.00043	39
MS(cohort1)	13.429	0.00038	43
MS(cohort3)	13.4705	0.00037	43
MS(cohort2)	14.6409	0.00021	43
general	15.3904	0.00014	44
TE(COHORT)	22.2854	0	35
TE(cohort2cohort3)	24.1547	0	36
global	31.2143	0	54
no group	63.7914	0	17

Model Estimates

Marine survival

Marine survival was indistinguishable between juvenile life history strategies, most likely due to the small sample size of returning E state adults. For the A=2+ data set, marine survival was estimated at 0.017 (0.012-0.025) for cohort one, 0.016 (0.009-0.026) for cohort two and 0.028 (0.017-0.046) for cohort three (Figure 8). For the A=J data set, marine survival was estimated at 0.024 (0.016-0.036) for cohort one, 0.027 (0.018-0.042) for cohort two and 0.049 (0.033-0.074) for cohort 3 (Figure 9). Although marine survival was indistinguishable between juvenile life histories, the point estimates of the general model were quite different, at least in cohort 2 (Appendix). For the A=2+ dataset, the difference in marine survival point estimates between spring migrants and early migrants for cohort 2, was 0.020 and for the A=J data set it was 0.031. For this reason, the point estimates of cohort 2 were used as the parameters to generate the simulated data for the power analyses.

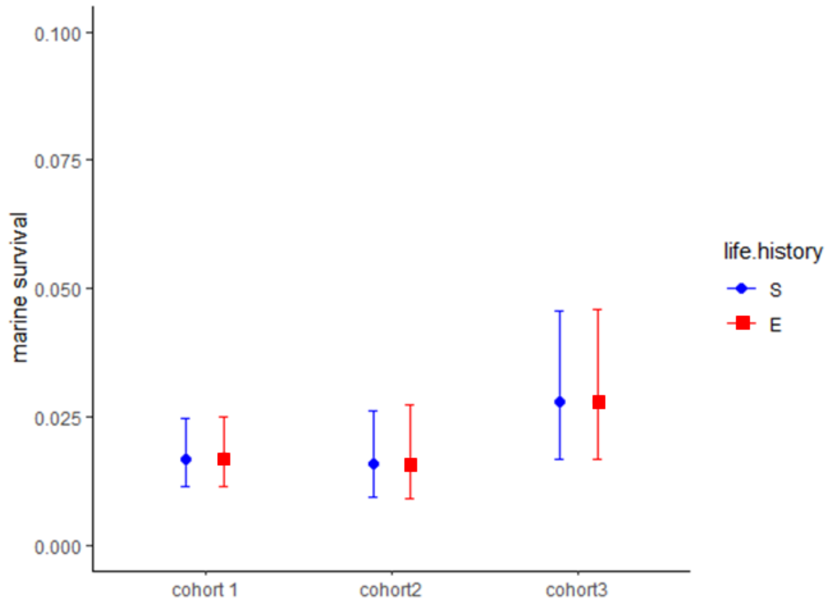

Figure 8. A=2+ marine survival of spring (blue circle) end early migrating (red square) juvenile Coho Salmon in Freshwater Creek, spanning three cohorts from 2013-2018.

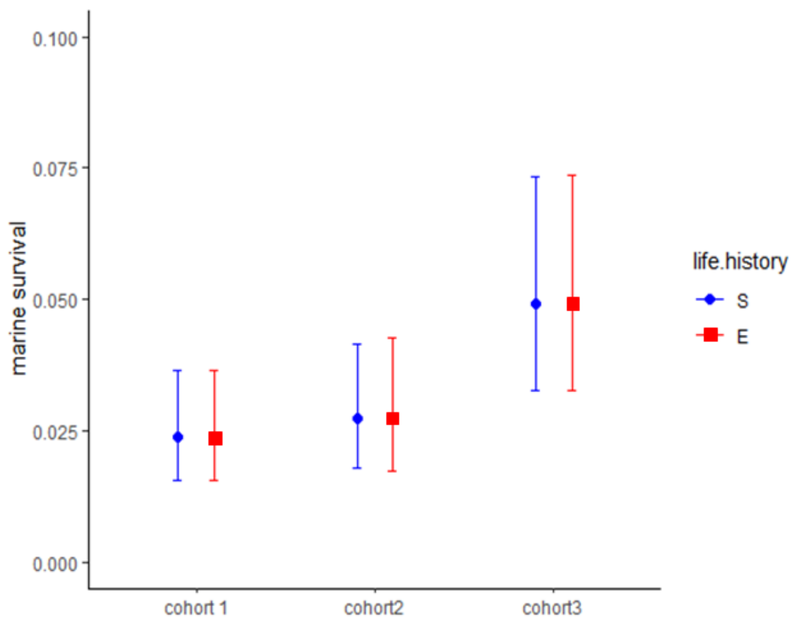

Figure 9. A=J marine survival of spring (blue circle) end early migrating (red square) juvenile Coho Salmon in Freshwater Creek, spanning three cohorts from 2013-2018.

<u>Overwinter survival</u>

In both data sets and for the first cohort only, overwinter survival of spring migrants was substantially higher than that of the early migrants. Overwinter survival was indistinguishable in cohort 2 and 3. In the A=2+ data set, cohort 1, overwinter survival for the spring migrants was estimated as 0.382 (0.348-0.416) and the early migrants as 0.257 (0.214-0.304). Cohort 2 was estimated as 0.561 (0.427-0.681) and cohort 3 was estimated as 0.401 (0.345-0.455) (Figure 10). In the A=J data set, overwinter survival for spring migrants was estimated as 0.528 (0.358-0.692) and early migrants as 0.259 (0.206-0.316). Cohort 2 was estimated as 0.735 (0.659-0.796) and cohort 3 was estimated as 0.414 (0.359-0.470) (Figure 11).

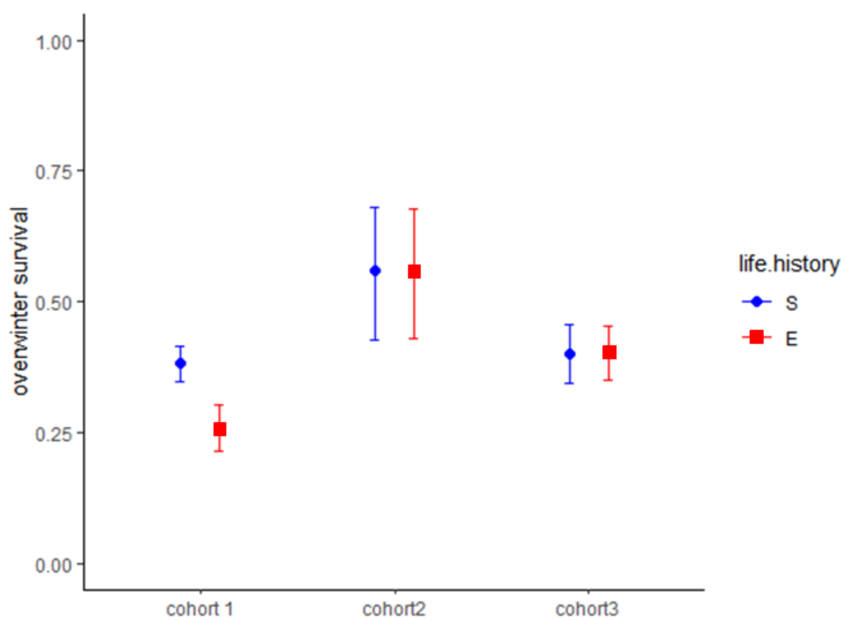

Figure 10. A=2+ overwinter survival of spring (blue circle) end early migrating (red square) juvenile Coho Salmon in Freshwater Creek, spanning three cohorts from 2013-2016.

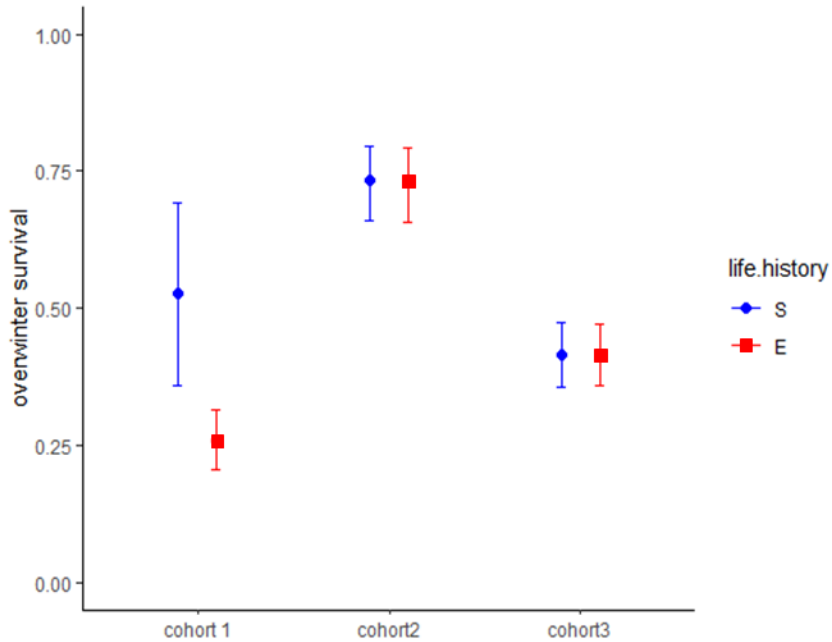

Figure 11. A=2+ overwinter survival of spring (blue circle) end early migrating (red square) juvenile CohoSalmon in Freshwater Creek, spanning three cohorts from 2013-2016.

<u>S to E transition</u>

The transition probability from S to E was significantly different for each cohort. For A=2+ data set, S to E transition was estimated at 0.221 (0.182-.265) for the first cohort, 0.114 (0.081-0.265) for the second cohort and 0.339 (0.251-0.440) for the third cohort (Figure 12). For the A=J data set, S to E transition was estimated at 0.221 (0.178-0.271) for the first cohort, 0.115 (0.078-0.167) for the second cohort and 0.332 (0.242-0.436) for the third cohort (Figure 13).

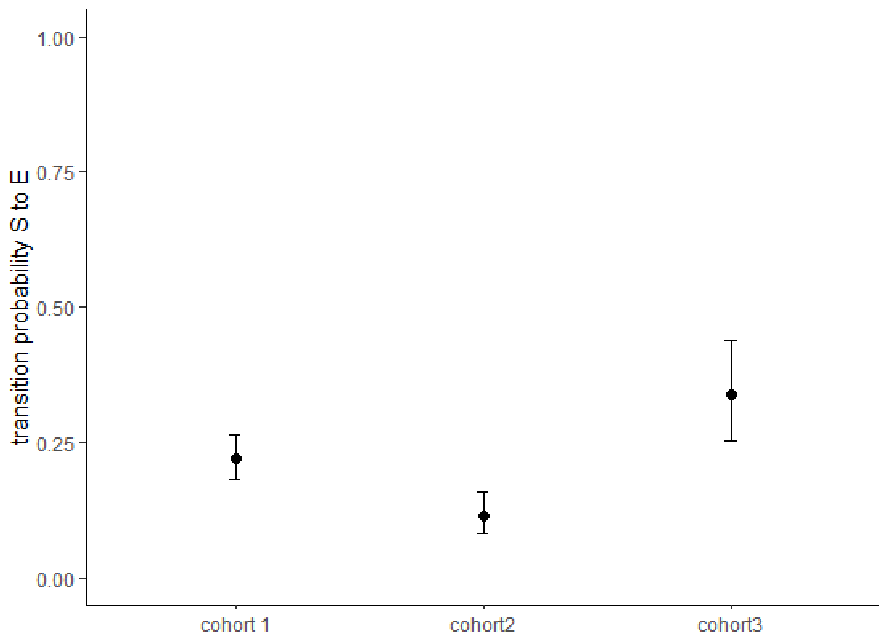

Figure 12. A=2+ Transition probability of fall tagged juvenile Coho Salmon to the early migrant life history strategy. Spanning three cohorts from 2013-2016.

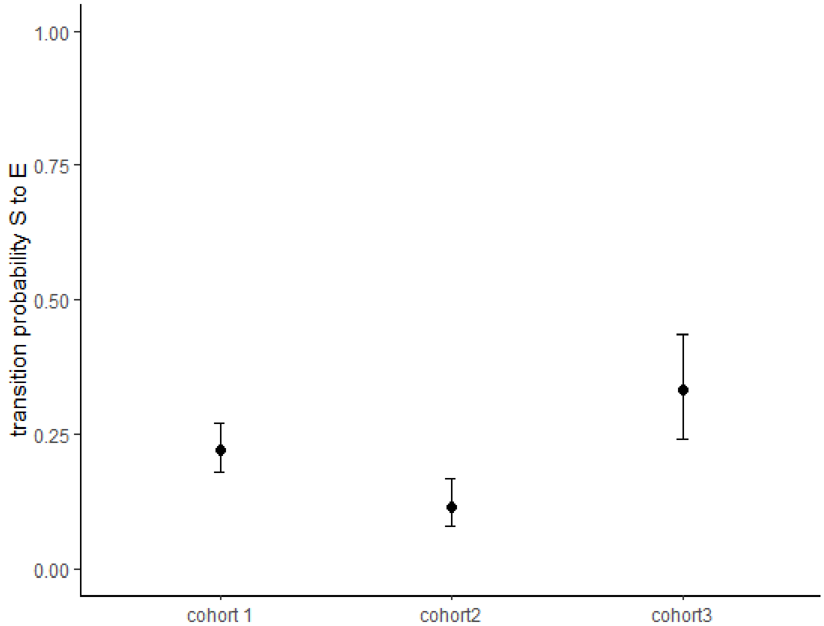

Figure 13. A=J Transition probability of fall tagged juvenile Coho Salmon to the early migrant life history strategy. Spanning three cohorts from 2013-2016.

Transition to J

Although the transition probabilities to the jack state were fixed to be the same for S and E fish in the top model, there is some evidence that this transition may differ between the two life histories. In *TJ(COHORT*), the top ranked model, the transition probability to J was set equal between S and E states in each cohort. However, the next top ranked model *TJ(cohort2cohort3)* allowed the probability to be estimated separately for S and E states in the first cohort. The next ranked model *TJ(cohort1cohort2)* allowed the probability to be estimated separately for S and E states in the second cohort. And the next top ranked model *TJ(cohort1cohort3)* allowed the probability to be estimated separately for S and E states in the third cohort. Since these models held a significant $QAIC_c$ weight (>0.10), the transition probabilities to the jack state were estimated as slightly different between juvenile life history strategies. For the first cohort of the A=2+ data set, the transition probability from S to J was estimated at 0.021 (0.002-0.198) and E to J was estimated at 0.015 (0.001-0.262). For the second cohort, the transition probability from S to J was estimated at 0.161 (0.048-0.423) and E to J was estimated at 0.096 (0.011-0.513). For the third cohort, the transition probability from S to J was estimated at 0.061 (0.011-0.281) and E to J was 0.041 (0.003-0.348) (Figure 14). For the first cohort of the A=J data set, the transition probability from S to J was estimated at 0.344 (0.161-0.589) and E to J was estimated at 0.216 (0.030-0.709). For the second cohort, the transition probability from S to J was estimated at 0.513 (0.313-0.709) and E to J was estimated at 0.504 (0.202-0.803). For the third cohort, the transition probability

from S to J was estimated at 0.463 (0.274-0.663) and E to J was 0.558 (0.158-0.894) (Figure 15).

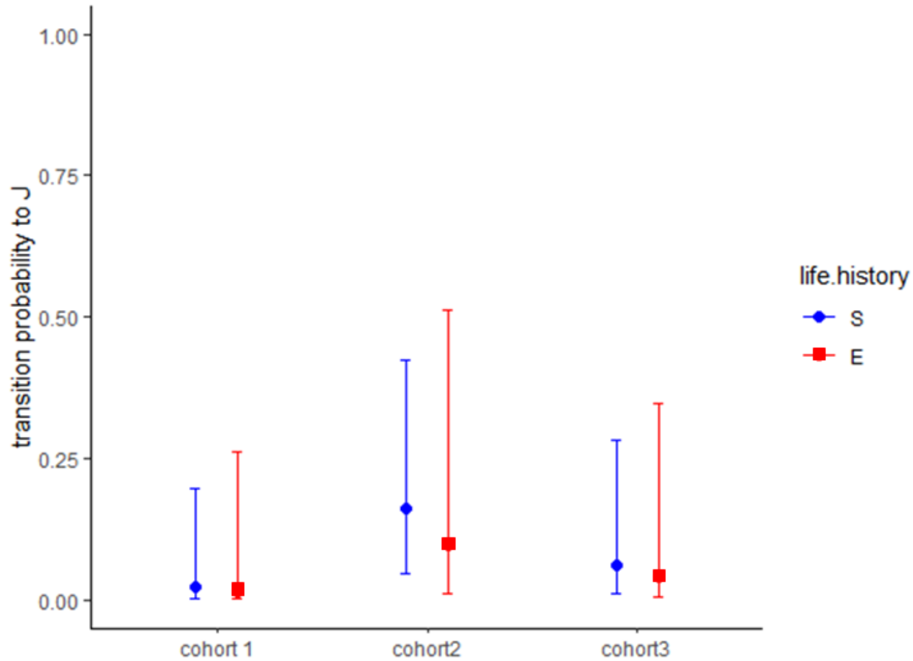

Figure 14. A=2+ Probability of transition to the jack state. Spring migrating juveniles (blue circle), early migrating juveniles (red square), separated by cohort.

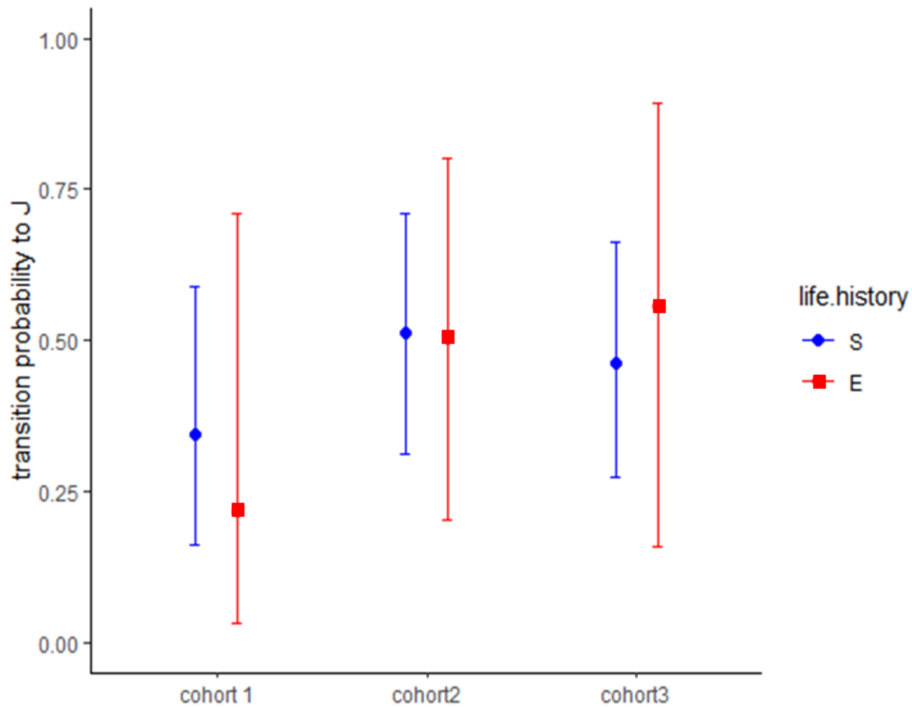

Figure 15. A=2+ Probability of transition to the jack state. Spring migrating juveniles (blue circle), early migrating juveniles (red square), separated by cohort.

Simulations

Both power analysis simulations demonstrate a low probability of detecting a 0.020 and 0.031 difference in marine survival between spring and early migrants with the current number of tagged juveniles. When the ambiguous fish were assumed to be 2+ juveniles (A=2+), the LRT demonstrated that we would need to tag 6000 juveniles in the fall to consistently detect a difference in survival of 0.020. On average, the likelihood of the reduced model is less than 0.05 when the sample size is 6000 (Table 11). When the ambiguous fish were assumed to be jacks (A=J), the LRT demonstrated that we would need to tag more than 3500 juveniles in the fall to consistently detect a difference in survival of 0.031. On average, the likelihood of the reduced model is less than 0.05 when the sample size is greater than 3500 (Table 12). Results of the simulation are shown in Figures 16 and 17. As the sample size of fall tagged fish increases, the model estimates converge on the true values.

Table 11. A=2+ power analysis simulation. The sample size of fall tagged juveniles was incrementally increased until the likelihood of the reduced parameter model was less than or equal to 0.05

sample size	% top model	mean ΔAICc	evidence ratio	likelihood
500	57	2.36	3.26	0.31
1000	61	2.59	3.65	0.27
2000	47	2.98	4.45	0.22
3000	63	3.67	6.27	0.16
4000	78	4.39	8.98	0.11
5000	72	4.91	11.66	0.09
6000	87	6.01	20.18	0.05

Table 12. A=J power analysis simulation. The sample size of fall tagged juveniles was incrementally increased until the likelihood of the reduced parameter model was less than or equal to 0.05.

sample size	% top model	mean ΔAICc	evidence ratio	likelihood
500	52	2.60	3.66	0.27
1000	59	2.98	4.43	0.23
2000	74	4.16	8.00	0.12
3000	81	5.07	12.64	0.08
3500	83	5.69	17.22	0.06
4000	86	6.34	23.83	0.04

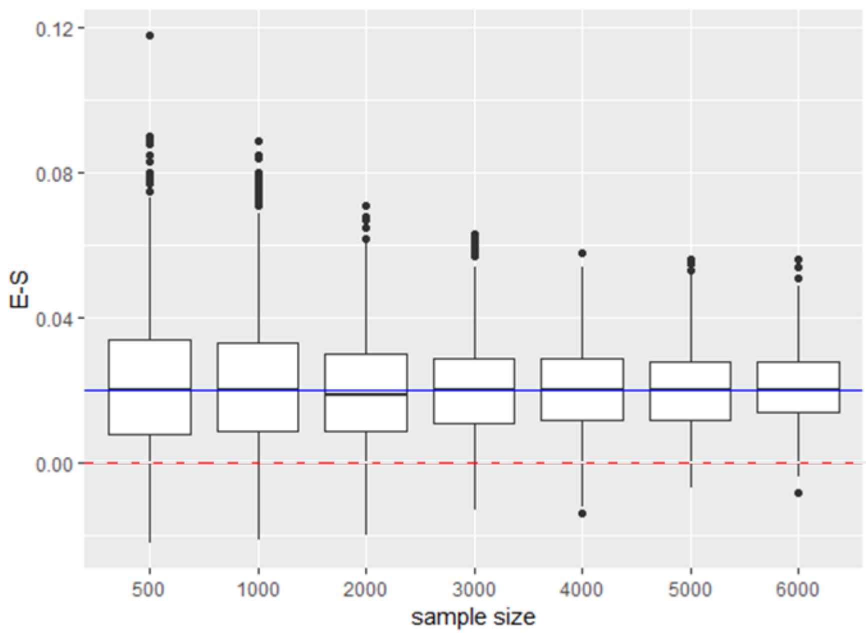

Figure 16. A=2+ Power analysis. Simulations with increasing sample sizes of fall tagged juveniles on the x axis. The difference in marine survival parameter estimates between early migrants (E) and spring migrants (S) on the y axis. The solid blue line is the true value of 0.020, the dashed red line is zero.

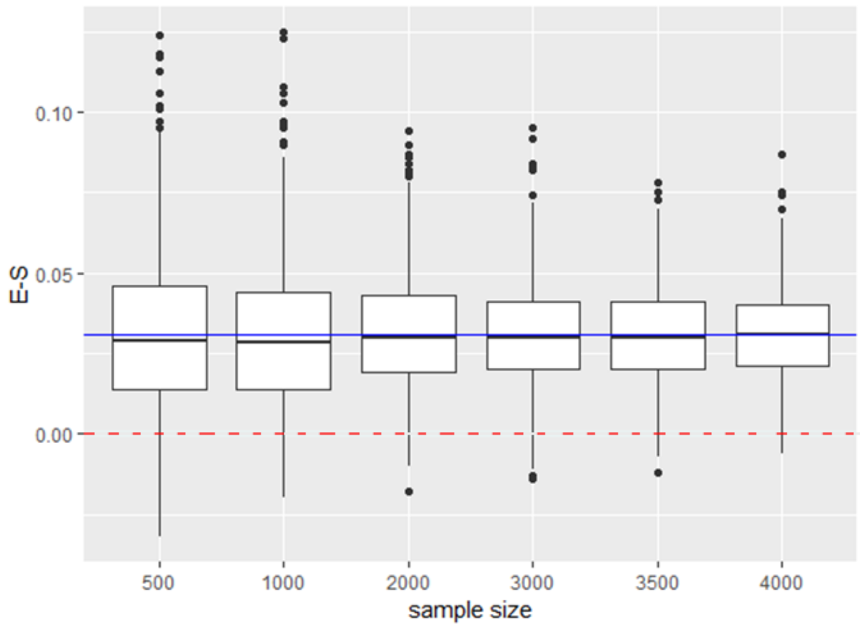

Figure 17. A=J Power analysis. Simulations with increasing sample sizes of fall tagged juveniles on the x axis. The difference in marine survival parameter estimates between early migrants (E) and spring migrants (S) on the y axis. The solid blue line is the true value of 0.031, the dashed red line is zero.

DISCUSSION

Through the use of a full life-cycle multistate model I was able to gain new insights into patterns of Coho Salmon life history expression in Freshwater Creek and estimate key demographic rates of the population. Firstl, I found that fish that reared in the estuary as juveniles survived to adulthood, indicating that this life history can contribute to population growth. I was then able to estimate overwinter survival for each juvenile life history strategy and demonstrate that there are differences in overwinter survival between the two in some years. Additionally, I demonstrated that the expression of the early migrant life history fluctuates on an annual basis. While limited sample size prevented me from making strong conclusions about whether freshwater life history affects the marine survival or whether males return as jacks, my power analysis allowed me to estimate the number of tags needed in order to detect potential differences in marine survival between the juvenile life histories. No previous studies have estimated overwinter survival or marine survival of early migrating Coho Salmon using multistate mark recapture modeling.

Overwinter Survival

Overwinter survival for the juvenile Coho Salmon varied by year; estimates ranged from 0.25-0.53 for the first cohort, 0.56-0.73 for the second cohort and 0.40-0.41 for the third (these ranges include both life history strategies and ambiguous fish designations). Although I did not examine environmental covariates in this analysis, it is

noteworthy that the first cohort experienced a low water year and the third cohort experienced a high water year compared to historic averages (Eureka 2019) (Figure 18). Extreme flow events such as drought and winter floods have been negatively correlated to Coho Salmon overwinter survival (Lawson et al. 2004); this may explain the trend of higher relative overwinter survival in the second cohort. Further investigation of these trends should be examined using covariate analysis in a modeling framework.

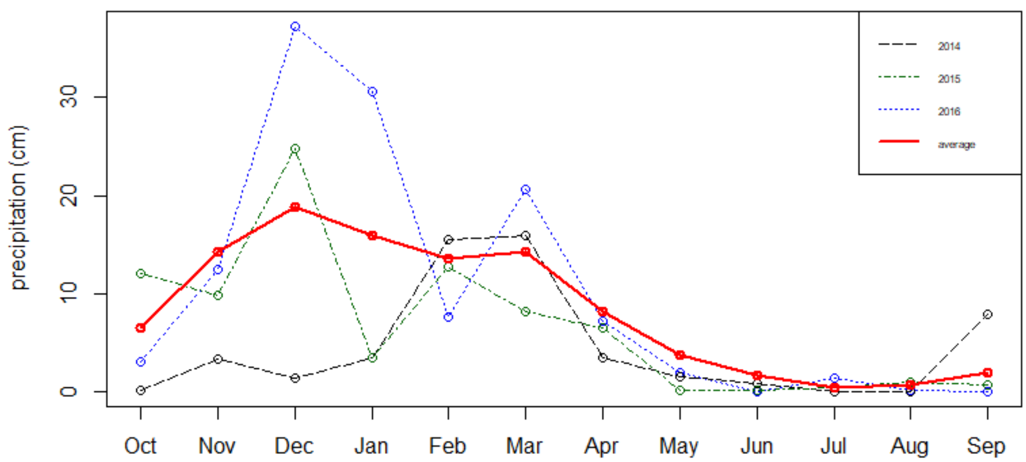

Figure 18. Monthly precipitation on Woodley Island in Eureka, California for water years 2014-2016. Solid red line represents 50 year historic average.

The overwinter survival estimate of spring migrants was significantly higher than that of the early migrants in the first cohort, yet indistinguishable in the second and third cohorts. This demonstrates that there can be differences in freshwater survival between life history strategies, depending on year. In the first cohort, the overwinter survival of spring migrants was estimated as 38-53% (depending on ambiguous fish designation) compared to the early migrants at 26%. My overwinter survival estimates of spring migrants in 2013-2016 (22-53%) are on the high end of the range compared to other Coho Salmon overwinter survival studies (13-49%) (Peterson et al. 1994, Brakensiek and Hankin 2007, Roni et al. 2012, Hauer 2015). This is likely due to the fact that other studies fail to account for early emigration.

Weybright and Giannico (2018) conducted a study similar to mine in Palouse Creek in Oregon, examining differences in survival between sedentary and mobile juvenile Coho Salmon over the winter. They found that sedentary juveniles had higher rates of overwinter survival than those that were mobile. Although I found a similar pattern with the spring migrants and early migrants in cohort 2, our results are not analogous since their classification of mobile was not defined by estuary habitat use like mine was.

The multistate model is more inclusive when compared to the modeling approaches currently being used to calculate Coho Salmon overwinter survival. By accounting for each life history and the potential for fish to transition between life history states, the multistate approach addresses some of the concerns about estimating these parameters that were raised in previous studies (e.g. Bennett et al. 2015, Rebenack et al.

2015). However, the multistate approach is still subject potential to bias. The overwinter capture occasions in my model are months long, violating the assumption that sampling is instantaneous and the that individuals in a state are subject to the same survival, capture, and transition. Early migrants move downstream at different times over the winter so that their overwinter intervals vary in length. In the multistate modeling framework implemented in Program MARK, individuals survive and then transition, so this violation affects the estimate for spring migrant overwinter survival. Most likely, the overwinter survival estimate for spring migrants is biased high, since a portion of the population (the S to E transitioners) survived to outmigration (they were detected in the E state) and did not necessarily survive the whole interval (they died before becoming smolts in the spring). Even with the bias, the multistate approach is superior to other mark recapture methods because it does not make the faulty assumption that all early migrants are mortalities (Rebenack et al. 2015).

Marine Survival

Marine survival estimates from the multistate model ranged from (1.6-4.9%), inclusive of both life history strategies and ambiguous fish designations. These estimates are within the range of other studies estimating smolt to adult return (SAR) rates (0.2-17%) (Gallagher et al. 2013, Bennett et al. 2015, Anderson and Ward 2016). The marine survival parameter of my model represents a juvenile's survival between outmigration and return to freshwater. This is a combination of the survival of the jack and adult fish in a single cohort, where interval lengths vary: 6 months for jacks and 18 months for adults.

This is analogous to the survival estimate currently reported for Coho Salmon populations in CMP monitoring programs, but is difficult to interpret as a demographic rate because the jacks returning at 6 months to not contribute to population growth like a three-year-old adult. Future modeling efforts should treat return rates of jacks and adults separately.

Marine survival for cohort 3 was high when compared to the other two cohorts. Environmental covariates were not analyzed in this study; however, these results were consistent with the Northwest Fisheries Science predictions of salmon marine survival using ocean ecosystem indicators (Peterson et al. 2018). NOAA researchers use a combination of physical, biological and ecosystem indicators within the California current to predict salmon survival in advance; they use metrics such as sea surface temperature, copepod biodiversity, and biological spring transition. Ocean indicators in 2015 and 2016 predicted the poorest juvenile salmon survival documented in over twenty years. In 2017, ocean conditions were considered fair for salmon survival and in 2018 they were considered neutral. The marine survival that I estimated follows this trend, greatly increasing for adults returning in 2018 (cohort 3), suggesting that marine survival of Coho Salmon in Freshwater Creek may correlate to ocean indicators.

With the current sample sizes, estimates of marine survival were indistinguishable between juvenile life history strategies. However, I estimate that it is necessary to deploy 3500-6000 tags in the fall in order to detect a difference of 0.02-0.03 between the juvenile life history strategies. The Freshwater Creek monitoring program aims to tag 2000 juveniles each fall, using a combination of FDX and HDX tags (Table 13); usually

less than 1000 per year are HDX tags (my analysis was limited to HDX tags). With the current antenna structure, an increase to 3500-6000 HDX tags is likely not feasible as many of the fish are too small to receive these larger tags during fall tagging. However, if an FDX antenna was installed upstream of the weir, FDX tags could be used for the analysis, and administering 3500-6000 tags to fish each fall may be possible.

Without either increasing the number of tagged fish or changing antenna structure to capture FDX tags at more locations, precise and unbiased estimates of marine survival for estuary-rearing fish are not possible for the Coho Salmon on Freshwater Creek. Another approach that may prove useful to evaluate the juvenile life history of adult returns is otolith microchemistry (Zimmerman 2005). Using otolith microchemistry, Nordholm (2014) concluded that 30-42% of the spawning adults in Larson and Palouse Creeks utilized the estuary as juveniles. Although this method could not provide estimates of marine survival, it could estimate the proportion of spawning adults that reared in the estuary as juveniles and help inform future plans for the Freshwater Creek monitoring program.

Transition to Jack

The phenotypic expression of the jack versus hooknose (three-year-old male) life history is thought to be a result of freshwater conditions the individuals experience as juveniles before migrating to sea (Koseki and Fleming 2007). For this reason, I tested whether the expression of the jack state was different between freshwater life history strategies. The transition probabilities from S to J and from E to J were indistinguishable

for each cohort examined. These results are likely due to small sample sizes of returning jacks. Even when ambiguous fish were assumed jacks (A=J), the number of jacks detected that transitioned from the early migrant life history strategy was very small: zero for the first cohort and three in both the second and third cohorts (Figure7).

The estimated transition probabilities to the jack state ranged from 1.5-16.1% for the A=2+ data set (Figure 14) and 21.6-55.8% for the A=J data set. This includes both juvenile life histories. There is a considerable difference between estimates depending on the designation of ambiguous antenna detections during the winter but comparing the two lends some insight into a potential solution to the ambiguity. The capture probability for migrating spawners at the weir was estimated separately from the multistate model, using opercular punches at the weir and carcass surveys (0.59, 0.41, and 0.45 for the three cohorts). Because only 3, 12 and 0 jacks were captured in hand at the weir for each respective cohort, it is highly unlikely that 16, 22, and 23 jacks would be detected on upstream antennas in the winter for each cohort, like the A=J data set assumes (Figure 7). Either the A=J data set is highly unlikely, or the assumption that jacks and adults have the same detection probability is faulty. At present, the demographic rates of jacks cannot be further examined until a better method of detection is developed.

Transition to the Early Migrant State

The probability of fall tagged juveniles migrating early was significantly different each year, ranging from 11-33%. These values represent the minimum proportion of juveniles migrating early, since they do not include those juveniles that migrated before

fall tagging. No covariates were analyzed in this study, however early migration has been correlated to discharge (Bramblett et al. 2002, Cederholm and Scarlett 1981 and Rodgers et al. 1987), location in the watershed (Rebenack et al. 2015, Weybright and Giannico 2018, Bennett et al. 2011), food limitation and aggression (Chapman 1962), and length (Bennett et al. 2015).

Study Critique

The multistate mark recapture modeling approach has greatly enhanced our ability to study wildlife populations in that it allows us to analyze individual movement and transition between ecologically important states. Before we design a study, it is necessary to consider the assumptions of the model, and the consequences of violating those assumptions. Along with the basic assumptions of the CJS model, the multistate model includes the assumption that animals survive, and movement happens right before the next occasion. If the intervals between occasions are long, and individuals transition at different times during that interval, then there is heterogeneity between members of the same state and the assumption is violated. This was certainly true in my study. Individuals transitioning to the E or J states over the winter transitioned at different times during that interval. As a result, estimates of survival and movement may have been confounded, causing both estimates to be biased (Hestbeck 1995). Unfortunately, given the biology of juvenile salmon, it is impossible to sample the whole population instantaneously.

Another important source of uncertainty in this study was the ambiguous tags. These tag detections in upstream areas during the spawning months could have been jacks returning from the sea, juveniles that remained in freshwater an additional year, or ghost tags (free tags from a fish that has died) (Bond et al. 2018). The assumptions about the ambiguous tags greatly affected the parameter estimates of interest, particularly the overwinter survival estimates and transition probabilities to the jack state. The issues raised by tag detections that do not fit the "typical" life history patterns are only starting to be addressed (Bond et al. 2018, Cochran et al. 2019). As more research and monitoring programs develop large databases of mark-recapture data, we will need to develop new sampling techniques and modeling approaches to deal with these issues.

Even with these biases, I believe the use of a multistate model, is superior to other modeling frameworks that do not allow for the inclusion of multiple life histories. In the practical application, this model can be used as an index to measure life history diversity of Freshwater Creek through time.

Conclusions

This study highlights the importance of updating monitoring protocols to include alternative life history variants. Life cycle monitoring stations in California and other states report overwinter survival estimates that do not include early migrants. In Freshwater Creek, I demonstrated that overwinter survival between the two life histories can differ, which means current methods of estimating overwinter survival are biased. Monitoring programs should strongly consider the use of multistate models to estimate

the demographic rates of at least spring and early migrants and consider tagging more juveniles in order to have the statistical power to do so. In this study I was unable to include two-year-old juveniles in the model, however they represent a portion of the juvenile population and should be included in monitoring and estimation of demographic rates as well.

This study contributes to a growing body of work that overturns the historical perspective that early migrants represent surplus juvenile production that does not contribute to adult return (Wallace et al. 2015, Bennett et al. 2015, Koski 2009, Cochran et al. 2019). Given access to habitat, early migrants can be successful evidenced by their survival to adulthood. As most estuarine wetland habitat on the California coast is highly degraded, this result highlights the potential value of habitat restoration work in these areas. It is still unknown whether early migrants represent a successful portfolio effect that can reduce the extinction risk for the Freshwater Creek population (Scheer 2017). For this to be true, survival rates for early migrants would have to respond to varying environmental conditions in ways that are distinct from spring migrants, such that a bad year for stream-rearing fish could be a good year in the estuary With long term monitoring of separate life history variants, this topic could be investigated further

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APPENDIX

Parameter estimates for Cohort two, used to simulate data for power analysis. Parameter type: phi represents survival, p represents detection probability and psi represents transition probability. State: S represents the spring migrant state, E the early migrant state and J the jack state. Model estimates, standard error and upper and confidence intervals are reported. The model is parameterized the same as *general*, except using only including cohort two data.

					95% CI		
parameter #	parameter type	state	estimate	SE	lower	upper	
1	ϕ	S	0.983	0.088	0.002	1.000	
2	ϕ	S	0.747	0.184	0.304	0.952	
3	ϕ	S	0.025	0.004	0.018	0.035	
4	ϕ	S	1.000	0	1.000	1.000	Fixed
5	ϕ	E	0.732	0.115	0.463	0.896	
6	ϕ	E	0.749	0.139	0.412	0.927	
7	ϕ	E	0.056	0.025	0.023	0.129	
8	ϕ	E	1.000	0	1.000	1.000	Fixed
9	ϕ	J	1.000	0	1.000	1.000	Fixed
10	p	S	0.148	0.022	0.110	0.196	
11	p	S	0.618	0.143	0.331	0.841	
12	p	S	0.410	0	0.410	0.410	Fixed
13	p	S	0.635	0.129	0.370	0.838	
14	p	E	0.904	0.045	0.772	0.963	
15	p	E	0.832	0.153	0.366	0.977	

parameter #	parameter type	state	estimate	SE	95% CI lower	95% CI upper	
16	p	J	0.590	0	0.590	0.590	Fixed
17	p	J	0.691	0.087	0.502	0.832	
18	ψ	S to E	0.104	0.016	0.075	0.141	
19	ψ	S to J	0.523	0.084	0.363	0.679	
20	ψ	E to J	0.474	0.205	0.152	0.819	