

OVERWINTER SURVIVAL AND REDISTRIBUTION OF JUVENILE COHO
SALMON, *ONCORHYNCHUS KISUTCH*, IN PRAIRIE CREEK, CALIFORNIA

By

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ABSTRACT

Overwinter Survival and Redistribution of Juvenile Coho Salmon, *Oncorhynchus kisutch*, in Prairie Creek, California

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During the summer of 2012, juvenile coho salmon (*Oncorhynchus kisutch*) in Prairie Creek, California and its tributaries were marked using PIT tags to monitor winter redistribution and estimate overwinter growth and survival. Since a substantial number of juvenile coho salmon in the Prairie Creek watershed may rear in freshwater for two years, a scale sample analysis was also conducted to determine what proportion of the 2012 population was exhibiting a two-year freshwater residency. The Cormack-Jolly-Seber model and Program MARK were used to examine how rearing location, size at tagging, habitat unit depth, and volume of large woody debris affected overwinter survival. I found that 98.6% of juveniles in 2012 were age 0, and apparent overwinter survival was 39.4%. On average, juveniles experienced a 0.13% increase in length per day and 0.35% increase in weight per day, with the smallest fish experiencing the highest growth rates. Fish that were larger in fall and tagged closer to the confluence of Prairie Creek had higher apparent overwinter survival, but habitat depth and quantity of large woody debris did not appear to impact survival probability. Large juveniles appeared to have low survival near the confluence of Prairie Creek; however, the model could not distinguish deaths from emigration, meaning the high mortality rate for large juveniles near the mouth may actually reflect a pattern of early emigration from the study area.

Since juveniles that migrate to sea prior to spring trapping are typically treated as mortalities, these results have important implications for the way managers estimate freshwater survival for coho salmon.

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INTRODUCTION

Coho salmon (*Oncorhynchus kisutch*) in southern Oregon and northern California have suffered precipitous populations declines over the past several decades due to habitat degradation and overfishing, warranting their protection under the Endangered Species Act (Ly et al. 2011). Juveniles typically spend at least one year rearing in freshwater, where they may experience high mortality due to lack of winter habitat (Solazzi et al. 2000) and high flow events (Sandercock 1991). Juvenile coho salmon respond to increasing discharge in fall by leaving the main channels of rivers and streams and migrating to low velocity areas, seeking refuge in off-channel ponds (Swales and Levings 1989), tributaries (Bramblett et al. 2002), and lakes (Swales et al. 1988). Juveniles also associate with large woody debris (LWD), root wads and overhanging banks, a behavior that helps them avoid predation and prevents displacement during periods of high flow (Sandercock 1991).

Numerous studies have examined factors that influence overwinter survival and growth of juvenile coho salmon. The presence of large woody debris (Quinn and Peterson 1996; Johnson et al. 2005) and adult salmon carcasses (Giannico and Hinch 2007) have been linked to increased overwinter survival, and when in combination, higher overwinter growth rates (Giannico and Hinch 2007). Location in the watershed may also impact both survival and overwinter movement patterns, although this effect varies regionally (Quinn and Peterson 1996; Ebersole et al. 2006; Ebersole et al. 2009; Roni et al. 2012). A juvenile's size also influences its ability to survive winter

conditions, as individuals that are larger in the fall are more likely to survive to the spring migration phase (Quinn and Peterson 1996; Brakensiek and Hankin 2007). When population density is high, juvenile coho salmon often experience lower growth rates (Roni and Quinn 2001), especially subdominant juveniles, which may be forced into lower quality habitat by more aggressive, dominant individuals (Rosenfeld et al. 2005). Even in low density populations, smaller individuals experience lower survival due to their decreased energy reserves and inability to tolerate stress (Ebersole et al. 2006; Pess et al. 2011).

Recent advances in PIT (passive integrated transponder) tag technologies have made it possible assign unique identification numbers to individual juvenile salmonids, allowing researchers to examine how individual characteristics affect growth, survival, and behavior. After fish have been tagged, movement patterns can be remotely monitored by placing RFID (radio frequency identification) arrays in the stream. The usage of these devices has greatly increased knowledge of the diversity of coho salmon life histories and improved juvenile survival estimates by accounting for early emigration. For example, Roni et al. (2012) found that more than 50% of juvenile coho salmon in two Washington Rivers actually migrated to sea in fall rather than spring. Another study in Freshwater Creek, a northern California stream, documented substantial fall and winter emigration into a tidally influenced marsh (Hauer 2013). Since spring migrant trapping is typically used to estimate overwinter survival, these early emigrants would have previously been considered mortalities (Roni et al. 2012).

In Prairie Creek, California, Brakensiek and Hankin (2007) found that 15% of juvenile coho salmon PIT tagged in fall migrated from the upper reaches of the stream before early March and either attempted to complete overwintering in the lower reach or migrated to the ocean. A peak of downstream movement occurred in November, and juveniles that were smaller than average were more likely to migrate downstream early. Scarlett and Cederholm (1984) observed a similar phenomenon in Clearwater River, Washington, where smaller juvenile coho salmon migrated downstream in the late fall and early winter. Downstream movements by small individuals may reflect their increased risk of being displaced during winter flows (McMahon and Hartman 1989) or forced out of habitat by larger, dominant fish (Chapman 1962), although these movements may be an adapted life history trait. In Alaska, Murphy et al. (1997) documented juvenile salmonids migrating from the upper Taku River to downstream habitat during summer and fall, suggesting river's headwaters may be more suitable for spawning, but the lower region of the watershed is better for rearing. A similar phenomenon has been observed on the Klamath River in northern California, where juvenile coho salmon from the upper reaches of the watershed have been documented utilizing off-channel ponds located in two Lower Klamath tributaries (Yurok Tribal Fisheries Program 2013).

In 2000, a PIT tag study in Prairie Creek found that 28% of spring migrants were juveniles that had spent two years in freshwater, a life history that had previously only been observed in the northern extent of the coho salmon range (British Columbia and Alaska). This life history is utilized by individuals that require an extra year to reach the

critical size needed to migrate to sea in spring (Bell and Duffy 2007). A more recent study documented extended freshwater rearing in five of six northern California streams surveyed, and the number of two-year old individuals was higher after winters with low stream flow (Ransom 2007). During milder winters, small juveniles (i.e., ones that would likely become two-year freshwater residents) may be less prone to displacement or experience higher survival. In Prairie Creek and its tributaries, the proportion of individuals in a cohort utilizing freshwater for two years (age 1+) varied greatly by year, ranging from 2% to 30% in mainstem Prairie Creek (Ransom 2007).

In this study, four hundred juvenile coho salmon in Prairie Creek and its tributaries were PIT tagged in fall and monitored until spring to examine overwinter survival, growth, and movement. Since previous studies in the area have focused on upper Prairie Creek above the Strelow Creek confluence (Duffy 2011), this study expanded monitoring efforts to include the previously unsurveyed lower reach of this stream. A set of dual pass-through RFID antennas was placed between upper and lower Prairie Creek to monitor overwinter migration patterns, and a set of antennas and a rotary screw trap were used to examine spring migration timing and overwinter growth. Apparent overwinter survival was estimated using these detection occasions and the Cormack-Jolly-Seber (CJS) model in Program MARK. Because the CJS model cannot distinguish early emigration from mortality, survival estimates from this model are referred to as “apparent” survival.

Although PIT tags offer many advantages over other mark-recapture methods, mortality associated with this technology may be substantial. For example, Brakensiek

and Hankin (2007) found a 33.0% difference in survival when comparing the overwinter survival rates of a group of juvenile coho salmon contaminated with PIT tag mortality with survival rates representing true overwinter mortality. Another study found that PIT tagged juvenile Atlantic salmon (*Salmon salar*) had lower survival in the first interval after tagging, especially smaller individuals (Sigourney et al. 2005). In contrast, Peterson et al. (1994) found no differences in overwinter growth or survival between wild juvenile coho salmon marked with coded wire tags and those injected with PIT tags, even for the smallest tagging group (53 – 70 mm). Acolas et al. (2007) reported similar results for a laboratory experiment using juvenile brown trout (*Salmo trutta*), observing negligible effects on growth and survival as long as the fish was greater than 57 mm at the time of tagging. In this study, PIT tag mortality rates were estimated by tagging juvenile coho salmon in two temporally spaced groups according to methods outlined by Brakensiek and Hankin (2007).

This study addressed five distinct goals: 1) determine if water depth, habitat location, large woody debris, and fork length at tagging influenced overwinter survival; 2) determine the overwintering location of the fall migrants from the upper watershed; 3) estimate the number of two-year freshwater resident juveniles; 4) estimate PIT tag mortality; and 5) determine if fork length at tagging and habitat location influenced overwinter growth. I hypothesized that fish tagged in deeper water with abundant large woody debris would have higher overwinter survival, and fish that were smaller at tagging would experience lower survival and greater overwinter growth. Based on the overwinter movement study of Brakensiek and Hankin (2007), I predicted some smaller

than average juveniles would migrate from upper Prairie Creek in fall in response to fall freshets.

STUDY SITE

Prairie Creek is a fourth-order tributary whose confluence with Redwood Creek occurs near Orick, California (Figure 1). Draining a watershed of 34.4 km², this stream flows for 20 km and is located almost entirely within the boundaries of Redwood National and State Parks (Duffy 2011). The climate of the study area is characterized by dry, foggy summers and rainy winters with rare snowfall. The mean annual precipitation is 177 cm, most of which falls between November and March (77%). Only 5% of yearly rain falls between June and September, and 30 day periods without precipitation are common during these months. The area's proximity to the Pacific Ocean helps maintain a mild climate and stable year-round temperatures (Janda et al. 1975).

The Prairie Creek watershed supports a variety of plant and animal species. Coast redwood (*Sequoia sempervirens*) dominate the old growth forests, though the following trees can also be found in the area: Sitka spruce (*Picea sitchensis*), tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), big-leaf maple (*Acer macrophyllum*), California bay or laurel (*Umbellularia californica*), and red alder (*Alnus rubra*). Sword fern (*Polystichum munitum*) and redwood sorrel (*Oxalis oregana*) are common in the understory, along with rhododendron (*Rhododendron macrophyllum*), huckleberry (*Vaccinium* spp.), salal (*Gaultheria shallon*), and azalea (*Rhododendron occidentale*) (NPS 2010).

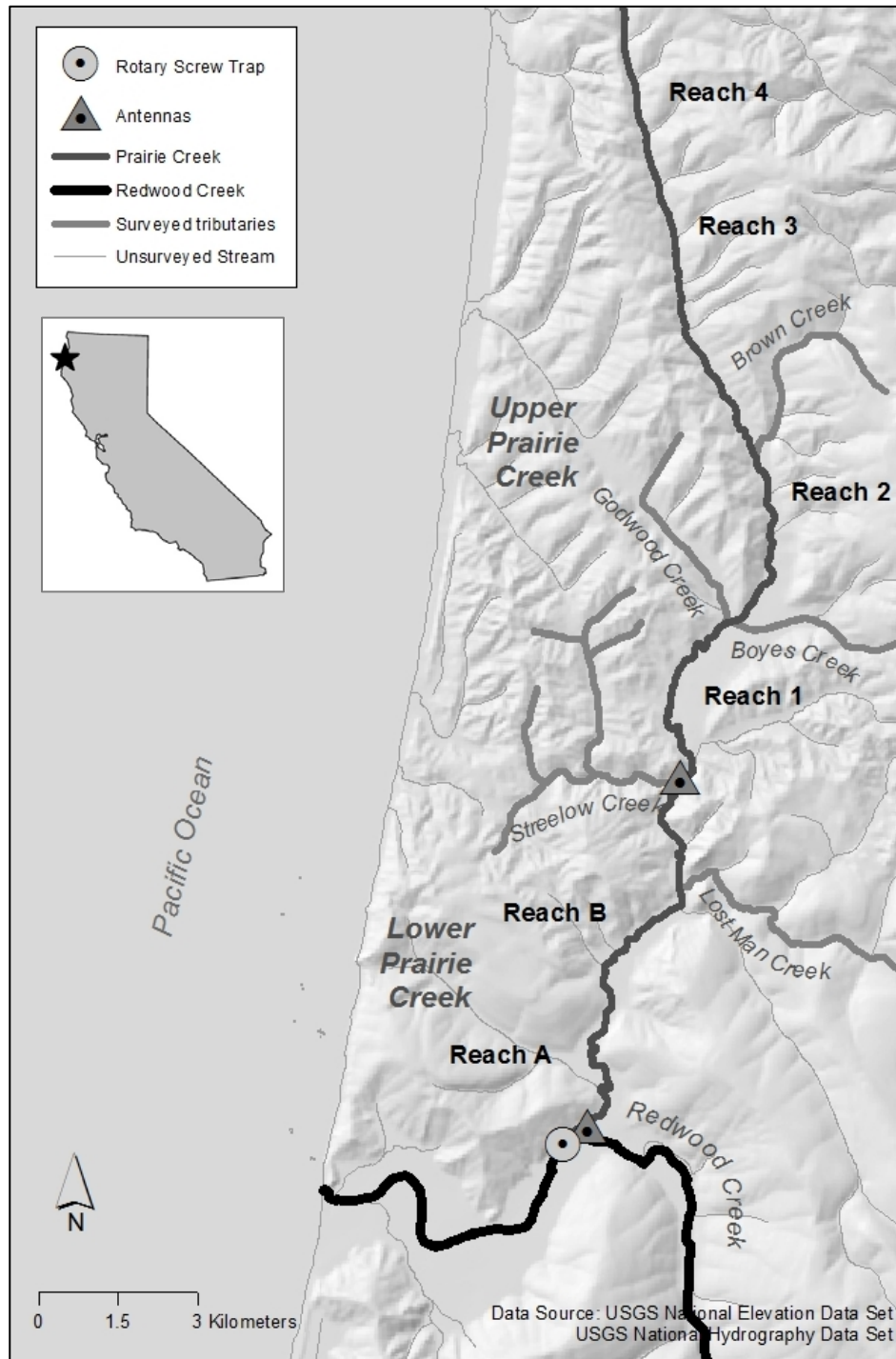


Figure 1. Map of Prairie Creek study site, located near Orick, California in Redwood National and State Parks (Environmental Systems Research Institute, Inc., Redlands, California).

Prairie Creek hosts several species of anadromous salmonids, including steelhead (*Oncorhynchus mykiss*), coastal cutthroat trout (*O. clarki clarki*), coho salmon, and Chinook salmon (*O. tshawytscha*). Runs of coho salmon and steelhead in northern California are listed as threatened under the federal Endangered Species Act (NOAA 2011). Threespine stickleback (*Gasterosteus aculeatus*), coastrange sculpin (*Cottus aleuticus*), prickly sculpin (*Cottus asper*), and Pacific lamprey (*Lampetra tridentata*) are also found in Prairie Creek (Cannata et al. 2006).

While upper Prairie Creek (UPC) is characterized by shallow runs and riffles, lower Prairie Creek (LPC) has numerous deep pools. Trees and thick understory surround UPC, which has particularly dense canopy cover in the upstream reaches. LPC is located in an area with more open prairie and cattle grazing on private land. Prior to this study, the California Cooperative Fish and Wildlife Research Unit divided UPC into four reaches (Figure 1), each ranging between 2500 and 4000 meters in length: reach one (from the Streeflow Creek confluence to the Boyes Creek confluence), reach two (from the Boyes Creek confluence to the Brown Creek confluence), reach three (from the Brown Creek confluence to a bridge that crosses the creek 3500 m upstream), and reach four (the 2500 m of stream above this bridge). For the purposes of this study, LPC was divided into two reaches, both of which are approximately 3500 m in length: reach A (from the bridge at Bald Hills Road to the bridge at Davidson Road) and reach B (the bridge at Davidson Road to the beginning of reach one of UPC). The lower 200 meters of Prairie Creek's major tributaries were also included in this study: Streeflow Creek,

Boyes Creek, Brown Creek, and Godwood Creek were considered to be part of UPC, and Lost Man Creek was grouped with mainstem LPC.

METHODS

Habitat Surveys

Each stream reach contained multiple habitat units, sections of stream that begin and end at a distinct hydraulic break. Only habitat units that contained pools (areas of deep, low velocity water) were sampled since these are the preferred habitat of juvenile coho salmon (Bisson et al. 1988). Moving in an upstream direction from the beginning of the reach, every third habitat unit was sampled provided the unit had a pool. If the unit did contain a pool, the closest pool habitat unit upstream was sampled. This process resulted in a total of 70 habitat units, each of which had either a scour pool, plunge pool, or deep pool according to criteria outlined by the California Salmonid Stream Habitat Restoration Manual (Flosi et al. 2010). Scour pools are defined as pools that are formed where fluvial processes displace the sediment, plunge pools are created by the movement of water over an object, scouring the streambed below, and dam pools are created when a partial blockage in the stream results in a pool of backed up water. For each habitat unit, the following measurements were taken: length, two widths (one 1/3 of the way into the unit and one 2/3 of the way into the unit), two depths (same spots as the two widths), a maximum depth (deepest point in the habitat unit), and a pool tail depth. Large woody debris (LWD) in each habitat unit was also recorded according to protocols outlined by Bouwes et al. (2011), but modified for this study. Qualifying large woody debris included wood pieces measuring at least 10 cm in diameter that extended into the water 1 m during summer flow conditions. Logs that spanned the channel above the water but

were not physically submerged were not included in this count. Each piece was classified into one of three length classes (1 to 3 m, 3.1 to 6 m, and > 6 m) and one of three diameter classes (10 to 15 cm, 16 to 30 cm, and > 30 cm). The amount of large woody debris in each habitat unit was quantified by using the median value for each length and diameter category to calculate volume of wood in m^3 , and dividing this amount by the length (m) of the habitat unit. Fish sampling occurred immediately after taking habitat measurements and quantifying large woody debris (see “Marking Techniques” section below). Habitat units were flagged with the date, habitat unit number, and number of fish tagged in the unit. GPS coordinates of each unit were recorded using a Garmin GPS unit (model GPSMAP 60CSx).

Marking Techniques

Fish were marked using Passive Integrated Transponder (PIT) tags made by Oregon RFID, 12 x 2.12 mm electronic tags (half-duplex) that can be injected into a fish’s body cavity. All tagging and handling procedures were approved by the Humboldt State University Institutional Animal Care and Use Committee (permit number 11/12 F14A). Each tag contained a unique code, which could be detected by a reader or RFID array without having to sacrifice or handle the fish. Fish were collected using a 3 x 1.2 m seine net with 4.7 mm mesh, and all processing and tagging was done streamside. All fish were anesthetized using MS-222 (tricaine methanesulfonate) prior to handling. Five juvenile coho salmon were randomly selected from each habitat unit for obtaining length

and weight measurements in order to estimate the average size of juveniles throughout the watershed. Five coho salmon having a fork length (FL) ≥ 60 mm were then selected from the unit for tagging. Prior to tagging, each fish receiving a tag was weighed, measured, and given an adipose clip as a secondary marker. Tags were inserted by making a small (1 mm) incision on the fish's abdomen using a sanitized razor blade and immediately sliding a sterilized PIT tag into this incision. Scale samples were collected from the first twenty fish tagged in each reach using a sanitized razor to remove approximately ten scales from the area posterior to the dorsal fin. After handling was complete, fish were allowed to fully recover in a mesh basket placed in an area of the stream with abundant circulation and then released into the habitat unit from which they were collected.

Capture Occasions

For the purpose of estimating PIT tag mortality, fish were tagged in two events approximately 30 days apart following methods outlined by Brakensiek and Hankin (2007). Since PIT tag mortality was assumed to happen in the first month after tagging, the survival interval between September and spring for the August tagging cohort was considered to represent true overwinter mortality, uncontaminated with PIT tag mortality. In contrast, this time period for the September tagging group included both natural overwinter mortality and PIT tag mortality, meaning a lower survival rate for the September tagging group would indicate a tagging effect. To get an accurate estimate of

PIT tag mortality, it was necessary to recapture as many August-tagged fish as possible during the September tagging event, and therefore the same 70 habitat units were used for both rounds of tagging. Both tagging rounds followed the same procedure, although no new fish were tagged in the tributaries during September. If an August-tagged fish was recaptured in September, it was weighed and measured. One of these August-tagged fish recaptured in September had shed its tag; however, due to time constraints, secondary fin clips were not checked for all fish captured during September, and therefore tag shed rate was not calculated for time period between August and September. A total of 277 fish were tagged during the August event (August 1, 2012 to August 19, 2012) and 123 were tagged in September (September 1, 2012 to September 30, 2012). The number of tagged fish marked within each stream reach are summarized in Table 1.

A set of dual pass through antennas with Oregon RFID half duplex PIT tag readers were located at the start of reach one and were considered to be the dividing line between upper and lower Prairie Creek (Figure 1). Constructed using 10 m x 1 m loops of eight gauge copper wire, antennas were placed in pairs approximately 20 m apart to allow for determining directional movement. The antennas collected data from August 1, 2012 until August 1, 2013 with the exception of days when the equipment was inoperable due to high flows and technical issues (Table 2).

To monitor spring migrants, a second set of two antennas were placed at the bridge on Bald Hills Road, 500 m upstream of the mouth of Prairie Creek. These antennas were in operation from August 8, 2012 until August 1, 2013, although

Table 1. Number of juvenile coho salmon tagged in each stream reach of Prairie Creek during August and September tagging events.

Reach/Tributary	Region	August	September
<i>Reach A</i>	Lower Prairie Creek	42	20
<i>Reach B</i>	Lower Prairie Creek	39	20
<i>Lost Man Creek</i>	Lower Prairie Creek	10	0
<i>Reach 1</i>	Upper Prairie Creek	40	20
<i>Reach 2</i>	Upper Prairie Creek	40	22
<i>Reach 3</i>	Upper Prairie Creek	40	19
<i>Reach 4</i>	Upper Prairie Creek	35	22
<i>Streelow Creek</i>	Upper Prairie Creek	10	0
<i>Boyes Creek</i>	Upper Prairie Creek	10	0
<i>Brown Creek</i>	Upper Prairie Creek	1	0
<i>Godwood Creek</i>	Upper Prairie Creek	10	0

Table 2. Number of days each month that monitoring at the Prairie Creek antennas was suspended due to high flow and technical issues.

Month	Upstream Antennas	Confluence Antennas
August 2012	0	0
September 2012	0	1 day – technical issues
October 2012	3 days – technical issues	2 days – technical issues
November 2012	2 days – high flow	7 days – high flow
December 2012	8 days – high flow 2 days – technical issues	18 days – high flow
January 2013	0	0
February 2013	0	0
March 2013	0	1 day – high flow
April 2013	0	1 day – high flow
May 2013	0	3 days – technical issues
June 2013	1 day – technical issues	0
July 2013	0	0

monitoring was periodically suspended due to high flows and technical problems (Table 2). Spring migration to the ocean was also monitored by a five foot rotary screw trap installed at the mouth of Prairie Creek and operated from March 10, 2013 until August 13, 2013. All juvenile coho salmon collected at the trap were scanned for PIT tags using a RS601 series portable PIT tag reader (Allflex, DFW Airport, TX). Overwinter tag shed rate was obtained by calculating the percentage of fish observed with a clipped adipose fin but no PIT tag.

Apparent Overwinter Survival Analysis

Apparent overwinter survival and recapture probabilities were estimated using the Cormack-Jolly-Seber model. The model is based on the following assumptions (Pollock and Alpizar-Jara 2005):

1. All animals in the population that are alive at the time of sampling have an equal chance of being captured.
2. All animals in the population have an equal chance of survival for a given time interval.
3. No errors are associated with tagging (i.e. no tag loss or misread tags).
4. Sampling is instantaneous.
5. If an animal emigrates from the study site, it does not return.

In the Cormack-Jolly-Seber model, a series of 0's and 1's are used to code the capture history of each animal. A "1" means the animal was sighted, and a "0" means the

animal was not seen, either because the animal is dead or because it was alive but not resighted on that occasion. The first “1” in the series indicates when the animal was marked. For example, a capture history of 111 would represent an individual marked on occasion one and resighted on the subsequent two occasions, while 010 would mean the individual was marked on occasion two, and not resighted on occasion three. Survival rates between capture occasions are represented by ϕ , and encounter rates are represented by p (Figure 2). For example, ϕ_1 would be the survival rate between t_1 and t_2 , the first and second capture occasions, while p_2 would be used to indicate the probability of recapture at t_2 , given survival to t_2 . The survival and recapture rates can be used to calculate the probability of an encounter history. For example, the probability of encounter history 101 would be $\phi_1(1 - p_2)\phi_2 p_3$. The last two parameters, in this case ϕ_2 and p_3 are not separately identifiable (Lebreton et al. 1992).

In this study, fish were either marked on the first capture occasion in August or the second occasion in September. Observations at the other three encounter occasions, the upstream antennas, confluence antennas, or rotary screw trap, represent whether or not the fish was encountered at these sites during the spring migration to the ocean. The beginning of the spring migration period was considered to be March 4, 2013 since this was the first day a fish migrating downstream was encountered at either set of antennas. These last three occasions only represent detections that occurred on or after March 4, 2013 and do not include fish detected at the antennas during fall or winter. Although the rotary screw trap was not installed until March 10, 2013, migration that occurred between

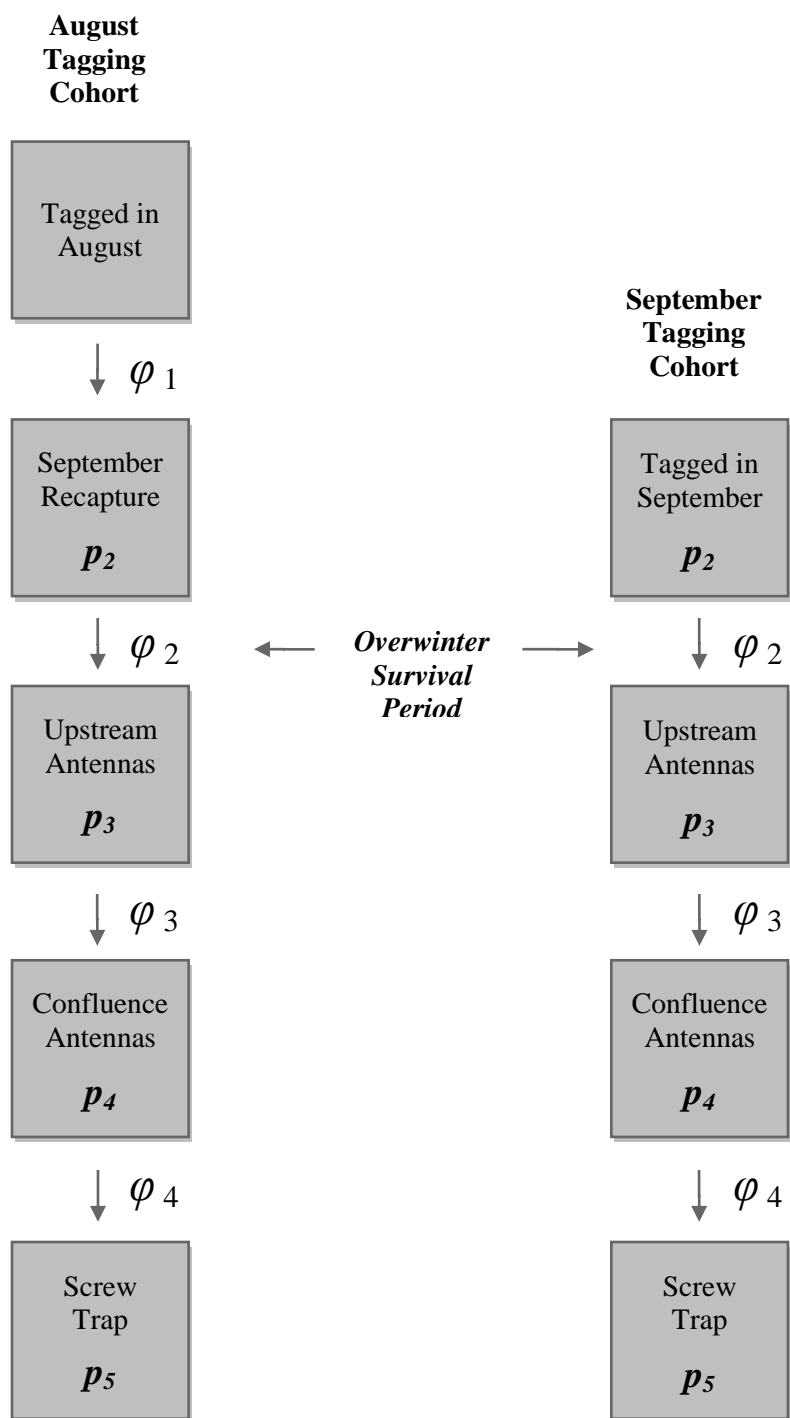


Figure 2. Recapture histories for the two tagging cohorts (September and August). The survival rate φ_2 represents overwinter survival for all juvenile coho salmon in this study, whether they were tagged above or below the upstream antennas.

March 4, 2013 and March 10, 2013 was considered to be minimal since only one fish was encountered at the confluence antennas during this time period. The ϕ for the period between the September occasion and the upstream antennas (ϕ_2) represents the overwinter survival rate for all fish, both those tagged above the upstream antennas and those tagged below. Although fish tagged in reaches A and B were not likely to be encountered at the upstream antennas during spring migration, they could still potentially be detected at the recapture points following the upstream antennas: the confluence antennas (fourth recapture occasion) and rotary screw trap (fifth recapture occasion), and thus considered to be overwinter survivors. For example, a fish with the encounter history 10001 (seen at the August and trap occasions only) is still considered to survive the overwinter period (September – upstream antennas) because it was encountered on at least one subsequent occasion after the upstream antennas. Furthermore, survival between the upstream and confluence antennas was nearly 100%, and survival between the confluence antennas and rotary screw trap was assumed to be to 100% due their close proximity (less than 500 m) and the need to estimate the confounded last recapture parameter. This means any overwinter mortality experienced by fish from reaches A and B likely occurred during the period between the September occasion and the upstream antenna occasion, further confirming the decision to use this period to define overwinter survival. However, this approach significantly biases the recapture efficiency of the upstream antennas, since the Cormack-Jolly-Seber model assumes an equal probability of recapture for all individuals. To account for this, a grouping variable based on whether

the fish was tagged above or below the upstream antennas (*tagged*) was applied to the recapture model (described in greater detail below). This allowed the recapture efficiency of the upstream antennas to be calculated separately for fish tagged above and below the antennas.

The overwinter survival analysis was conducted by building models using the RMark package (Laake 2012) found in R (R Development Core Team 2011) and importing these models into Program MARK (Cooch and White 2011). Candidate models were assessed using AICc, a variant of Akaike's Information Criterion that includes a bias correction term for improving performance with small sample sizes. AICc is calculated as follows (Anderson 2008):

$$\text{AICc} = -2\log_e(L(\hat{\theta})|x) + ((2K(K+1))/(n-K-1))$$

where $L(\hat{\theta})|x$ is the maximized value of the likelihood function given the data (x) and indicates goodness of fit, and K is the number of estimated parameters. The values of $L(\hat{\theta})|x$ can be improved by adding more parameters. However, adding more parameters is penalized by the “ $((2K(K+1))/(n-K-1))$ ” term, thus this form of model selection balances predictive power with parsimony (Anderson 2008). For this study, the best model was considered to be the simplest model within approximately two AICc values (Δ_i) of the best fitting model. The logit link function was used for all models, restricting survival and recapture rate estimates to the interval (0,1) (Lebreton et al. 1992).

Overwinter survival models included combinations of the following explanatory variables: tag month (whether the fish was tagged in August or September – used to assess PIT tag mortality as described in the “Capture Occasions” section above), fork length at time of tagging, maximum depth (deepest point in fall habitat unit), amount of large woody debris present in the habitat unit (volume of wood in m^3 , divided by length of the habitat unit in m), and some form of location, either as distance from the confluence of Prairie Creek or as the grouping variable *tagged*, which categorized fish based on whether they were tagged above or below the upstream antennas (not both). Models with a length and location interaction (*length:distance* or *length:tagged* grouping variable, never both in one model) were also included in the analysis. Since time intervals between capture occasions ranged from an entire season (ϕ_2), to less than a day (ϕ_4), a parameter that allowed survival rate to vary by time interval (*interval*) was included in all models. Explanatory variables used in the overwinter survival analysis are summarized in Table 3.

The recapture rate model used with all survival models included the following parameters: the location grouping variable *tagged* (tagged above or below the upstream antennas), *occasion* (allowed probability of recapture to vary by capture event since several different recapture methods were used), and the interaction of *tagged* with *occasion* p_2 and *occasion* p_3 . The interaction terms *tagged:occasion* p_2 and *tagged:occasion* p_3 were included since location at time of tagging would only impact the recapture rates p_2 and p_3 . The recapture rate in September (*occasion* p_2) was effected by

Table 3. Model parameters used in the overwinter survival and recapture analysis. The term φ refers to a parameter that affects survival, and p refers to a parameter that affects recapture rate.

Model Parameter	Parameter Description
φ (<i>interval</i>)	Survival parameter that allows survival rate to vary by time interval
φ (<i>length</i>)	Individual covariate that describes the fork length of the fish at the time of tagging
φ (<i>max depth</i>)	Individual covariate describing the deepest point in the habitat unit where the fish was tagged
φ (<i>LWD</i>)	Individual covariate that describes the volume of large woody debris present in the habitat divided by the length of the habitat
φ (<i>distance</i>)	Individual covariate that refers to the habitat unit where the fish was tagged in the fall. Indicates the habitat unit's distance from the confluence of Prairie Creek
φ (<i>tagged</i>)	A grouping variable that refers to whether the fish was tagged above or below the upstream antennas. Models included φ (<i>tagged</i>), φ (<i>distance</i>), or neither φ (<i>tagged</i>) or φ (<i>distance</i>), never both.
φ (<i>tag month</i>)	A grouping variable that refers to the month the fish was tagged and assesses tagging effect.
p (<i>occasion</i>)	Recapture parameter that allows recapture rate to vary by capture occasion
p (<i>tagged</i>)	A grouping variable that refers to whether the fish was tagged above or below the upstream antennas.
p (<i>tagged:occasion p₂</i>)	Recapture parameter that refers to the interaction between the recapture occasion p_2 and the location grouping variable <i>tagged</i>
p (<i>tagged:occasion p₃</i>)	Recapture parameter that refers to the interaction between the recapture occasion p_3 and the location grouping variable <i>tagged</i>

whether or not fish were tagged above the upstream antennas due to logistical difficulties with seining the deep water in lower Prairie Creek. Also, fish tagged above the upstream antennas (probability of recapture at this event represented by *occasion p₃*) were far more likely to pass by this location when migrating in spring than fish marked below these antennas, which would have to swim upstream to be detected. The decision to use this model was confirmed by a preliminary comparison of two models: the full interactive model (recapture model $\text{logit}(p) = \text{intercept} + \beta_1(\text{tagged}) + \beta_2(\text{occasion}) + \beta_3(\text{tagged}:\text{occasion interaction})$) and the more parsimonious model with the *tagged* interaction applied only to *occasion p₂* and *occasion p₃*. This analysis revealed that the full interactive model was always ranked lower than its counterpart that had fewer interactions, with an AICc value of less than 3 units higher. This model also received more than 0.99999 of model weight when compared with the alternative models $\text{logit}(p) = \text{intercept} + \beta_1(\text{tagged}) + \beta_2(\text{occasion})$ and $\text{logit}(p) = \text{intercept} + \beta_2(\text{occasion})$, further confirming the usage of this model for the survival analysis. The parametric bootstrapping and the median \hat{c} goodness of fit tests in Program MARK were used to estimate the variance inflation factor, \hat{c} . Because these tests in Program MARK are unable to handle models containing individual covariates (only grouping variables), the survival model $\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{tagged})$ and the recapture model $\text{logit}(p) = \text{intercept} + \beta_1(\text{occasion}) + \beta_2(\text{tagged}) + \beta_3(\text{tagged}:\text{occasion } p_2, \text{occasion } p_3 \text{ interactions})$ were used to assess general goodness of fit. A \hat{c} greater than 3 indicates

there is either excess variation in the data or the model does not accurately reflect the structure of the data (Lebreton et al. 1992).

Overwinter Growth

Overwinter growth was analyzed using the fish recaptured at the rotary screw trap that had retained their PIT tags. Specific growth rates were calculated using the following formulas (Busacker et al. 1990):

$$G(\text{length}) = ((\log_e \text{FL}_2 - \log_e \text{FL}_1) / (T_2 - T_1)) \times 100$$

$$G(\text{weight}) = ((\log_e \text{WT}_2 - \log_e \text{WT}_1) / (T_2 - T_1)) \times 100$$

where G is overwinter growth in percentage per day, FL₁ and WT₁ represents initial fork length and weight, FL₂ and WT₂ represents spring fork length and weight, T₁ represents the date of the initial tagging event and T₂ represents the date the fish was recaptured at the trap. The effects of fall fork length and tagging location on specific growth in length were analyzed using the following general linear model in R: *specific growth in length* = $\beta_1(\text{fork length}) + \beta_2(\text{distance}) + \beta_3(\text{fork length}:\text{distance}) + e$, $e \sim N(0, \sigma^2)$.

1+ Life History

All scale samples were collected during the first round of tagging to minimize the amount of size at age variation in the age-length key. Multiple scales from each fish were dry mounted on glass slides, viewed at a magnification of 63x using Nikon SMZ800 stereomicroscope (Nikon Corp., Tokyo, Japan), and photographed using an attached Spot

Insight 2 megapixel digital camera and Spot software version 4.6 (Spot Imaging Solutions, Sterling Heights, Michigan). Twenty five percent of the scales were aged by a second person to assess the accuracy of age determination. A second individual was also consulted if the presence of annuli was in question. To minimize aging bias, scales were aged without prior knowledge of the fish's characteristics (i.e., size or location at time of tagging).

RESULTS

Apparent Overwinter Survival

During spring migration to sea, 66, 97, and 26 unique fish were encountered at the upstream antennas, confluence antennas, and the screw trap, respectively. Releases and recaptures are presented in an m-array (Table 4), which represents a summary of mark/recapture data. In this table, the bold number numbers represent the total number of fish encountered at each occasion, and the line separates number of fish that were released or rereleased (left) from number of first recaptures (right) (Burnham et al. 1987).

The top four overwinter survival models out of the candidate set accounted for 0.73 of the total weight and included the following predictors: *max depth*, *length*, *distance*, *the length/distance interaction*, and *tag month* (Table 5). The best model was considered to be the simplest model within approximately two AICc units (Δ_i) of the model with the lowest AICc score. Based on this criteria, the model with the parameters *length*, *distance*, and the *length:distance interaction* was considered to be the best model, excluding the *max depth*, *tag month*, and *LWD* parameters. The parameter *length* (fork length at the time of tagging) was present in every top ranked model, and corresponding models without this parameter had less than 0.00001 AICc weight, indicating the fork length of the fish at the time of tagging was most likely an important predictor of apparent survival through winter. Since the top model with the *tagged* grouping variable ($\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{max depth}) + \beta_3(\text{length}) + \beta_4(\text{tagged})$) had an AICc weight of only 0.01, *distance* was most likely a better parameter for describing the

Table 4. M-array table summarizing the number of fish marked and recaptured at each occasion. A total of 400 juvenile coho salmon were marked in Prairie Creek, California over two tagging events (August and September). Fish could then potentially be encountered at the upstream antennas, confluence antennas, and the rotary screw trap at the confluence of Prairie Creek.

Releases	Number released (R_i)	Spring Recapture Occasions				Total recaptured for first time (r_i)	Never recaptured ($R_i - r_i$)	
		Second occasion in September	Third occasion at upstream antennas	Fourth occasion at confluence antennas	Fifth occasion at rotary screw trap			
August (initial [1])	277	140	16	16	1	173	104	
September	263	[11]	140	31	24	2	57	83
		[01]	123	19	16	0	35	88
			263				92	171
Upstream antennas	66	[101]	16	10	1	11	5	
		[111]	31	16	4	20	11	
		[011]	19	15	1	16	3	
			66				47	19
Confluence antennas	97	[1001]		16	3	3	13	
		[1101]		24	4	4	20	
		[1011]		10	2	2	8	
		[1111]		16	2	2	14	
		[0101]		16	4	4	12	
		[0111]		15	2	2	13	
			97			17	80	

Table 5. AICc table for the overwinter survival (ϕ) analysis. In addition to the parameters listed, all survival models include the parameter *interval*, which accounts for the difference in time intervals between capture occasions. The model for the recapture rate (p) for all models was $\text{logit}(p) = \text{intercept} + \beta_1(\text{occasion}) + \beta_2(\text{tagged}) + \beta_3(\text{tagged}:\text{occasion } p_2, p_3 \text{ interactions})$. A colon denotes an interaction between two parameters.

Explanatory variables in the survival model	AICc	Δ AICc	AICc Weights	K
<i>max depth, length, distance, length:distance</i>	1222.95	0.00	0.23900	13
<i>length, distance, length:distance</i>	1223.55	0.60	0.17700	12
<i>tag month, length, distance, length:distance</i>	1223.62	0.67	0.17100	13
<i>tag month, max depth, length, distance, length:distance</i>	1224.00	1.05	0.14100	14
<i>LWD, max depth, length, distance, length:distance</i>	1224.96	2.01	0.08720	14
<i>LWD, length, distance, length:distance</i>	1225.55	2.60	0.06510	13
<i>LWD, tag month, length, distance, length:distance</i>	1225.64	2.69	0.06210	14
<i>max depth, length, tagged</i>	1228.74	5.79	0.01320	12
<i>max depth, length, tagged, length:tagged</i>	1229.84	6.89	0.00762	13
<i>max depth, length, distance</i>	1230.05	7.10	0.00685	12
<i>length, tagged</i>	1230.52	7.57	0.00543	11
<i>length, distance</i>	1230.57	7.62	0.00530	11
<i>LWD, max depth, length, tagged</i>	1230.62	7.67	0.00516	13
<i>length, tagged, length:tagged</i>	1231.42	8.47	0.00345	12
<i>LWD, max depth, length, tagged, length:tagged</i>	1231.73	8.78	0.00296	14
<i>LWD, max depth, length, distance</i>	1232.08	9.13	0.00249	13
<i>LWD, length, tagged</i>	1232.35	9.40	0.00217	12
<i>LWD, length, distance</i>	1232.58	9.63	0.00194	12
<i>LWD, length, tagged, length:tagged</i>	1233.29	10.34	0.00136	13
<i>length</i>	1237.16	14.21	0.00020	10
<i>max depth, length</i>	1237.89	14.94	0.00014	11
<i>LWD, length</i>	1239.08	16.13	0.00007	11
<i>LWD, max depth, length</i>	1239.81	16.86	0.00005	12
<i>max depth, tagged</i>	1247.17	24.22	0.00000	11
<i>LWD, tagged</i>	1248.51	25.56	0.00000	11
<i>max depth, distance</i>	1248.62	25.67	0.00000	11
<i>LWD, max depth, tagged</i>	1249.07	26.12	0.00000	12
<i>LWD, distance</i>	1249.45	26.50	0.00000	11

relationship between apparent overwinter survival and location at the time of tagging.

The top seven models (combined 0.94 model weight) included the *length* and *distance* interaction, and the model $\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{length}) + \beta_3(\text{distance})$ had approximately 33 times less weight than its corresponding equivalent with the *length* and *distance* interaction. These results indicated that overall survival increased with length, but this effect was more pronounced for fish higher in the watershed than fish near the confluence (Figure 3). Larger fish tagged at the maximum (20,350 m) and mean (7,150 m) distances from the confluence had higher survival than small fish, while at the minimum distance from confluence (660 m), smaller fish appeared to have higher survival than large fish (Figure 4). However, since the Cormack-Jolly-Seber model cannot distinguish mortalities from emigration, the survival of larger fish near the confluence may be artificially low due to early emigration. To test for any potential confounding issues involving fork length and location (for example, if fish in downstream habitats were larger at the time of tagging), a simple linear regression was used to examine the average length of fish throughout the watershed. The general linear model $\text{average fork length} = \beta_1(\text{distance}) + e$, $e \sim N(0, \sigma^2)$ produced a value of -0.00021 for the *distance* coefficient (SE = 0.00014, p = 0.138), suggesting that any confounding effect was negligible.

The apparent overwinter survival estimate produced by the best model ($\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{length}) + \beta_3(\text{distance}) + \beta_4(\text{length}:\text{distance interaction})$) for the average length fish at that average distance from confluence was 0.39 (SE = 0.04)

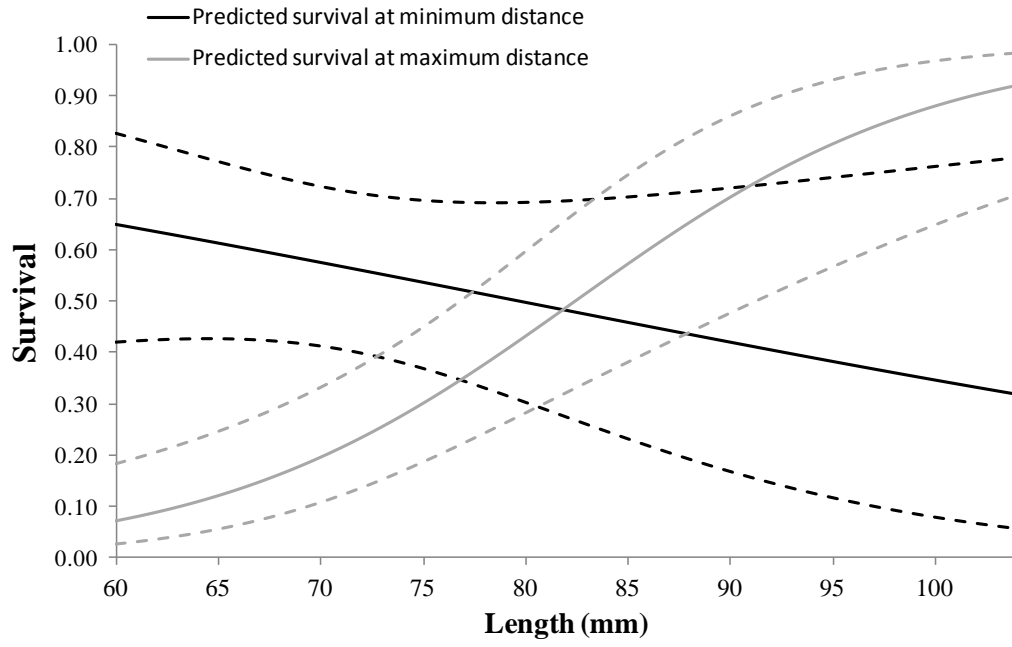


Figure 3. Effect of fall fork length on apparent overwinter survival at the minimum (660 m) and maximum (20,305 m) distances from confluence in fall.

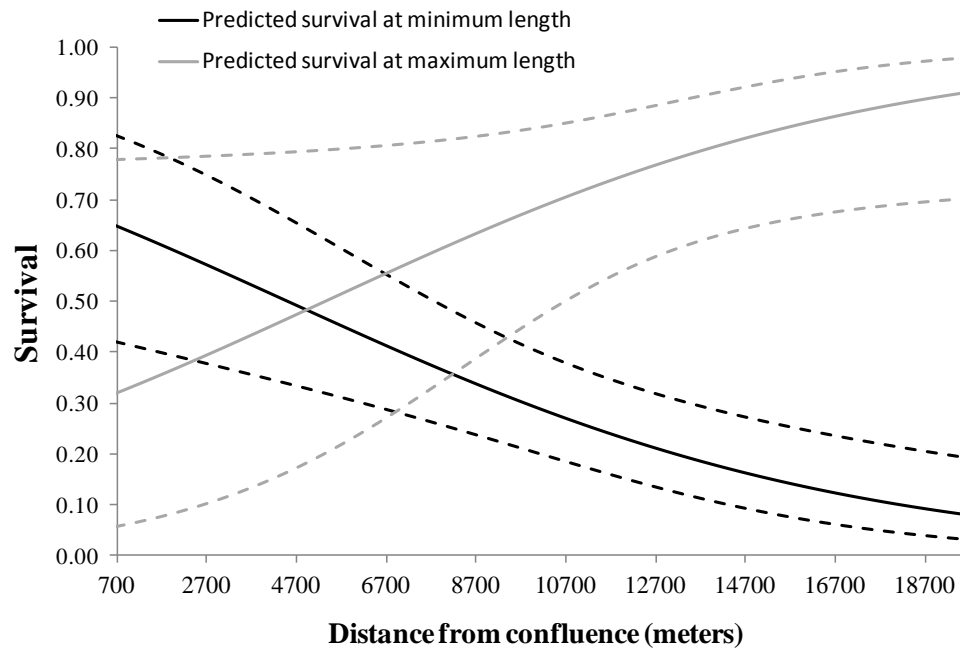


Figure 4. Effect of fall distance from confluence on apparent overwinter survival for juveniles of minimum (60 mm) and maximum (104 mm) fall fork lengths.

(Table 6). This value may be multiplied by 100 to estimate the percentage of fish that survived the winter. Coefficients (β estimates) produced by the model are summarized in Table 7. Of the 30 fish encountered at the trap, 4 had shed their tags. Since these fish could not be uniquely identified, they were excluded from the survival analysis, thus true apparent survival may be 13.3% higher. The apparent overwinter survival estimate also does not include fish that may have migrated from Prairie Creek earlier than March 4, 2013 (including the two fish that were detected at the confluence antennas in fall and never encountered again), or fish that would be spending a second winter in Prairie Creek as 1+ fish (at least one fish was encountered in September 2013), hence the term “apparent” survival. Although the best overwinter survival model did not include PIT tag mortality, models containing the PIT tag mortality parameter totaled 0.38 of the model weight. The model averaged survival estimates using all models in the survival analysis were 0.41 (95% confidence interval = 0.31 – 0.52) survival for the August group, and 0.38 (95% confidence interval = 0.28 – 0.49) for the September group, indicating PIT tag mortality was approximately $100 * (1 - (37.6/41.1)) = 8.5\%$.

The parametric bootstrap test (100 simulations) in Program MARK was used to estimate two values of \hat{c} for the survival model with the *interval* and *tagged* parameters and the recapture model with the *occasion*, *tagged*, *tagged:occasion* p_2 interaction, and *tagged:occasion* p_3 interaction parameters. For the first approach, the deviance of the data was divided by the deviance of the simulated data, producing a \hat{c} value of 1.22. The second approach consisted of dividing the observed \hat{c} (model deviance/deviance degrees

Table 6. Survival and recapture rate estimates for the survival model $\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{length}) + \beta_3(\text{distance}) + \beta_4(\text{length:distance interaction})$ and the recapture rate model $\text{logit}(p) = \text{intercept} + \beta_1(\text{occasion}) + \beta_2(\text{tagged}) + \beta_3(\text{tagged:occasion } p_2, p_3 \text{ interactions})$. Since Program MARK had difficulty estimating parameters that are close to 1, survival for the time period between the upstream and confluence antennas (φ_3), probably close to 100%, is not listed.

Parameter	Description	Estimate	Standard Error	Confidence Interval	
φ_1	Survival rate between August and September tagging occasions	0.91	0.06	0.71	0.98
φ_2	Survival rate between September and upstream antennas (overwinter)	0.39	0.04	0.32	0.48
φ_4	Survival rate between the confluence antennas and the rotary screw trap.	1.0*	-	-	-
$p_2(\text{above})$	Recapture rate during the September tagging occasion for fish tagged above the upstream antennas	0.63	0.05	0.52	0.72
$p_3(\text{above})$	Recapture rate at the upstream antennas for fish tagged above the upstream antennas	0.68	0.06	0.56	0.78
$p_4(\text{above})$	Recapture rate at the confluence antennas for fish tagged above the upstream antennas	0.69	0.05	0.58	0.78
$p_5(\text{above})$	Recapture rate at the rotary screw trap for fish tagged above the upstream antennas	0.21	0.04	0.14	0.29
$p_2(\text{below})$	Recapture rate during the September tagging occasion for fish tagged below the upstream antennas	0.44	0.06	0.34	0.55
$p_3(\text{below})$	Recapture rate at the upstream antennas for fish tagged below the upstream antennas	0.08	0.03	0.04	0.18
$p_4(\text{below})$	Recapture rate at the confluence antennas for fish tagged below the upstream antennas	0.51	0.07	0.37	0.64
$p_5(\text{below})$	Recapture rate at the rotary crew trap for fish tagged below the upstream antennas	0.11	0.03	0.07	0.18

*Assumed to be 100% survival and fixed to 1.

Table 7. Coefficient (beta) estimates for the survival model $\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{length}) + \beta_3(\text{distance}) + \beta_4(\text{length:distance interaction})$ and the recapture model $\text{logit}(p) = \text{intercept} + \beta_1(\text{occasion}) + \beta_2(\text{tagged}) + \beta_3(\text{tagged:occasion } p_2, p_3 \text{ interactions})$. Survival at time interval four (φ time 4) was fixed to 1 since survival was assumed to be 100% between the confluence antenna and the trap. Since it is difficult for Program MARK to estimate parameters that are close to 1, survival for time 3, probably close to 100%, is not listed.

Parameter	Coefficient estimate (β)	Standard Error	Confidence Interval	
			Lower Limit	Upper Limit
φ intercept	5.68	2.44	0.91	10.46
φ time 2	-2.79	0.84	-4.43	-1.15
φ time 3	-	-	-	-
φ time 4	-	-	-	-
φ length	-0.04	0.03	-0.10	0.03
φ distance	-0.06	0.02	-0.10	-0.02
φ length:distance interaction	7.34×10^{-4}	2.51×10^{-4}	2.43×10^{-4}	1.23×10^{-3}
p intercept	0.52	0.23	0.08	0.97
p time 3	0.23	0.34	-0.43	0.89
p time 4	0.27	0.29	-0.29	0.83
p time 5	-1.87	0.30	-2.45	-1.28
p tagged below	-0.76	0.23	-1.21	-0.30
p time3:tagged below interaction	-2.38	0.53	-3.42	-1.35

of freedom) by the mean \hat{c} from the bootstrap simulations. This method estimated \hat{c} to be 1.24. The median \hat{c} test in Program MARK also produced a \hat{c} close to 1 (1.14, SE = 0.06), suggesting the data was not overdispersed.

Migration

Prior to spring migration (March 4, 2013), detections at the upstream antennas were limited to 10 encounters of eight unique fish, three from the reach immediately upstream from the upper antennas (reach 1), three from the reach immediately downstream of the upper antennas (reach B), one from a habitat unit in the tributary Streelow Creek (less than 300 m from the upper antennas), and one fish tagged close to the confluence antennas. The first detection at the upstream antennas occurred on October 16, 2012 and half of the unique fish detected before spring migration were encountered between December 26, 2012 and January 6, 2013. At the confluence antennas, a total of three fish were encountered before spring migration; one during August, one during October, and one during November. The first two fish were both encountered at the upstream loop in the confluence antenna set, then immediately detected at the downstream loop, implying the fish was swimming downstream. Since neither fish was encountered again, they may have left the system.

Because the antennas were inoperable during high flows, the sparse detection history may not accurately reflect the amount of winter movement. During these periods, some fish may have migrated into Lower Prairie or left Prairie Creek entirely. To assess

the possibility of missed movement from upper Prairie Creek during high flows, the 66 spring detections at the upstream pair of antennas were used to construct a three encounter recapture history. All fish were “marked” on the first occasion (“1” for all fish in the encounter history), and the other two occasions represent the two antennas in the upstream array. Since only fish that were encountered in the spring were used in this analysis, survival was set to 1 for both the interval between the initial marking and the first antenna and the interval between the antennas. For the 66 spring detections, Program MARK estimated the efficiency of the antennas to be 0.65 and 0.79, meaning the chance of being detected by at least one antenna was $1 - (1 - 0.65) * (1 - 0.79)$, or 0.93. The best survival model ($\text{logit}(\varphi) = \text{intercept} + \beta_1(\text{interval}) + \beta_2(\text{length}) + \beta_3(\text{distance}) + \beta_4(\text{length:distance interaction})$) estimated the spring antenna efficiency for fish tagged above the upstream antennas to be much lower (0.68). Though not definitive, these results indicate that some portion of the fish tagged in upper Prairie Creek moved into lower Prairie Creek before the spring migration period, making the spring antenna efficiency seem artificially low.

Median travel time between the antenna locations during the spring migration to the ocean was calculated using the last day the fish was encountered at the upstream antennas and the first day the fish was encountered at the confluence antennas. For the forty fish detected at both antennas during the spring, median travel time was 1.5 days, and 80% were detected at the confluence antennas within 3 days. Three fish utilized the habitat between the antennas (lower Prairie Creek) for more than 40 days and one fish

spent 92 days in this area, suggesting it may be an important stopover for some juveniles during spring migration. Number of spring migrants per day at the confluence antennas and the screw trap are summarized in Figure 5.

Overwinter Growth

Fit of the model $\text{specific growth in length} = \beta_1(\text{fork length}) + \beta_2(\text{distance}) + \beta_3(\text{fork length}:\text{distance}) + e$, $e \sim N(0, \sigma^2)$ was assessed using a normal probability plot of the residuals (Q-Q plot) and a residuals versus fitted plot, which revealed no departures from normality or violations of the assumption of homogeneity of variance. There was strong evidence that initial fork length was associated with growth, but no evidence that distance was either associated with growth or modified the effects of initial fork length (Table 8). Fish that were smaller at the time of tagging experienced a greater increase in length (Figure 6). For fish captured at the trap, mean fall fork length was 77.0 mm (SD = 12.5 mm) and mean spring fork length was 108.5 mm, with a average daily growth rate of 0.13%/day (SD = 0.05%). Using the specific growth rate calculation for weight (second expression) growth rate in weight was estimated at 0.35%/day (SD = 0.16%), ranging from 0.10%/day to 0.73%/day. Juveniles recaptured at the rotary screw trap had a mean fall weight of 5.9 g and mean spring weight of 13.5 g.

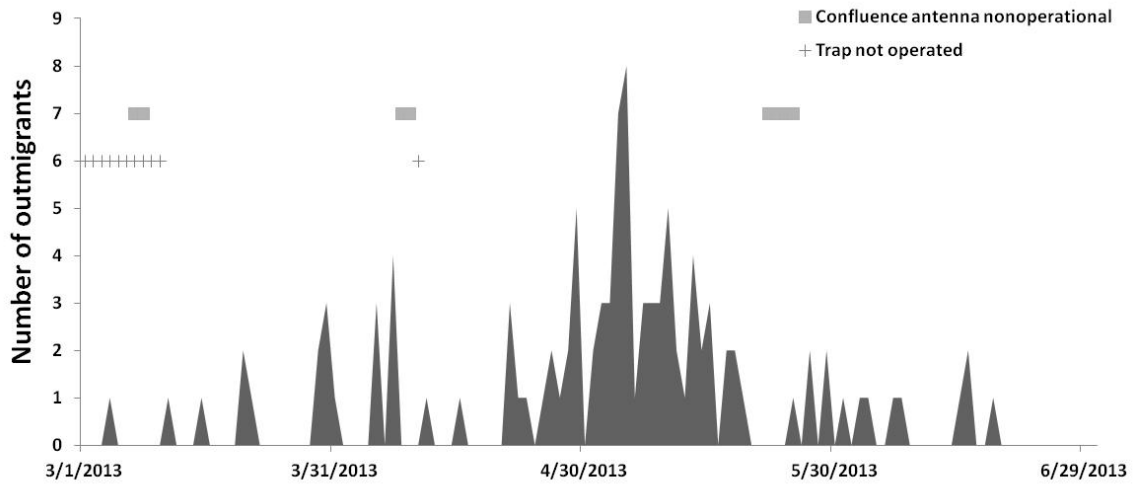


Figure 5. Combined number of unique spring migrants per day at the confluence antennas and rotary screw trap.

Table 8. F statistics, degrees of freedom, and R^2 for the model *specific growth in length* = $\beta_1(\text{fork length}) + \beta_2(\text{distance}) + \beta_3(\text{fork length:distance}) + e$, $e \sim N(0, \sigma^2)$ and its explanatory variables *fork length*, *distance*, and the *fork length:distance* interaction.

Explanatory variable	F statistic	Degrees of freedom	p value	R^2
<i>full model</i>	33.33	3,22	2.32×10^{-08}	0.80
<i>fork length</i>	33.32	1,22	8.31×10^{-06}	-
<i>distance</i>	1.58	1,22	0.22	-
<i>fork length:distance</i> interaction	1.41	1,22	0.25	-

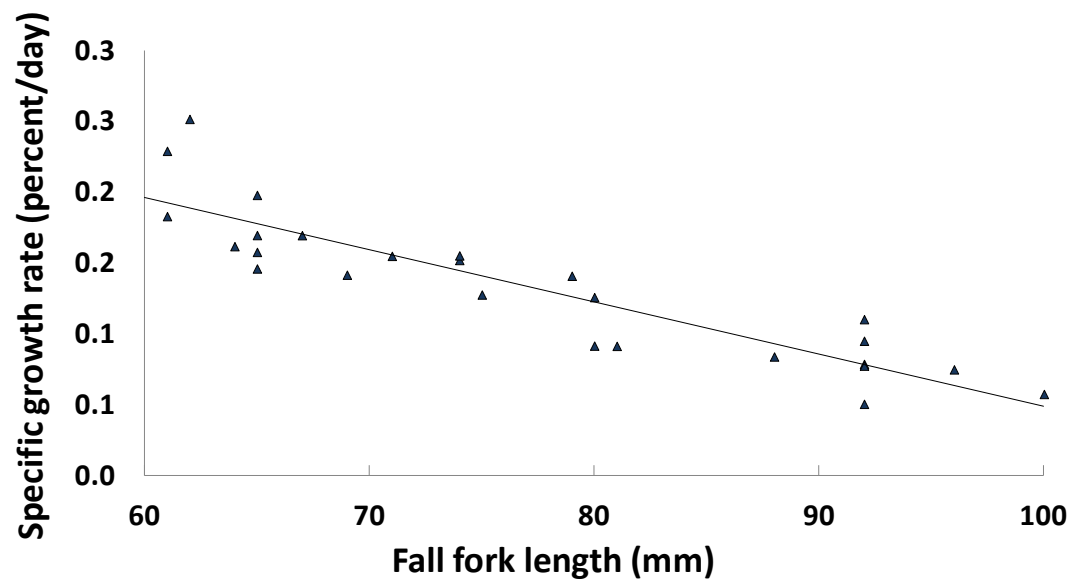


Figure 6. Effect of fall fork length on specific growth rates of juvenile coho salmon over winter (percentage increase in length per day).

1+ Life History

An age length key was constructed using 132 scales samples and lengths from 317 randomly selected fish from throughout the watershed (5 per habitat unit, unless less than five were found in the unit). Scales samples were only collected from fish that were 60 mm and greater since smaller fish were assumed to be age 0. Based on the random population sample, mean fish size was estimated at 57.7 mm (SD = 10.1). The average size of 1+ (two-year freshwater resident) juveniles in the scale sample analysis was 86.2 (SD = 6.5), and the age length key estimated the percentage of fish exhibiting a 1+ life history to be 1.4% (Figure 7). There was some overlap in the age classes, with the largest age 0 fish being 82 mm and the smallest age 1+ fish being 74 mm (Figure 8). A second person that aged 25% of the scale samples was in agreement with the primary individual aging the scales 90.9% of the time.

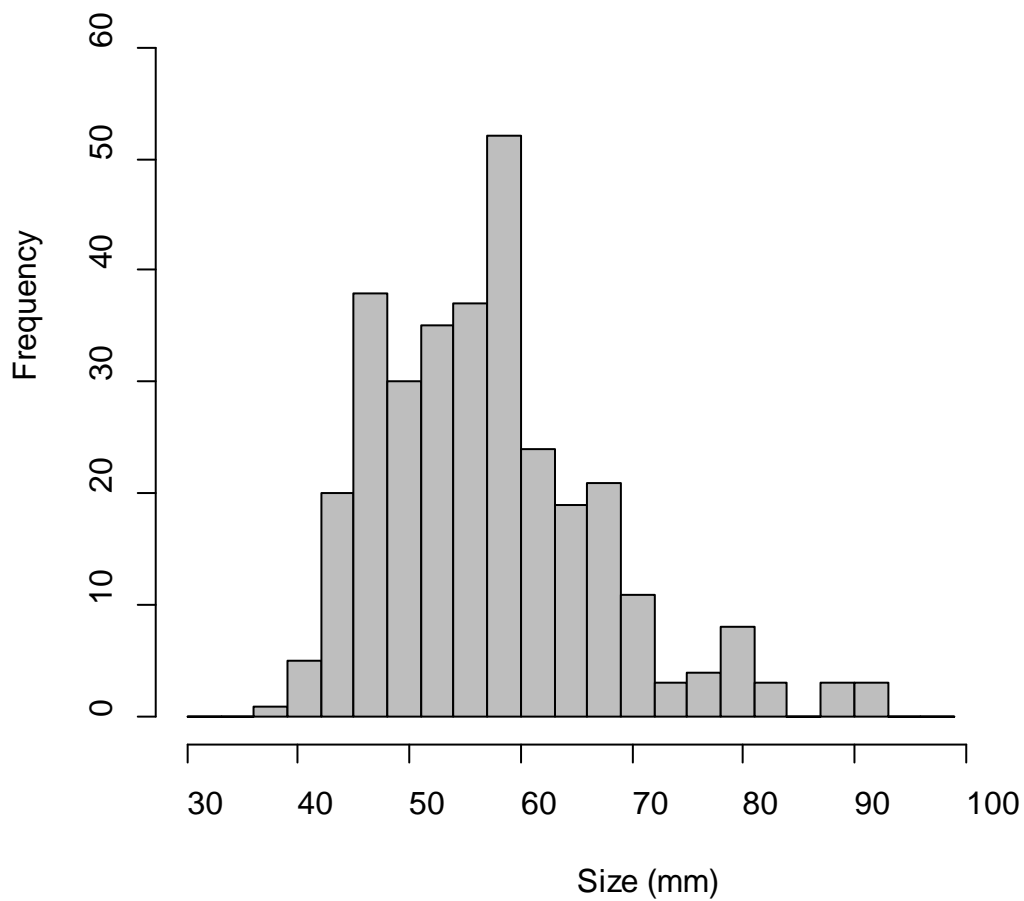


Figure 7. Length (FL) distribution of a random sample of 317 juvenile coho salmon from the Prairie Creek watershed (mean fork length = 57.7 mm).

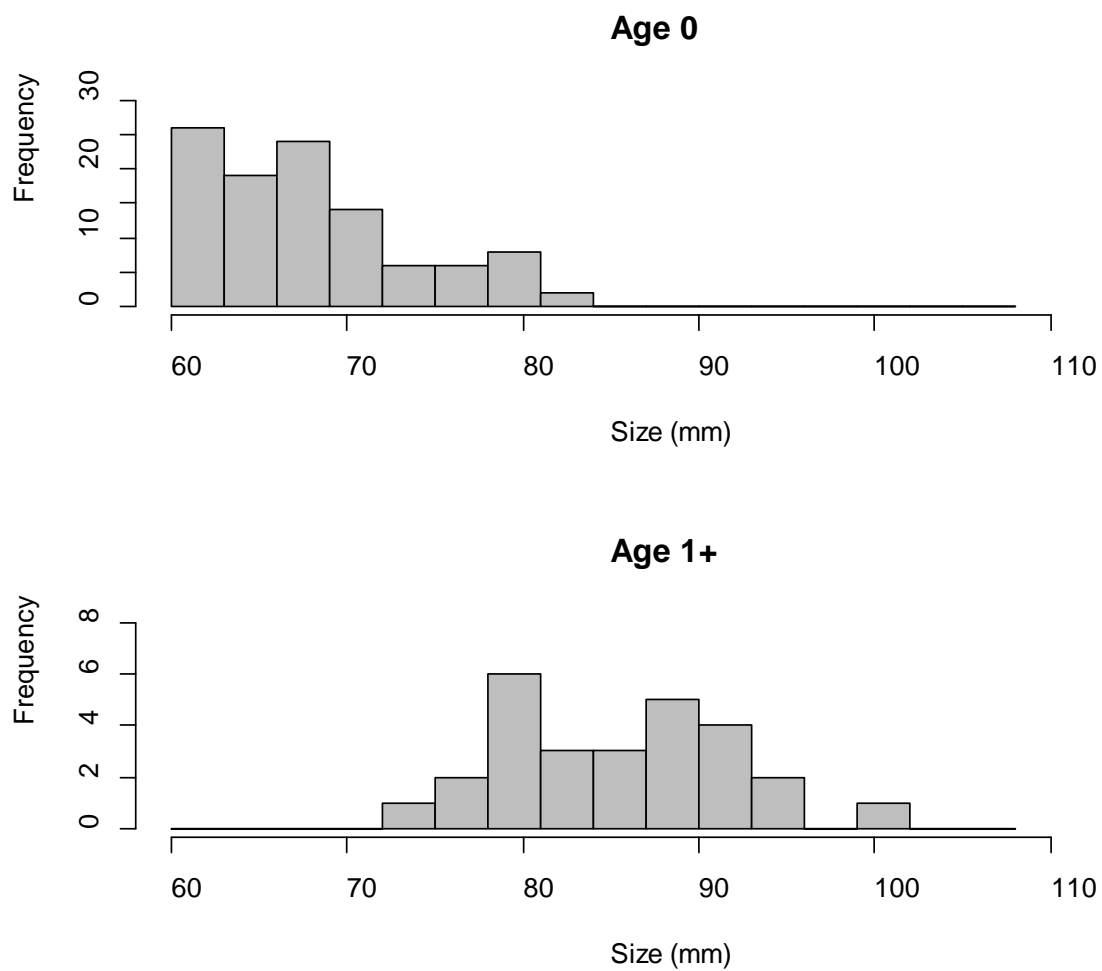


Figure 8. Size (FL) distribution of age 1+ juveniles and age 0 juveniles greater than 60 mm. Distributions are based on 132 scales samples collected throughout the Prairie Creek watershed.

DISCUSSION

In northern California, coho salmon are listed as threatened and are continuing to experience population declines (Ly et al. 2011). This study contributes to the understanding of factors that influence survival during freshwater residency, a period when juveniles may experience high mortality due to winter flow events (Sandercock 1991) and lack of winter habitat (Solazzi et al. 2000). With the exception of large individuals tagged near the confluence of Prairie Creek (see explanation below), I found that juveniles that were larger in fall were generally more likely to survive the winter. The positive influence of fall size on overwinter survival rates has previously been observed in Prairie Creek (Brakensiek and Hankin 2007) and other watersheds (Quinn and Peterson 1996; Ebersole et al. 2006; Pess et al. 2011). However, all fish that did not migrate before the summer of 2013 would be considered mortalities by my model, meaning estimated survival may be biased low for small individuals due to their higher probability of spending a second year in freshwater (Bell and Duffy 2007).

Juveniles that were tagged lower in the watershed in fall had elevated apparent overwinter survival relative to fish tagged higher in the watershed with the exception of large juveniles tagged near the confluence, which appeared to have very poor survival. However, large fish in other watersheds have been documented migrating to sea earlier than the rest of the cohort (Irvine and Ward 1989; Giannico and Hinch 2007), meaning the low survival of large fish near the confluence may actually reflect a pattern of early emigration by the most mature fish. March 4, 2013 was considered to be the start date of

spring migration since this was the first day that a fish was detected at the antennas since February, and several more individuals were encountered in the days that followed. However, migration could have occurred before this date but been undetected by the antennas. Additional migrants may have been missed on March 8, 2013 and March 9, 2013, days when neither the confluence antennas nor the trap were in operation.

Alternatively, the individuals that experienced poor apparent survival near the confluence may represent fall emigrants, a life history recently documented in other streams. Although only two potential fall migrants were encountered in Prairie Creek (fish that were last encountered at the confluence antennas in fall and were swimming in a downstream direction), more may have emigrated when high flow events rendered the confluence antennas inoperable for a total of 25 days in November in December. In nearby Freshwater Creek, Hauer (2013) reported that up to 27% of juvenile coho salmon emigrated from the stream in fall and overwintered in a tidally influenced marsh. In East Twin and West Twin Rivers, Washington, Roni et al. (2012) observed that more than 50% of juveniles migrated to sea in fall, with a consistent peak of downstream movement in early November. In both of these studies, juveniles that were lower in the watershed had a higher probability of migrating in fall. Juveniles migrating from Prairie Creek in fall might overwinter in the Redwood Creek estuary and its tributaries, although the amount of habitat in this area has been greatly reduced from its historical state by an Army Corps of Engineers flood control project. Since the completion of these flood levees in 1968, 50 percent of the estuary has filled with ocean derived sediments or

become isolated from the embayment (Janda et al. 1975; Ricks 1995). However, coho salmon juveniles have recently been documented in Strawberry Creek, a tributary of the south slough of the Redwood Creek estuary, indicating this area still has some viable rearing habitat. Since no spawning is thought to occur in Strawberry Creek due to degraded habitat conditions, these juveniles likely represent non-natal migrants (Redwood National Park 2014). The maximum depth measurement of habitat units had no effect on apparent overwinter survival. This is consistent with the results of Quinn and Peterson (1996), who found that overwinter survival in Big Beef Creek was not influenced by residual pool depth of the habitat unit. Volume of large woody debris in the habitat unit also had no impact on overwinter survival, although this may be a reflection of the limitations of the sampling methodology. Future habitat surveys in Prairie Creek may be improved by utilizing a more precise method of quantifying large woody debris or by recording the amount of large wood debris in the bankfull channel rather than amount at summer base flow, which may not be an accurate reflection of available cover during winter conditions. Alternatively, characteristics of a juvenile's summer habitat unit may be a poor predictor of survival because juveniles in Prairie Creek are unlikely to remain in the same habitat unit during winter; Bell et al. (2001) found that juveniles in upper Prairie Creek had low habitat unit fidelity over winter - a mean of 16% in both years surveyed. In this case, aggregating large woody debris counts at a larger spatial scale (for instance, within 500 m of the tagging location) may be a better measure of how much cover is available to juveniles.

The apparent overwinter survival rate for juvenile coho salmon in Prairie Creek was estimated at 39.4% (SE = 4.1%), and is close to the survival rate reported by Brakensiek and Hankin (2007) for the winter of 1999-2000 (45.5% survival). This estimate is well within the broad range of overwinter survival rates (5 - 74%) published from other studies from throughout the coho salmon range (Bustard and Narver 1975; Quinn and Peterson 1996; Solazzi et al. 2000; Ebersole et al. 2006; Pess et al. 2011; Roni et al. 2012; Hauer 2013). Some caution should be used when interpreting the estimates produced by my overwinter survival analysis since I was limited to tagging juveniles 60 mm FL or larger. Approximately two thirds of the fish I encountered in August were smaller than 60 mm FL, meaning results reported here are only applicable to the largest individuals, which likely had higher survival than the rest of the population.

The model averaged overwinter survival estimates for the August and September tagging groups were 41.1% and 37.6%, respectively, indicating PIT tag mortality was 8.5% . Brakensiek and Hankin (2007) estimated the difference between their October and November tagging groups to be much higher (33%), although this may be partially attributed to the fact they tagged juveniles as small as 55 mm compared to 60 mm in this study. Overwinter tag loss rate in this study was relatively high (13.3%), however, this estimate was derived from a small sample size (30 fish captured at the rotary screw trap), and so it should be interpreted with this limitation in mind. Although most PIT tag studies of juvenile salmonids have reported a tag shed rate of less than 5% (Ombredane et al. 1998; Bell et al. 2001; Gries and Letcher 2002; Brakensiek and Hankin 2007; Sloat et

al. 2011), Acolas et al. (2007) found up to 20% of juvenile brown trout between 57 and 63 mm rejected their PIT tag one month after implantation, and smaller fish were more likely to lose their tag than larger fish. Since juveniles that shed their tag were not detected at the antennas, they were considered to be mortalities by my model. All juveniles that did not migrate to the ocean in the spring of 2013 were also considered mortalities, including one fish that was encountered the following fall. When adjusted for this known two year old resident, PIT tag mortality, and PIT tag loss, apparent overwinter survival rate increases to 48.0%.

Although a previous study reported a pulse of downstream movement by juvenile coho salmon from upper Prairie Creek in November (Brakensiek and Hankin 2007), I did not observe any evidence of fall redistribution. However, this may be due to the fact that the fyke trap used by Brakensiek and Hankin (2007) to monitor fall migrants was much farther upstream than my upper antennas (approximately 7.3 km farther from the confluence). Fall redistribution may be more common in this upstream region, which would explain the lack of overwinter encounters at the upstream antennas. Alternatively, downstream movement in fall may have occurred, but been missed by the upper antennas during high flow events. In order to assess this possibility, a capture efficiency rate for the upper antennas was calculated using the 66 individuals encountered during spring migration. By considering the two antenna loops to be separate encounter occasions, the probability of being detected by at least one antenna in spring was estimated to be 92.6%. This figure is significantly higher than the efficiency estimate produced by the full

overwinter survival model for fish tagged above the upstream antennas (67.9%), indicating a possible violation of the survival model's assumption that no fish migrated from upper Prairie Creek prior to March. However, the treatment of the antenna loops as separate occasions relies on the assumption that they are independent encounters, which may not be the case. Although the antenna loops collected data separately, they still transmitted data to the same readers system and received power from the same battery source, meaning if one loop was not functional the other was most likely not operating either. Nevertheless, the disparity between the efficiency estimations indicates the need for more research into how juveniles in Prairie Creek redistribute during and after peak flow events.

The proportion of two year old residents in the Prairie Creek watershed was estimated to be 1.4% in the fall of 2012. This estimate is slightly lower than the range reported by Ransom (2007), who found that the proportion of age 1+ individuals from the 2000-2002 cohorts varied from 1.9% to 29.5% in mainstem Prairie Creek, 3.6% to 15.3% in Streelaw Creek, and 1.6% to 8.9% in Boyes Creek. In his study of these streams and three others in northern California, Ransom observed that the number of juveniles residing in freshwater for a second year did not appear to be related to initial class year strength (as measured by density) or mean size of juveniles in that cohort. The highest summer proportion of 1+ individuals was observed after a winter with very low stream flow, suggesting milder conditions allow a greater number of small individuals (future two-year freshwater residents) to survive the winter. High discharge rates during the

spring preceding my sampling (Figure 9) may have displaced smaller individuals downstream, ultimately leading to a reduced proportion of two-year residents during the fall I was sampling.

Specific growth rate over winter (0.35% in weight/day) was within the range of growth rates reported by Justice (2007) for another northern California stream, East Fork Mill Creek (0.35% to 0.45% in weight/day) and the Giannico and Hinch (2003) for artificial side channels in the Cheakamus and Mamquam Rivers (0.23 to 0.66% in weight/day). Mean overwinter growth rate for Prairie Creek was higher than the rate observed by Bratty (1999) in Lemieux and Mann Creeks, British Columbia, (0.08% in weight/day) but lower than the rate reported by Ebersole et al. (2006) in West Fork Smith River, Oregon (0.58% in weight/day). A linear regression of the relationship between size in fall and overwinter growth revealed that juveniles that were smaller at the time of tagging experienced the highest growth rates. This trend is consistent with the von Bertalanffy growth function, which assumes growth rate slows as a fish becomes larger. The tendency for smaller juvenile coho salmon to experience higher growth rates was previously noted by Ransom (2007) in Boyes, Streeflow, and Prairie Creek and Hauer (2013) and Roni et al. (2012) in other watersheds. Contrary to studies in other areas (Swales et al. 1988; Quinn and Peterson 1996; Ebersole et al. 2006), I did not find that location in the watershed influenced growth rate, meaning juveniles tagged near the headwaters and juveniles tagged near the confluence likely experienced similar growth. Alternatively, distance from confluence alone may not accurately describe the complex

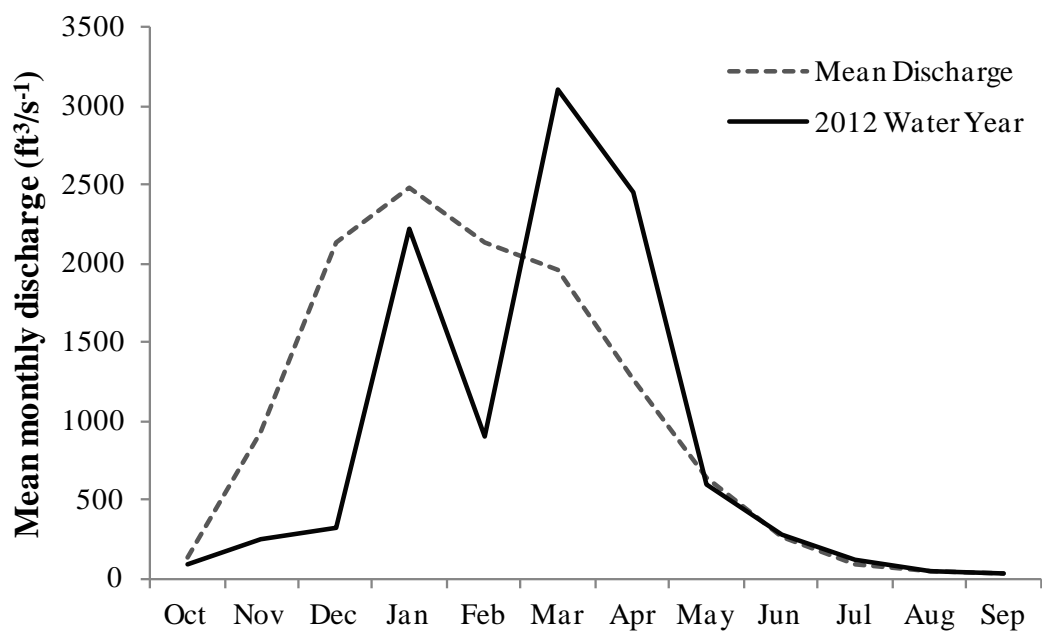


Figure 9. Mean monthly discharge at the Redwood Creek USGS stream gage near Orick, California (2012). Mean discharge line represents average monthly discharge rates for water years 1911 – 2012.

relationship between fall location and growth rate, especially if juveniles did not remain in their original tagging location over winter.

This study demonstrates the advantages of PIT tags, which allowed for the examination of how size and habitat characteristics affect survival and growth of juvenile coho salmon. However, the caveats of this technology, including PIT tag induced mortality and tag loss, must be considered since the accuracy of a survival model depends on individuals surviving the tagging process and retaining their tags throughout the study. To reduce loss of PIT tags, I recommended making the smallest incision necessary to implant the tag and incorporating the use of a veterinary tissue adhesive to close incisions. I also suggest considering alternatives to pass through antennas when examining fall redistribution, especially in streams that are prone to high flow events. Utilizing an antenna design that is less susceptible to storm damage or sampling in areas where juveniles may potentially be migrating may help illuminate overwinter movement patterns in watersheds where pass through antennas are difficult to maintain. For example, in lower Prairie Creek, a seine or a handheld PIT tag reader with a wand could be used to search for migrants from the upper part of the watershed.

It is clear from this study that fisheries managers must consider migration patterns and alternative life histories when conducting population estimates. Studies that estimate freshwater survival of juvenile coho salmon often do not account for individuals that migrate to sea prior to spring migrant trapping (Roni et al. 2012). However, my results indicate the practice of treating these individuals as mortalities may lead to biased

overwinter survival rates, especially for larger individuals that may be more prone to early migration. More research is essential to determine the fate of these potential early migrants and how they may be utilizing downstream habitat.

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