

COHO SALMON (*ONCORHYNCHUS KISUTCH*) DISPERSAL AND LIFE HISTORY
VARIATIONS AMONG HUMBOLDT BAY WATERSHEDS

By

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ABSTRACT

COHO SALMON (*ONCORHYNCHUS KISUTCH*) DISPERSAL AND LIFE HISTORY VARIATIONS AMONG HUMBOLDT BAY WATERSHEDS

Madison J. Halloran

The decline of Coho Salmon (*Oncorhynchus kisutch*) in California is the result of various anthropogenic effects across the landscape, affecting all stages of their anadromous life history. Monitoring a subset of the remaining populations is essential to evaluate the success of management actions and develop new restoration projects. Defining the appropriate spatial scale for this monitoring and restoration depends on the frequency and extent of dispersal of individuals across watershed boundaries. Coho Salmon life-cycle monitoring projects in California estimate the abundance of juveniles and adults over time in selected focal watersheds. If individuals frequently enter or leave the monitored watersheds for rearing or spawning, these abundance estimates might not accurately reflect the production and survival of individuals in the focal watershed. To address this issue, I assessed movement of Coho Salmon among watersheds along Humboldt Bay, including the life-cycle monitoring population in Freshwater Creek. Using individual tags and mark-recapture multi-state modeling, I quantified the frequency of juvenile and adult movement between Freshwater, Wood, Ryan, and Jacoby Creek over two years of life-cycle monitoring (2017-2019). Wood Creek and Ryan Creek are two connected sub-watersheds that share an estuary with Freshwater Creek, while

Jacoby Creek is separated from these other watersheds by Humboldt Bay. Straying of adults among watersheds was rare (only 2 individuals out of 51 tagged adult returns strayed into a stream with potential spawning habitat). Movement of juveniles through the full marine habitat in Humboldt Bay (between Jacoby Creek and the three other streams) occurred, but at low rates (3 fish out of 2492 individuals tagged in 2017 and 5 fish out of 2614 individuals tagged in 2018). Movement of juveniles among Freshwater, Wood, and Ryan Creeks was relatively common (ranged from 250 fish out of 2492 individuals tagged in fall 2017 to 354 fish out of 2614 individuals tagged in fall 2018).

I developed a multi-state model structure to estimate the probability of individuals moving among watersheds while accounting for survival and imperfect detection, but parameter estimates from the global model were unreliable due to small sample size and violations of mark-recapture assumptions. A reduced model with fewer parameters provided more reliable estimates. Apparent survival in the second interval of the most parsimonious reduced model was 47.5% in 2017-18 and 29.5% in 2018-19. The reduced model estimated that <0.2% of juvenile fish crossed the bay in both years. However, 17% and 23% of juvenile fish moved between Freshwater, Ryan, and Wood Creeks in 2017-18 and 2018-19 respectively. I also performed a power analysis with simulated data to demonstrate that a greater sample size of fall-tagged individuals would likely not provide more accurate model estimates for transition probability, as many of the transition probabilities are very close to zero. These results suggest the importance of scaling up monitoring efforts to include all connected areas upstream of marine habitats and suggest that it is less essential to monitor adjacent watersheds separated by full marine habitat.

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INTRODUCTION

Pacific salmon are ecologically important throughout their region and often used as an indicator species to characterize the health and productivity of watersheds. Salmon remain economically important throughout their range in both commercial and recreational fisheries (Quinn 2011). In the 20th century, California's salmon and steelhead populations experienced extreme declines in their distribution and abundance, leading many of the state's salmonids to be listed under the California Endangered Species Act (CESA) and the Federal Endangered Species Act (ESA) as either threatened or endangered (Adams et al. 2011). Monitoring and recovering these listed populations requires a clear understanding of the spatial scale of dispersal during juvenile rearing and reproductive integration of populations of salmon living in nearby watersheds. For my thesis, I addressed these issues for an intensively-monitored population of Coho Salmon (*Oncorhynchus kisutch*) in Freshwater Creek and adjacent watersheds that flow into Humboldt Bay, California.

Salmon that are born in different watersheds intermingle during their time in the ocean, but most individuals have a precise tendency to return to their natal rivers to spawn (Quinn 2011). Because of this, fisheries biologists have long recognized reproductive isolation of independent populations that spawn in different watersheds as a defining characteristic of Pacific salmonids (Waples 1991, Dittman and Quinn 1996, Hendry et al. 2000). This isolation allows for genetic divergence, local adaptation, and

life history variation among populations with increasing spatial separation, based on regionally specific genetic diversity (Spence et al. 2008).

The National Oceanic and Atmospheric Administration (NOAA) defines an independent population of any Pacific salmonid as “a collection of one or more local breeding units whose population dynamics or extinction risk over a 100-year time period is not substantially altered by exchanges of individuals with other populations” (McElhany et al. 2000). To manage for and conserve the local genetic and life history diversity of protected salmon, NOAA has defined groups of salmon populations in spatially-clustered watersheds along the West Coast as Evolutionary Significant Units (ESUs). The National Marine Fisheries Service (NMFS) has listed 27 salmon ESUs under the ESA since 1989 and created recovery plans and delisting criteria for these groups of salmonids (Spence et al. 2008). The ESA is primarily concerned with the viability and persistence of an ESU as a whole, not all of the individual populations within each ESU (McElhany et al. 2000), under the assumption that the ESU scale captures the spatial scale of local adaptation.

While the legal protection for salmonids operates at the ESU level, which incorporates many watersheds, the practice of protecting them through monitoring and evaluation of restoration activities typically take place at the population level, within a single watershed. Though much of the focus in modern salmon management has been placed on the conservation of genetic diversity in local, independent populations, Pacific salmonids have persisted for millennia through the exchange of individuals between spatially discrete populations (Rich 1939; Schtickzelle and Quinn 2007). Recent studies

have demonstrated that straying in wild populations is not merely a “failure to home”, but rather a critical evolutionary feature of salmonid biology, allowing a buffer to protect a population against natural variation in resources, as well as environmental catastrophes (Keefer and Caudill 2014). The Southern Oregon/Northern California Coast (SONCC) Coho Salmon ESU Recovery Plan acknowledges the potential for interactions between neighboring populations through their labeling of “core” and “dependent” populations, implying that a “core” population of a salmonid species will be able to assist the recovery of their neighbors through the movement of individuals (NMFS 2014), providing resilience to both anthropogenic stressors and catastrophic natural events (Adams et al. 2011). Because of this and other potential life history variations, recovery plan designs include strategies that account for the potential movement of individuals between populations, however, the frequency and importance of interactions between populations of different watersheds is often unknown (Lawson 2009). As salmon habitat becomes more fragmented through human actions, the need to better understand interactions between connected salmonid populations only grows.

Previous investigations of salmon dispersal among watersheds have most often focused on adult straying during their reproductive migration (Quinn 2011). Straying of adults has a clear effect on a donor population, as an adult that strays from its natal stream to reproduce elsewhere displaces its demographic contribution from one watershed to another. Straying can have varying effects on a small recipient population beyond the demographic contribution. Strays potentially contribute traits that improve the fitness and viability of the donor population, but the opposite can also happen. For

example, even very low (~1 percent) stray rates from large donor populations can “swamp” smaller, locally-adapted populations with an influx of individuals that lack adapted traits (Keefer and Caudill 2014).

In addition to straying as adults, salmon may also disperse among watersheds as juveniles. Juvenile dispersal occurs when a pre-smolt salmon leaves its natal stream to rear in another watershed before going to sea. This form of dispersal provides no direct demographic contribution of recruitment to the non-natal stream, unless the fish also returns as an adult to reproduce there. However, if a non-natal juvenile salmon is included in monitoring activities for a watershed or not included in production estimates for its home watershed, then frequent juvenile dispersal could bias estimates of population survival and outmigration. Movement of different life stages among watersheds could have important consequences for Pacific salmon populations, and has been investigated in Washington (Bennett et al. 2015, Roni et al. 2012), yet this scale of dispersal has not been studied rigorously in California.

Coho Salmon are a species of anadromous salmon, found along the West Coast of the United States and Canada. Aptos Creek, in central California, now represents the southernmost extent of their range, although historically they were found as far south as the San Lorenzo River in Santa Cruz County (Olswang 2017). Where populations remain, the abundance of Coho Salmon in California is a small fraction of historic levels. The decline of Coho Salmon in California is a result of various anthropogenic activities across the landscape, affecting all stages of their anadromous life cycle. These activities include stream alterations, urbanization, mining, logging, loss of genetic integrity due to reduced

stocks and hatchery salmon production, overharvest of adults, damming and climate change (Bradford and Irvine 2000, Brown et al. 1994; Spence et al. 2008 and references therein).

Coho Salmon throughout the Pacific Northwest typically follow a three-year life cycle. Juveniles remain in fresh water for one full year before migrating out to the ocean as smolts during the spring, usually between the months of March and May (Sandercock 1991, Brown et al. 1994). Most adults spend approximately 18 months at sea, before returning to their native stream to spawn and die. However, there are several common variations to this typical life history, including “jacks” (males that return at age two) and adults that stray from their natal stream to spawn. Some juvenile Coho Salmon migrate downstream to tidal estuary habitat prior to the spring smolt migration (Chapman 1962); the survival and reproductive success of these early emigrants is not well documented, but some do survive to return and spawn (Jones et al. 2014; Ghrist 2019). These variations provide temporal and spatial separation within populations, buffering against variable environmental conditions (Schtickzelle and Quinn 2007). However, they may also cause biased population estimates (Rebenack et al. 2015, Cochran et al. 2019) or affect the long-term viability of populations through transferred genetic adaptations (Spence et al. 2008).

The Coho Salmon fry that move downstream early in their life cycle are referred to as “nomads” (Koski 2009). Initial research attributed nomad’s downstream movement to displacement by dominant, territorial individuals upstream, leading to the inference that nomads are forced into low-quality habitat and not likely to contribute to adult

returns (Chapman 1962). Juvenile Coho Salmon were historically thought to be intolerant of saline-waters found in estuaries (Crone and Bond 1976), making them unlikely candidates for volitional early migrations outside of their natal stream. More recent studies have since shown that nomad Coho Salmon can not only tolerate brackish water, but that the estuary ecotone may provide crucial, highly productive habitat for these individuals (Koski 2009). There is evidence that nomadic juvenile life histories can successfully contribute to adult returns, and are not merely “surplus production” as previously thought (Bennett et al. 2015, Gorman 2016, Osterback 2017). Adult Coho throughout the West Coast have also been shown to stray from their natal streams (Keefer and Caudill 2014, Quinn 2011), although due to a lack of analysis of juvenile movement data, it is difficult to say if adult straying is linked to non-natal movement at another life stage.

My study on Coho Salmon dispersal and life history variations was located within the Humboldt Bay watershed. This area has some of the southernmost streams with robust spawning populations of Coho Salmon, and thus is crucial to the conservation and recovery of Coho Salmon. The Humboldt Bay population was included under the Southern Oregon/Northern Californian Coast (SONCC) ESU of Coho Salmon listed as threatened in 1997 (NMFS 2014). Humboldt Bay tributaries include Freshwater Creek, the site of a long-term, intensive Coho Salmon monitoring effort. The tributaries of Humboldt Bay outside of the Freshwater Creek watershed have not been regularly surveyed for juvenile Coho Salmon. Researchers have conducted spawner surveys throughout additional potential spawning tributaries to Humboldt Bay, but these adult

counts are intended to produce a single abundance estimate for the bay, not separate assessments of each tributary. Past studies of the Freshwater Creek population have assessed one life history variation – early emigration of smolts (Rebenack et al. 2015) and the effects this life history strategy might have on marine survival rates (Ghrist 2019). More data is needed to analyze the population for additional non-natal life history variations that may further impact population abundance estimates or marine survival rates.

Within the Humboldt Bay watershed, there have been indications for years that some Coho may display other alternative life history strategies, moving beyond the stream-estuary ecotone of their natal stream as either a juvenile or adult. Anecdotal evidence includes Freshwater Creek-tagged juveniles that were observed outmigrating as smolts from other streams (M. House, personal communication, 2017). Reports throughout the Pacific Northwest have documented similar alternative life history strategies for Coho Salmon, including juveniles entering saltwater before smoltification, and potentially moving between watersheds as pre-smolts, or later straying as returning adults (Bennett et al. 2015, Faulkner et al. 2017, Koski 2009, Roni et al. 2012, Weybright and Giannico 2017). Based on these observations, Anderson et al. (2019) called for monitoring efforts at Freshwater Creek to be expanded to include nearby streams and seasonal habitat within Humboldt Bay, in order to better capture what specific habitat attributes outside of the natal stream might be needed to improve survival rates of juvenile Coho Salmon.

I used passive integrated transponder (PIT) tags and mark-recapture multi-state modeling to evaluate the movement of rearing juveniles and returning adults between four Humboldt Bay tributaries. It is important to increase our understanding of this population to develop more robust monitoring approaches that account for these variations in juvenile life history. These four tributaries form a spectrum of connectivity – Freshwater, Ryan, and Wood Creeks are all connected within an estuary system, while the mouth of Jacoby Creek is several miles away across Humboldt Bay, which represents a lower degree of connectivity by both distance and a more challenging salinity barrier. I hypothesized that there would be some movement between all four study creeks, with increased transition probability between creeks that were closer to each other and thus more connected. If there are enough Coho Salmon moving between these watersheds throughout their juvenile life stages, it may significantly alter the estimates of key demographic rates from the monitoring data that is collected entirely within Freshwater Creek. Effective management and monitoring protocols, as well as data analysis of the Freshwater Creek life-cycle monitoring station would then need to be expanded to include nearby watersheds.

STUDY SITE

I evaluated movement of juvenile and adult Coho Salmon among four streams in the Humboldt Bay watershed: Freshwater, Wood, Ryan, and Jacoby Creeks. Humboldt Bay is located in Humboldt County, California, and is the second largest estuary in California. The Humboldt Bay watershed, which drains an area of 578 square kilometers, is mainly forested, and used for a mix of agricultural, residential, commercial, extractive or industrial purposes (HBWAC 2005). Most of the surrounding lands are used for timber production, with some residential areas and a small amount of agricultural and commercial use (HBWAC 2005). There are five tributaries to Humboldt Bay with known spawning populations of Coho Salmon every year: Jacoby, Freshwater, Ryan, and Salmon creeks, and Elk River. Numerous additional small tributaries may provide seasonal rearing habitat for Coho Salmon (NMFS 2014), for example, fish have been caught and observed on antennas in Wood Creek (Wallace et al. 2015). Freshwater Creek is the largest watershed in Humboldt Bay and the focus of most ongoing population monitoring efforts (Anderson and Ward 2016). Jacoby Creek and Ryan Creek are the Humboldt Bay tributaries closest to Freshwater Creek with documented adult Coho Salmon spawning and juvenile rearing habitat.

Freshwater Creek is a 24 km stream and drains an 83 square-km watershed. There is a 6-meter waterfall approximately 14.5 kilometers up the main channel that is a barrier to anadromy (Rebenack et al. 2015). The surrounding land is mostly forested and has experienced considerable timber harvest, with some agricultural land use. Several small

residential communities are located throughout the watershed. Freshwater Creek is connected to Humboldt Bay by Freshwater Slough, which then drains into Humboldt Bay. There is a permanent weir in the main stem of Freshwater Creek managed by the California Department of Fish and Wildlife (CDFW) and Humboldt State University Sponsored Programs Foundation as part of a Life Cycle Monitoring (LCM) station. In California, LCM stations are intended to allow CDFW to assess the response of Coho Salmon populations to freshwater habitat management while accounting for fluctuations in abundance caused by changing ocean conditions (Adams et al. 2011). To meet this goal, the Freshwater Creek LCM is operated to fulfill several main objectives, which include estimating juvenile and adult abundance, as well as freshwater and marine survival rates of Coho Salmon. Data from the LCM station also helps to characterize the diversity of life history patterns present in this watershed. An adult trap is installed at the weir each winter to sample Coho Salmon returning to spawn, a smolt trap is used at the weir each spring to sample emigrating smolts, and radio frequency identification (RFID) antenna arrays are installed on Freshwater Creek annually to detect PIT-tagged juveniles and adults (Figure 1). Historically, fisheries data in Humboldt Bay has largely focused on Freshwater Creek due to the presence of this sampling infrastructure. Annual estimates of juvenile Coho Salmon smolt emigration using mark-recapture procedures at the weir trap sampling location ranged between 5,000 and 17,000 from 2007-2018 (Anderson et al. 2019). Annual mark-recapture estimates of spawner abundance ranged from 600 and 1,800 individuals for the years 2002-2017.

Jacoby Creek is an 18-km-long stream and drains a 45 square-km watershed. The anadromous reach ends approximately 9 km upstream from the mouth due to a waterfall that is impassable for salmonids (HBWAC 2005). The mouth of Jacoby Creek is approximately 5 km north of the mouth of Freshwater Slough, connected by Humboldt Bay. Two restoration ponds were constructed on upper Jacoby Creek in 2016 and a lower channel network was constructed in 2018. During the first year of this study, two RFID antenna arrays were maintained at the upper Jacoby restoration pond, one at the off-channel pond entrance and one just below the pond on the main stem of Jacoby Creek. During the second year of the study, one array was maintained near the upper Jacoby restoration pond, while two additional arrays were installed in lower Jacoby Creek, one at the entrance to the new off-channel restoration pond, and one on the main stem of Jacoby just below that pond entrance.

Ryan Creek is a 10-km-long tributary that drains a 38 square-km watershed into Freshwater Slough. The lower one kilometer of Ryan Creek is tidally influenced. Ryan Creek was historically believed to provide poor salmon habitat due to its silty water and lack of coarse gravel substrate preferred by salmonids; however, significant numbers of adult Coho Salmon have been observed in the limited spawning habitat and juveniles have been captured throughout the creek from October to December. Previous PIT tagging studies have confirmed that Ryan Creek and its estuary also provides seasonal rearing habitat for juvenile fish originating from Freshwater Creek and its tributaries (Wallace et al. 2015). Ryan Slough provides approximately 4.5 km of anadromous habitat (HBWAC 2005). Until recently, approximately 76% of the Ryan Creek watershed

was owned by Green Diamond Resource Company and managed as timber lands. Green Diamond conducted some Coho Salmon monitoring at the site and CDFW conducted additional tagging and monitoring on Ryan Creek from 2013 – 2016 (Wallace 2015). Ryan Creek is connected to Freshwater Creek through Ryan Slough, so juveniles do not have to enter the bay to move between the two creeks. Ryan Creek has one PIT antenna array, located approximately 1 km upstream of its confluence with Freshwater Creek (Figure 1).

Wood Creek is a 1.6 km stream that drains a <2 square-km watershed. There is no Coho Salmon spawning habitat in Wood Creek, but it feeds into a recently restored tidal wetland intended to provide rearing habitat for non-natal juveniles. The Wood Creek restoration contains a network of channels and ponds that were built in two phases. Phase 1 was completed in 2010, and included the removal of a tidal gate, the construction of tide channels and the construction of an off-channel pond in the tidally-influenced area of Wood Creek. Phase 2 was completed in 2016, and included the construction of more tide channels to increase overwinter habitat for salmonids (Wallace et. al 2015). CDFW monitored the Phase 1 project area from 2007 until August 2017, and the Phase II project site from November 2016 through August 2017. In September of 2017, the National Marine Fisheries Service (NMFS) began monitoring water quality and fish assemblages in both Phase 1 and Phase 2 of the project area. This sampling occurs monthly from October to June (Pagliuco 2018). Two antennas arrays are maintained annually during the same months within the Wood Creek restoration site, one at the tide gate and one in the Phase 2 project area (Figure 2).

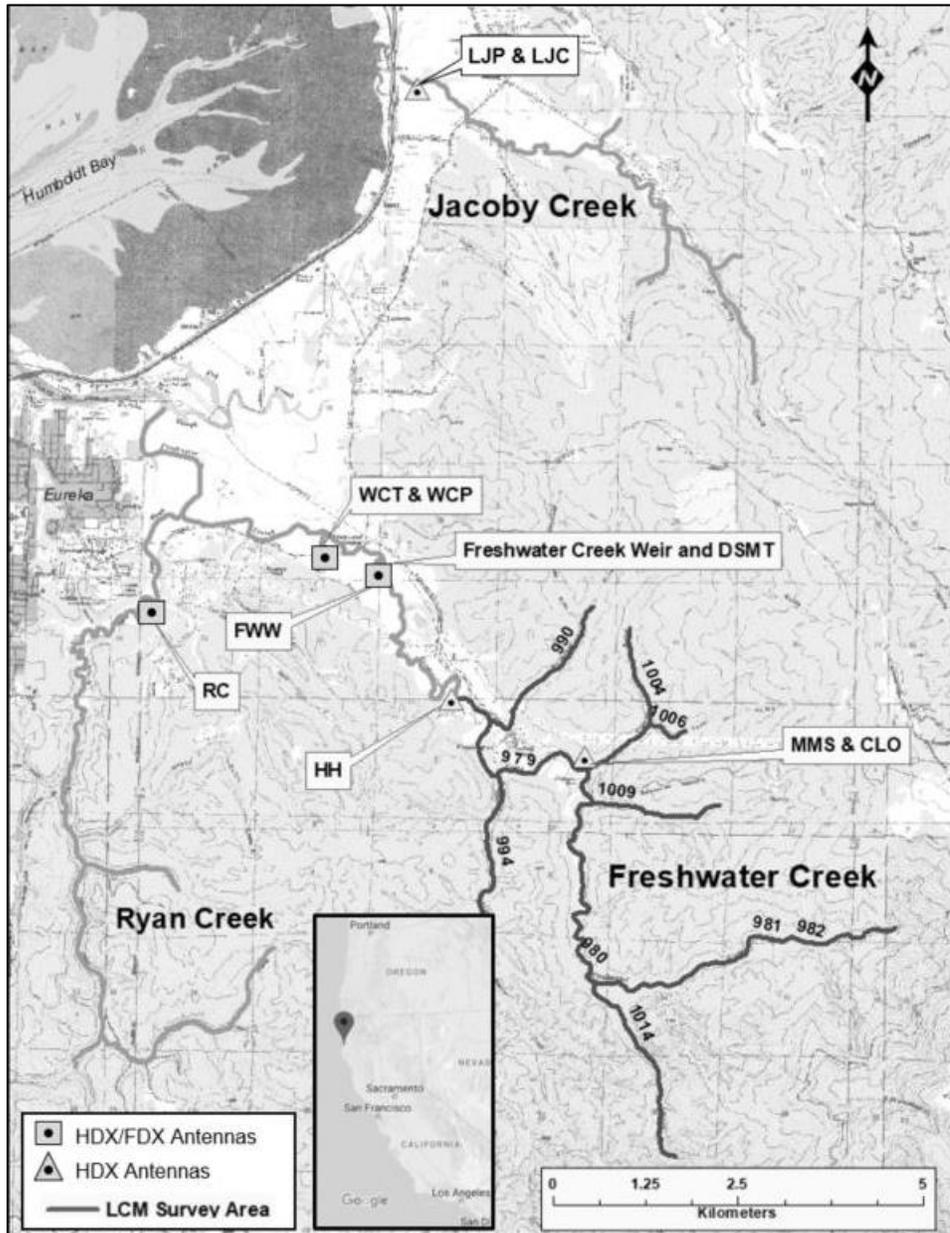


Figure 1. Humboldt Bay Tributaries, RFID antenna locations (triangles and squares), and spawner survey reaches (numbered) in the Freshwater Creek LCM station and adjacent streams for the 2018-19 monitoring season (Anderson et al. 2019). Antenna locations are abbreviated as: Lower Jacoby Creek/Pond (LJC & LJP), Wood Creek Tide Gate and Wood Creek Phase II (WCT & WCP), Freshwater Weir (FWW), Ryan Creek (RC), Howard Heights (HH), Middle Mainstem and Cloney Gulch (MMS & CLO). DSMT indicates the location of the downstream migrant trap. WCT & WCP also mark the location of the Wood Creek restoration study site (Figure 2). Inset shows location of Humboldt Bay on the West Coast of the United States (Google Maps).

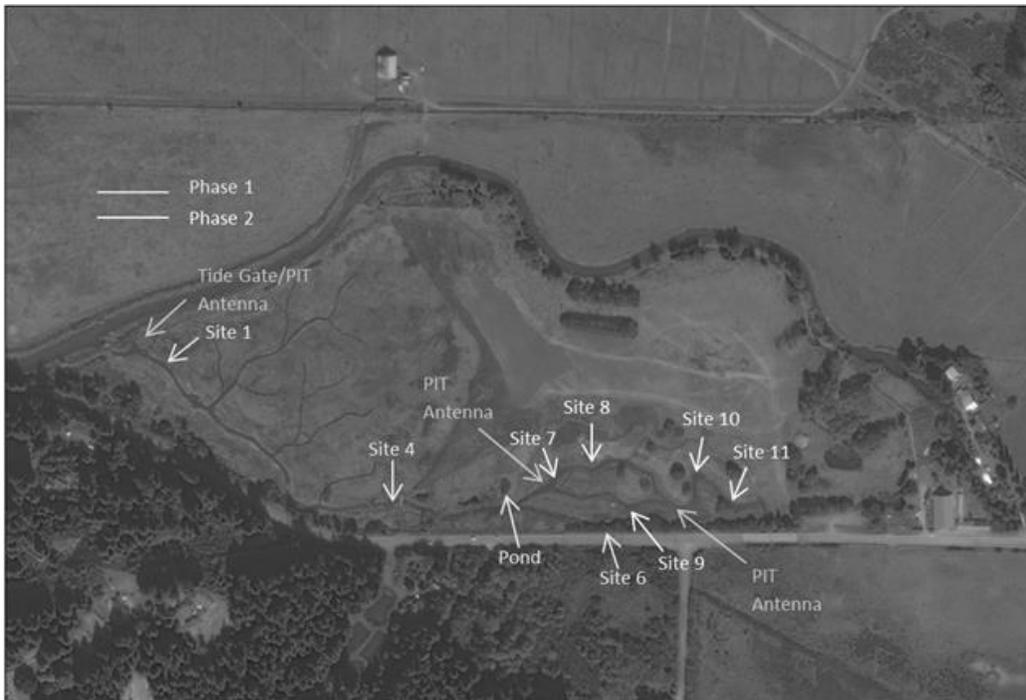


Figure 2. Map of the Wood Creek restoration study site, courtesy of Bob Pagliuco. Eight sites (labeled Site 1, 4, and 6-11) were sampled monthly using seining and minnow trapping. Three PIT tag antennas are labeled, only the Tide Gate and Phase 2 (middle) antennas are currently operational.

MATERIALS AND METHODS

I monitored movement for two juvenile (birth years 2017 and 2018) and two adult (return years 2017-18 and 2018-19) cohorts of Coho Salmon. I relied on the life-stage specific seasonal sampling and fish tagging efforts of the Freshwater Creek LCM program, supplemented with additional tagging and recapture efforts that I conducted at sites outside of the scope of the Freshwater Creek program. Each cohort was first sampled as young of the year (YOY) in the fall and subsequently detected at sampling events (described in detail below), stationary antennas arrayed through the study sites, or at the downstream migrant trap on Freshwater Creek. By June, most surviving juveniles had become smolts and migrated downstream to the ocean. Returning adults that were tagged as juveniles could also be detected at the stationary antennas or at an adult trap on Freshwater Creek.

For the study years 2017-19, the staff of the Freshwater Creek LCM sampled and marked juvenile Coho Salmon in Freshwater, Jacoby, and Ryan Creeks each fall. I worked with employees from the Northcoast Regional Land Trust, NOAA Fisheries, and volunteers to conduct monthly sampling in Wood Creek from November to June each year. I also worked with the LCM staff and volunteers from HSU to conduct seine and minnow trap surveys several times each winter in the Jacoby Creek restoration ponds. In the upper pond, we used a 3-4 m x 1.5 m x 3.2 mm mesh seine net to sample the pond in two sections, with approximately 4 seine pulls in each direction, pulling towards the mouth of the restoration pond. We also placed 10 minnow traps baited with hatchery

feed while we seined (at least 30 minutes). Seining was generally a more successful method than trapping in this pond. In the lower restoration area, volunteer crews used the same methods to sample twice during the 2018-2019 winter.

The LCM staff maintained a downstream migrant trap annually from March to June on Freshwater Creek. Detailed field methods are described in Anderson and Ward (2016), and relevant aspects for a typical year are summarized below. In this monitoring structure, an individual fish may be encountered at one or more of the following steps as a cohort completes its life cycle: fall tagging and fall/winter antenna detections as a YOY, spring outmigrant tagging at the trap (Freshwater Creek only), outmigrant detection on the antennas, adult capture at the trap, adult detection at antennas, and adult detection on spawning ground surveys.

The Institutional Animal Care and Use Committee (IACUC) approval number for this research was 15/16.F.79-A, which was first approved February 22, 2016.

Fall Tagging

The main stem and tributaries of Freshwater Creek were divided up into 10 reaches, and all reaches have been sampled each year since 2010. The average number of pools sampled and fish tagged per pool vary by reach to balance the number of tags deployed across areas in each watershed. Jacoby and Ryan Creeks were similarly divided into reaches and sampled annually starting in 2017.

The fall tagging effort for all three creeks (Freshwater, Jacoby, and Ryan) used systematic sampling, in which we seined every third pool along each reach for juvenile

Coho Salmon. Surveyors used a 3-4 m x 1.5 m x 3.2 mm mesh seine net to sample each pool until we captured the appropriate number of individuals to mark (goal of 9-12 per pool, depending on the reach). All salmonids were placed in a bucket and individually worked up by recording their fork length (FL) and wet weight before being tagged and released.

Juvenile Coho Salmon with a FL greater than or equal to 60 mm were marked with a PIT tag. Individuals with a FL between 60-69 mm received a 9 mm tag (Biomark FDX), while those with a fork length longer than 69 mm received a larger 12 mm tag (Biomark HDX). Prior to tagging, all fish were anesthetized using tricaine methanesulfonate (<150 mg/L) or Alka Seltzer. PIT tags were inserted into the body cavity through a <2 mm incision made with a sterile scalpel anterior to the pectoral fin. We allowed fish to recover for approximately 20-30 minutes before returning them to the pool where they were sampled.

Continued Tagging

The Jacoby Creek restoration pond sites were seined approximately once a month during the winter and spring to supplement antenna detections. Two people pulled a 4 m x 1.5 m x 3.2 mm mesh seine net to sample an area for YOY. Any individual caught in the net was scanned for a PIT tag. Any individuals without a PIT tag already implanted received a PIT tag using the same technique described above for fall tagging. Some sites were sampled with roe-baited minnow traps that were left in place for 30 minutes to an hour.

Sampling in Wood Creek began in 2007, and since September 2017, the National Marine Fisheries Service (NMFS) has conducted monthly sampling of eight sites within two restoration areas there. Some sites were sampled with baited minnow traps, a 9.1m x 1.8m x 6.4 mm mesh beach seine, or both (Pagliuco 2018). The same scanning and tagging procedure as described in Jacoby Creek was followed on Wood Creek.

Antenna Detections

Six antenna arrays located throughout Freshwater Creek (Figure 1) were operated continuously from mid-November to early June each year. In January of 2018, we installed an additional antenna array in lower Jacoby Creek. Ryan Creek has had one antenna array installed since 2015. The arrays were a mix of dual-platform readers that detect both HDX and FDX tags and single-platform readers that only detect HDX tags, so some were unable to detect the 9 mm PIT tags (Figure 1). Antennas located in Jacoby Creek, upper Freshwater Creek and its tributaries were only able to detect the 12 mm/HDX tags, while the Freshwater weir antenna arrays, Ryan Creek array, Wood Creek tide gate (WCT) and pond (WCP) antenna arrays read both half and full duplex tags (Anderson and Ward 2016). All antennas were operational for different periods of time throughout each study year (Table 1).

Table 1. Date ranges all RFID antennas were operational for each study season.

Antenna name	2017-2018 Season	2018-2019 Season
Upper Jacoby Creek Pond	01/03/2018 - 04/30/2018	10/23/2018 – 3/6/2019
Lower Jacoby Pond	N/A	11/24/2018 – 7/1/2019
Lower Jacoby Creek	N/A	11/23/2018 – 7/1/2019
Ryan Creek	08/29/2017 - 07/12/2018	11/20/2018 – 7/8/2019
Middle Main stem Freshwater Creek	10/18/2021 - 07/12/2018	10/15/2018 – 1/13/2019
Howard Heights, Freshwater Creek	11/08/2017 - 07/12/2018	10/18/2018 – 6/28/2019
Freshwater Creek Weir	10/18/2017 - 07/12/2018	11/20/2018 – 7/6/2019
Wood Creek Tide Gate	8/24/2017 - 7/09/2018	10/30/2018 – 6/17/2019
Wood Creek Phase 2	8/24/2017 - 7/09/2018	11/18/2018 – 6/23/2019

Smolt Trapping

A downstream migrant, or “smolt” trap is installed annually at the Freshwater Creek weir in early March (weather and flow dependent). The LCM staff continued to use similar methods to the past 16 years of smolt trap operation (Anderson and Ward 2016). The trap was checked daily, and all individual fish were scanned with a handheld scanner to check for PIT tags. Each day, a sample of previously unmarked age 1+ Coho were marked with PIT tags. Both individuals recaptured from fall tagging and newly marked individuals had their fork length and weight recorded. The LCM staff typically estimates capture efficiency of the weir by releasing marked fish upstream of the weir and tracking how many are recaptured in the trap. These smolts could also potentially be detected on one or more of the Freshwater Creek antennas during their outmigration. Tagged juveniles in the other two creeks were detected by the stationary antennas during this time of year.

Adult Returns

Adult Coho Salmon were detected at the adult trap at the weir on Freshwater Creek, or as antenna detections as the adults return to any of the study tributaries from Humboldt Bay. Tagged adults were also recorded during spawner surveys in the winter between November and February, but these were less common than detections from the antennas or weir. During these surveys, field technicians walked all reaches of Freshwater Creek and counted both live and dead fish that were encountered. Carcasses were scanned for PIT tags when possible.

Multi-state Modeling Framework

The Freshwater Creek LCM has used the Cormack-Jolly-Seber (CJS) mark-recapture model (Cormack 1964; Jolly 1965; Seber 1965) to estimate overwinter survival of juvenile Coho Salmon that are marked in fall and recaptured during the spring smolt outmigration for nine years. In a CJS model, sampling events are called “occasions” and the time between events is an “interval”. The CJS model estimates two key parameters: detection probability (p) for each occasion, as well as apparent survival (Φ) for each interval. In this modeling strategy, the survival parameter is referred to as “apparent survival” because there is no way to determine if a marked fish permanently left the sampling system (the stream) or died. This basic model structure highlights the importance of understanding movement across a watershed, because a fish that simply moves to another stream before the expected migration period would be considered dead

in a single stream monitoring approach. If this happens at large enough rates, “apparent” survival may experience a significant negative bias as an estimate of “true” survival.

For my modeling purposes, I expanded the basic CJS model into a multi-state mark-recapture (MSMR) model. In this modeling strategy, each stream is a different “state” (s) and each season in the sampling structure represents an “occasion” (t). In my global model, apparent survival (Φ) and transition probability (Ψ) are estimated for the intervals (v) between occasions and vary with time and state (s). For example, the estimate of apparent survival in the first interval (between occasions 1 and 2) will be different depending on if a fish is in Freshwater Creek or Jacoby Creek, thus $\Phi_{1,F} \neq \Phi_{1,J}$.

During each interval (v) between occasions, the fish must survive before it can either move to a new “state” or remain in the same one. To determine the rate of juvenile dispersal, Program MARK estimated the parameter “p” (detection probability) for each occasion for each stream ($p_{t,s}$) as well as two parameters for each interval (represented by arrows in Figure 3): $\Phi_{v,s}$ or apparent survival during the interval in each state, and $\Psi_{v,s}$, the conditional probability that an animal moved from one state to another at the end of said interval. In my global model, all of these parameters vary between occasions. For example, in the global model, detection probability at Occasion 2 is different for Freshwater Creek fish (state “F”) and Jacoby Creek fish (state “J”), thus $p_{2,F} \neq p_{2,J}$. This parameter “p” is estimated from the total antenna detections, including individuals that are known to be alive (because they are detected at subsequent occasions) but are not detected. Fish that are tagged in different locations may have different detection probabilities because of the many factors that can vary in each stream, antenna array,

trap, or sampling effort. This variation is captured by allowing the detection probability to vary by stream, occasion, and tag type (HDX versus FDX PIT tags).

Survival was estimated for each interval based on the fish that are detected at time $i + 1$ compared to time i , after accounting for p . No evidence of tag-induced mortality was identified using analysis of tagging effects during a tag study conducted in the 2010 and 2011 field seasons for this study area (Hauer 2013). The movement parameter is conditional on the fact that the individuals first survived the interval. The probability that an animal moved from one state to another between each occasion (Ψ) is complimentary for all four states, i.e. the four Ψ estimates, plus the probability of remaining in the current state must add up to 1 for each interval in each capture history.

I constructed capture histories for each individual that were based on a series of four occasions that correspond to the different types of encounters at different times of the year: fall juvenile tagging, winter antenna detections, and spring smolt trapping, tagging, and antenna detections (Tables 2 and 3). Fish that were detected were assigned a state based the stream where the detection occurred (F=Freshwater, W=Wood, R=Ryan, J=Jacoby). Occasions were defined by the corresponding data collection methods. For example, the “spring” occasion starts when the smolt trap is installed, which varies from year to year (Tables 3 and 4). These are biologically arbitrary dates that have no direct correlation to salmon life history, but my modeling structure is confined to this because of how the sampling protocol is structured. Fish that emigrate before the smolt trap is installed will have a different probability of detection than individuals that do not, because the early emigrants will not be caught at the trap. Because of this modeling

structure, it is not possible to conduct a temporal covariate analysis, as the seasonal intervals I used were too long to capture the short-term response to discrete events. I analyzed years separately in the global model.

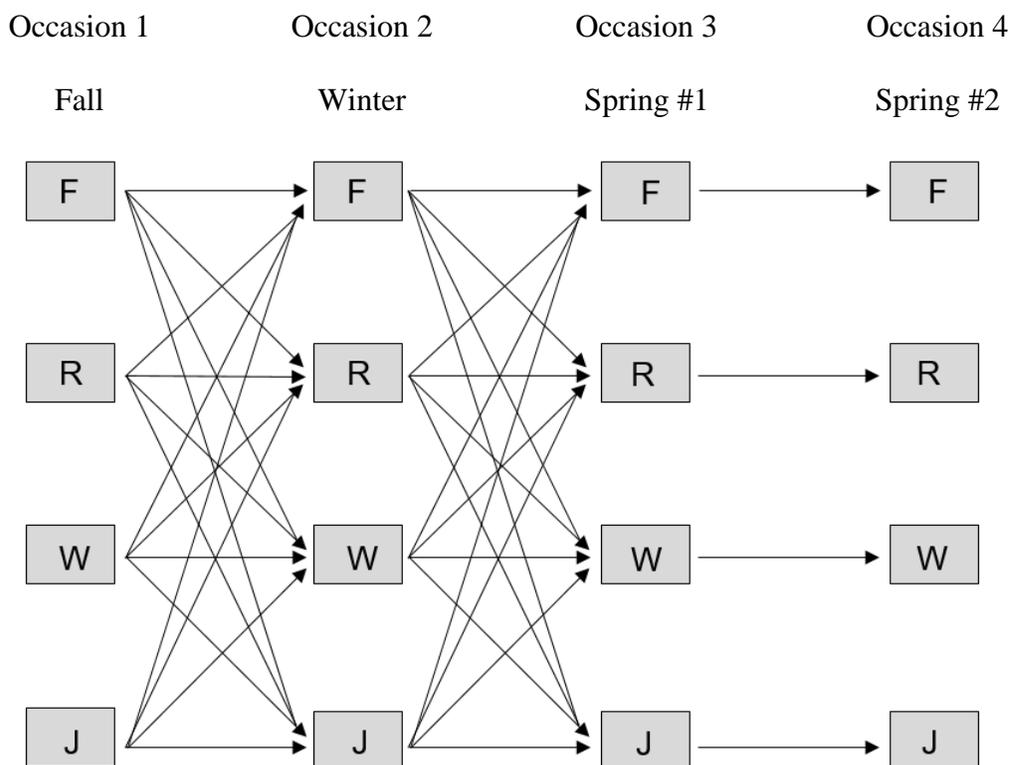


Figure 3. A conceptual diagram of the general model for one cohort. Each column corresponds to one of the four mark-recapture occasions: occasion one is in-hand tagging of YOY during the fall (October-November), occasion two is antenna detections and in-hand capture during winter seining events (November-March), occasion three is spring antenna detections and occasion four is either a secondary, downstream antenna detection or an in-hand detection at the weir downstream migrant trap. Rectangles represent occasions, and letters represent states, which are the four study creeks: Freshwater (F), Jacoby (J), Ryan (R), and Wood (W). All arrows represent $\Phi \times \Psi$, where individuals first must survive (Φ) and then transition to a new state (Ψ). In the final interval of this model, survival is fixed to 1 and transition probability is fixed to zero.

The global model has a large number of parameters, so I also constructed a reduced model to increase the likelihood of model convergence. For this model, I made simplifying assumptions to reduce the number of parameters. First, I assumed that apparent survival (Φ) is occasion-dependent, but is constant among the four states (creeks). Second, I assumed that the probability of transitioning to a new state (Ψ) only varies between two groups: the individuals that cross the bay at some point (from Jacoby to the Freshwater complex, or vice versa) or those that do not, so reciprocal transitions are the same parameter. For example, in this model structure, for the first occasion, $i, j = R, W, F$, and $\Psi_{i,j,1} = \Psi_{j,i,1}$ where $i \neq j$, while $\Psi_{FJ,1} = \Psi_{RJ,1} = \Psi_{WJ,1} = \Psi_{JF,1} = \Psi_{JR,1} = \Psi_{JW,1}$ (Figure 4). In this reduced model I retain a covariate for tag group (HDX or FDX) to account for the variation in detection probability between antenna types.

To find the most parsimonious model with this data set, I conducted a model selection test for four alternatives of the reduced model, combining both years of data (2017-2018 and 2018-2019). The models were constructed as follows, with the final transition fixed to zero in each model structure:

- Model 1: Apparent survival (Φ) and transition (Ψ) vary between years;
- Model 2: Apparent survival (Φ) and transition (Ψ) are constant between years;
- Model 3: Vary apparent survival (Φ) between years;
- Model 4: Vary transition (Ψ) between years.

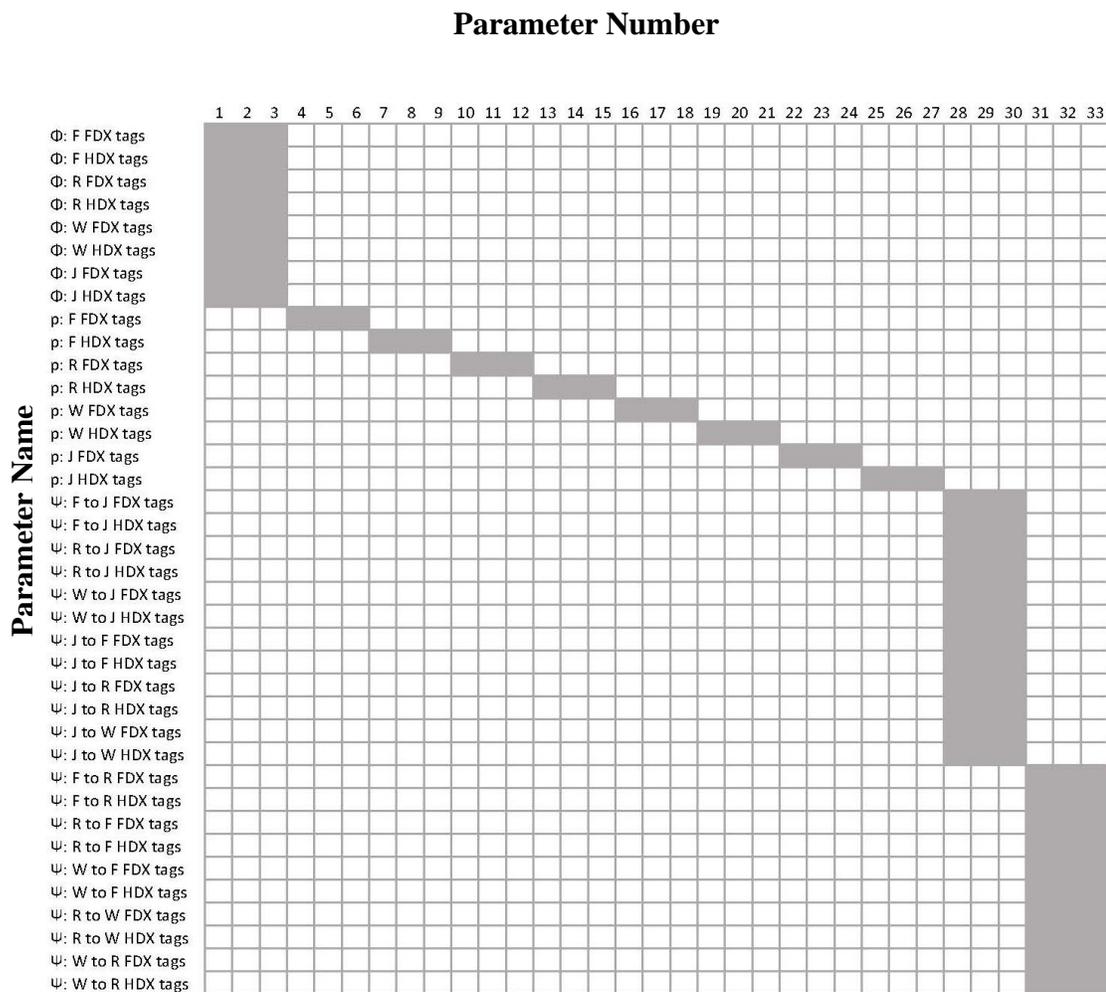


Figure 4. Parameter index matrix diagram, showing the model structure for my original reduced model. The top row shows the parameter numbers for the model. The first column shows the name of each parameter, which are apparent survival (Φ), detection probability (p), and the probability of transitioning to a new state (Ψ). Letters denote the “state”, which is one of the four study creeks: Freshwater (F), Jacoby (J), Ryan (R), and Wood (W). If two parameters are set to be equal, they will have boxes shaded in gray for the same parameter number. In the final interval, survival is fixed to one (Parameter 3) and transition probability is fixed to zero (Parameter 33).

Simulations

I tested the full model structure on a set of encounter histories generated in Microsoft Excel using preliminary estimates of model parameters from my raw data, and sample sizes similar to my field study. I ran the simulated data set as a data input file in Program MARK to demonstrate the validity of a four state mark-recapture model for estimating survival and movement among locations for Coho Salmon in the study tributaries. This preliminary model was able to accurately estimate the input parameters (Appendix A).

To test how parameter estimates could be improved with increased sample size, I conducted a power analysis using the simulations function in Program MARK. For this, I used beta values that reflected biologically plausible estimates for this system. Survival between occasions 1 and 2 were based on actual overwinter “apparent survival”, or the percentage of fall-tagged fish that migrated during the spring smolt trapping period in the 2017-18 season, which ranged from 14-25%. Detection probabilities were set to be 60% for all occasions and all creeks. Transition estimates for the input parameters were approximately twice the rates we observed, allowing for imperfect detections in the empirical data. I fixed the survival parameter in the final interval to 1 for all fish, and the transition probability to 0, constraining the fish to stay in the same creek between occasions 3 and 4, which reflected how I ran my empirical models. I created four levels of sample sizes, varying the number of tagged fish released in the first occasion (Table 2), in order to simulate the fall tagging occasion in my model (Figure 3). The first level is

an approximate number of tags that is put out annually in our monitoring effort (2350 tags total, of which 1000 each go into Freshwater and Jacoby, 250 in Ryan and 100 in Wood Creek), and the three levels after that double (Power 2), triple (Power 3), and quadruple (Power 4) the number of tags from the initial level.

Table 2. Set up of power analysis, number of releases per simulated “creek”. Power 1 approximates the number of fish that are actually fall-tagged in each creek during our study years.

	Power 1	Power 2	Power 3	Power 4
Freshwater	1000	2000	3000	4000
Jacoby	1000	2000	3000	4000
Ryan	250	500	750	1000
Wood	100	200	300	400
Total	2350	4700	7050	9400

Data Analysis

After completing each season of field work, the data was entered into an Access database and checked for accuracy of transcription. I cleaned the antenna detections using an R code developed by a previous graduate student (G. Scheer, personal communication, 2018), queried the data to isolate the years and individual fish relevant to this study, exported this as an Excel file, and created a capture history for each fish. Ultimately, my final database contained a series of detections for each fish that was marked with a PIT tag. These detections were transformed into capture histories for each individual (Appendix B) and analyzed using a multi-state Cormack-Jolly-Seber (CJS) mark-

recapture model in Program MARK (version 8.2). Due to the variation throughout this study in RFID antennas, not all antennas were able to detect both FDX and HDX tags, which reduced my overall detection capability.

The assumptions of a multi-state CJS 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; and (7) all emigration from the sample area was permanent. If one or more of these assumptions is violated, there may be overdispersion of the data leading to less accurate parameter estimates. I used a median \hat{c} test in Program MARK to evaluate goodness of fit.

The estimates for survival and detection probability are confounded in the final interval of a mark-recapture model, so in order to estimate the parameters for my main interval of interest, overwinter survival and transition probability (“Interval B”), I needed one additional occasion, which is why the “spring” time period is divided into Occasions 3 and 4, or “Spring #1” and “Spring #2” (Figure 3). In Freshwater and Wood Creeks, I was able to use two different antenna arrays (or in the case of Freshwater, an array and the downstream migrant trap) for these two spring occasions. In Ryan and Jacoby Creeks, I had to split an array to use the upper and lower antennas as separate occasions (Appendix B). This may violate the 5th assumption of CJS models, that every individual represents an independent sample, as environmental conditions or power source issues

that affect detection efficiency would affect antennas in the same array similarly.

Regardless of if the detection method used separate or split arrays for detections in

Occasions 3 and 4, all of those locations are spatially very close to each other, so I fixed

the survival parameter (Φ) to 1 and the transition probability (Ψ) to 0 for the third interval

in all of the creeks.

Table 3. Occasion structure for the 2017-18 study season, detailing the data input for each seasonal occasion for each state: Freshwater, Wood, Ryan, and Jacoby Creeks.

	Occasion 1 Fall	Occasion 2 Winter	Occasion 3 Spring #1	Occasion 4 Spring #2
	10/1/17-11/20/17	11/21/17-03/09/18	Spring #1 and #2 (3/10/18 - 6/13/18)	
Freshwater	Fall tagging	Winter antenna (any)	FWW antenna	FW Weir DSMT
Wood	Detection/in-hand	Detection/in-hand	WC Phase 2	WC Tidegate
Ryan	Fall tagging	Winter antenna (any)	RC1 antenna	RC2 antenna
Jacoby	Fall tagging	Winter antenna (any)	JC1 antenna	JC2 antenna

Table 4. Occasion structure for the 2018-19 study season, detailing the data input for each seasonal occasion for each state: Freshwater, Wood, Ryan, and Jacoby Creeks.

	Occasion 1 Fall	Occasion 2 Winter	Occasion 3 Spring #1	Occasion 4 Spring #2
	10/2/18 - 11/8/18	11/9/18 - 3/18/19	3/19/19 – 6/24/19	
Freshwater	Fall tagging	Winter antenna (any)	FWW antenna	FW Weir DSMT
Wood	Antenna/in-hand	Antenna/in-hand	WC Phase 2	WC Tidegate
Ryan	Fall tagging	Winter antenna (any)	RC1 antenna	RC2 antenna
Jacoby	Fall tagging	Winter antenna (any)	LJP antenna	LJC antenna

In addition to the juvenile data analysis outlined above, I used adult return data from the weir trap, carcass surveys, and antenna detections. Originally I had intended to use these data to model adult returns in a separate analysis from the juvenile dispersal model, and thus examine the rate of adult straying by comparing the last detection of their smolt state and the basin of adult return. Unfortunately, there are too few tagged adults returning for capture-recapture modelling, so I evaluated stray rate simply by tabulating the number of tagged adults that return to streams other than their natal stream relative to the total number of tagged returns and the total number of tagged outmigrants. An evaluation of the proportion of adults that stray from their natal stream has not been conducted before, so even this single documentation represents a valuable contribution to the monitoring program.

RESULTS

The results of this study are separated into four sections: a summary of the 2017-18 data, a summary of the 2018-19 data, results of the empirical multi-state modeling analysis, and results from the model evaluation using simulated data.

2017-2018 Data Summary

2492 PIT tags were applied to juvenile Coho in the 2017-18 study season across the four study creeks (Table 5). Of these fall- and winter-tagged fish, 697 (28%) were detected again on at least one occasion. There were 55 unique capture histories that occurred in this study season, 26 of which had greater than 5 occurrences (Figure 5). Fish that were tagged in the fall and never detected again (J000, F000, R000) were among the most common capture histories. These individuals represented approximately 96.9% of Jacoby fall-tagged fish, 49.1% of Freshwater fall-tagged fish, and 69.4% of Ryan fall-tagged fish. Three fish moved across Humboldt Bay in this cohort year, with one individual and two individuals exhibiting the capture histories 0JFF and J00W, respectively (Table 6). Movement occurred at a much higher rate between Freshwater, Ryan, and Wood creeks through the shared estuary/slough area.

Table 5. The number of fish that were tagged in each of four Humboldt Bay Tributaries: Freshwater Creek, Ryan Creek, Wood Creek and Jacoby Creek in each season of the 2017-18 study year.

Creek	Fall	Winter
Freshwater	1153	0
Ryan	248	0
Wood	0	67
Jacoby	1091	97

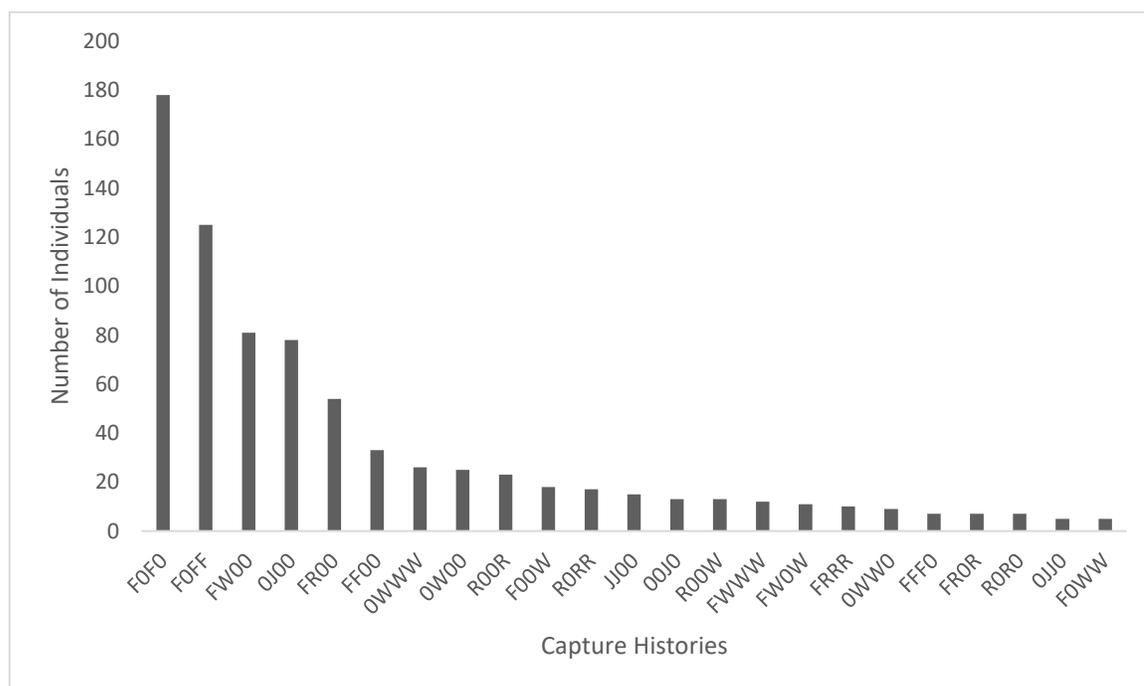


Figure 5. All capture histories that had 5 or more individuals and in which the individual was detected at least once after fall-occasion release for study year 2017-2018.

Table 6. Summary table of fish detected in a creek in either the winter or spring occasions that was different than where they were tagged as a YOY in the fall of 2017 or winter of 2017-18. The number of fall tags applied in each creek are noted in parentheses in the first column. Creeks are listed in order of connectedness. Shaded boxes denote a movement across Humboldt Bay. An individual fish could be counted in more than one creek if they moved between occasions.

		Detection Creek			
		Freshwater	Wood	Ryan	Jacoby
Tagging Creek	Freshwater (1153)	355	139	84	0
	Wood (67)	3	38	1	0
	Ryan (248)	0	20	55	0
	Jacoby (1188)	1	2	0	27

There were 2058 juveniles tagged in the 2015-16 season throughout Freshwater, Wood, and Ryan creeks. This is the cohort that returned to Humboldt Bay as adults in the winter of 2017-18. Seven juvenile-tagged adults returned to Freshwater Creek and were caught at the weir. Only three of these individuals were ever detected on RFID antennas, and all seven were tagged at the Freshwater Creek weir downstream migrant trap in the spring of 2016 during the juvenile migrant trapping survey. A total of 23 juvenile-tagged adult fish were detected on antennas at least once, and three of these adults were detected in non-natal streams. All three of the adults detected in non-natal streams had been tagged during a Freshwater Creek juvenile survey. Two were detected as adults on a Ryan Creek antenna, and one was detected on a Wood Creek antenna. Wood Creek does

not provide any spawning habitat, so adult detections here do not represent straying that would have any effect on reproduction demographics.

In total, 31 fish were detected on antennas during the 2017-18 data year that were tagged as YOY in the fall of 2016 or as pre-smolts and smolts in the spring of 2017. All of these were tagged at the Freshwater Creek weir downstream migrant trapping in the spring of 2016 during the juvenile migrant trapping survey. Without having them in hand, it is difficult to say whether these ambiguous individuals detected on the antennas were fish that outmigrated and came back after less than a year at sea (jacks) or if they never outmigrated and remained in the system as two year old smolts. Six additional fish were described as jacks when they were caught in hand during the 2017-18 Freshwater Creek HFAC weir Adult Trapping survey.

Four of these adults were detected on antennas in “non-natal streams” (they were tagged during a Freshwater Creek survey and detected on a Wood Creek or Ryan Creek antenna). One of these fish displayed exploratory movement behavior, and was detected on three different Freshwater Creek antenna arrays as well as detected on the Ryan Creek array (Appendix C). This fish was tagged during the 2016 Freshwater Creek over-winter survival fall tagging event as a YOY. It was next detected on the Freshwater Creek weir, middle main stem, and Howard Heights antennas in January and February of 2018. Its final detection occurred moving upstream on the Ryan Creek antenna array on February 2, 2018, approximately 5 hours after its final detection on the weir antenna. Because this fish was never captured in hand again after the initial tagging event, it is not possible to

say where it spawned. Additionally, this individual is another example of an ambiguous adult – I cannot determine if it is a jack or a two-year old smolt from this antenna data.

2018-2019 Data Summary

2614 PIT tags were applied to juvenile Coho in the 2018- 19 study season in the four study creeks (Table 7). Of these fall and winter tagged fish, 974 were detected again at some point. There were 64 unique capture history types detected in the study year 2018-19. Twenty-nine of these capture history types had 5 or more fish detected in this study year (Figure 6), and 35 capture history types had fewer than 5 occurrences. Fish that were tagged in the fall and never detected again (J000, F000, R000) were overwhelmingly the most common capture history again in this study year. These individuals represented approximately 72.4% of Jacoby fall-tagged fish, 52.2% of Freshwater fall-tagged fish, and 76.5% of Ryan fall-tagged fish. The detection percentage of Jacoby fall-tagged fish improved between the two study years, associated with the additional antenna installed at the new restoration site, while the detection of fall-tagged fish in the other two creeks declined slightly.

There were 340 non-natal fish detections (fish that were tagged in one creek and detected in another) in this study year (Table 8). Five fish exhibited cross-basin movement behavior in this cohort year with the capture histories JF00, JR00, JW00, R0JJ, and FOJ0. None of these histories occurred in the 2017-18 study year.

Table 7. The number of fish that were tagged in each of four Humboldt Bay Tributaries: Freshwater Creek, Ryan Creek, Wood Creek and Jacoby Creek in each season of the 2018-19 study year.

Creek	Fall	Winter
Freshwater	1331	0
Ryan	380	0
Wood	0	1
Jacoby	903	52

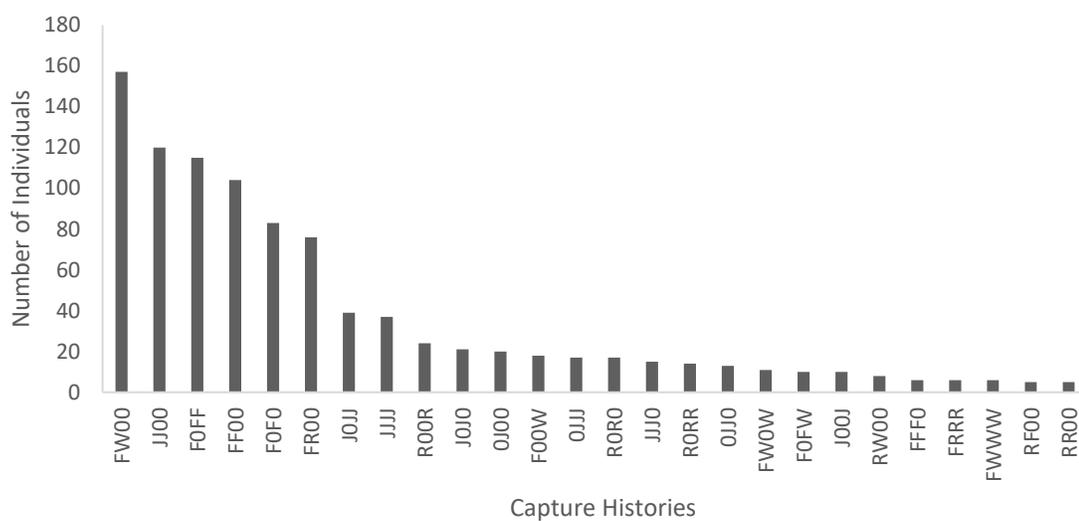


Figure 6. All capture histories that had 5 or more individuals and in which the individuals were detected at least once after fall-occasion release for study year 2018-2019.

Table 8. Summary table of fish detected in a creek other than where they were tagged as a YOY in the fall of 2018. The number of fall tags applied in each creek are noted in parentheses in the first column. Creeks are listed in order of connectedness. Shaded boxes denote a movement across Humboldt Bay. An individual fish could be counted in more than one creek if they moved between occasions.

		Detection Creek			
		Freshwater	Wood	Ryan	Jacoby
Tagging Creek	Freshwater (1331)	336	220	103	1
	Wood (1)	1	0	0	0
	Ryan (380)	11	14	63	1
	Jacoby (903)	0	2	1	283

There were 2037 juveniles tagged in the 2016-17 season throughout Freshwater, Wood, and Ryan creeks. This is the cohort that returned to Humboldt Bay as adults in the winter of 2018-19. Three juvenile-tagged adults returned to Freshwater Creek and were caught in hand at the weir. All were tagged at the Freshwater Creek weir in the spring of 2017 during the juvenile migrant trapping survey, and all were detected at least once on antennas during 2018-19. 21 total adult fish were detected on antennas at least once (including the three caught in hand at the weir), and two of these adults were detected in “non-natal streams”, but both of these were tagged during a Freshwater Creek survey and detected on a Wood Creek antenna. As Wood Creek does not provide any spawning habitat, these adult detections do not represent straying that would have an effect on reproduction demographics, provided these adults eventually were able to spawn successfully elsewhere.

In December of 2018, one juvenile-tagged fish was described as a “jack” when it was captured in hand during the Freshwater Creek HFAC weir Adult Trapping survey. A total of 16 fish were detected on antennas during the 2018-19 data year that were tagged as YOY in the fall of 2017. Three of these individuals were detected in non-natal streams (they were all tagged as YOY in Freshwater Creek and detected in Ryan or Wood Creek). Without having them in hand, it is difficult to say whether these ambiguous fish were individuals that outmigrated and came back after less than a year at sea (jacks) or if they never outmigrated and remained in the system.

Multi-state Modeling Results

While the global multi-state model was able to converge in Program MARK v. 8.2, it provided clearly erroneous estimates for many of the parameters in the model. The global model estimates (Appendix D) for detection and movement were obviously biased based on comparisons to results from previous studies (Rebenack et al. 2015, Anderson and Ward 2016, Ghrist 2019) and the raw data. For example, in 2017, the model estimated transition probabilities from both F to J and from J to F of >0.5 in the second interval, even though no fish were observed making the transition from F to J, and only one transitioned from J to F for the entire sampling season (Table 6). This was likely due to the model being over-parameterized, as well as the violation of many key CJS modeling assumptions. Even with the introduction of additional covariates, such as PIT tag type, I was unable to diagnose or account for these assumption violations because there were so few observations for many of the state transitions.

Program MARK was unable to complete a goodness-of-fit test on the 2018-19 data using the global model, because every one of the simulated values generated a median \hat{c} of less than the observed value. The 2017-18 data also exhibited very poor goodness of fit. This means that there is likely an issue within the dataset, and indicates that that this model was not able to capture the reality of the system, or that the data violated some key assumptions of a CJS model.

The reduced parameter model estimated that Φ (apparent survival) was approximately the same between the two study years (Figure 7). For the 2017-18 data year, the model estimated <0.2% of the fish crossed the bay throughout the first two intervals, but approximately 17% moved between Freshwater, Ryan, and Wood Creeks. For the 2018-19 data year, this model estimated <0.2% of the fish cross the bay throughout the first two intervals, whereas approximately 23% moved between Freshwater, Ryan, and Wood Creeks. The bootstrapped median \hat{c} test in Program MARK for this model was 2.11 for the 2017-18 data and 2.25 for the 2018-19 data, which indicated that the data were indeed over-dispersed.

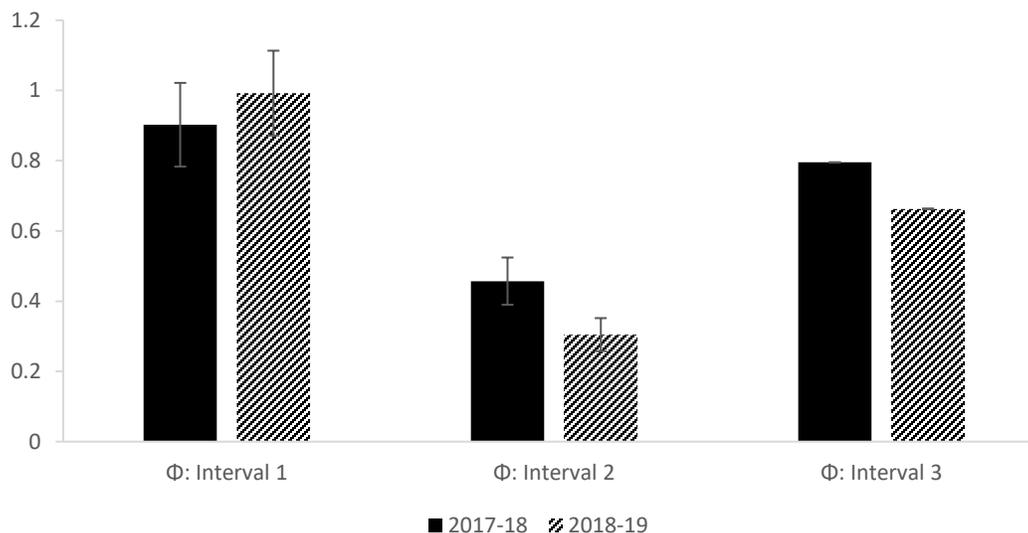


Figure 7. A bar graph comparison of apparent survival (Φ) results from the initial reduced MSMR model for the two study years (2017-2019). In this model, survival is time-dependent but does not vary between the four states. Error bars represent the standard deviation for the model estimates.

Next, I combined both years of data (2017-2018 and 2018-2019) and conducted a model selection test for four alternatives of the reduced model. The bootstrapped median \hat{c} test in Program MARK for the most parameterized model (Model 1) was 2.14, which indicated that the data were again over-dispersed. To account for over-dispersion in the data, I used quasi-likelihood adjusted AIC (QAICc) values for model selection instead of AIC. QAICc values adjust for overdispersion and correct for small sample size (Burnham and Anderson 2002). I determined Model 3 (survival varies by year) to be the most parsimonious model by comparing QAICc values (Table 9). This indicates that survival varied between years, but transition probabilities were constant between years. In both years, apparent survival was higher in the first interval, and much lower in the second

interval, and cross-bay transitions were less likely than non-cross-bay transitions in intervals 1 and 2 (Table 10).

Table 9. Model selection table for four variants of the reduced model structure, ranked by QAICc value. Models are listed in order from best supported to least supported model. Δ QAICc is the difference in QAICc from the top model (Model 3) and QAICc Weight indicates the level of support for a given model. The number of parameters provided is the total number of parameters for the model, minus the number of parameters fixed when the model was run.

Model	ΔQAICc	QAICc Weight	No. of Parameters
3: Φ varies by year	0	1.00	56
2: Φ and Ψ are constant between years	71.83	0.00	54
1: Φ and Ψ vary by year	323.75	0.00	60
4: Ψ varies by year	11012.38	0.00	58

Table 10. Real estimates for apparent survival (Φ) and transition (Ψ) from the top reduced model (Model 3). Survival varies by year, and is fixed to 1 in interval 3 for both years. The probability of transitioning to a new state (Ψ) varies between two groups: individuals that cross the bay at some point from Jacoby to the Freshwater complex, or vice versa (“cross-bay”) or those that do not (“no cross”), so reciprocal transitions are the same parameter. Transition is fixed to zero for interval 3 in both groups.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Φ : Interval 1 (2017)	0.877463	0.056154	0.72011	0.9522223
Φ : Interval 2 (2017)	0.474842	0.033858	0.409305	0.5412577
Φ : Interval 3 (2017)	<i>Fixed to 1</i>	-	-	-
Φ : Interval 1 (2018)	0.999999	4.16E-04	0.906E-298	1
Φ : Interval 2 (2018)	0.295312	0.013402	0.26974	0.322239
Φ : Interval 3 (2018)	<i>Fixed to 1</i>	-	-	-
Ψ : Interval 1 (Cross-bay)	0.001232	6.97E-04	4.06E-04	0.00373
Ψ : Interval 2 (Cross-bay)	0.001889	0.001119	5.91E-04	0.0060179
Ψ : Interval 3 (Cross-bay)	<i>Fixed to 0</i>	-	-	-
Ψ : Interval 1 (No cross)	0.164996	0.007974	0.149955	0.1812233
Ψ : Interval 2 (No cross)	0.039673	0.006917	2.81E-02	0.0556854
Ψ : Interval 3 (No cross)	<i>Fixed to 0</i>	-	-	-

Multi-state Power Analysis Results

While the reduced model provided some reasonable estimates and informative results, it does not have the resolution to answer questions regarding the variation in survival and movement among the individual states. To mitigate this shortcoming, I tested the full model structure on simulated data in Program MARK. These data were generated using preliminary estimates of model parameters from the raw empirical data, which better met the CJS assumptions. The model was able to accurately estimate the input parameters in Program MARK at sample sizes similar to the field study (Appendix E). I then used Program MARK to generate and analyze multiple data sets ($n = 1000$) simulations over a range of sample sizes of fish released in the first occasion to conduct a power analysis, where the number of releases increased for each set of 1000 simulations. For the movement parameter Ψ in the second interval, a key parameter of interest for this study, the set of simulations with the highest accuracy for the Freshwater (F) to Jacoby (J) transition was the in the largest sample size, with 4000 fish released in two “states” representing Freshwater and Jacoby creeks, and 1000 and 400 released in “Ryan” and “Wood” states, respectively. This is evident in the parameter estimates for the second “J to F” transition as well as the second “F to J” transition, although the estimates for these rare transitions still converge on zero for some iterations of the simulation (Figures 8 and 9). Estimating parameters that are naturally very small is likely to pose challenges for any analysis of empirical data sets with limited sample sizes, due to the difficulties posed by the boundary of zero.

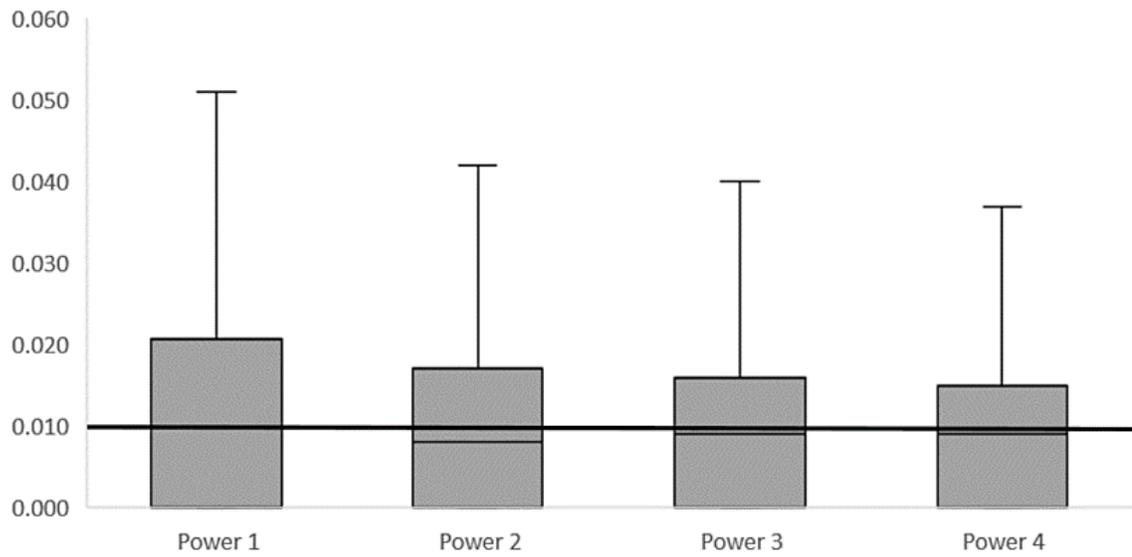


Figure 8. Box and whisker plot showing the results of a power analysis for the estimate of Ψ in the second interval for the transition from Freshwater to Jacoby, with the lowest sample size represented by the box on the far left, increasing along the x axis to the right. The horizontal line represents the true beta value of 0.01. “Power” labels on the x axis refer to the power analysis laid out in Table 2.

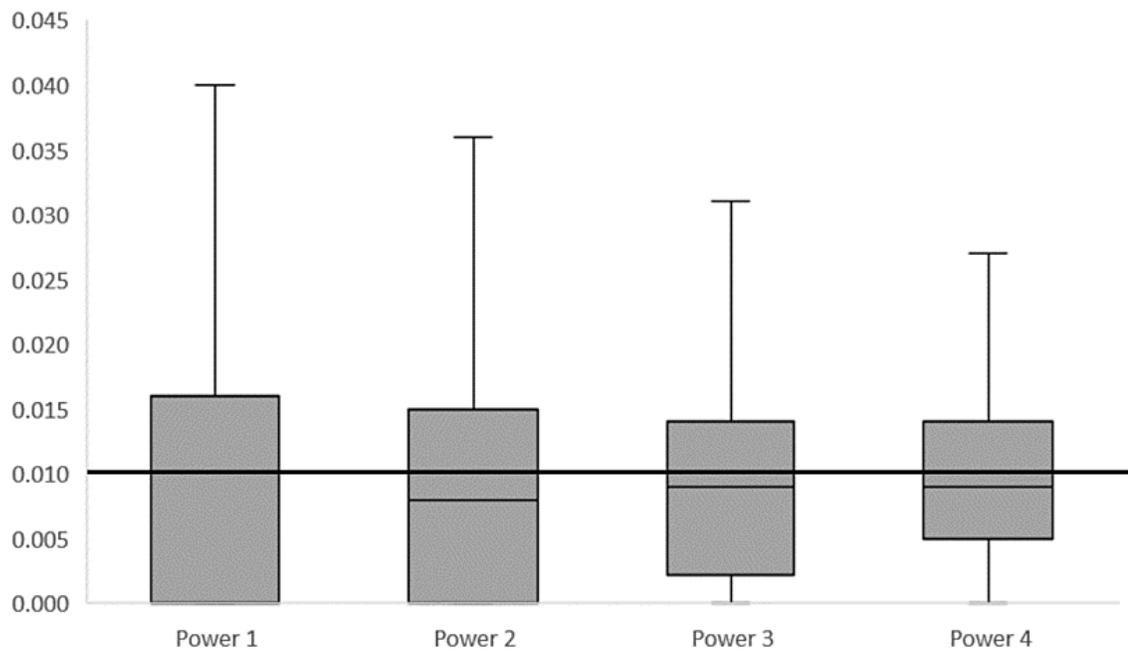


Figure 9. Box and whisker plot showing the results of a power analysis for the estimate of Ψ in the second interval for the transition from Jacoby to Freshwater, with the lowest sample size represented by the box on the far left, increasing along the x axis to the right. The horizontal line represents the true beta value of 0.01. “Power” labels on the x axis refer to the power analysis laid out in Table 2.

DISCUSSION

Researchers and managers along the Pacific Coast have an extensive history of studying Coho Salmon population ecology. In recent years, it has become apparent that alternative life histories may not be captured by traditional monitoring (Moberg et al. 1997, Bell and Duffy 2007, Koski 2009, Lawson 2009, and Bennett et al. 2015), which presents problems for accurate life-cycle modeling. When individuals with these life history variations are not accounted for, estimates of key demographic parameters such as overwinter survival and smolt abundance may be biased.

Due to the many challenges of monitoring highly migratory fish populations in marine environments, salmon researchers primarily estimate marine survival rates by using the number of smolts outmigrating from a given watershed and the number of adults that return there (Cochran et al. 2019). These analyses make many assumptions about the consistency of Coho Salmon life history types, including that they always rear in their natal stream, outmigrate uni-directionally at the same time in the spring, and return to their natal stream as adults (Sandercock 1991, Brown et al. 1994). However, the literature has also acknowledged extensive examples of diversity, both within and among Coho populations, including variations in juvenile behavior, developmental rates, and physiology (McElhany et al. 2000).

Various studies throughout the Pacific Northwest have begun to investigate juvenile life history diversity, including pre-smolt migration out of their natal streams. In general, the ability to accurately estimate demographic rates is impeded by a lack of

methodology to address alternative life history strategies used by juvenile Coho (Hauer 2013), even as we understand this diversity is important to maintain populations. To more accurately understand population structure, the spatial and temporal scales of juvenile Coho dispersal throughout their range and their relative reproductive success following dispersal must be investigated more thoroughly (Schtickzelle and Quinn 2007).

Researchers in Humboldt Bay have expanded the spatial and temporal scope of population studies several times as we learn more about the potential life history variation within the Coho Salmon life cycle in Freshwater Creek: first to include non-natal rearing habitat in the lower main stem (Rebenack et al. 2015) and then lower-basin wetlands and estuaries (Ghrist 2019). By conducting a more rigorous analysis of juvenile Coho movement between adjacent watersheds, this study sought to inform local fisheries managers if they need to expand the study of Freshwater Creek to nearby streams, in order to get a more accurate picture of Coho Salmon in this watershed.

Anecdotal evidence from previous monitoring studies (Mike Wallace and Bob Pagliuco, personal communication) identified at least seven tagged Coho Salmon juveniles that travelled between tributaries of Humboldt Bay between 2005 and 2017. These fish were caught in hand during various restoration activities, and would not have been captured in the typical sampling schedule of the current life cycle monitoring program. After two years of monitoring specifically directed at detecting fish moving among basins, I found that movement between streams happened at relatively low rates. Even with this more focused monitoring of adjacent watersheds, I found low rates of juvenile dispersal and straying throughout the winter, which were comparable to the

annual rates observed within the anecdotal evidence. This is in agreement with other study systems along the West Coast that have documented similar alternative life history strategies for Coho salmon, including juveniles entering salt water before smoltification and moving between coastal watersheds as pre-smolts (Koski 2009, Keefer and Caudill 2012, Bennett et al. 2015, Faulkner et al. 2017). These non-natal transition estimates are usually low and frequently reported as raw data within a larger study.

During their evaluation of downstream migrants, Bennett et al. (2015) identified a similar movement pattern among juveniles tagged in adjacent rivers that discharge to the Strait of Juan de Fuca in Washington. The Bennett et al. study tagged an average of 4330 juvenile fish each fall for 6 years, and recorded 20-50 juveniles per year (0.46 - 1.15%) that left their fall tagging stream and were detected in another nearby stream after swimming through 1-4 kilometers of salt water. I observed a lower rate of only 0.12% (2017) and 0.19% (2018) of my tagged juveniles make a transition across Humboldt Bay, but the order of magnitude of this type of movement is similar between the two studies. Additionally, almost all of their juvenile movement was east to west, and I did not see a preference for movement direction across Humboldt Bay when data was corrected for detection issues. In general, it is difficult to directly compare study systems like these that cover a large area, include a variety of habitat, and may experience many differences in environmental factors that are difficult to categorize or quantify.

Other studies that identified juvenile movement into non-natal watersheds identified rates closer to mine. A study of five adjacent creeks on the coast of Santa Cruz County detected 5 juvenile Coho in their non-natal watershed out of 2,167 tagged (an

average of 0.28%) from 2013-2016 (personal communication E. Kanawi 2018).

Weybright and Giannico (2017) qualitatively evaluated juvenile Coho movement in one inlet of Coos Bay, Oregon and found the average maximum distance moved during the winter varied between 1.3 km – 5.7km, which is similar to the cross-bay distances traveled by the juveniles in my study. In 2013, a CDFW monitoring project identified two juvenile Coho in the Prairie Creek rotary screw trap (also in Humboldt County, CA) that were initially tagged in McGarvey and Hunter Creeks in Del Norte County, a journey that would have required 17 miles of ocean transit (Faukner et al. 2017). The total number of fall-tagged juveniles was not reported, but this was described as a “previously undocumented life history behavior” in juvenile Coho in the Klamath river, and thus assumed to be a rare occurrence.

Juvenile dispersal through Humboldt Bay to non-natal rearing habitat is relatively rare and does not occur uni-directionally (i.e. only from Jacoby towards the Freshwater basin, as might be expected for this particular outmigration route). This low number of cross-basin movements is an important result for the monitoring program, as it suggests that the alternative life history of juveniles moving between tributaries separated by Humboldt Bay is likely not introducing much, if any, bias into demographic estimates of Freshwater Creek. However, these results also suggest that future lifecycle monitoring in this system should account for juvenile movement throughout Wood, Ryan, and Freshwater Creeks, in order to more fully understand the Freshwater population estimates. Movements between these watersheds are frequent enough to potentially

introduce bias into our estimates, and monitoring should be scaled up to account for the area downstream of the Freshwater Creek DSMT where all three basins are connected.

My global multi-state model had a high number of parameters to estimate. Given the rarity of movement among states, low detection probabilities, and relatively small number of tagged fish, I discovered that some of the potential life histories will effectively never appear in capture histories. My data also clearly violated multiple assumptions of the multi-state CJS modeling criteria. I suspect that there is some heterogeneity in this dataset that are not accounted for in the model, for example that my survival and transition probabilities could vary among individuals or sub-groups within the same tagging group during one interval. Although I included covariates to account for differences in detection probabilities within tagging groups, it was not sufficient to solve these issues. I may have missed some explanatory variable for differences in detection and movement probabilities, or some other issue within the dataset. For example, not all juveniles will move around during the long overwinter occasion, and the fish that do move are more likely to be detected on antennas, but less likely to be captured at the smolt trap on the subsequent occasion, which skews the capture histories. Additionally, although I fixed the survival and transition parameters in the third interval for all of my study creeks, there may still be issues with my detection probability, especially in the creeks where I had to split my final detections between two antennas in the same array. Based on findings from Deibner-Hanson (2019) in a nearby, similar watershed, this lack of independence within sampling infrastructure may have biased our detection probability low, by violating the CJS assumption that all detection events are independent.

Although my fully parameterized global model was not functional, a simplified version of that model did converge and yield plausible estimates. Apparent survival in the second interval of the most parsimonious reduced model was 47.5% in 2017-18 and 29.5% in 2018-19. The estimates for apparent survival in both years fell within the large range of published values of between 5-49% (Crone and Bond 1976; Quinn and Peterson 1996; Solazzi et al. 2000; Brakensiek and Hankin 2007; Roni et al. 2012). It also supported my hypothesis that individuals tagged in creeks with a higher degree of connectedness (i.e. Freshwater, Wood and Ryan Creeks) will have a higher probability of transition than creeks with a lower degree of connectedness (i.e. Jacoby Creek to the others). This is in agreement with other studies that highlight the importance of estuarine habitat connectivity to support life history diversity in the juvenile stage (Beechie et al. 2013, Bottom et al. 2005, Roegner et al. 2010).

While this simplified model gives us some reasonable estimates and informative results, it unfortunately does not have the resolution to draw any conclusions regarding the variation in survival and movement among an individual's states. My model selection analysis of the two years of data combined indicated that the most parsimonious model allows survival to vary by year, while holding transition probability constant between years. This agrees with similar research that highlights variation in survival due to changing ocean conditions and stream conditions (Nordholm 2014), but it appears to disagree with previous studies that suggests juvenile Coho movement could be a response to a variety of factors that vary inter-annually, including fish density (Chapman 1962), food availability (Mason 1976), or physical conditions such as temperature or instream

flows (Hartman et al. 1982, Koski 2009, Lawson et al. 2004). This lack of agreement might be due to sample size, as my study was confined to two years of data, and there were few or no individuals for in many of the transition categories. Typically, LCM data for Freshwater Creek is analyzed on an individual year basis for the annual report. I suggest that this aggregate reduced model structure continue to be in the future to see if estimates can be improved with additional years of data.

Due to the lack of resolution in my empirical data analysis, I also ran series of simulations to evaluate the sample size needed to more accurately estimate cross-basin transitions, and the set of simulations with the highest accuracy was the largest sample size. This indicates that I may be able to get more accurate model results with a larger sample size, due to the difficulty of detecting such a low transition rate. However, the simulated model still converged with sample sizes similar to the empirical data, highlighting that sample size was not my only issue in the empirical analysis. The biggest problem I identified with my real data is that the small sample size makes it difficult to diagnose issues, and just one or two unusual capture histories can make it difficult to estimate the low probability estimates, such as the transition rates that are close to the zero boundary. Given the range in estimates in the simulations, we would likely never reach a sufficient sample size to accurately estimate these low-frequency transitions.

Importantly, this exercise demonstrates that this model is functional if all of our data meets the assumptions of a multi-state CJS model, which clearly the empirical data for these particular study years do not. The simulations do suggest that it might be possible to estimate these parameters of interest with a larger sample size. This could be

achieved if we aggregate multiple years of data for a small coastal stream population like ours, or if this study structure were applied to a much larger study population, such as the Columbia River estuary.

I did not have any of the same survival or detection parameter estimation issues in the simulated data that we had in the empirical data, which lead me to conclude that there may be one or more additional variables not accounted for in this model that are confounding the parameters for survival and detection in the monitoring dataset. This study was also limited in design because not all antenna arrays on every creek could detect both HDX and FDX tags, so some fish were not able to be detected on some antennas. RFID antennas are known to have reduced read capabilities in brackish or saline water (Bass et al. 2014), which may have affected detection in some of our estuary locations as well.

While this study was primarily focused on juvenile movement among Humboldt Bay tributaries, I also evaluated the rate of adult straying between the study creeks. In the Bennett et al. (2015) study described above, 4 out of 86 returning Coho adults had swapped streams as fall-tagged juveniles, and returned as adults to the stream where they had overwintered. Two were eventually detected returning to the original stream where they had been tagged, while the other two were not detected leaving again, and assumed to stay in the non-natal streams to spawn. These rates are similar to the adult returns in my study years, although I was unable to conclusively say if any adults spawned in a non-natal stream.

In other systems, adult Coho Salmon have been found to stray from a donor population at rates between 1-17% in California (Keefer and Caudill 2014). This low of a straying estimate would be difficult to correlate to juvenile movement in my study system, due to our small sample size and low overall adult return rate. This program first tagged Jacoby Creek YOY Coho in the fall of 2017, so 2020 will be the first year there are juveniles returning to Jacoby as adults that were tagged as juveniles in what we assume is their natal stream. With this additional data, a large sample size of tagged fish might be able to identify if any fish that move across the bay as juveniles come back to their non-natal stream. Other studies have been able to show that juvenile dispersal away from natal sites can lead to higher local straying by adults (Hamann and Kennedy 2012, Anderson et al. 2013), however it is relatively difficult to observe this phenomenon in a study system like ours, with such low return rates. With current tagging rates, the odds of identifying this in our system are very low, as there were only three known cross basin juveniles from Jacoby in the 2017 cohort, and two in the 2018 cohort. Starting with the winter of 2019-2020, it will be interesting to see if Jacoby Creek has the same level of site fidelity as Freshwater Creek in regards to the adults or if Jacoby Creek natal-rearing fish regularly stray up Freshwater Creek.

I recommend to continue monitoring the additional creeks in this study, in order to conduct an analysis of annual covariates as predictors for transition probability, such as water year or total rainfall, or the date of first fish movement between streams and the first flow event. This will test if there is increased cross-basin movement during wet years or high flow events within years, as observed by Van Vleet (2019). An analysis of

covariates, such as water year, might lend better insight into the mechanism for why juveniles would use the strategy of rearing in non-natal watersheds. I also support the recommendations of the LCM monitoring report for 2018 (Anderson et al.), which calls for continuing to focus on Coho movement in lower basin, off channel or seasonal habitat, in order to evaluate restoration opportunities. Continuing to collect and analyze movement data will be helpful in that effort. Overall, this multistate modeling approach is more inclusive of life history variation. Accounting for movement in and out of Freshwater removes potential bias that could arise from counting juveniles from other streams as Freshwater smolts at the downstream migrant trap

This study highlights the importance of long-term monitoring projects and the importance of adaptive monitoring. Demographic rates are typically estimated at a single watershed level due to existing monitoring structures, which may not account for the full spectrum of Coho Salmon life history diversity in a system. In my study system, movement between streams did not appear to drastically affect the apparent survival rates, but it might in other systems, depending on a variety of factors, including physical displacement, inherent life history traits, or environmental variables that we do not yet understand. Adjusting sampling techniques to ask new questions, such as adding PIT tagging and antenna array sites to Jacoby Creek for this study, are vital to increasing our understanding of Coho Salmon, in this and other study areas. So far, monitoring efforts have managed to expand the LCM through multi-agency collaboration between projects, but that has mostly been opportunistic. While it may not be necessary to include a large-scale movement parameter to improve demographic estimates in this system, we do need

to keep expanding the LCM focus to include the highly connected network with Wood and Ryan Creeks below the Freshwater Creek smolt trap. Future studies in Humboldt Bay and elsewhere along the West Coast should continue to ask questions of both the monitoring and modeling structures, to ensure we are getting the best demographic estimates of our wild and threatened populations of Coho Salmon.

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APPENDIX A

Initial Simulation Results and Figures

These initial simulations were based on empirical values of detection and survival of juvenile Coho Salmon, estimated from previous years of studies in the Freshwater Creek System. I first ran a simulation based on a dataset created in Excel to demonstrate that the model structure worked, and would produce similar ratios of capture histories to the empirical data (Figures A-1 and -2). One main difference between the data simulation and the empirical data was that in the Freshwater Creek fall-tagged fish. The empirical data had a much higher frequency of fish that were tagged in Freshwater Creek, not observed in Occasion 2, and then detected again at the Freshwater Creek Weir in Occasion 3 (Figure A-2).

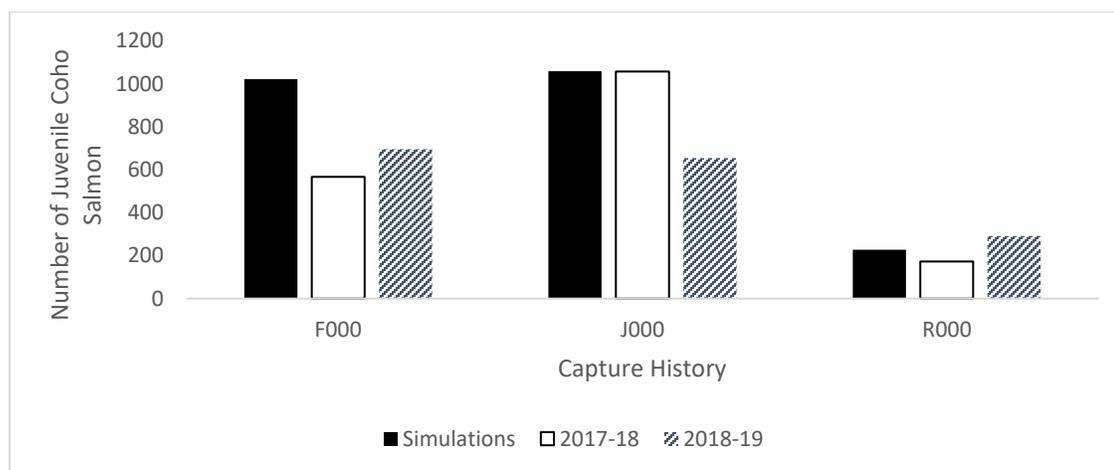


Figure A-1. Frequency histogram of capture histories F000, J000, and R000 observed in both study years compared to the simulations.

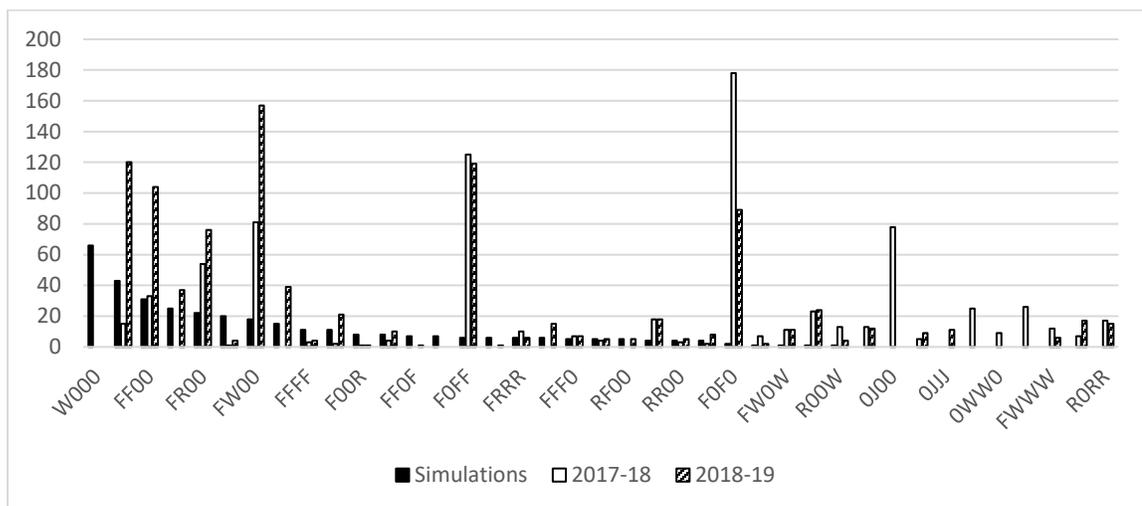


Figure A-2. Frequency histogram of all capture histories (except F000, R000, J000) observed in both study years compared to the simulated dataset created in Excel.

APPENDIX B

Humboldt Bay Monitoring Capture History Protocol

Protocol Outline

1. Obtain antenna detections and clean them up
2. Create query → export file as Excel
3. Process Excel file into capture histories
4. Create Tag Size Groups
5. Create .inp file for MARK

Procedures

1. Obtain antenna detections and clean them up (hours to days, depending on issues)

From year to year, antennas can move locations, work during different periods of time, and all are different brands, so we have to clean up this data and put all antenna detections into the same format in order to query them for this study. The general procedure for this step is to clean all antennas separately (because they are in different formats), then combine them into one large Excel file of all antenna detections.

I then verify that no zeros/digits were lost in cleaning using this formula:

`=IF(LEN(B2)<15, 1, " ")`

Then I search for “1” with “Look in = values” in that column, and verify that all tag numbers have at least 15 digits.

	A	B	C	D	E	F	G
1	date	tagid	basin	site	reader	ANT	
2	10/18/2017	900226000573067	FWC	FWW		1 U	
3	10/18/2017	900226000573067	FWC	FWW		1 U	
4	10/18/2017	900226000573067	FWC	FWW		1 U	
5	10/18/2017	900226000573067	FWC	FWW		1 U	
6	10/18/2017	1130380180914180000	FWC	FWW		1 U	
7	10/18/2017	1130380180914180000	FWC	FWW		1 U	

Figure B-1. An example of cleaned antenna data after formatting.

2. Create query → export file as Excel (~30 minutes)

- Import antenna detection excel file into Access
- Connect Header to Individual tables using "HeaderID", connect Individual to Tag using "IndividualID"
- In Header table, use "group by" and the field "SurveyID" to select which surveys (i.e. adults, creek, etc. - see "Survey types" excel)
 - taxonID = 1595 for COHO, but that should be most of them
 - In 2017-18 I used that to make a query for all 2017 Humboldt Bay fall tags applied (“2017 Fall tags”).
- Example query: Connect “2017 Fall tags” to: 2017-2018 AllDetections (only Fall/Winter) AND 2017_18 Spring Detections by *tag number*
- Query fields: tag number, length (for tax prefix check), GeoUnit (FW, Ryan, or Jacoby), ObsDate (from fall data), site and Date for each other occasion
- Full query might not run instantaneously (can take up to 20 minutes depending on file size and the computer used)
- Notes on queries:
 - “group by” to get rid of duplicate tags on same days (hit “totals” button)
 - “max” under Date to get only one detection for each tag number
 - TagID means different things in “Tag” table vs in my antenna detections
 - If one doesn’t open, right click, “open design view”

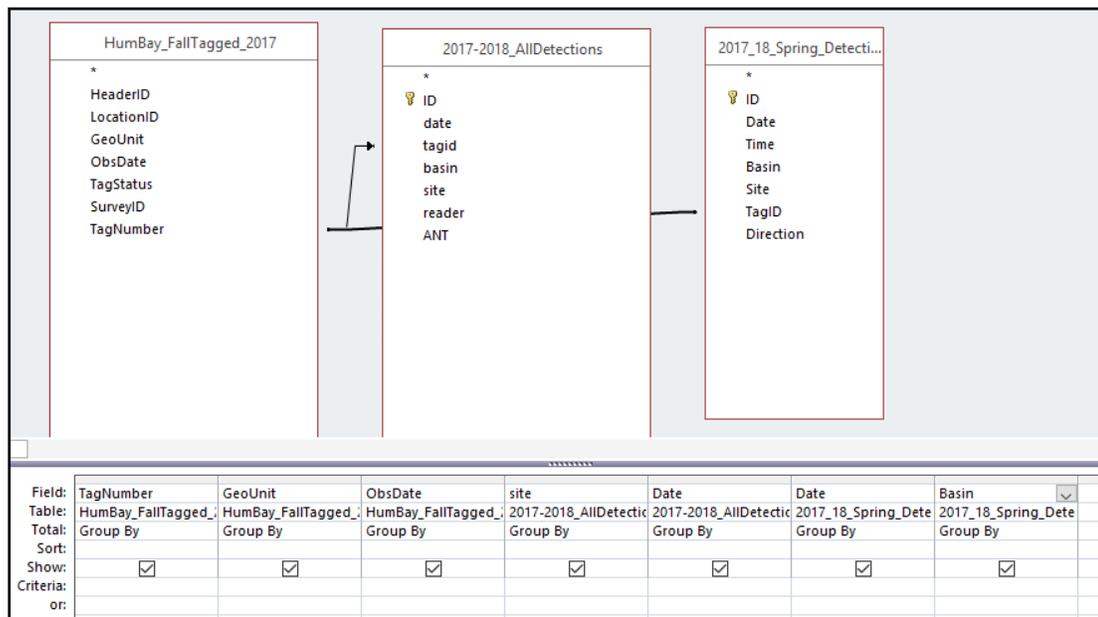


Figure B-2. A screen capture of the query used to create the detection file for one year of data.

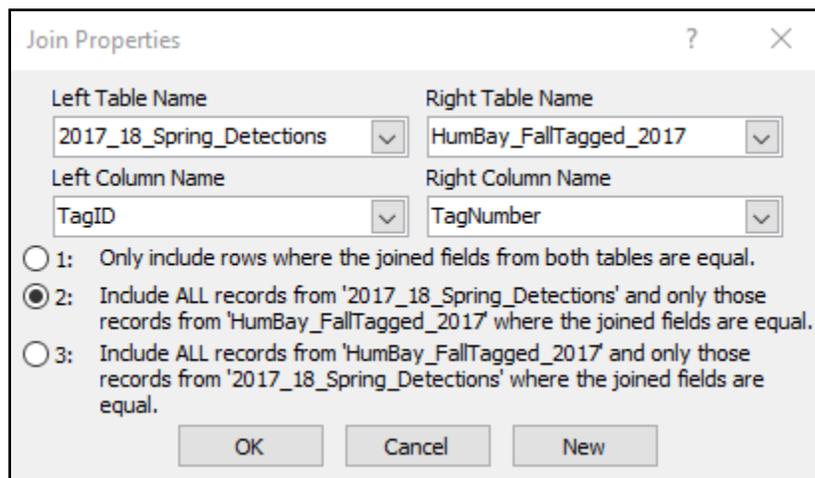


Figure B-3. A screen capture of the join property settings for this query.

4. Process Excel file into capture histories (~5 hours)

- Export Excel file from Access
- Copy sheet so you have a clean Access copy without capture history edits

- Add column for capture history, equation:
- Sort based on tag number
- Highlight duplicate tags using: Home tab > Conditional Formatting > Highlight Cells Rules > Duplicate Values.
- Assign 4-occasion capture histories manually using the rules below

Table B-1. The occasion structure from 2017-18.

	Occasion 1	Occasion 2	Occasion 3	Occasion 4
	10/1/17-11/20/17	11/21/17-03/09/18	3/10/18 - 6/13/18	
Freshwater	Fall tagging	Winter antenna (any)	FWW antenna	FW Weir DSMT
Wood	Detection/in-hand	Detection/in-hand	WC Phase 2	WC Tidegate
Ryan	Fall tagging	Winter antenna (any)	RC1	RC2
Jacoby	Fall tagging	Winter antenna (any)	JC1 or URP*	JC2

*URP = Upper Restoration Pond

Criteria for choosing which detection to count for an occasion

1. If it is detected making a state transition and then transitioning back to its original state during an occasion, use the state that it transitioned to in order to give it "credit" for making a transition.
2. If it is detected in two states other than its original state during an occasion, use the most distant one to give it credit for its longest movement.

3. This model constrains the final interval so transition probability (Ψ) is zero. If a fish is found in different streams in Occasions 3 and 4, Occasion 4 must be recorded as a 0.

The downside of these rules is that there's no straightforward way to automate them (e.g. you can't just use the one with the latest date). The upside is, it will give us the largest sample size for fish are moving to other states, particularly the more distant ones.

Table B-2. An example of using the above criteria to determine the final capture history. This fish was tagged in Freshwater Creek in October 2017 (Occasion = Fall), then detected on antenna arrays in Ryan and Wood Creeks in November (Occasion = Winter). It was not detected in Occasions 3 and 4. This fish will be assigned capture history **FR00**, as moving from Freshwater to the Ryan Creek antenna array is a bigger movement than Freshwater to the Wood Creek Tide Gate.

Antenna	Date Detected	Tag Number	Possible Capture History
RC	11/27/2017	982000402976259	FR00
WCT	11/26/2017	982000402976259	FW00

4. Create Tag Size Groups

- Create a column for tag size, fill with tag numbers
- Determine prefixes for each tag size (9mm and 11.5mm)
- Find and replace tag numbers with tag sizes based on prefixes
- Create another column for “attribute group” 0 1 or 1 0 based on tag size
- 2016 example:
All of the fish from 65mm to 69mm were tagged with the full duplex 9mm tags

and have the tag prefix "982000406 -". All fish larger than that use "9820004062 -", "982000403 -", or "989001004 -" and are the 11.5mm half duplex tags in fish 70mm and up.

5. Create .inp file for MARK

- Copy/paste columns for tag number and capture history to a new sheet.
Data > Remove Duplicates
- Use linking equation to create data line for inp files: ="/*"&A2&"*"/&B2&"&D2&";"
Should look like: **/*982126051768640*/00J0 1 0;**
- Copy column of capture histories, paste as "values only" in a new column.
- Copy/paste that column of values only into a text file using Notepad ++
 - Should look like figure below
- Comment title of data and short description of it using /* */
/* comment */
- Save as a .inp file

```

1  /*Capture histories for 2017-18*/
2  /*Three creeks (Freshwater, Ryan, Wood)*/
3  /*1460 fish total*/
4  /*no Jacoby records*/
5
6  /*900226000165015*/OW00 1;
7  /*900226000165044*/OW00 1;
8  /*900226000165046*/OW00 1;
9  /*900226000165067*/OW00 1;
10 /*900226000165076*/OW00 1;
11 /*900226000165080*/OW00 1;
12 /*900226000165085*/OW00 1;
13 /*900226000165089*/OW00 1;
14 /*900226000165097*/OW00 1;
15 /*900226000165101*/OW00 1;
16 /*900226000165115*/OW00 1;
17 /*900226000165120*/OW00 1;
18 /*900226000165121*/OW00 1;
19 /*900226000165123*/OW00 1;
20 /*900226000165125*/OW00 1;

```

Figure B-4. An screenshot example of an .inp file with individual capture histories.

APPENDIX C

Humboldt Bay Adult Data Example

This adult Coho Salmon was detected on the Freshwater Weir antenna (FWW) on 2/2/2018 and then detected on the Ryan Creek array (RC) a few hours later the same day. In order to determine the path of this individual, we have to look at the time of detection on each antenna.

Table C-1. The capture history for the adult Coho Salmon described anecdotally in the text of adult data for year 2017-18. It was tagged in Freshwater Creek on 11/3/2016, detected on multiple Freshwater Creek antennas (FWW, HHL, MMS) in 2018 before being detected on the Freshwater Weir antenna (FWW) and the Ryan Creek antenna array (RC) on the same day.

Tag Number	Survey Name	Stage	Antenna	Date Detected
982000403268301	NVA091616102419	yoy	FWW	1/8/2018
982000403268301	NVA091616102419	yoy	HHL	1/9/2018
982000403268301	NVA091616102419	yoy	MMS	1/11/2018
982000403268301	NVA091616102419	yoy	MMS	1/12/2018
982000403268301	NVA091616102419	yoy	FWW	2/2/2018
982000403268301	NVA091616102419	yoy	RC	2/2/2018

Table C-2. The raw antenna data for this individual, demonstrating that it moved into Ryan Creek after being detected on multiple Freshwater Creek antennas in the winter.

Antenna	Time	Date	Tag Number
Freshwater Weir Antenna	02:37:08	02/02/2018	982.000403268301
Ryan Creek Antenna Reader #1	07:39:11	02/02/18	982.000403268301
Ryan Creek Antenna Reader #2	07:39:11	02/02/18	982.000403268301

APPENDIX D

Global Model Results

Table D-1. Parameters estimates for the 2017-18 data year from the global model. Parameter type: Φ (phi) represents survival, p represents detection probability and Ψ (psi) represents transition probability. State: initials represent the four study creeks, F for Freshwater, J for Jacoby, W for Wood, R for Ryan. Estimates, standard error and upper and confidence intervals are reported.

Parameter Number	Parameter Type	State	Estimate	SE	Lower	Upper
1	Φ	F	1	7.71E-08	0.9999998	1.0000002
2	Φ	F	1	1.79E-05	0.9999649	1.0000351
3	Φ	F	0.7316612	22.680568	1.27E-98	1
4	Φ	J	0.0366837	0.0092746	0.0222599	0.0598813
5	Φ	J	0.0182229	3.1056896	3.20E-150	1
6	Φ	J	0.0756109	3.8989917	2.68E-49	1
7	Φ	R	0.8517139	0.1543486	0.3436166	0.9843796
8	Φ	R	0.4660959	0.6943208	0.003668	0.9951927
9	Φ	R	0.8916209	4.3541625	3.63E-38	1
10	Φ	W	0.5192508	0	0.5192508	0.5192508
11	Φ	W	0.4554537	0.0277845	0.4017372	0.5102272
12	Φ	W	0.8536479	21.899233	3.61E-149	1
13	p	F	0.1376166	0.0317582	0.0862961	0.2123639
14	p	F	0.9751387	0.0140953	0.9261978	0.9919086
15	p	F	0.5445604	19.257989	9.59E-67	1
16	p	F	0.0582458	0.0198051	0.0295767	0.1115108
17	p	F	0.949076	0.0493548	0.7157798	0.9928017
18	p	F	0.7521514	26.599399	1.06E-121	1
19	p	J	1	6.01E-05	0.9998822	1.0001178
20	p	J	0.0057262	0.005971	7.37E-04	0.0430502
21	p	J	0.7809996	120.78326	3.52E-304	1
22	p	J	0.5434699	0.3463883	0.0716213	0.9483722
23	p	J	1.11E-16	1.16E-09	-2.28E-09	2.28E-09
24	p	J	2.54E-11	3.05E-06	-5.98E-06	5.98E-06
25	p	R	1	2.77E-07	0.9999995	1.0000005
26	p	R	0.4744898	0.0724604	0.338116	0.6147782
27	p	R	0.9994439	0	0.9994439	0.9994439

Parameter Number	Parameter Type	State	Estimate	SE	Lower	Upper
28	p	R	1	1.44E-04	0.9997179	1.000282
29	p	R	0.2149588	0.0699982	0.1082929	0.3817136
30	p	R	0.3326812	0	0.3326812	0.3326812
31	p	W	0.1143406	0.0163213	0.0860343	0.1504272
32	p	W	0.8595519	0.0622759	0.6900788	0.943888
33	p	W	0.896156	22.98973	4.47E-210	1
34	p	W	0.1595467	0.0210086	0.1225302	0.2051316
35	p	W	0.3003162	0.0770371	0.1730201	0.4682398
36	p	W	0.7547376	19.362093	2.83E-89	1
37	Ψ	F to J	2.78E-16	8.10E-10	-1.59E-09	1.59E-09
38	Ψ	F to J	0.7592708	0.0521462	0.6432514	0.8465595
39	Ψ	F to J	1.11E-13	4.19E-08	-8.22E-08	8.22E-08
40	Ψ	F to R	0.0668426	0.0074067	0.0537088	0.0829067
41	Ψ	F to R	0.1869148	0.044559	0.1145744	0.2899717
42	Ψ	F to R	7.77E-16	2.91E-09	-5.69E-09	5.69E-09
43	Ψ	F to W	0.7277583	0.0421329	0.6379485	0.8021976
44	Ψ	F to W	1.43E-13	7.22E-08	-1.42E-07	1.42E-07
45	Ψ	F to W	0.115666	4.7564919	3.42E-41	1
46	Ψ	J to F	0.5325392	0.1236556	0.3008524	0.7509947
47	Ψ	J to F	0.6221937	106.04098	1.62E-304	1
48	Ψ	J to F	8.66E-13	4.87E-07	-9.55E-07	9.55E-07
49	Ψ	J to R	2.77E-13	1.18E-07	-2.32E-07	2.32E-07
50	Ψ	J to R	0.6781377	115.57263	2.08E-304	1
51	Ψ	J to R	3.88E-09	3.25E-04	-6.37E-04	6.37E-04
52	Ψ	J to W	6.72E-14	8.38E-08	-1.64E-07	1.64E-07
53	Ψ	J to W	2.35E-12	1.74E-06	-3.41E-06	3.41E-06
54	Ψ	J to W	0.6808645	34.3249	7.29E-135	1
55	Ψ	R to F	0.916195	0.0287044	0.8401039	0.957891
56	Ψ	R to F	8.12E-12	6.47E-07	-1.27E-06	1.27E-06
57	Ψ	R to F	3.82E-13	1.19E-07	-2.32E-07	2.32E-07
58	Ψ	R to J	1.32E-14	1.25E-08	-2.45E-08	2.45E-08
59	Ψ	R to J	0.0160541	1.5823647	8.79E-88	1
60	Ψ	R to J	0.0295363	4.4265188	1.07E-133	1
61	Ψ	R to W	0.0406746	0.0216096	0.014118	0.111534
62	Ψ	R to W	2.06E-11	1.40E-06	-2.75E-06	2.75E-06
63	Ψ	R to W	0.1689334	3.6132227	2.52E-23	1
64	Ψ	W to F	0.4626101	77.037193	1.44E-264	1
65	Ψ	W to F	0.7441983	0.0263874	0.6891661	0.7924219
66	Ψ	W to F	5.45E-12	5.01E-07	-9.82E-07	9.82E-07

Parameter Number	Parameter Type	State	Estimate	SE	Lower	Upper
67	Ψ	W to J	0.3950754	0	0.3950754	0.3950754
68	Ψ	W to J	3.99E-12	1.31E-06	-2.56E-06	2.56E-06
69	Ψ	W to J	9.01E-12	7.42E-07	-1.45E-06	1.45E-06
70	Ψ	W to R	0.4700631	0	0.4700631	0.4700631
71	Ψ	W to R	0.009877	0.0069654	0.0024637	0.0387313
72	Ψ	W to R	2.01E-12	3.78E-07	-7.42E-07	7.42E-07

APPENDIX E

Power Analysis Model Accuracy

I tested the full model structure on a simulated data set generated in Program MARK using preliminary estimates of model parameters from existing data and sample sizes similar to the field study. The model was able to accurately estimate the input parameters (Figures E-1 and E-2).

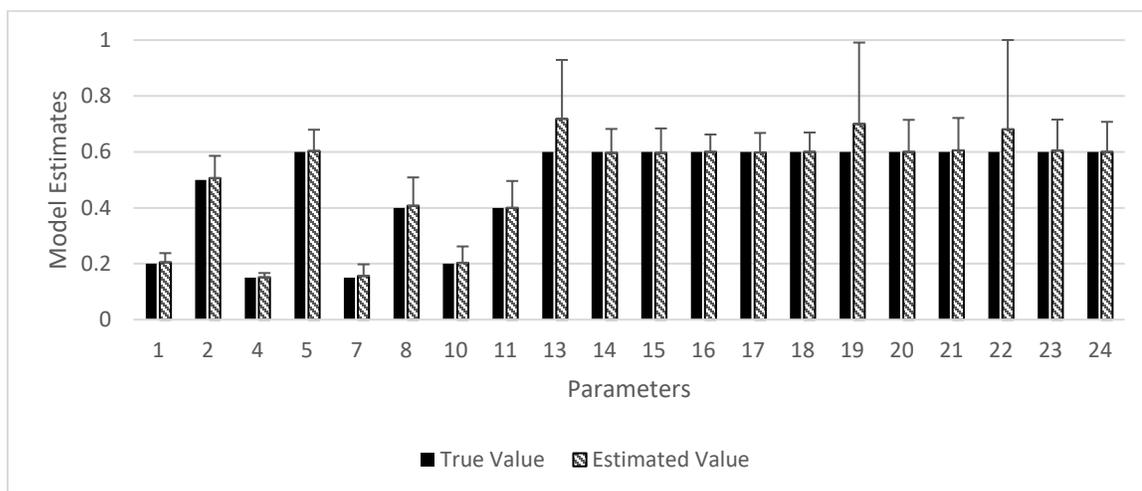


Figure E-1. Input values (“true” values) for Program MARK simulations in solid black bars and estimated values in hatched bars. Error bars represent the standard deviation for each of the model estimates, average from the 1000 simulations for the first level of the power analysis, which had comparable fish release numbers to our empirical dataset. Parameters 1-12 are survival (ϕ) for each of four states, which would be the four creeks in my model. Parameters 3, 6, 9, and 12 (survival for the final interval for each state) were removed from the figure, as they were all fixed to 1 in the model. Parameters 13-24 are detection probability for each state for occasions 2, 3, and 4.

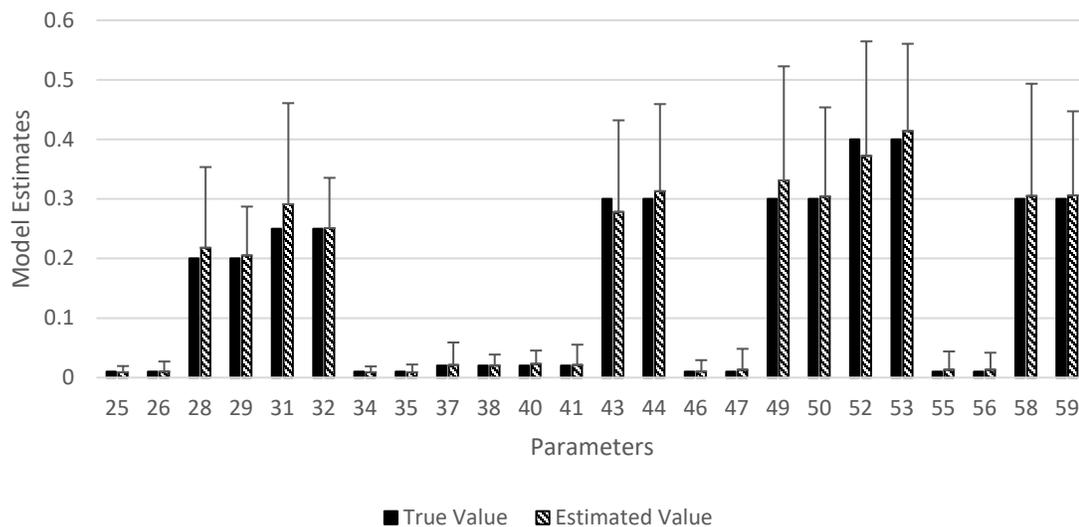


Figure E-2. Input values (“true” values) for Program MARK simulations are shown here in solid black bars and estimated values are in hatched bars. Error bars represent the standard deviation for the model estimates. Parameters 25-60 are transition probabilities (ψ) between different four different states. Parameters 27, 30, 33, 36, 39, 42, 45, 48, 51, 54, 57, 60 were removed from the figure, as they were all fixed to 0 in the model.