OVERWINTER SURVIVAL AND MOVEMENT OF JUVENILE COHO SALMON

(*ONCORHYNCHUS KISUTCH*) IN RELATION TO LARGE WOODY DEBRIS AND

LOW-VELOCITY HABITAT IN NORTHERN CALIFORNIA STREAMS

By

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ABSTRACT

OVERWINTER SURVIVAL AND MOVEMENT OF JUVENILE COHO SALMON,
ONCORHYNCHUS KISUTCH, IN RELATION TO LARGE WOODY DEBRIS AND
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John D. Deibner-Hanson

Some studies suggest that Coho Salmon populations are limited by overwinter survival as a result of insufficient winter habitat. While many small-scale projects aim to define reach and basin-level habitat requirements for Coho Salmon, large-scale studies that assess multiple independent populations remain few. For my research, I quantified large woody debris (LWD) by volume and low-velocity rearing habitat (LVH) as percent area in three coastal watersheds of similar size in northern California to untangle the relationships between Coho Salmon overwinter survival, emigration timing and specific winter habitats. I used mark-recapture techniques with PIT tags to formulate Cormack-Jolly-Seber models for each of three years (2013-2015) to (1) estimate apparent overwinter survival of juvenile Coho Salmon populations, (2) determine to what extent outmigration timing varies among basins, and (3) evaluate the relationships between reach-specific survival, movement and winter habitat. LWD volume ranged from 47.8 to 109.9 cubic meters per kilometer among stream reaches while LVH area spanned from 9.3% to 23.6% of total stream area per reach. Effects of LWD on apparent overwinter survival and early emigration were absent during all three years of the study. Effects of LVH were not observed during 2013 and 2014. In 2015, LVH correlated positively with

apparent overwinter survival and negatively with emigration. Larger Coho Salmon had higher apparent overwinter survival rates than small fish, whereas smaller fish had greater emigrations rates before spring. Mean apparent overwinter survival varied by basin from 0.052 to 0.567 but basins maintained consistency across years. Early emigration rates ranged even further by basin (0.023-0.773). Variation in both apparent overwinter survival and early emigration was much greater among basins than within basins. A lot remains to be learned regarding how habitat affects the migratory behavior of Coho Salmon in California and these results suggest the effects may vary significantly by stream. The drastic life history differences observed in neighboring Coho Salmon populations demonstrate the plasticity in a species once thought to be relatively inflexible. Moving forward, incorporating multi-basin approaches should be considered when evaluating freshwater survival and movement to inform large-scale restoration and conservation.

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INTRODUCTION

In recent decades, populations of Coho salmon (*Oncorhynchus kisutch*) throughout California have declined, and although no single mechanism is responsible, loss of freshwater habitat is often considered the largest culprit (Brown et al. 1994). This is not surprising, as Coho Salmon rearing habitat consists of low-gradient coastal landscapes, which often overlap with human settlement and development (Burnett et al. 2007). The need for remediation from combined effects of habitat degradation, hydropower, harvest and hatcheries (Lichatowich 1999) has led to multiple evolutionarily significant units (ESUs) of Coho Salmon being listed as endangered or threatened under the Federal and California Endangered Species Acts (ESAs). Multiple recovery plans have been developed for these Coho Salmon ESUs, which primarily occur at the southern extent of their range, and they primarily focus on prioritizing restoration implementation across regional landscapes (CDFW 2004; ODFW 2007; NMFS 2012, 2014, 2016). Unfortunately, as millions of dollars are spent annually to restore habitat for Coho Salmon populations throughout the southern end of their distribution, minimal funds are dedicated to monitoring project success. Moreover, the limited attempts to evaluate restoration effectiveness often fail to observe the effects on multiple populations, focusing instead on individual projects in a single stream or reach (Roni et al. 2018). Sampling within populations from multiple basins offers important advantages over single-basin sampling such as extending the spatial level of inference. Monitoring Coho Salmon populations in multiple basins will help us to understand how restoration

activities will affect multiple populations, which will provide a more direct link to species recovery goals.

Northern California represents the southern tip of Coho Salmon range, where they are currently threatened in the Southern Oregon Northern California Coast (SONCC) ESU and endangered in the Central California Coast (CCC) ESU. However, despite the species listings and collaborative efforts to restore salmon populations, no evidence of regional biological responses to widespread restoration programs is available in the literature. Restoration effectiveness monitoring in other states has included numerous studies on relationships between individual restoration projects and increases in local fish abundance (e.g., Fausch and Northcote 1992; Cederholm et al. 1997; Roni and Quinn 2001; Pess et al. 2012), but fewer studies compare population-level responses such as overwinter survival or growth to specific habitat attributes (Roni et al. 2014, 2018). Research on watersheds in coastal Oregon present correlative and experimental evidence that overwinter survival of Coho Salmon populations is limited by winter habitat including large woody debris (Johnson et al. 2005), slow-water area (Nickelson et al. 1992; Solazzi et al. 2000), and canopy cover (Ebersole et al. 2006). Nevertheless, attempts to identify key habitat features which affect juvenile Coho Salmon survival or early emigration in central and northern California remain few.

Coho Salmon in northern California typically remain in fresh water for a year or more after emergence. Many suggest that the availability of sufficient winter habitat during their prolonged freshwater residence is the most limiting factor for Coho Salmon (Nickelson et al. 1992, Solazzi et al. 2000; Gallagher et al. 2012). If true, overwinter

survival rates should be useful for measuring population responses to the restoration of various stream habitats. More specifically, understanding the effects of various winter habitats on overwinter survival in populations would contribute greatly to achieving species recovery goals in California and elsewhere.

Positive relationships between certain stream habitat attributes and local salmonid abundance are demonstrated in several small-scale studies in the literature. For example, one major focus in salmonid habitat research involves the role played by large woody debris (LWD). Fausch and Northcote (1992) show that during high flow periods, submerged LWD caused water to scour benthic substrates and stream banks increasing pool depth and channel width where aggregations of mixed-size debris formed, providing space and cover for a greater biomass of juvenile Coho Salmon. Other studies report positive correlations between abundance of juvenile Coho Salmon and LWD density in number of pieces (Roni and Quinn 2001; Sharma and Hilborn 2001) or wood volume (Fausch and Northcote 1992; Johnson et al. 2005) with wood loadings ranging from less than 100 pieces·km^{-1} or 200 m^3·km^{-1} in simple streams to greater than 400 pieces·km^{-1} or 600 m^3·km^{-1} in complex streams. Mellina and Hinch (2009) include data from 37 studies in a meta-analysis to evaluate the effects of streamside clear-cut logging and in-stream wood removal (termed, "stream cleaning") on species-specific salmonid densities. Their review reveals a common finding that LWD removal adversely affects densities of juvenile Coho Salmon and other salmonids. Velocity refuge provided by LWD in pools is likely important during winter, particularly for its role in providing refugia from high flow events during winter.

Coho Salmon are also found to favor low-velocity habitats often associated with pools, avoiding habitat types where average velocity exceeds 20 cm/s (Bisson et al. 1988). In the Pacific Northwest, enormous efforts are made each year to inventory freshwater habitat in the summer, but streams frequently lack winter habitat data due to unstable stream habitat and survey conditions. Nevertheless, a variety of slow water habitat types are associated with higher growth and abundance in Coho Salmon during the winter (Bustard and Narver 1975). Nickelson et al. (1992) demonstrates a strong preference of juveniles for backwaters, alcoves, dammed pools, floodplain ponds and side-channel ponds. This is supported through winter periods by Rosenfeld et al. (2008) suggesting these habitats may limit juvenile abundance in coastal streams, which often lack such pools and are prone to periods of heavy discharge. In Prairie Creek, increased fidelity and apparent overwinter survival were observed in juveniles occupying off-channel habitat units compared to main channel units (Bell et al. 2001).

While many small-scale projects aim to define reach and basin-level habitat requirements for Coho Salmon, large-scale studies that sample from multiple populations remain few. One example by Sharma and Hilborn (2001) compared Coho Salmon abundance and habitat in parts of 14 small streams in Washington showing that pool densities ($m^2 \cdot km^{-1}$) correlate more with abundance than numerous other predictor variables such as LWD, road density and drainage area. Their multi-basin approach was seen as valuable for planning restoration and predicting associated juvenile salmon increases across western Washington. More recently, Gallagher et al. (2012) evaluated basin-wide population monitoring data over an eleven-year span (2000-2011) in two

coastal streams in Northern California and found a negative correlation between winter survival and mean winter flows, supporting the existing evidence (Nickelson et al. 1992) that high flows can limit juvenile survival. Multi-basin studies such as this, although rare, still demonstrate value in prioritizing a regional approach to stream monitoring and restoration.

Large-scale projects unfortunately also come with their own difficulties as multi-basin monitoring is costly, time consuming, and must account for any environmental and biological variability in populations across space. For Coho Salmon, efforts to establish life-stage specific habitat requirements are challenged by spatial and temporal life history variations expressed by juveniles. It was once assumed that Coho Salmon escapement was simply a product of the outmigrant spring abundance of smolts and their smolt-to-adult (i.e., marine) survival rate (Shapovalov and Taft 1954). Until recently, life histories of Coho Salmon throughout their southern range were previously expected to entail freshwater occupancy for one or two years before a seaward migration followed in the spring (Brakensiek and Hankin 2007; Ricker and Anderson 2011). This life history provided a relatively simple framework for monitoring overwinter survival rates with short fish marking periods in the fall followed by short recapture periods in the spring (e.g., Solazzi et al. 2000). However, population monitoring and individual-based mark-recapture studies redefined the Coho Salmon life cycle model by revealing previously unidentified life histories strategies. In California, the regional expression of a unified life history in Coho Salmon was challenged by Rebenack et al. (2015) who observed early juvenile emigration from their natal stream during fall freshets in Humboldt Bay,

California. Similar life history diversity has also been documented in Oregon (Jones et al. 2014), Washington (Roni et al. 2012) and British Columbia (Scrivener et al. 1998) and likely affects current Coho Salmon survival estimates vital to species recovery efforts.

Estimation of overwinter survival based on comparing abundance estimates between fall and spring (e.g., Solazzi et al. 2000) was imperfect, partly because sampling methodology used for each estimate differed (i.e., fin clipping mark-recapture methods via seining in fall versus downstream migrant trapping in spring). The use of individual marks (e.g., passive integrated transponder (PIT) tags) allowed researchers to estimate winter survival by marking juvenile Coho Salmon before winter and recapturing them during outmigration, reducing potential bias (e.g., Quinn and Peterson 1996; Brakensiek and Hankin 2007; Ebersole et al. 2009). Although many environmental factors may affect the ability to recapture tagged fish (e.g., variable discharge, PIT tag antenna malfunctions), a variety of mark-recapture models are available which account for imperfect and variable detection probability. Strategically placed PIT tag arrays have helped mark-recapture models more accurately estimate overwinter survival of Coho Salmon by accounting for seasonal movement and early emigration from study areas (Roni et al. 2012; Jones et al. 2014; Rebenack et al. 2015). More accurate survival estimates are crucial to develop habitat suitability models that enable managers to prioritize restoration strategies (Beechie et al. 1994).

Evidence to date demonstrates that higher habitat complexity in streams has a positive influence on local salmonid abundance (McMahon and Hartman 1989, Cederholm et al. 1997, Roni and Quinn 2001, Rosenfeld et al. 2008, and several others),

but the benefits winter habitat provides for salmonid survival on a landscape scale are less clear (Solazzi at al. 2000; Johnson et al. 2005). In this project, I evaluated how survival and emigration relate to overwinter habitat features in three basins of northern California. The purpose of this study was to inform future stream restoration practices by (1) evaluating relationships between juvenile Coho Salmon overwinter survival and early emigration with in-stream LWD volume and low-velocity rearing area and (2) comparing overwinter survival and outmigration timing among basins and reaches across a northern California landscape.

STUDY AREA

The three streams included in the study area are Freshwater, Prairie and Mill

Creeks each located in small coastal basins in the SONCC evolutionary significant unit

(ESU) for Coho Salmon in Del Norte and Humboldt Counties, California (Figure 1).

Each study basin supports Coho Salmon, fall Chinook Salmon *O. tshawytscha*, resident

and anadromous rainbow trout (steelhead) *O. mykiss* and resident and anadromous coastal

cutthroat trout *O. clarkii clarkii*. Other fish species present within each basin include

threespine stickleback *Gasterosteus aculeatus*, prickly sculpin *Cottus asper*, coastrange

sculpin *C. aleuticus*, Sacramento sucker *Catostomus occidentalis*, Pacific lamprey

Entosphenus tridentatus and Western Brook Lamprey *Lampetra richardsoni*. Each of the

watersheds are vegetated in coniferous forest dominated by coast redwood *Sequoia*

sempervirens and Douglas-fir *Pseudotsuga menziesii*. Vegetative composition of riparian

forests also typically includes red alder *Alnus rubra* and big-leaf maple *Acer*

macrophyllum.

Mill, Prairie and Freshwater creeks all experience a similar coastal climate in

which total annual precipitation falls almost entirely as rain from large Pacific storm

systems between October and March (WRCC 2016). Summer fog frequently blankets the

coastal zones, contributing a small portion of the annual precipitation which helps to

moderate diurnal temperature shifts throughout the hottest months (Cannata et al. 2006).

To estimate overwinter survival and early emigration probability, each stream was

subdivided into two or three reaches depending on stream size and the number of fish

monitoring antennas available (see below). Reaches were selected based on existing antenna locations and contained a range of physical characteristics such as gradient, size, habitat quality and historical differences in land use and ownership. Reaches ranged from three to eight kilometers in length.

Mill Creek

Mill Creek is a fourth order tributary to the Smith River, the largest undammed river in California. Mill Creek sits at the northern end of the coast redwood (*Sequoia sempervirens*) range near Crescent City in Del Norte County, California. In this study, the Mill Creek basin (99.7 km^2) was partitioned into three anadromous reaches including the lower main stem Mill Creek (MSM; 9.3 km), and its two main tributaries, East Fork Mill Creek (EFM; 6.5 km) and West Branch Mill Creek (WBM; 9.2 km) (Figure 2). The East Fork, which drains a watershed of 37 km², and West Branch, which drains a 24 km² watershed, join to form the Mill Creek main stem. The main stem flows through preserved old-growth redwood forest within Jedediah Smith Redwoods State Park, which was established in 1939. Most of the upper watershed, including the entire East Fork and its confluence with West Branch, was managed for industrial timber production starting from the early 1850s. Most of the area was logged at least once since 1920 (Madej et al. 1986). The Mill Creek Property, which includes the East Fork and West Branch, was purchased from Stimson Lumber by California State Parks in June 2002. This 10,000-hectare acquisition put Mill Creek entirely within public ownership. The land is managed

by California State Parks to restore late successional forest conditions and to maintain

and enhance habitat for state- and federally-listed species (Porter et al. 2007).
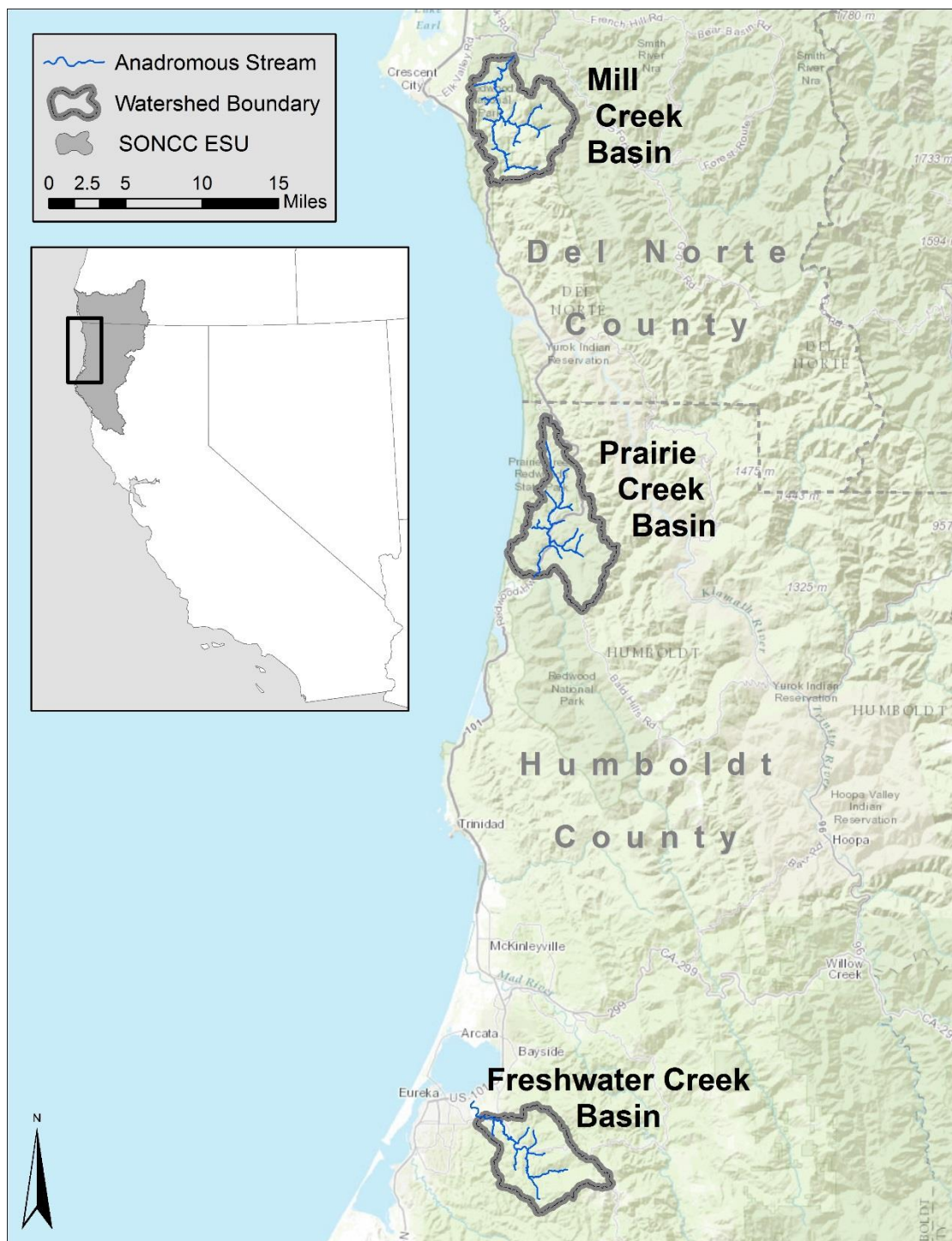
Figure 1. Map of the study area, including Mill, Prairie and Freshwater Creeks, tributaries to
Smith River, Redwood Creek and Humboldt Bay, respectively (California, U.S.A.).
The Coho Salmon Southern Oregon Northern California Coast (SONCC)
Evolutionary Significant Unit (ESU) boundary is displayed on the inset.
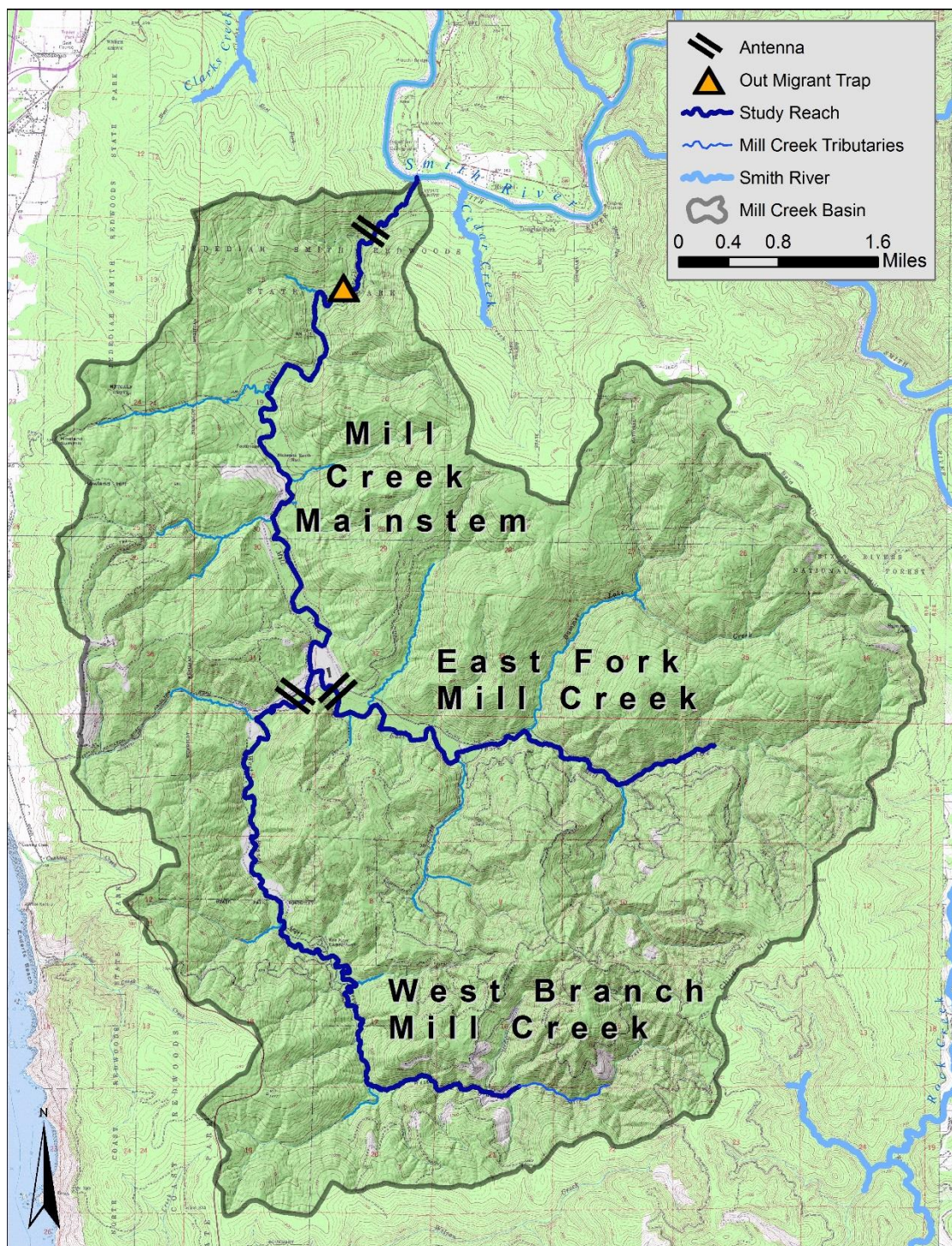
Figure 2. Mill Creek watershed, tributary to the Smith River, Del Norte County, CA (U.S.A.). Locations of PIT tag antenna arrays and the migrant trapping station are shown among the three stream reaches in Mill Creek.

Prairie Creek

Prairie Creek is a fourth-order tributary that enters Redwood Creek approximately 5 km upstream from its outlet to the Pacific Ocean near the town of Orick, California. The creek drains a 103 km² watershed, 98% of which is publicly owned and managed by Redwood National and State Parks (Cannata et al. 2006). Nearly half of the watershed area lacks history of logging or major development as the upper basin flows through an undisturbed forest of late seral coast redwood, making Prairie Creek the most pristine of the study basins (Janda et al. 1975). Although the lower basin and tributaries downstream from May Creek experienced heavy timber harvest throughout the 1960s and 1970s, its subsequent acquisition in 1978 by the National Park Service ensured future protection. The forest is now dominated by second growth coast redwood and Douglas-fir. (Cannata et al. 2006). For this study, the two Prairie Creek reaches were divided into Upper Prairie Creek (UPC; 13.7 km) and Lower Prairie Creek (LPC; 4.7 km) by PIT tag antennas just downstream from May Creek, a reach break that coincides with the two land use histories (Figure 3).
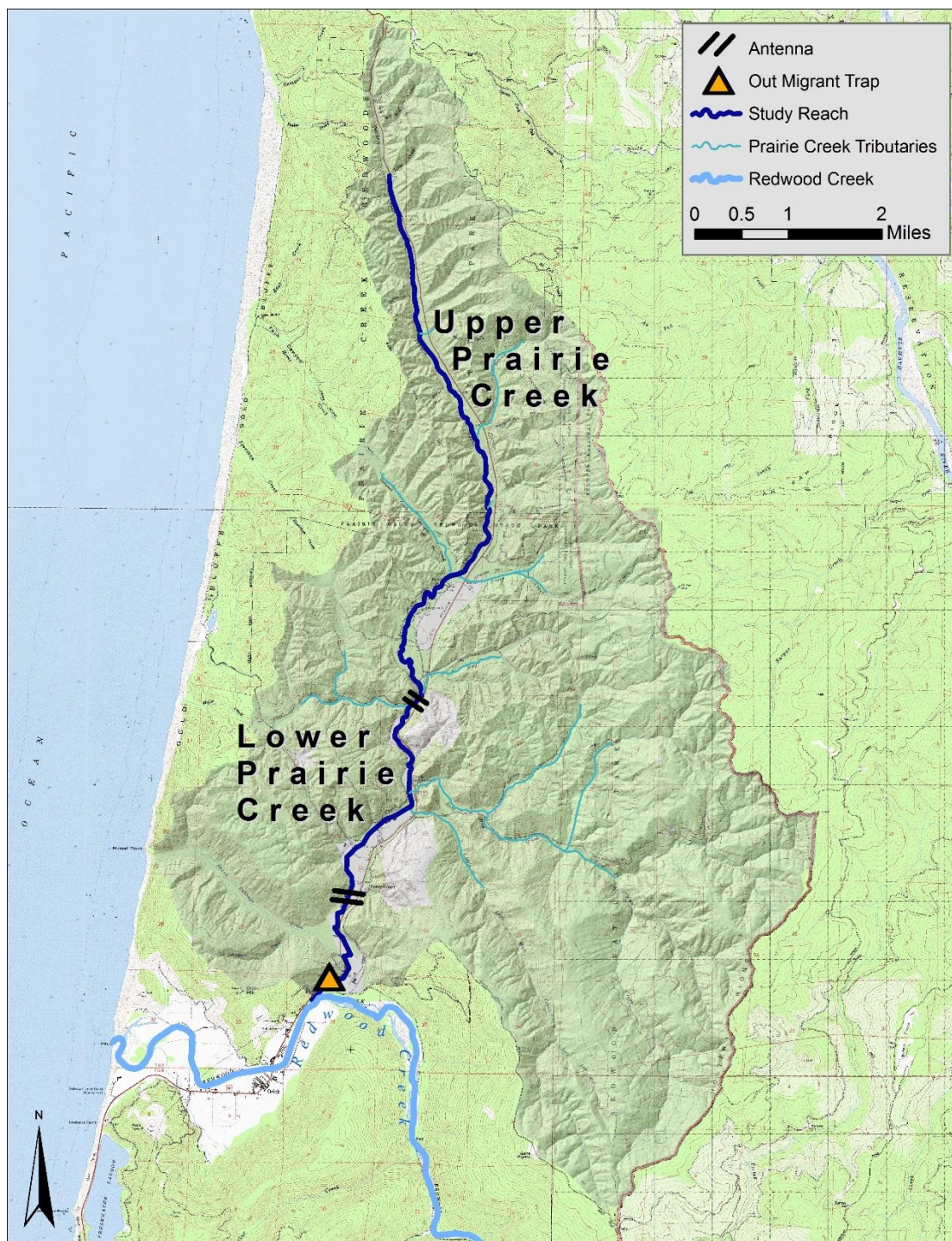
Figure 3. Prairie Creek watershed, tributary to Redwood Creek, Humboldt County, CA (U.S.A.). Locations of PIT tag antenna arrays and the migrant trapping station are shown throughout the basin.

Freshwater Creek

Freshwater Creek drains a 92.3 km^2 watershed into Humboldt Bay and the Pacific Ocean. The mainstem is approximately 23 km long, providing 14.5 km of habitat for anadromous fishes. Five tributaries each provide an additional two to four km of anadromous fish habitat (Mull and Wilzbach, 2007). Most of the watershed is managed for timber production, predominantly under the ownership of the Humboldt Redwood Company. The remainder of Freshwater Creek is predominantly under private ownership for agricultural or residential use. The lower six kilometers of the stream include estuarine Freshwater Slough. Lands in the lower watershed are primarily under private ownership and confined by levees for cattle grazing. A permanent weir currently operated by Humboldt State University (HSU), in collaboration with California Department of Fish and Wildlife (CDFW), is located on the mainstem along the stream-estuary ecotone to monitor migration of juvenile and adult salmonids (Figure 4). The weir serves as the lower boundary for the Freshwater Creek component of this study. The lowest of three reaches in Freshwater Creek is the lower main stem (LFW; 4.1 km), which extends from Cloney Gulch downstream to the weir. The second reach, upper main stem Freshwater (UFW; 5.8 km), runs from Cloney to the upper anadromous boundary of Freshwater. Two smaller Freshwater Creek tributaries, Cloney Gulch and South Fork Freshwater, compose the third reach and from here forward will be called Freshwater tributaries (FWT; 3.0 total km).
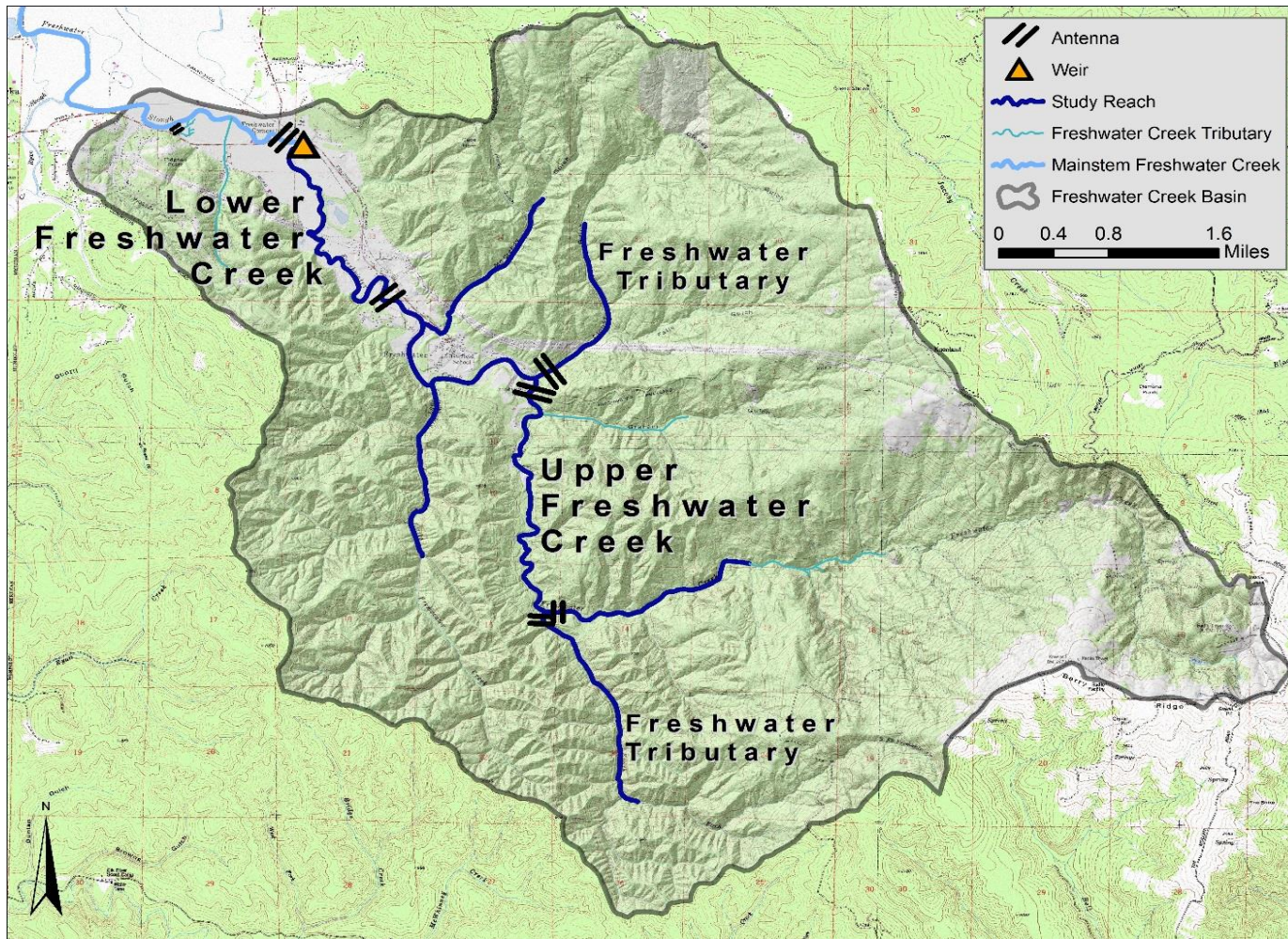
Figure 4. Freshwater Creek watershed, tributary to Humboldt Bay, Humboldt County, CA (U.S.A.). Locations of PIT tag antenna arrays and the migrant trap are indicated. The three stream reaches are labeled in text. The Freshwater tributaries reach includes both Cloney Gulch and South Fork Freshwater.

FIELD METHODS

Habitat data was collected from the three study basins during summer and winter

of 2014 while three years (2013 – 2015) of fish monitoring data was collected by CDFW

and HSU field crews in each basin including fall tagging and spring outmigrant trapping.

Each season of fish monitoring and corresponding model is referred to by the year in

which fish were tagged during fall (e.g., 2013 refers to the cohort monitored from

October 1, 2013 through September 30, 2014). The habitat data included classifications

of LWD size, volume, and abundance and low velocity rearing habitat area. The fish

monitoring data included data collected when juvenile Coho Salmon were tagged during

the fall, detected by passive integrated transponder tag antennas during the winter and

spring, and captured in outmigrant traps during the spring. The data collected from these

efforts was adapted to form basin-specific capture histories needed for mark-recapture

models to estimate overwinter survival and early emigration of Coho Salmon from natal

rearing areas.

Habitat Data Collection

Large Woody Debris

Following the Columbia Habitat Monitoring Program (CHaMP) protocol

(Bouwes et al. 2013), I counted and classified LWD pieces that existed inside the

bankfull channel (i.e., within bankfull width and beneath bankfull height). Dimensions of

the bankfull channel were visually assessed in the field using indicators including scour

lines, vegetation limits, changes in bank slope, changes between bed and bank materials, and presence of flood-deposited silt (USFS 1995). Bankfull indicators are present year-round, which allowed me to complete LWD surveys during summer months when instream pieces are most visible and accessible. LWD data was collected once over the course of the three-year study and took place during summer 2014 between the first and second years of biological data collection. To compare one season of reach-specific LWD data across each cohort of juvenile Coho Salmon, I assumed that annual LWD gains and losses to each reach were proportional across reaches for the study duration.

As described in the CHaMP protocol, I surveyed upstream classifying all pieces of wood ≥ 1.0 m long × 0.1 m diameter within bankfull into one of four length classes and one of four diameter classes to estimate wood volume per stream kilometer (Table 1). Due to high variability in size and low frequency of extra-large LWD pieces, all pieces greater than 15 m long or 60 cm in diameter were individually measured for accuracy (nearest 0.1 m). All LWD located beneath bankfull height was tallied regardless of its surrounding habitat type.

There was one specific way my LWD field methods diverged from the CHaMP protocol. CHaMP specifies that LWD pieces are classified if they are in (1) the bankfull channel (i.e. in the channel beneath bankfull elevation) or (2) the bankfull prism (i.e., the area directly above bankfull elevation). Instead, I only counted pieces which existed within the bankfull channel that have expected intervals of inundation every few years. For LWD existing partially beneath bankfull height, only the portion within the bankfull channel was measured and tallied. Pieces protruding from the stream bank or benthos

Table 1. Length-diameter classification bins used for large woody debris.

Size Class (length-diameter)	Length (m)	Diameter (cm)
Small-Small	1 to 3 m	10 to 15 cm
Small-Medium	1 to 3 m	15 to 30 cm
Small-Big	1 to 3 m	30 to 60 cm
Medium-Small	3 to 6 m	10 to 15 cm
Medium-Medium	3 to 6 m	15 to 30 cm
Medium-Big	3 to 6 m	30 to 60 cm
Big-Small	6 to 15 m	10 to 15 cm
Big-Medium	6 to 15 m	15 to 30 cm
Big-Big	6 to 15 m	30 to 60 cm
XL (Measured[a])	>15m	> 60 cm

a: XL Pieces measuring > 15 m long *or* > 60 cm in diameter were individually measured to exact length and diameter to achieve precise volumes

were counted only if the exposed volume satisfied measurement criteria. The entire reach

lengths for all reaches was surveyed for LWD without gaps, except for approximately 4

km in main stem Freshwater Creek due to restricted access.

LWD pieces were counted in individual stream segments comprised of three

pools and any accompanying riffles or runs within the three-pool sequence. Segment

totals were added to calculate reach totals for each LWD size class. LWD volume per

reach (V_{reach}) was calculated as

$$V_{reach(i)} = N_{reach(i)}M_i$$

where N_{reach} is the total number of pieces per reach in each size class (i) and M_i is the

corresponding geometric mean LWD volume for each size class bin based on

measurements of more than 75,000 pieces of LWD collected by the U.S. Forest Service

in Oregon and Washington (Rentmeester, 2014; Appendix A). Reach-specific volume

estimates and LWD counts were expressed in terms of density as pieces•km^{-1} and

m^3•km^{-1}, respectively, to account for varying stream lengths within the study area.

Low-Velocity Winter Rearing Habitat

I estimated the area of low-velocity habitat (LVH) available for juvenile Coho

Salmon within each reach during periods of the most typical winter flows between

November 2014 and March 2015. Streams were divided into individual habitat units

separated by distinct hydraulic breaks to assess each unit by area (m^2) and type. To

ensure channel unit data was representative of winter habitat during typical winter flows

and standardized across streams, all surveys were completed between the 25th and 50th

percentile (2nd quartile) median flow statistics for November through April according to

Unites States Geological Survey (USGS) streamflow records (USGS 2014). The 2nd quartile flows were chosen as the survey range to capture the most common flow range during winter months and ensure a relatively stable stage height for eight-hour survey days. I monitored flows in each stream using the nearest USGS gauging station as a proxy to determine sufficiency of flow conditions prior to surveying, since historical flow records for small-scale watersheds are typically unavailable.

Winter habitat data was collected once throughout each stream to compare with three years of biological data forcing the underlying assumption that the relationship between LVH area and stream discharge was consistent throughout the course of the study. For example, if a stream reach flowing at 100 cubic meters per second (cms) is observed with 25% LVH, the reach would be expected to contain 25% LVH throughout the study duration on any day where flows are 100 cms. However, because I did not observe flows at any other quartile, I cannot make extrapolations based on my observations about what LVH might look like in any other flow conditions.

A modified classification system developed from the Columbia Habitat Monitoring Program (CHaMP 2013) was used to classify habitat units. I worked upstream from the start of each reach, classifying units as either fast-water (FW) or slow-water (SW). FW units were defined as those with over 50% of the unit area characterized by turbulent or swift flows identified by white-caps, ripples and noise. SW units had less than 50% area with turbulent or swift water, mostly characterized by low-velocities and laminar flows.

Due to variability in water velocities within some individual units, these units were visually broken down into within-unit SW and FW proportions of total the unit area (e.g., a SW unit may have a proportion of FW area estimated visually at 25%). Consistency in visual divisions of SW and FW was verified each day by taking cross-sectional measurements of water velocity in the first few units with a flow meter (Marsh-McBurney Model 2000 Flo-Mate™) at 60% depth from the water surface. Water velocities in units that were visually classified as SW typically traveled at speeds of ≤ 0.1 m•s^{-1} while FW units were always > 0.1 m•s^{-1}.

Estimates for low velocity rearing area (m^2) were generated using the basin visual estimation technique (BVET) developed by Dolloff et al. (1993). Total unit areas were estimated for all SW and FW units and adjusted by within-unit slow or fast proportions if necessary. Every fifth unit of each type, fast or slow, was estimated and subsequently measured. Measured values were used to calculate calibration coefficients of the visual estimates for slow and fast unit types made by each surveyor. Once the SW and FW areas were properly adjusted and calibrated, the areas were compiled by reach to compute reach-specific proportions for use in habitat modeling.

Fish Monitoring

Fish Handling Procedures

All fish handling procedures were approved by the HSU Institutional Animal Care and Use Committee and the National Oceanic and Atmospheric Administration (NOAA) Fisheries Authorizations and Permits for Protected Species (No. 13/14.F.123-

A). Fish tagging was conducted within each basin by its respective field crew each fall before the first freshets, when rearing fish are still associated with their summer rearing habitat. A stratified sample of pools throughout each basin was identified and sampled for juvenile Coho Salmon using seine nets. To minimize effects of added stress and weight on small Coho Salmon, restrictions on minimum taggable fish size were followed for using 12-mm passive integrated transponder (PIT) tags suggested by NOAA, CDFW and Tiffan et al. (2015). Recommendations for minimum fish size using 12-mm PIT tags changed over the course of the study; minimum lengths varied between 60 and 70 mm each year (see Table 4 in the Results section). Given the size restrictions on tagging, Coho Salmon fall size distributions were approximated using a length-frequency probability distribution to emphasize the proportion of the population on which inference could be made (Appendix B). Sizes for the length-frequency distribution were obtained by recording measurements of a random sample of Coho Salmon from each fall sampling unit before tagging. Fish too small to tag were counted, measured if necessary, allowed to recover from handling, and released. Taggable fish were anesthetized by immersion in tricaine methanesulphonate (MS-222), measured for length and weight, and tagged by insertion of a PIT tag through a small incision in the body cavity following the tagging methodology of Prentice (1990) and Rebenack et al. (2015). Tags were inserted by hand through a 1-2 mm ventral incision slightly posterior to the pectoral fins. Tagged individuals were given time to recover from the procedure before their release back into the pool from which they were captured. Using this procedure, Rebenack et al. (2015) found no effect of PIT tagging on survival of Coho Salmon $\geq$ 65 mm.

<u>Passive Integrated Transponder (PIT) Tag Mark-Recapture Techniques</u>

Coho Salmon life cycle monitoring stations have been operated in each study basin for several years by researchers from CDFW and HSU. Monitoring goals are consistent across stations and aim to deliver population estimates useful for status and trend monitoring including adult escapement, juvenile overwinter survival, juvenile outmigrant abundance, and marine survival. I incorporated juvenile Coho Salmon survival and abundance data from Mill, Prairie and Freshwater Creek projects into survival models to investigate habitat-survival relationships. Field staff in each watershed collected mark-recapture data using PIT tag antenna systems and downstream-migrant traps. Fish detections recorded at the traps and antennas were integral to this study, collectively forming capture histories needed for mark-recapture modeling.

PIT tag antenna systems are typically used in fisheries research and monitoring for recording passive detection of tagged fish in space and time (Prentice et al. 1990; Peterson et al. 1994; Horton and Letcher 2008). The antenna arrays in each of the study watersheds were stationary systems which included adjacent pairs of channel-spanning antennas that detected upstream or downstream passage of individually PIT-tagged salmonids. Throughout the study duration, each stream and some large tributaries were bounded by paired PIT tag antennas at the downstream end to track seaward movement from the basins (Figure 2; Figure 3; Figure 4). Two additional antennas were installed prior to the third year of data collection approximately 18 km downstream from the mouth of Mill Creek on two tributaries to the lower Smith River, which became important to the results of this study.

Although PIT tag antennas are widely used and often considered essential tools in some areas of fisheries science, caution must be taken when used in certain applications—especially when estimating abundance or survival. Since PIT tag antenna efficiencies in natural settings are rarely close to 100%, multiple antennas or other capture methods (i.e., downstream migrant trapping) can be used jointly to account for imperfect detection (Zydlewski et al. 2006).

Downstream migrant traps aim to capture stream fish and come in many different styles and sizes depending on stream size and discharge. Small coastal streams in northern California which receive most precipitation as rainfall are limited to migrant trapping during spring and summer months when flow levels are lower and more predictable. Traps in Mill, Prairie and Freshwater Creeks are installed each year in late March and operate through summer until the last of the Coho smolt population has emigrated. Migrant traps generally only capture a small proportion of the passing fish, and this capture efficiency must be estimated to extrapolate the trap catch to a total abundance estimate. This is done by marking a subsample of captured fish and releasing them back upstream for recapture on subsequent days. This 'single trap' design was implemented in each of the study basins and usually served as the last detection point for Coho smolts in each basin.

Estimating survival rates with mark-recapture models is challenging in "open populations", where both mortality and emigration processes occur within the same occasion. When emigration and mortality are confounded, survival is termed 'apparent' and will always be lower than 'true' survival whenever permanent emigration from the

study area is not zero (Kéry and Schaub 2012). In the case of overwintering Coho,

individuals that emigrate before spring are less likely to depend on instream winter

habitat due to the shorter residency period. Therefore, to understand the relationship

between stream habitat and overwinter survival of stream-dwelling Coho Salmon, I used

a second CJS model to estimate the proportion of the population that exhibited early

emigration.

STATISTICAL METHODS

I followed the general Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) arrangement used in Rebenack et al. (2015) to separately estimate "apparent" overwinter survival and early emigration of juvenile Coho Salmon using data obtained from multiple PIT tag antenna arrays continuously operated throughout the year. In this case, survival is termed "apparent" because emigration cannot be separated from mortality (Cooch and White 2011). Although overwinter survival remains 'apparent', the additional analysis of early emigrations models for each year helped inform potential bias in the survival estimates. I modeled survival and emigration during each of three years with individual CJS models (6 total models) with all three study basins incorporated in each model. Three occasions (i.e., capture periods) in each model included one marking occasion in the fall before the first seasonal freshets and two independent recapture occasions situated at or near each stream outlet. The apparent overwinter survival and early emigration models were mathematically identical, differing only by the way data were specified as occasions in each model.

Conceptualizing Overwinter Survival and Emigration Models

As with all modeling approaches, careful examination of the model assumptions is paramount. The standard CJS model is based on the following assumptions (Williams et al. 2002):

1. Tags or marks are not lost or misread;

2. Tags do not affect survival or recapture probability;

3. Initial capture, marking and release at time *t* is instantaneous relative to interval from time *t* to time *t*+1;

4. Each capture and recapture of animals is regarded as an independent random sample from the population;

5. All individuals *i* have equal recapture (p_i) and survival probability (ϕ_i) at or after a given interval, unless accounted for by covariates; and

6. All emigration from the sampling area is permanent.

The assumptions of the CJS model have been well studied and some are more flexible than others. Violations of the first four assumptions may require additional parameters, which can be estimated with an adequate study design. The last three assumptions are more flexible, and violations of these assumptions can be accounted for by including individual (e.g. size), or group (e.g. release group), covariates in the model (Kéry and Schaub 2012).

In all study basins for the apparent overwinter survival model, the first occasion was the initial marking period, the second occasion occurred downstream at a channel spanning PIT tag antenna array and the third occasion occurred at the downstream migrant trap (Figure 2; Figure 3; Figure 4). Apparent overwinter survival estimation did not account for Coho Salmon that emigrated before migrant traps were installed because the migrant traps only operate effectively in spring once winter flows subside. Consequently, 'apparent' overwinter survival in this study may be more accurately

interpreted as the joint probability that individuals stay in the study area through winter and survive to emigrate in spring.

For the early emigration model, the first occasion incorporated the same fall tag group of Coho Salmon used in the survival model. However, since downstream migrant traps were inoperable in winter, recaptures for the early emigration model were based solely on antenna detections (Figure 5). Without a migrant trap operating during fall and winter, two or more independently operated PIT tag antennas near the outlet of each basin would be ideal for use as recapture occasions. Unfortunately, antenna configurations were variable depending on the year and Creek and more than two PIT tag antennas were only deployed near the outlet in Freshwater Creek (all three years). Prairie Creek included two antennas (all three years), though one was located almost 3 km upstream from the antenna at the mouth, which could cause bias if individuals decided to overwinter between the antennas instead of emigrating early. During year three only, additional antennas located downstream of the Mill Creek confluence with the Smith River provided the critical secondary capture points. Without additional antennas operating in or downstream of Mill Creek during years one and two, the early emigration model could only be fulfilled by splitting the lower antenna array into two occasions. This strategy was made possible with each antenna site in the study area set up to detect directionality by including one upstream and one downstream antenna. However, splitting the lower antenna into two occasions may violate the assumption that recapture of animals is an independent random sample from the population (assumption 4).
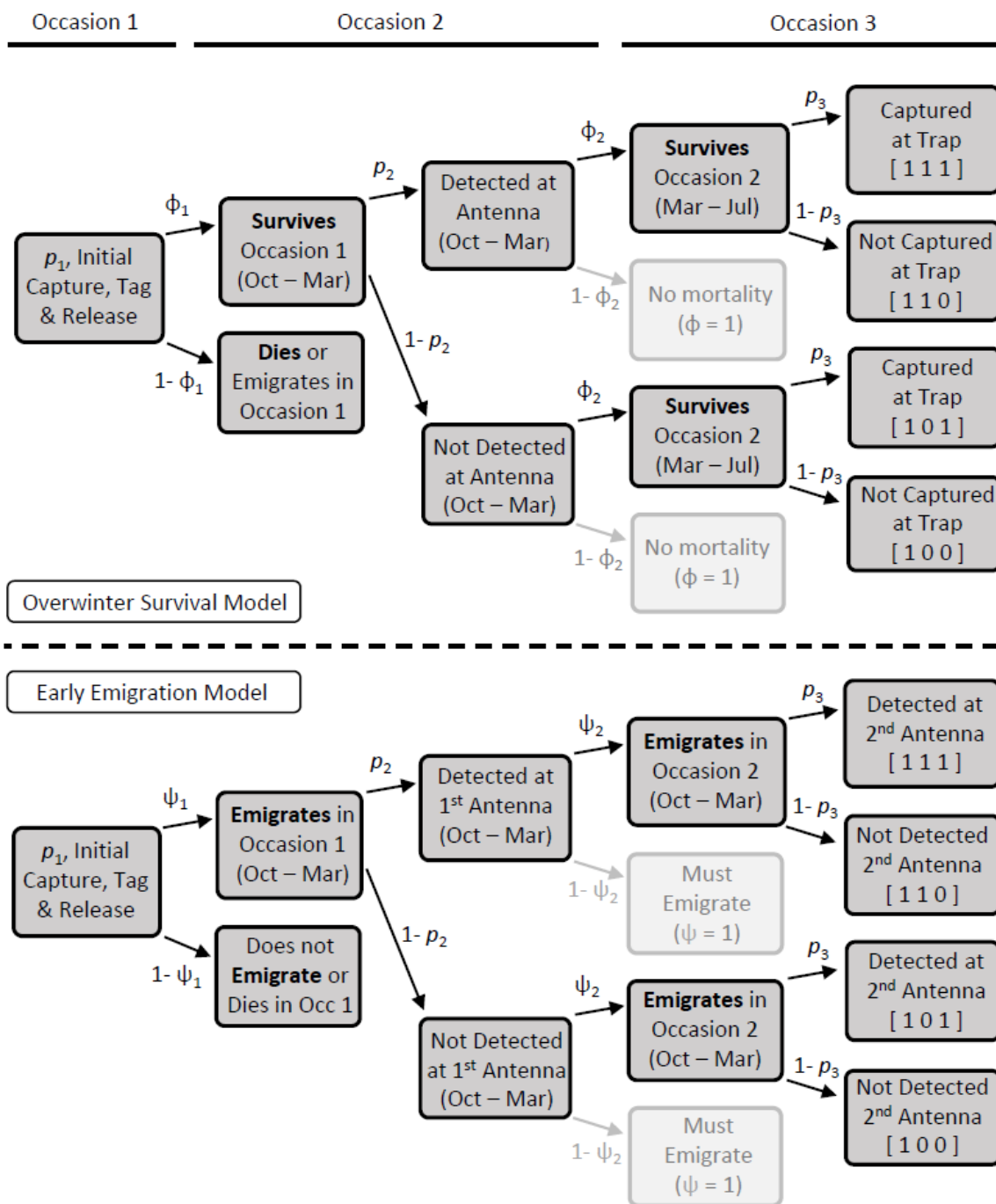
Figure 5. Cormack-Jolly-Seber model flow diagrams. Fish have a probability of surviving (ϕ_i) or emigrating (ψ_i) during occasion *i* and are detected at the next occasion with a probability p_{i+1}. Parameters ϕ_2 and ψ_2 are fixed to 1 assuming survival over short distance from antenna to trap is perfect (overwinter survival model) and all Coho emigrate the same year of tagging (early emigration model). Encounter histories indicate fish detection [1] or non-detection [0] at each of three occasions.

There are two potential reasons these two antennas may lack independence. First, they are within a few meters of each other, where environmental or biological conditions affecting one antenna's efficiency (e.g., a large flow event or a fish swimming near the surface) are likely to affect detection on both antennas. Second, these antennas rely on the same power source. Unfortunately, with no other PIT tag antenna arrays available throughout this system, I had no other way to estimate emigration.

Cormack-Jolly-Seber Model Formulation

I used the state-space formulation of the CJS model introduced by Royle (2008), a hierarchical approach where the observation process (i.e. observed or not observed) is conditional on the state process (i.e. alive or dead). Binary capture histories of three occasions were built for all tagged individuals each year with dimensions $i \times t$, where i is the number of marked individuals and t is the number of capture occasions. Capture histories consisted of 1's and 0's indicating whether an individual was observed (1) or not (0) at a given occasion. For example, a fish that was tagged in the fall, passed the antenna array undetected in the spring and detected at the migrant trap was assigned the capture history 101. Individuals like this, whose capture histories include 0's followed by 1's yield vital information the model needs to separately estimate survival probability (ϕ) and recapture probability (p). In standard CJS models, the last ϕ and p parameters are confounded, and therefore are not separately identifiable (Lebreton et al. 1992).

Although the two CJS models I used to estimate apparent survival and early

emigration were given different capture histories, the underlying mathematical models

were identical. To reduce confusion moving forward when discussing model parameter

estimates, apparent survival will be referred to as ϕ (or phi) while early emigration is

termed ψ (or psi). Since the survival and emigration models are constructed identically, I

describe the following model using only phi parameters to minimize redundancy.

As described in Kéry and Schaub (2012) the following equation defines the state

process used to estimate survival probability ϕ of individual i at time t:

$$z_{i,t+1} \mid z_{i,t} \sim Bernoulli\left(z_{i,t}\phi_{i,t}\right)$$

where $z_{i,t}$ represents the true state of individual i at time t taking value of 1 if the

individual is alive or 0 if the individual is dead. z is always 1 for the first occasion since

animals are always alive at tagging and the individual's state each subsequent occasion is

modeled as Bernoulli trials. The Bernoulli success parameter is the product of $z_{i,t}$ (1 or 0)

and survival probability, $\phi_{i,t}$, ensuring that if an individual is dead (z=0), it remains dead.

The observation process is defined similarly:

$$y_{i,t} \mid z_{i,t} \sim Bernoulli\left(z_{i,t}p_{i,t}\right)$$

where $y_{i,t}$, the observation of individual i at time t (observed or not) is conditional on its

true state $z_{i,t}$ (alive or dead). The success parameter is the product of $z_{i,t}$ (1 or 0) and

detection probability $p_{i,t}$, ensuring that if an individual is dead (z=0), it is not observed.

Within the CJS framework, a Bayesian mixed effects model adapted from Kéry

and Schaub (2012) was analyzed using Just Another Gibbs Sampler (JAGS) software

(Plummer 2016) to estimate the effect of reach-specific stream habitat on the overwinter

survival and early emigration of Coho Salmon tagged within the reaches in the fall. The

Bayesian model runs by executing Markov Chain Monte Carlo (MCMC) algorithms,

drawing many dependent (i.e. autocorrelated) samples from parameter distributions

(Gelman et al. 2014). Each model was run using three concurrent MCMC chains for each

parameter. The chains were then formally tested for convergence with the R-hat test

criterion available in the model posterior summary printout in JAGS, which compares the

among- and within-chain variance (Kéry and Schaub 2012). R-hat values of < 1.1 suggest

the absence of a "chain effect" and therefore adequate convergence (Brooks and Gelman

1998). Secondly, convergence was visually inspected in time-series plots for each

parameter to ensure chains were strongly interspersed (i.e., well-mixed, randomly

bouncing around while occupying the same space). Once the MCMC algorithms (i.e.,

chains) converge upon a common distribution for each parameter, all subsequent draws

are summarized for making inference about the posterior parameter distributions (i.e.,

posteriors).

Nested random group effects for the basin and reach of Coho Salmon capture in

fall were specified in the model to account for variation in overwinter survival due to

basin and reach variability. Fish fork length at time of tagging was also included as a

continuous individual covariate in the model. All covariates were standardized by

subtracting the mean and dividing by the standard deviation (Bring 1994) to help stabilize

the MCMC algorithms (i.e., improve convergence). Survival and detection parameters

were modeled on the logit scale ensuring that the estimated probabilities remain within

the interval [0, 1]. Survival over the second interval (ϕ_2) from t_2 to t_3 (between the antenna and migrant trap) was fixed to 1 to reduce the number of model parameters. This approach was reasonable because the time traveled and distance between the antenna and trap were minimal (typically less than 3 days and less than 1 km). The full linear model for survival was modeled on ϕ_1 from t_1 to t_2 as

$$logit\left(\phi_{i,j(k)}\right) = \alpha_{reach_{j(k)}} + \beta_1 LWD_{reach_j} + \beta_2 LVH_{reach_j} + \beta_3 FL_i$$

where LWD_{reach} is the LWD volume per km of reach j, LVH_{reach} is the percent LVH area per reach and FL is the fork length at tagging of individual i. The random group effect α_{reach} of reach j is nested within the random group effect α_{basin} of basin k as

$$\alpha_{reach_{j(k)}} \sim Normal(\alpha_{basin(k)}, \sigma^2_{reach})$$

where σ^2_{reach} is the variance of logit survival among all reaches and

$$\alpha_{basin(k)} \sim Normal(\bar{\alpha}, \sigma^2_{basin})$$

where σ^2_{basin} is the variance of logit survival among basins. Capture probability p of individual i at time t was modeled to vary by basin and occasion with no random effect specified:

$$logit(p_{i,t}) = \delta_{basin(k)} + \varepsilon_{basin(k)} IT_{i,t}$$

where $\delta_{basin(k)}$ represents the fixed effect of basin on capture probability, $\varepsilon_{basin(k)}$ represents the different fixed effects of occasion, and IT is an indicator function of dimensions $i \times t$ that equals 0 at t_1 and 1 at t_2.

While incorporating random effects for basin and reach extended the scope of inference outside the study area, I also refit each CJS model without the random effects

and habitat covariates to analyze survival inside the study area. In doing so, the scope of inference was reduced to within the study area in exchange for better convergence (as suggested by Kéry and Schaub 2012) and a direct comparison of survival among study basins and reaches. To compare posterior distributions of basin-specific survival, ϕ was modeled with a fixed group effect for basin as

$$logit(\phi_{i,t}) \ = \ \delta_{basin_k} \ + \ \varepsilon_{basin_k} IT_{i,t} \ + \ \beta_1 FL_i$$

where δ_{basin_k} represents the fixed effect of basin on ϕ, and ε_{basin_k} represents the different fixed effects of occasion. The fixed effect model for reach was structured similarly, except with $reach_k$ specified as the fixed effects:

$$logit(\phi_{i,t}) \ = \ \delta_{reach_k} \ + \ \varepsilon_{reach_k} IT_{i,t} \ + \ \beta_1 FL_i$$

Model Goodness-Of-Fit

Goodness-of-fit (GOF) tests for statistical models typically evaluate the difference between observed values from the data and expected values based on the model. Bayesian methods generally involve comparing the lack-of-fit of the model to the "real" data versus the lack-of-fit of the model to simulated data from the model's posterior parameter distributions (Gelman et al. 1996). I followed suggestions from Agresti and Hitchcock (2005) for making inference about binomial parameters with the Bayesian *p*-value, a statistic that represents the probability, given the data, that a future observation is more extreme that the observed.

As each model converged on its posterior distributions, while the model

summarized MCMC draws to form the "real" (i.e., observed) posterior distributions,

additional data was simulated conditionally on the parameters drawn at each subsequent

iteration. The simulated draws were summarized to populate a distribution of "ideal"

observations. I calculated Bernoulli discrepancy measures (i.e. a type of residual) from

each model iteration for the "real" (i.e., observed as 1 or 0) and "ideal" (i.e., predicted as

1 or 0) data and calculated the Bayesian p-value as the probability the predicted number

of survivors was more extreme than the observed (Agresti and Hitchcock 2005). A

Bayesian p-value close to 0 or 1 suggests lack-of-fit of the model to the data is likely.

Conversely, Bayesian p-values close to 0.5 suggest no lack-of-fit where both the

observed and predicted data have similar chances of being more extreme than the other

(i.e., the observed and real data are from similar distributions).

RESULTS

Large Woody Debris Summary

Given the study area contains two stream reaches passing through groves of some of the world's largest trees in Jedediah Smith Redwoods and Prairie Creek Redwoods State Parks (Madej et al. 1986; Cannata et al. 2006), I expected LWD volume to span a wide range and have a greater impact on survival than LWD counts due to its correlation with pool area (Bilby and Ward 1989). Therefore, LWD volume per km was the *a priori* LWD metric used as a covariate in the overwinter survival models. LWD counts and volume estimates were expressed for each reach as density (pieces•km^{-1} and m^3•km^{-1}) to account for variable reach lengths within the study area (Table 2). Highest LWD volume densities were observed in Freshwater tributaries and West Branch Mill Creek whereas lowest values occurred in lower Prairie Creek and upper Freshwater (Table 2). Unexpectedly, Prairie Creek averaged lower LWD volume densities that Mill and Freshwater Creeks. Figure 6 displays the spatial distribution of LWD volume throughout the study area in smaller reaches. The size of each bubble on the map corresponds to LWD volume density observed in stream reaches ranging from 1.5 to 4 km. Reaches with highest densities of LWD pieces were in lower Freshwater and Prairie creeks, which have riparian zones devoid of second or old growth timber. Lower Freshwater Creek had 758.6 pieces•km^{-1}, over two times higher than any other reach (Figure 7). Lower Freshwater Creek had the lowest mean volume per piece while Mill Creek reaches had the highest.

Table 2. Large woody debris (LWD) habitat statistics quantified by basin and reaches within each basin. Reach-specific LWD volume values were used as the LWD covariate in the overwinter survival model. Bold values indicate the three highest ranking reaches in each LWD category.

Basin / Reach	Stream Length (km)	Volume LWD ($m^3 \cdot km^{-1}$)	Number LWD (pieces$\cdot km^{-1}$)	Mean Volume per piece LWD (m^3)
Mill Creek	25.01	93.8	208.1	0.45
East Fork Mill Creek	6.54	72.4	231.1	0.31
West Branch Mill Creek	9.19	**109.9**	289.5	**0.38**
Mainstem Mill Creek	9.28	**92.9**	111.3	**0.83**
Prairie Creek	18.47	73.8	288.8	0.26
Upper Prairie Creek	13.73	82.8	284.4	0.29
Lower Prairie Creek	4.74	47.8	**301.6**	0.16
Freshwater Creek	12.84	93.8	422.6	0.18
Freshwater Tributaries	2.96	**106.1**	**315.9**	**0.33**
Upper Freshwater Creek	5.83	61.8	243.6	0.25
Lower Freshwater Creek	4.05	80.6	**758.6**	0.10
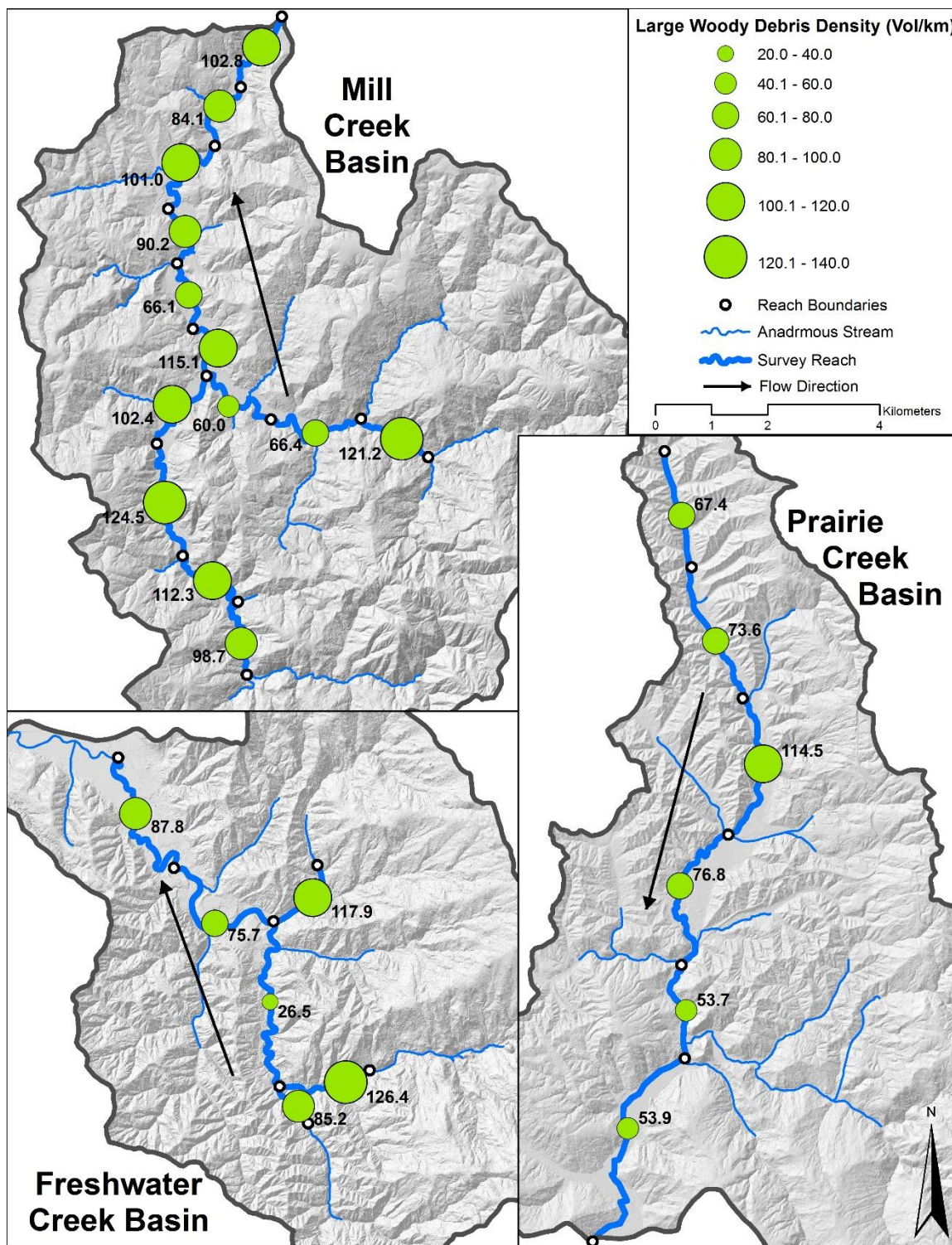
Figure 6. Large woody debris density distribution throughout each study basin. Bubble sizes correspond to reach-specific large woody debris density values ($m^3 \bullet km^{-1}$).
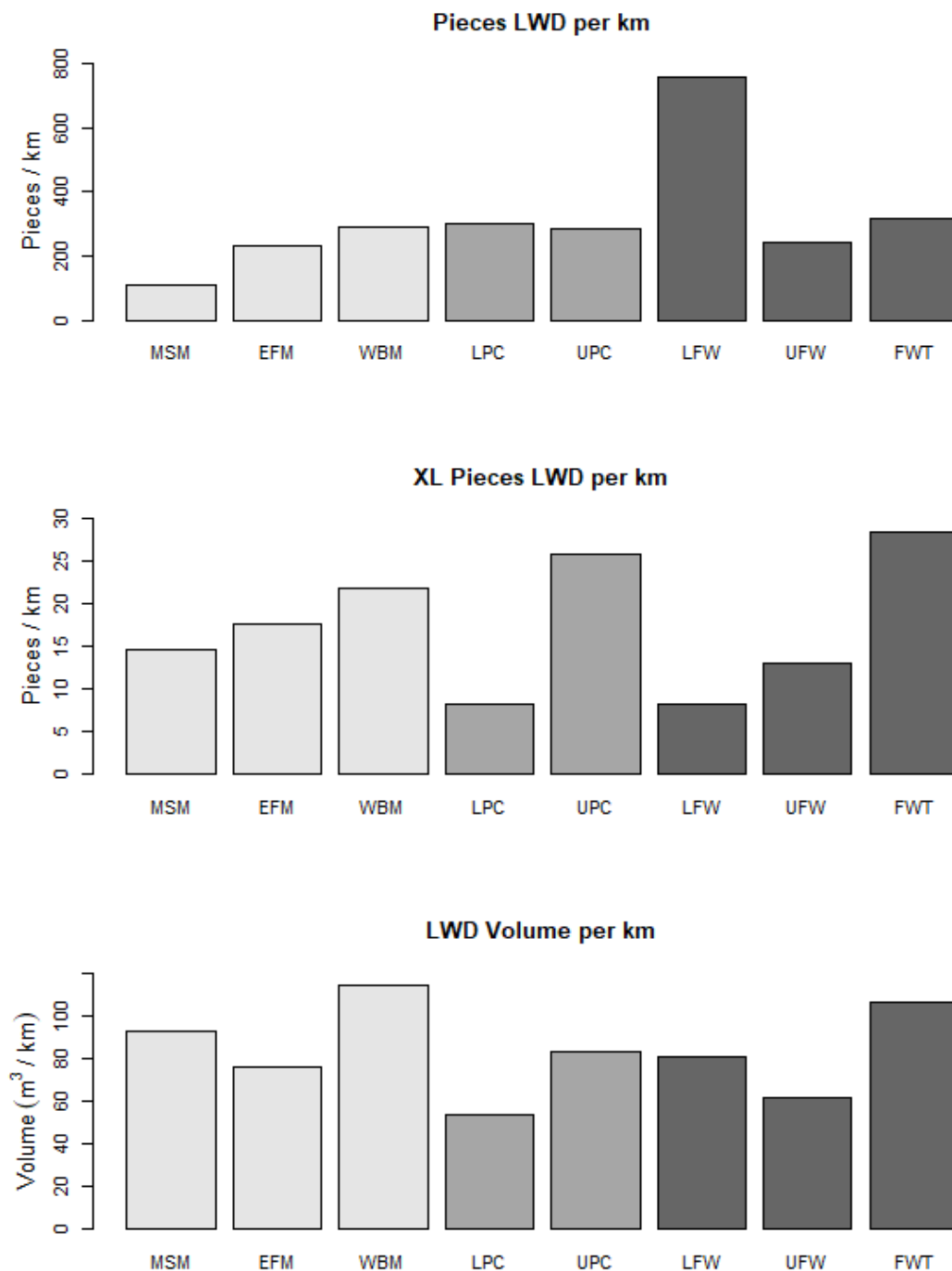
Figure 7. Large woody debris (LWD) density statistics by reach. XL pieces had diameters greater than 60 cm. Basins are shaded in light gray (Mill), gray (Prairie) and dark gray (Freshwater). MSM = Mainstem Mill, EFM = East Fork Mill, WBM = West Branch Mill, LPC = Lower Prairie, UPC = Upper Prairie, LFW = Lower Freshwater, UFW = Upper Freshwater, FWT = Freshwater Tributaries.

Low-Velocity Rearing Habitat Summary

Low-velocity rearing habitat (LVH) data was collected for its expression by reach as density (m²•km⁻¹) and proportion (i.e. percent) of total stream area (Table 3). Although I initially expected LVH densities per kilometer to best predict survival and emigration, I found densities correlated strongly with watershed location (i.e., upper reaches all had considerably less LVH area that lower reaches) (Figure 8). This was likely due to greater stream surface areas farther downstream in each watershed. Although previous studies in Freshwater and Prairie creeks demonstrated correlations between overwinter survival and location in watershed (i.e. reach) (Hauer 2013; Drobny 2016), I chose to use a relative measure of LVH independent of stream size. Instead, I used percent LVH area (i.e., slow area divided by total area) to avoid collinearity with watershed area, channel width, gradient, etc. Not surprisingly, a much different pattern emerged with lower Freshwater Creek, Freshwater Creek tributaries and upper Prairie Creek ranking highest and denoted in bold. Percent LVH was chosen as a covariate for the overwinter survival model and its spatial distribution throughout the study area is displayed in Figure 9. LVH observed in off-channel backwaters and alcoves was included in the reach-specific LVH density and percent estimates but was also totaled separately to evaluate floodplain connectivity in each reach (Table 3).

Table 3. Low-velocity rearing habitat (LVH) statistics quantified by basin and reaches within each basin. Reach-specific % LVH area was used as a covariate in the survival model. Bold values specify the three top ranked values for each LVH category.

Basin / Reach	Reach Length (km)	LVH Area (%)	LVH Density ($m^2 \cdot km^{-1}$)	Off-channel habitat ($m^2 \cdot km^{-1}$)
Mill Creek	25.01	12.1	1378.9	459.1
East Fork Mill Creek	6.54	9.3	979.3	376.5
West Branch Mill Creek	9.19	11.2	924.9	**434.2**
Main Stem Mill Creek	9.28	14.1	**2185.2**	**569.5**
Prairie Creek	18.47	18.7	1494.9	358.2
Upper Prairie Creek	13.73	**19.5**	1369.0	318.5
Lower Prairie Creek	4.74	17.2	**1859.3**	**473.3**
Freshwater Creek	12.84	19.0	1312.1	202.4
Freshwater Tributaries	2.96	**21.5**	895.2	119.3
Upper Freshwater Creek	5.83	14.2	973.6	147.4
Lower Freshwater Creek	4.05	**23.6**	**2103.9**	342.0
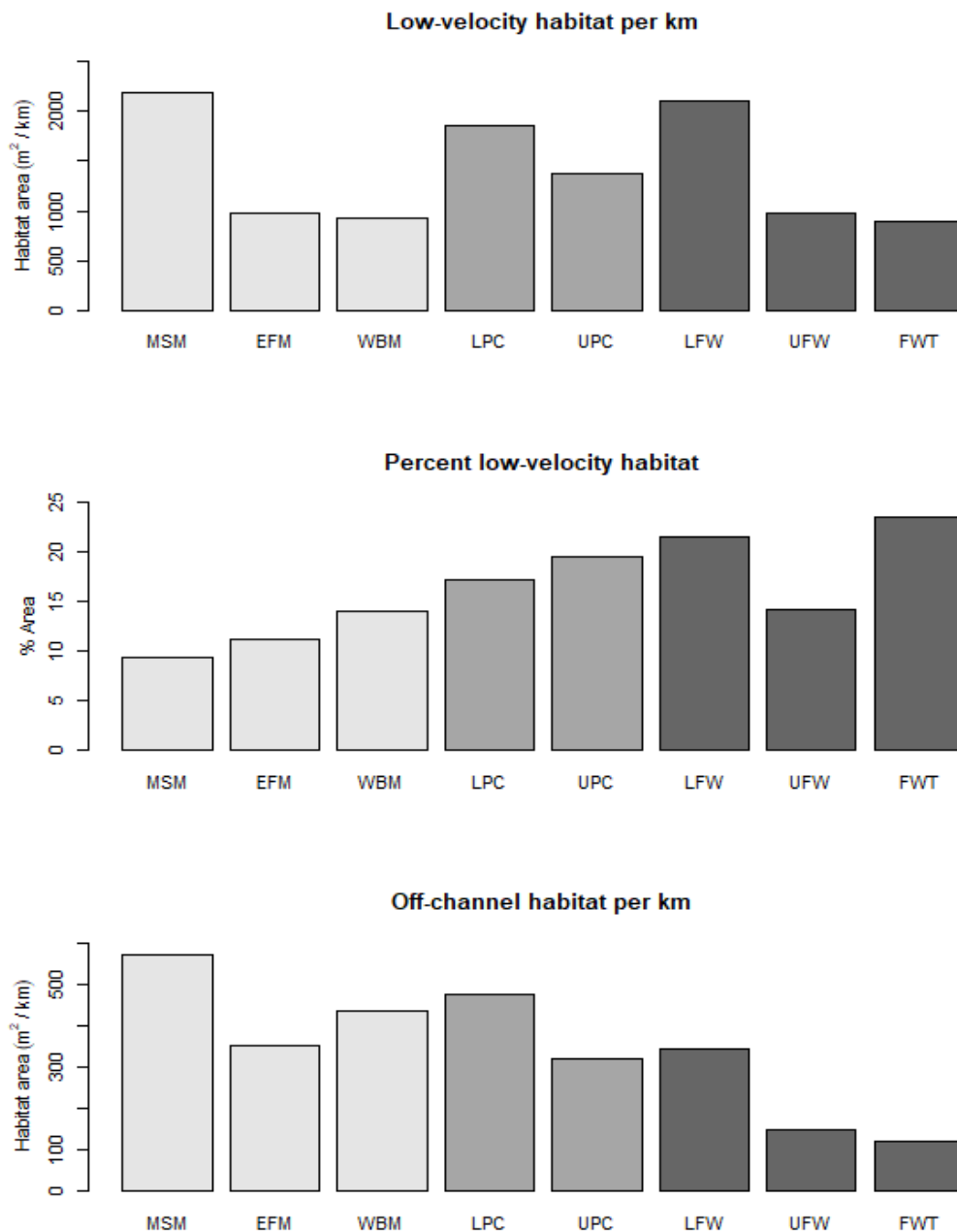
Figure 8. Three variations of low-velocity habitat densities by reach. Basins are shaded in light gray (Mill), gray (Prairie) and dark gray (Freshwater). MSM = Mainstem Mill, EFM = East Fork Mill, WBM = West Branch Mill, LPC = Lower Prairie, UPC = Upper Prairie, LFW = Lower Freshwater, UFW = Upper Freshwater, FWT = Freshwater Tributaries.
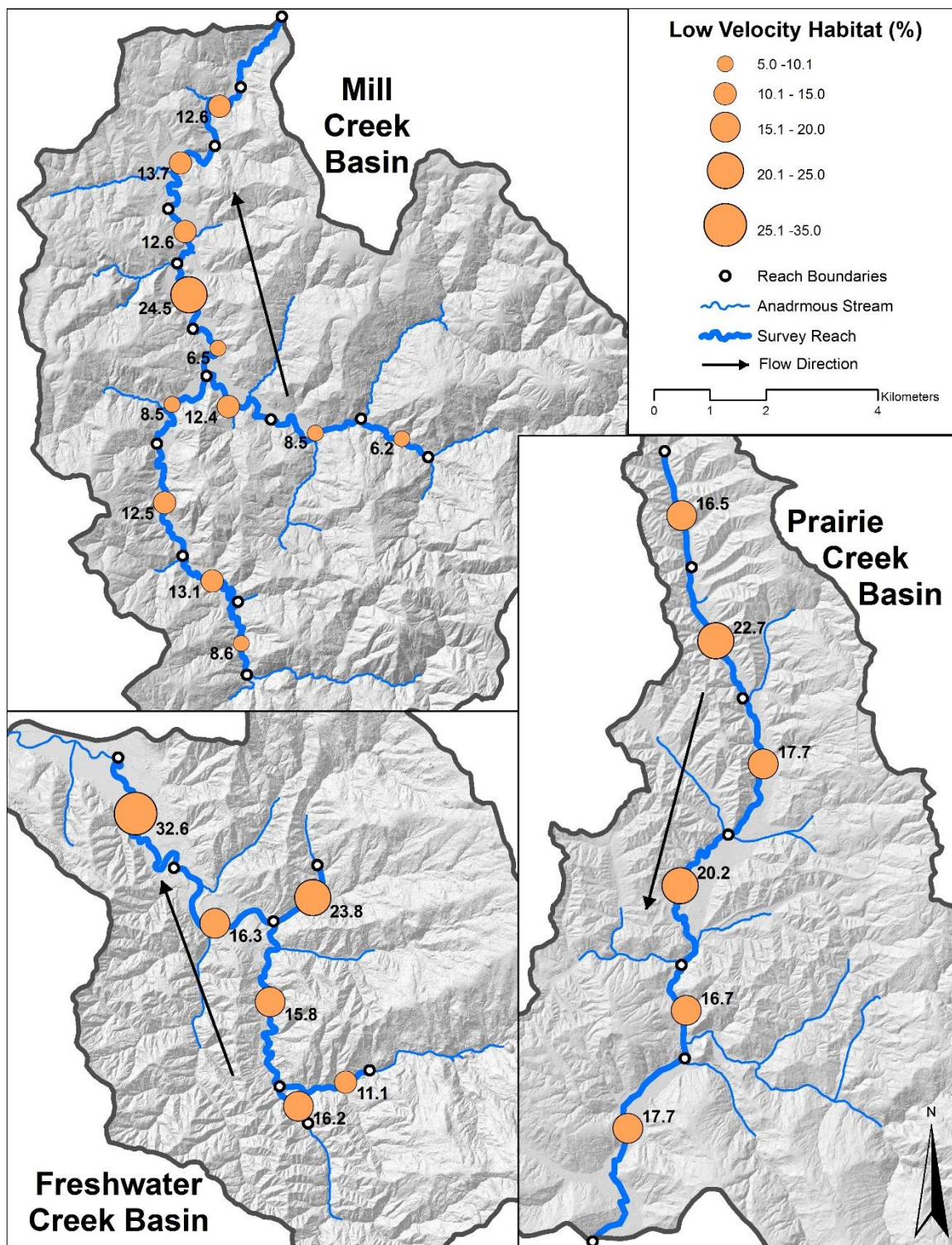
Figure 9. Percent low-velocity habitat distribution across all study basins. Bubble sizes correspond to percent low-velocity habitat values by reach.

Apparent Overwinter Survival Analysis

A total of 7,041 fish were tagged over the course of the study divided throughout Mill Creek, Prairie Creek and Freshwater Creek each October in 2013-2015 (Table 4). The number of Coho Salmon tagged in each reach was dependent on annual fish sizes, fish densities and available field crew resources and ranged from 61 (Freshwater Creek tributaries, 2015) to 550 fish (West Branch Mill Creek, 2014). All seven reaches in the study area were sampled every fall, except for 2015 when early rains prevented field crew from tagging fish in lower Mill Creek (Table 4). The proportion of the fish sampled that were large enough to tag each year based on NOAA's taggable fish size restrictions was 56.1% in 2013, 61.4% in 2014 and 33.7% in 2015. The taggable fish proportion also varied by basin every year where mean annual Coho Salmon fork lengths ranged from 70.0 to 70.8 mm in Mill Creek, 63.9 to 66.8 in Prairie Creek and 58.8 to 62.0 in Freshwater Creek (Table 4). Complete mark-recapture summaries by basin and reach are displayed in M-array tables for each CJS apparent overwinter survival model for the 2013 (Appendix C), 2014 (Appendix D) and 2015 (Appendix E).

A general pattern emerged across years and basins where waves of early emigration coincided with the first seasonal flow events in late fall or winter, followed by a winter period of reduced movement and a final spring migration typically extending into early June (Figure 10). However, a subtle difference separates the Mill Creek pattern from Freshwater and Prairie Creek, where the early pulses of emigrants are consistently

Table 4. Number of PIT tags applied to Coho Salmon by year, basin and reach. Basin-specific population statistics include the minimum fork length allowed to apply tags and the portion of each population within the taggable range. Mean fork lengths for each population are reported followed by standard deviation in parentheses.

Tag Location	Total Tagged Coho Salmon	Population Mean Fork Length (mm)	Minimum Length Taggable Fish[a] (mm)	Taggable Population (%)
2013	2,784	66.9 (11.3)		56.1
Mill Creek	1,442	70.2 (9.07)	65	74.5
East Fork Mill	472	69.5 (9.17)		
West Branch Mill	493	69.4 (8.86)		
Mainstem Mill	477	72.5 (8.88)		
Prairie Creek	637	66.8 (13.5)	60	67.5
Upper Prairie Creek	447	64.7 (13.8)		
Lower Prairie Creek	190	73.0 (10.2)		
Freshwater Creek	705	61.5 (11.2)	65	33.9
Freshwater Tribs	191	59.8 (10.8)		
Upper Freshwater	293	60.3 (9.85)		
Lower Freshwater	221	67.1 (12.6)		
2014	2,603	67.0 (11.1)		61.4
Mill Creek	1,385	70.8 (9.06)	63	81.6
East Fork Mill	467	67.4 (8.23)		
West Branch Mill	550	69.3 (8.13)		
Mainstem Mill	368	78.2 (7.38)		
Prairie Creek	718	63.9 (10.2)	60	65.6
Upper Prairie Creek	441	62.3 (10.0)		
Lower Prairie Creek	277	68.8 (9.00)		
Freshwater Creek	500	62.0 (12.6)	65	34.6

Tag Location	Total Tagged Coho Salmon	Population Mean Fork Length (mm)	Minimum Length Taggable Fish[a] (mm)	Taggable Population (%)
Freshwater Tribs	105	56.8 (10.7)		
Upper Freshwater	170	57.9 (7.36)		
Lower Freshwater	225	76.4 (11.7)		
2015	1,654	64.9 (11.7)		33.7
Mill Creek	821	70.0 (8.57)	70	57.8
East Fork Mill	415	70.0 (7.94)		
West Branch Mill	406	70.0 (9.11)		
Mainstem Mill	0[b]	-		
Prairie Creek	504	66.4 (14.0)	70	35.5
Upper Prairie Creek	241	63.8 (14.2)		
Lower Prairie Creek	263	73.6 (10.3)		
Freshwater Creek	329	58.8 (10.8)	70	16.0
Freshwater Tribs	61	54.5 (9.81)		
Upper Freshwater	107	58.0 (8.69)		
Lower Freshwater	161	69.2 (9.60)		
Total Fish Tagged:	7,041			

a: Minimum size of taggable fish set for each watershed each year using 12mm half-duplex PIT tag

b: No Coho Salmon tagged in mainstem Mill Creek in 2015 due to early rains causing flows too high to sample
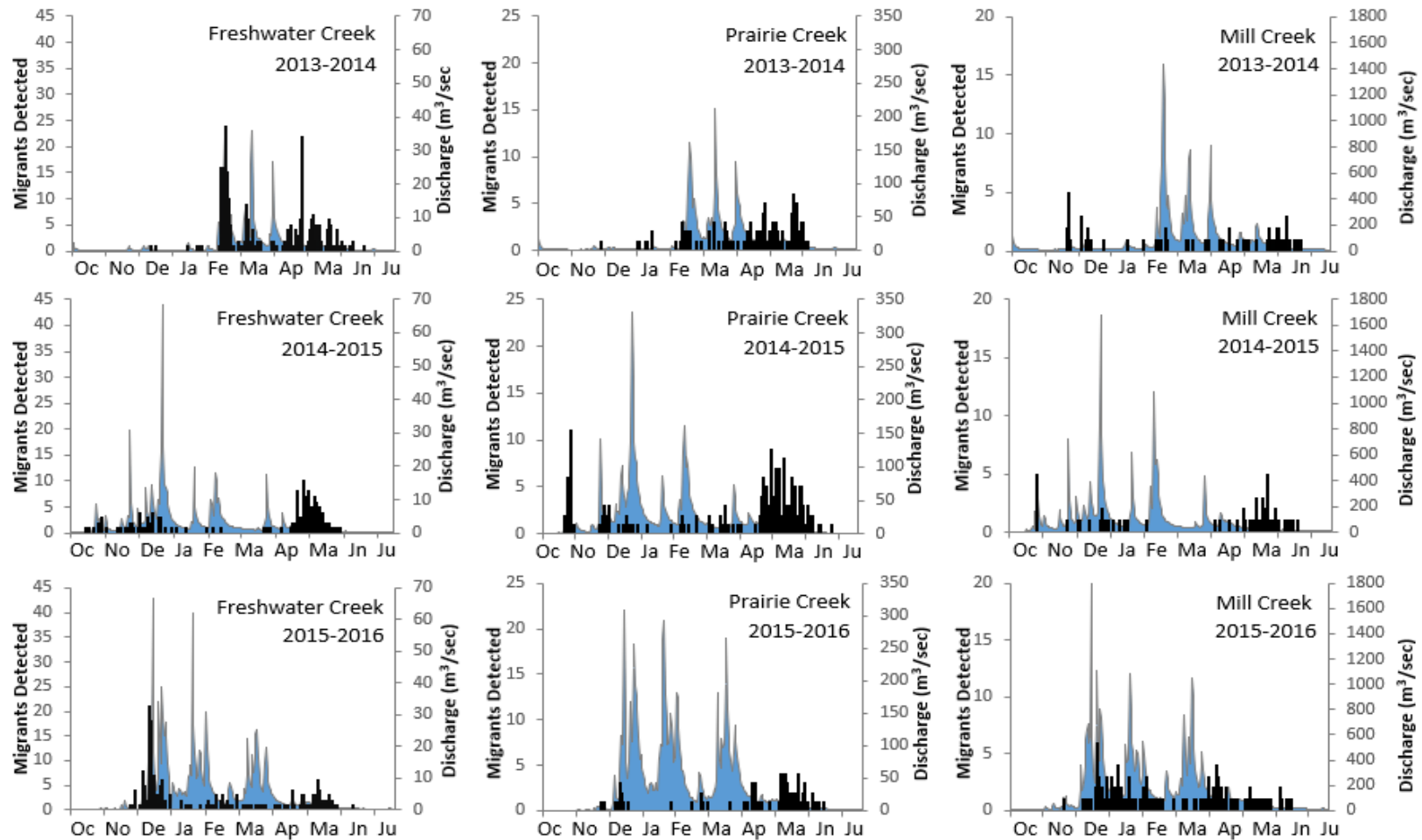
Figure 10. Outmigrant detection timing (October – July) of juvenile Coho Salmon for the three years (by row) and three streams (by column). Black bars (primary axis) represent daily counts of unique individuals detected leaving the stream. Blue shaded area (secondary axis) represents mean daily discharge at the nearest stream gauge.

larger in fall than in spring and the migration decrease in winter is less pronounced than in the other basins (Figure 10).

Chain convergence was confirmed for all posterior parameter distributions in each model where all R-hat values were below 1.1 (Brooks and Gelman 1998). Additionally, all MCMC chain plots appeared interspersed. When testing models for goodness-of-fit, Bayesian p-values for all models were between 0.45 and 0.55 suggesting no lack-of-fit in the models prior to proceeded with inference (Gelman et al. 2014).

Each annual apparent overwinter survival and early emigration model included LWD and LVH covariates (measured once in 2014-15) and an individual fork length covariate standardized over each season. Given mean covariate values for each year, mean apparent overwinter survival from the random effect posterior distributions for each year were 0.36 (95% CI: 0.05 – 0.84) in 2013, 0.42 (95% CI: 0.04 – 0.95) in 2014, and 0.42 (95% CI: 0.02 – 0.93) in 2015 (Table 5). Models produced wide credible intervals (CIs) around survival estimates due to high variability in reach-specific survival and the small number of basins (3) and reaches (7) used to inform the survival distribution. Considering the wide CIs, it is important to emphasize that when using random effects, some certainty around parameter estimates is sacrificed to extend inference from the specific study basins to a regional level.

Coho salmon fall fork length consistently exhibited positive relationships with overwinter survival (Figure 11). Based on the annual model results (Table 6), the 95% CIs suggested that for every 1 standard deviation increase in fork length ($SD \approx 8$ mm), overwinter survival probability was likely to increase by 1.24 to 1.61 times in 2013 (i.e.,

a 24% to 61% increase) and increase by 1.16 to 1.6 times in 2014 (i.e., a 16% to 60%

increase). Stated another way, there is greater than a 99% chance fall fork length has a

positive effect of on overwinter survival. The 95% CI in 2015 suggested an increase in 1

standard deviation fork length yielded a range from a 7% decrease to 36% increase in

survival probability; still, an 88% chance of a positive effect.

Effects of LWD volume and LVH area on overwinter survival were inconsistent

across yearly models. Beta estimates showed LWD volume had no effect on survival for

any year as 95% CIs of the posterior distributions clearly encompassed zero for each year

(Figure 12). Similar results were observed for LVH effects on survival, although a mostly

positive effect was suggested in 2015 where the model predicts the LVH effect to be

positive 96% of the time (Figure 13). This result is interesting because the 2015 model

included the additional PIT tag antennas downstream of Mill Creek, reducing bias in the

estimates of survival and emigration from the watershed that provides the least LVH.

Nevertheless, this can only be considered anecdotal evidence until more years of

monitoring data are collected with the additional antenna locations.

Table 5. Annual estimates for response variable mean apparent overwinter survival of juvenile Coho Salmon from each model for each year throughout the study.

Year	Overwinter Survival (mean)	SD	2.50%	97.50%
2013	0.36	0.17	0.05	0.84
2014	0.42	0.21	0.04	0.95
2015	0.34	0.21	0.02	0.93

Table 6. Coefficients on the log-odds scale for three survival predictor variables with 95% credible intervals from each model for each year throughout the study.

Predictor Variables	Year	Coefficient	SD	2.50%	97.50%
Fall Fork Length (mm)	2013	1.42	0.10	1.24	1.61
	2014	1.36	0.11	1.16	1.60
	2015	1.12	0.11	0.93	1.36
Low-Velocity Habitat (%)	2013	1.22	1.09	0.44	3.00
	2014	1.08	1.32	0.25	3.07
	2015	2.01	1.57	0.85	5.23
LWD Volume (m^3/km)	2013	0.89	1.08	0.37	1.87
	2014	0.84	0.64	0.23	2.04
	2015	1.32	0.85	0.62	2.43
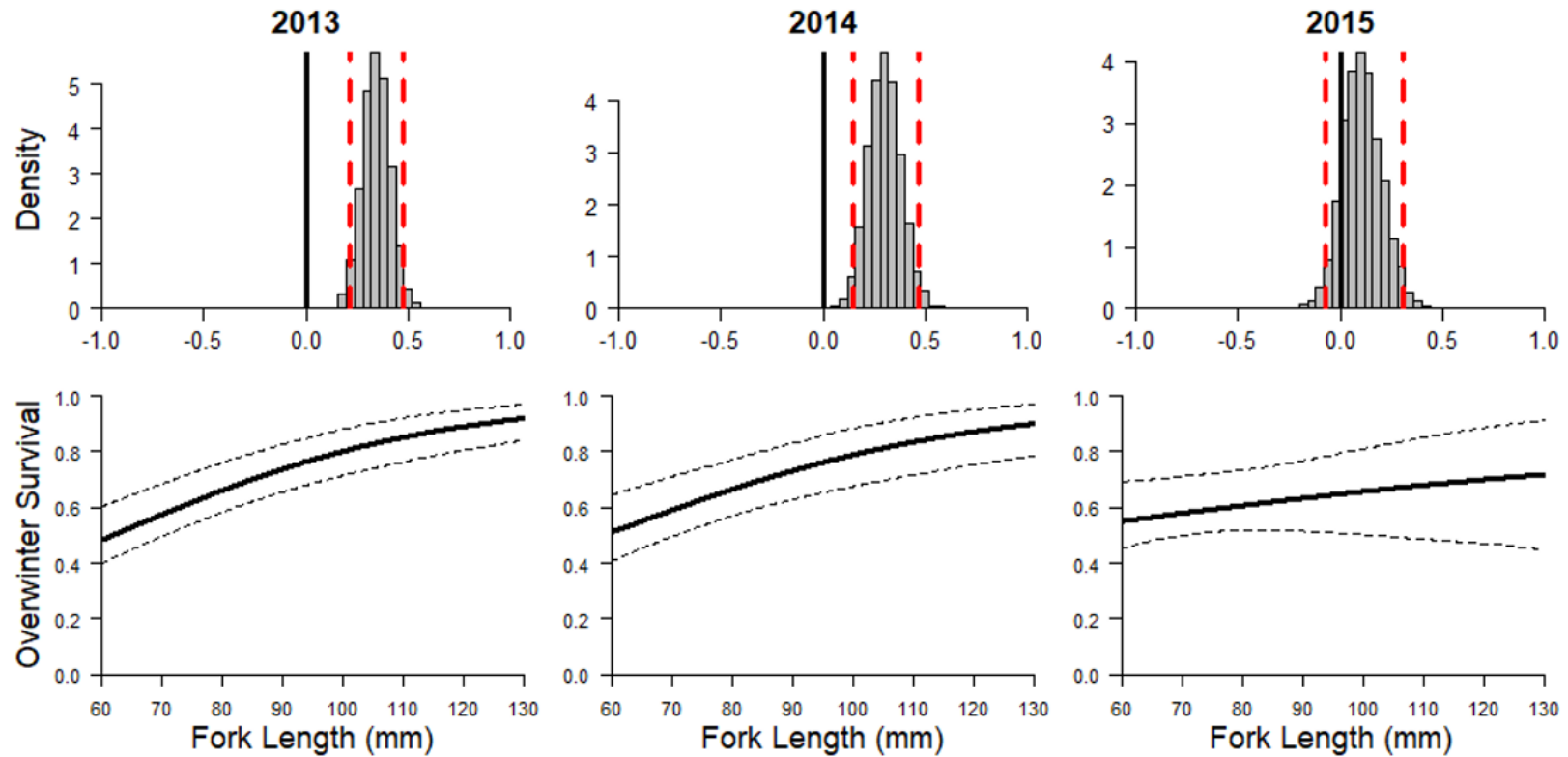
Figure 11. Posterior distributions of beta estimates (top row) and back-transformed effects (bottom row) of fall fork length on apparent overwinter survival of juvenile Coho Salmon each year, given mean values for low velocity habitat (16.3%), large wood volume (81.8 $m^3 \cdot km^{-1}$) and reach within basin random effects. Random effects for basin and sub-basin were included to account for spatial variability. Dashed lines represent 95% credible intervals.
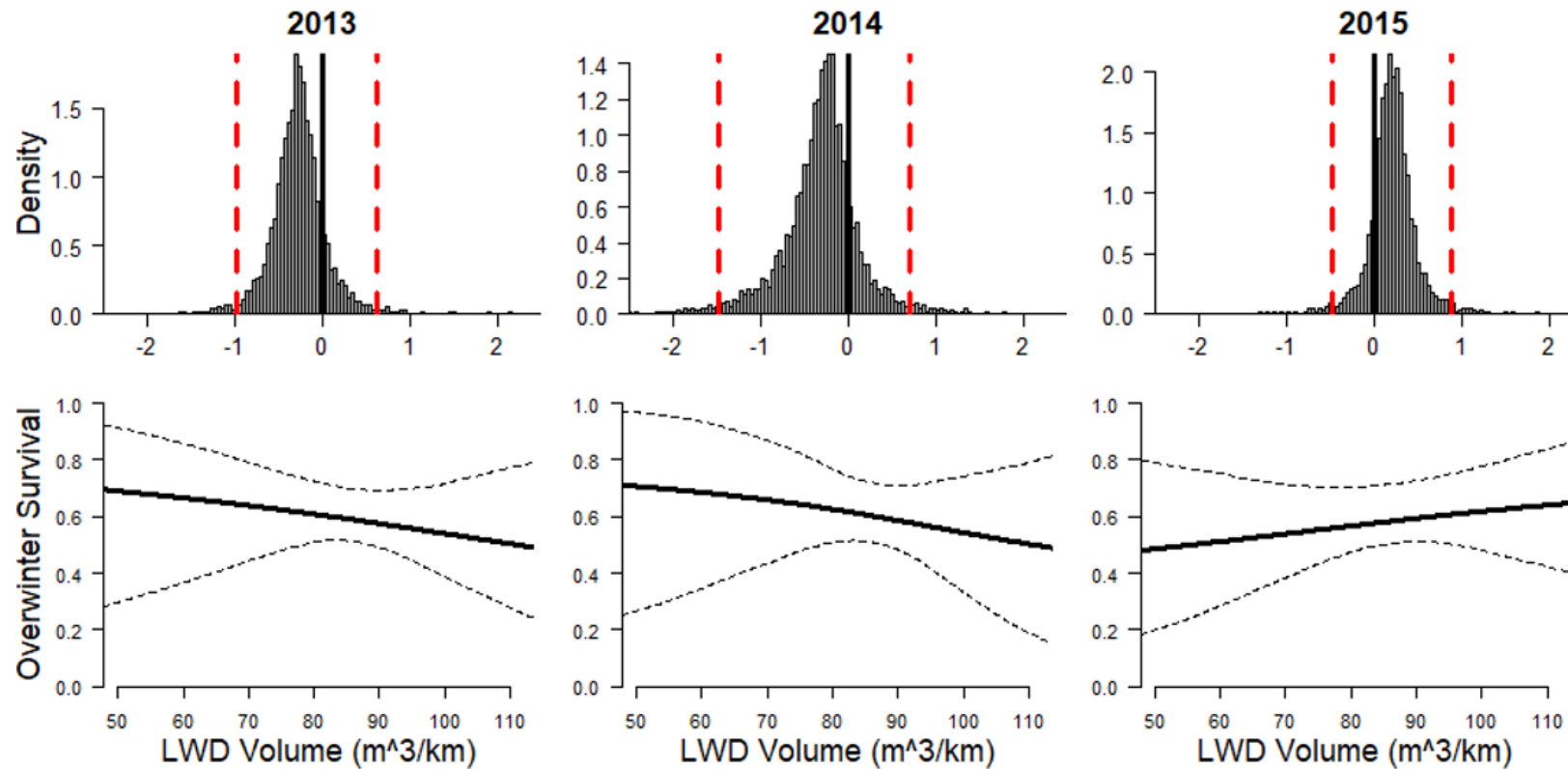
Figure 12. Posterior distributions of beta estimates (top row) and back-transformed effects (bottom row) of large woody debris (LWD) volume on apparent overwinter survival of juvenile Coho Salmon each year, given mean values for low velocity habitat (16.3%), fall fork length (71.6 mm) and reach within basin random effects. Random effects for basin and sub-basin were included to account for unexplained differences in survival among basins. Dashed lines represent 95% credible intervals.
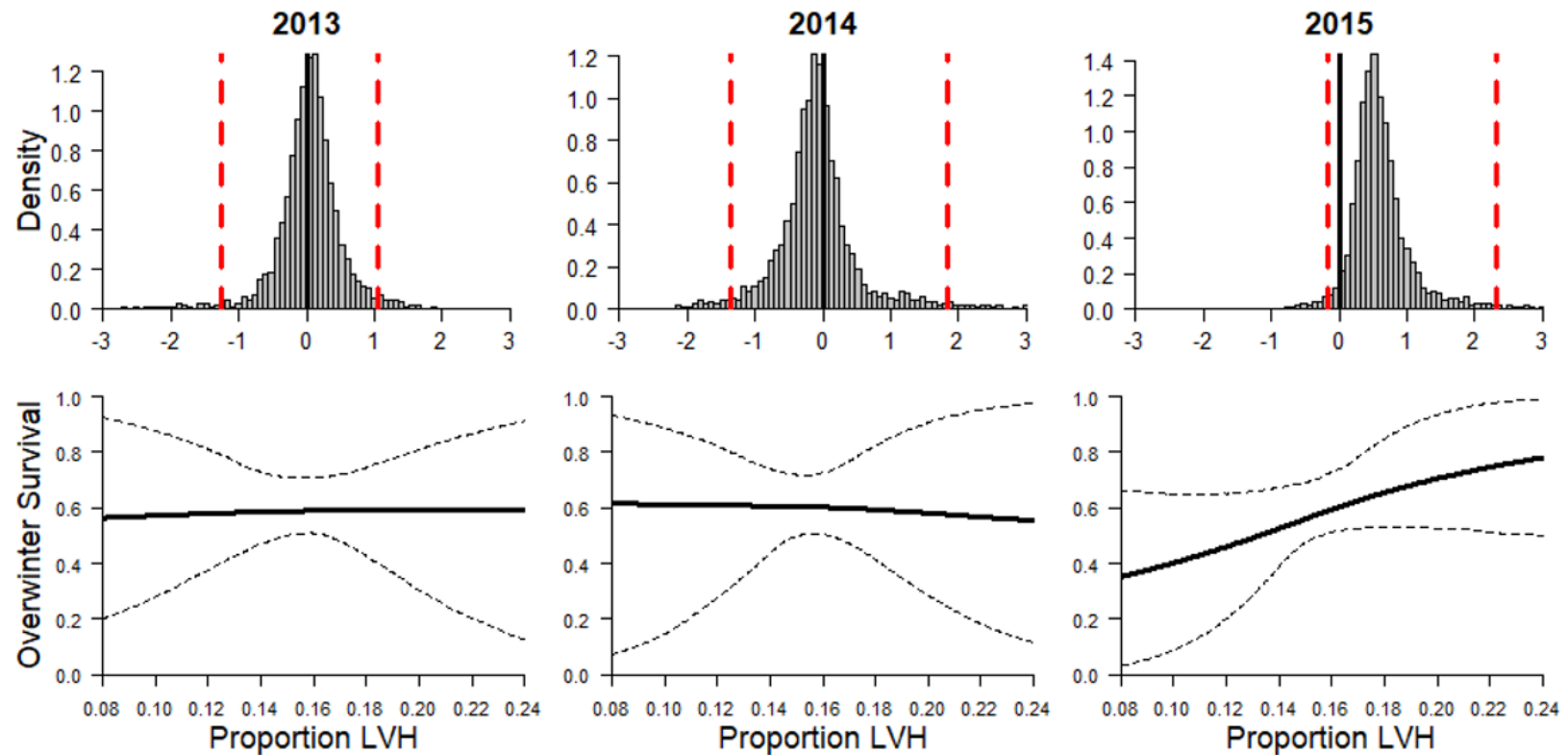
Figure 13. Posterior distributions of beta estimates (top row) and back-transformed effects (bottom row) of proportional low-velocity rearing habitat (LVH) on apparent overwinter survival of juvenile Coho Salmon each year, given mean values for fall fork length (71.6 mm), large wood volume (81.8 $m^3 \cdot km^{-1}$) and reach within basin random effects. Basin and sub-basin random effects were used in each model to account for spatial variability in survival among stream reaches. Dashed lines represent 95% credible intervals.

Early Emigration Analysis

All 7,041 tagged Coho Salmon across the three seasons in three basins that were used in the overwinter survival models were also used in the early emigration models (Table 4). All R-hat values were less than 1.1, indicating convergence of the three chains (Gelman et al. 2014). Bayesian *p*-values for all emigration models were between 0.45 and 0.55 suggesting no lack-of-fit was apparent in the models (Gelman et al. 2014). Based on these diagnostics, I proceeded with inference.

Given the standardized covariate values for each year, mean early emigration from the random effects posterior distributions were 0.29 (95% CI: 0.00 – 1.00) in 2013, 0.21 (95% CI: 0.00 – 0.95) in 2014, and 0.31 (95% CI: 0.00 – 0.99) in 2015 (Table 7). Like the survival models, the emigration models produced extremely wide CIs around mean early emigration estimates due to high variability in reach-specific emigration and the small number of basins used to inform the emigration distribution. I reiterate here that when using random effects, some certainty around parameter estimates is sacrificed to extend inference outside of the study area.

Models consistently suggested Coho Salmon fall fork length has a negative relationship with early emigration where smaller fish were more likely to migrate towards the estuary before spring (Figure 14). The 95% CIs of the parameter distributions showed no significant effect of fall fork length on early emigration in 2013, but in 2014 and 2015 models suggest there was greater than a 91% and 99% chance the relationship was negative, respectively (Figure 14). More specifically, the 95% CI from the model for

2015 suggested that for every 1 standard deviation increase ($SD \approx 8$ mm) in Coho Salmon fall fork length, early emigration probability was likely to decrease by 8% to 53% (Table 8).

Effects of LWD volume and LVH area on early emigration were inconsistent across yearly models. Beta estimates for LWD volume had no clear relationship with early emigration rates with 95% CIs surrounding zero, though regression coefficients for LWD were generally positive (Figure 15). LVH also showed no effect on early emigration in the first two study years. However, a weak negative effect was observed in 2015 where the model predicted that streams with an increase in low-velocity rearing area would reduce early emigration rates 89% of the time (Figure 16).

Table 7. Annual estimates for response variable mean early emigration of juvenile Coho Salmon from each model for each year throughout the study.

Year	Early Emigration (mean)	SD	2.50%	97.50%
2013	0.29	0.31	0.00	0.99
2014	0.21	0.24	0.00	0.95
2015	0.31	0.29	0.00	0.99

Table 8. Coefficients on the log-odds scale for three early emigration predictor variables with 95% credible intervals from each model for each year throughout the study.

Predictor Variable	Year	Coefficient	SD	2.50%	97.50%
Fall Fork Length (mm)	2013	0.98	0.12	0.78	1.25
	2014	0.87	0.10	0.70	1.06
	2015	0.69	0.12	0.47	0.92
Low-Velocity Habitat (%)	2013	2.15	2.95	0.12	10.02
	2014	1.57	1.76	0.29	4.77
	2015	0.68	1.24	0.07	2.50
LWD Volume ($m^3 \cdot km^{-1}$)	2013	1.19	2.07	0.10	5.03
	2014	0.94	1.15	0.18	2.28
	2015	0.80	1.50	0.10	2.54
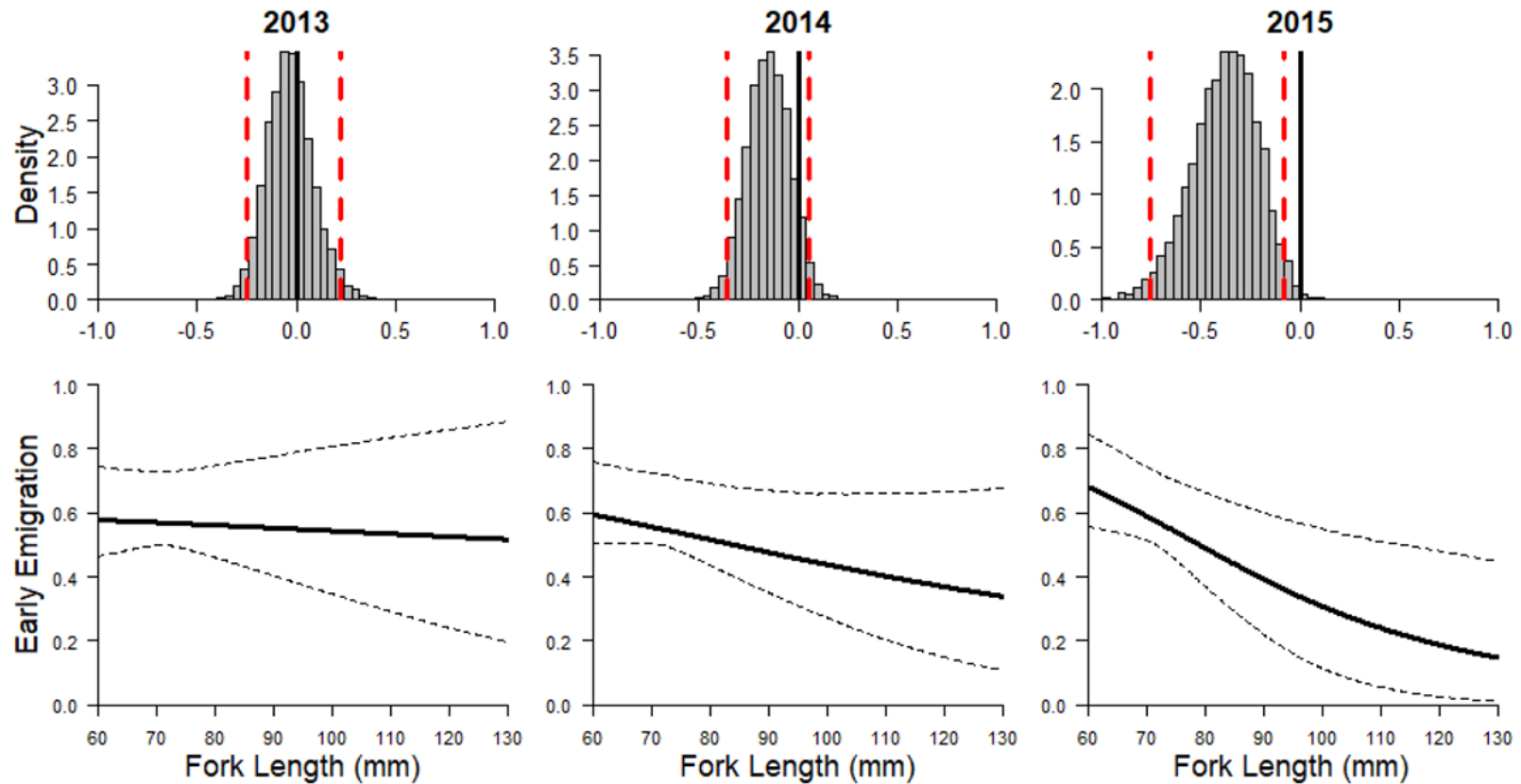
Figure 14. Posterior distributions of beta estimates (top row) and back-transformed effects (bottom row) of fall fork length on early emigration of juvenile Coho Salmon, given mean values for low velocity habitat (16.3%), large wood volume (81.8 $m^3 \cdot km^{-1}$) and reach within basin random effects. Random effects for basin and sub-basin were included each year to account for spatial variability. Dashed lines represent 95% credible intervals.
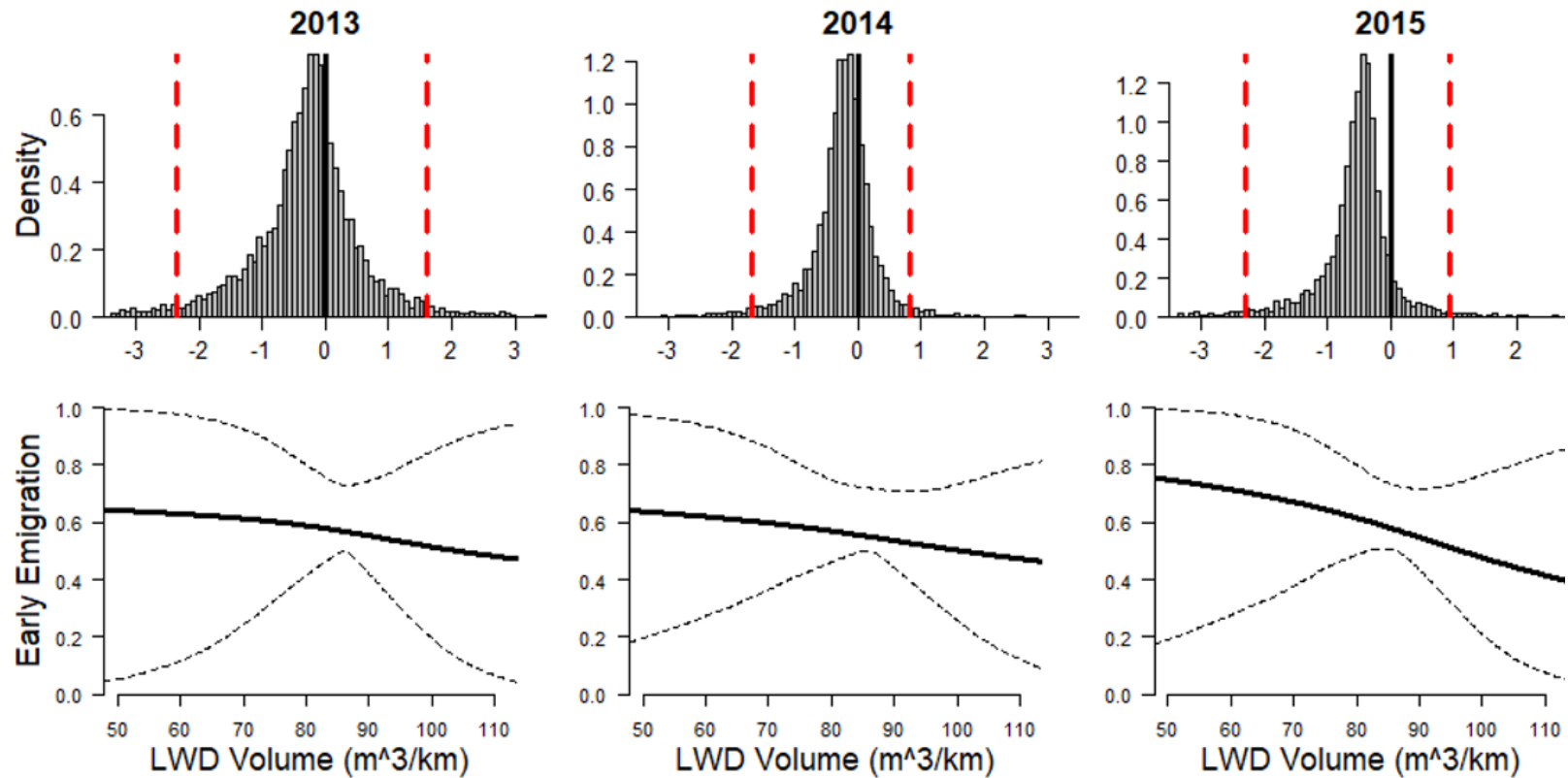
Figure 15. Posterior distributions of beta estimates (top row) and back-transformed effects (bottom row) of large woody debris (LWD) volume on early emigration of juvenile Coho Salmon each year, given mean values for low velocity habitat (16.3%), fall fork length (71.6 mm) and reach within basin random effects. Random effects for basin and sub-basin were included to account for unexplained differences in survival among basins. Dashed lines represent 95% credible intervals.
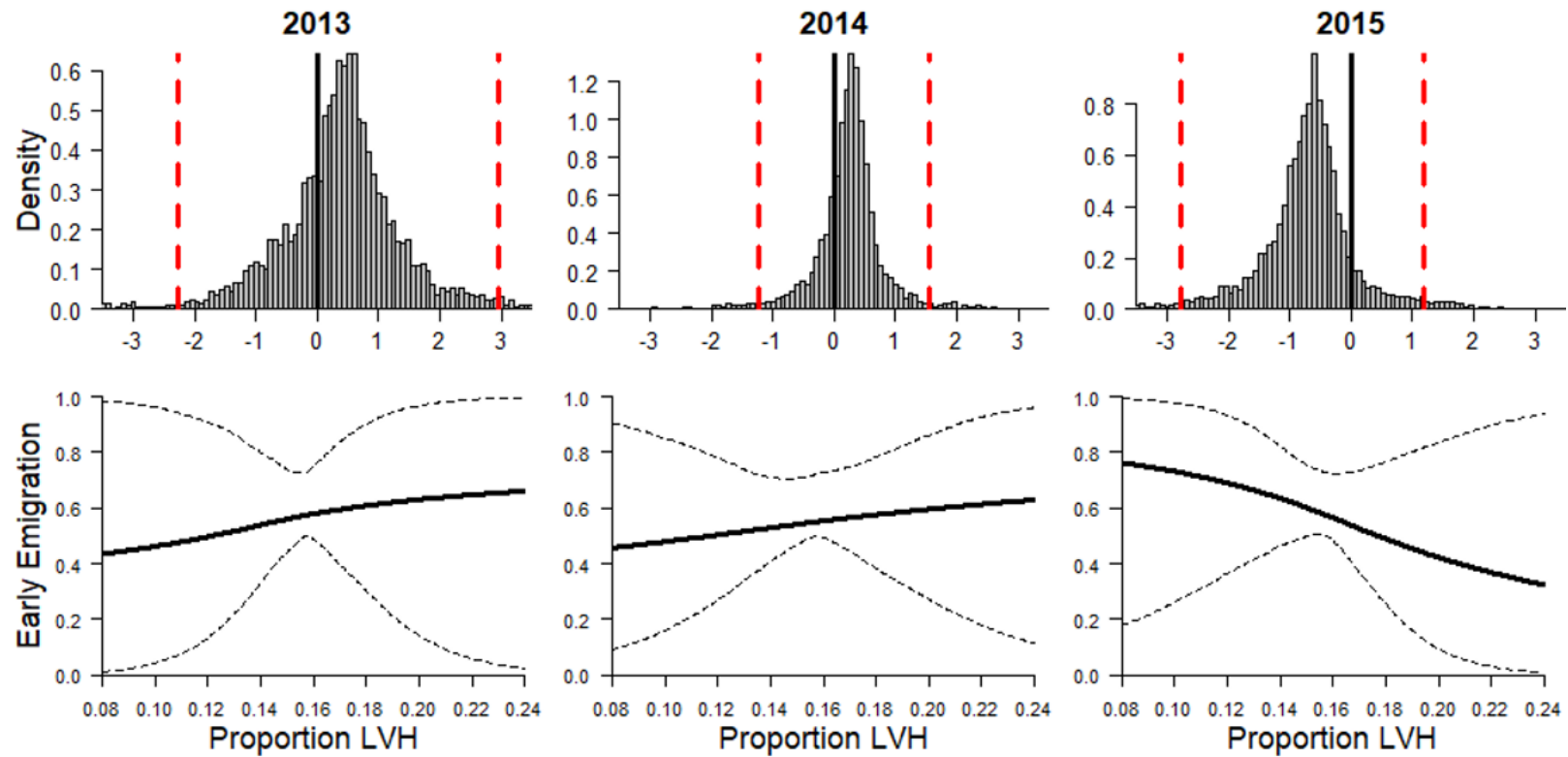
Figure 16. Posterior distributions of beta estimates (top row) and estimated effects (bottom row) of proportional low-velocity rearing habitat (LVH) on early emigration of juvenile Coho Salmon from mixed effects models for each year, given mean values for fall fork length (71.6 mm), large wood volume (81.8 m^3·km^{-1}) and reach within basin random effects. Random effects for basin and sub-basin were used in each model to account for spatial variability in survival among stream reaches. Dashed lines represent 95% credible intervals.

Spatial Variation in Survival and Emigration

To assess the spatial variability in survival and emigration across basins and reaches, I estimated reach and basin-specific parameters using fixed group effects for basin and reach. All seven reaches in each basin were sampled each year except for 2015 when high flows prevented field crew from seining mainstem Mill Creek (Table 4). Based on results from previous studies (Hauer 2013, Drobny 2016) I hypothesized that overwinter survival rates would be higher in upstream reaches than in downstream reaches, but this pattern was not evident (Figure 17). Instead, the obvious determinant for survival was basin. Additionally, I anticipated higher early emigration rates in the lower reaches of each basin, which was hardly apparent. While lower reaches in Freshwater and Prairie creeks had higher mean early emigration rates in every year, credible intervals overlapped considerably on most occasions (Figure 18). Furthermore, Mill Creek estimates were affected by the change in antenna infrastructure midway through the study, making it difficult to discern or trust patterns. Mean apparent overwinter survival by basin from ranged from as low as 0.052 (95% CI: 0.037-0.071) in Mill Creek during 2013 to as high as 0.567 (95% CI: 0.424-0.765) in Freshwater Creek in 2014 (Figure 19). Note that estimates for Mill Creek in 2015 only include the two upstream reaches since no fish were tagged in mainstem Mill Creek that year. However, I would expect an even higher rate of emigration would occur if mainstem Mill was included given it produced more early emigrants than upper reaches in 2013 and Freshwater and Prairie creeks showed similar patterns each year. Apparent overwinter survival distributions from each

year in Mill Creek were consistently and drastically lower than the ranges of survival in

Prairie Creek and Freshwater Creek.
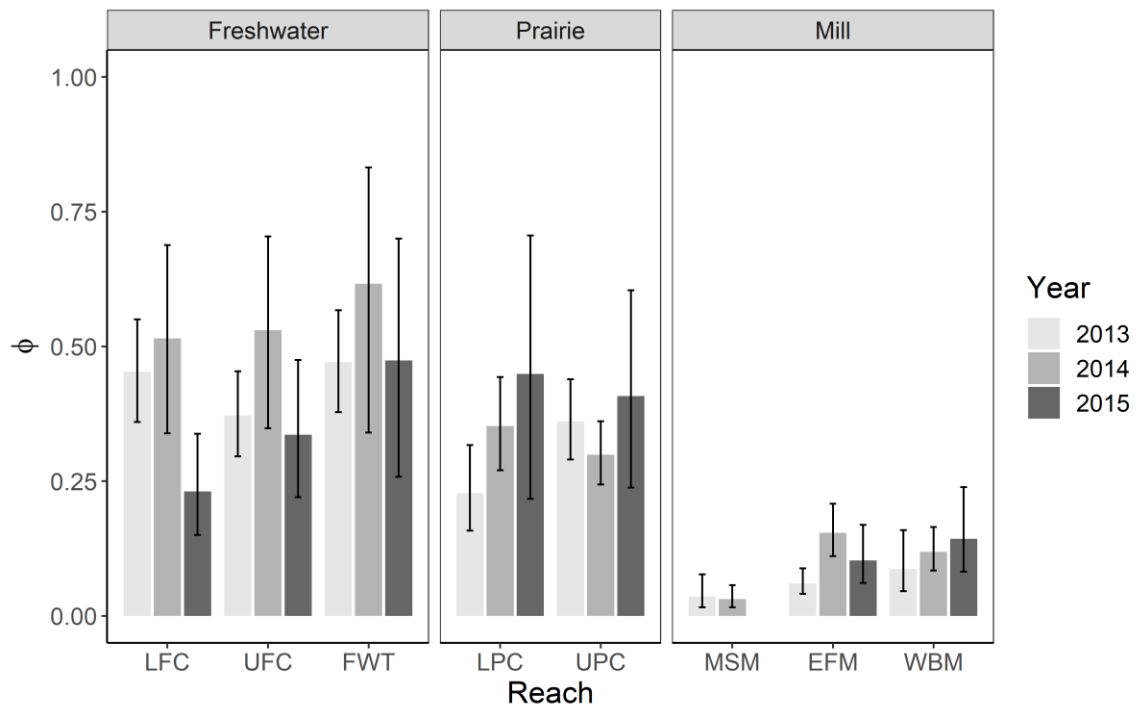
Figure 17. Reach-based apparent overwinter survival (ϕ) estimates with error bars representing 95% CIs for each study year, given mean fall fork length values. No fish were marked in Mainstem Mill Creek in 2015; no estimates available. Reach abbreviations are as follows, from left: lower Freshwater Creek (LFC), upper Freshwater Creek (UFC), Freshwater tributaries (FWT), lower Prairie Creek (LPC), upper Prairie Creek (UPC), mainstem Mill Creek (MSM), East Fork Mill Creek (EFM) and West Branch Mill Creek (WBM).
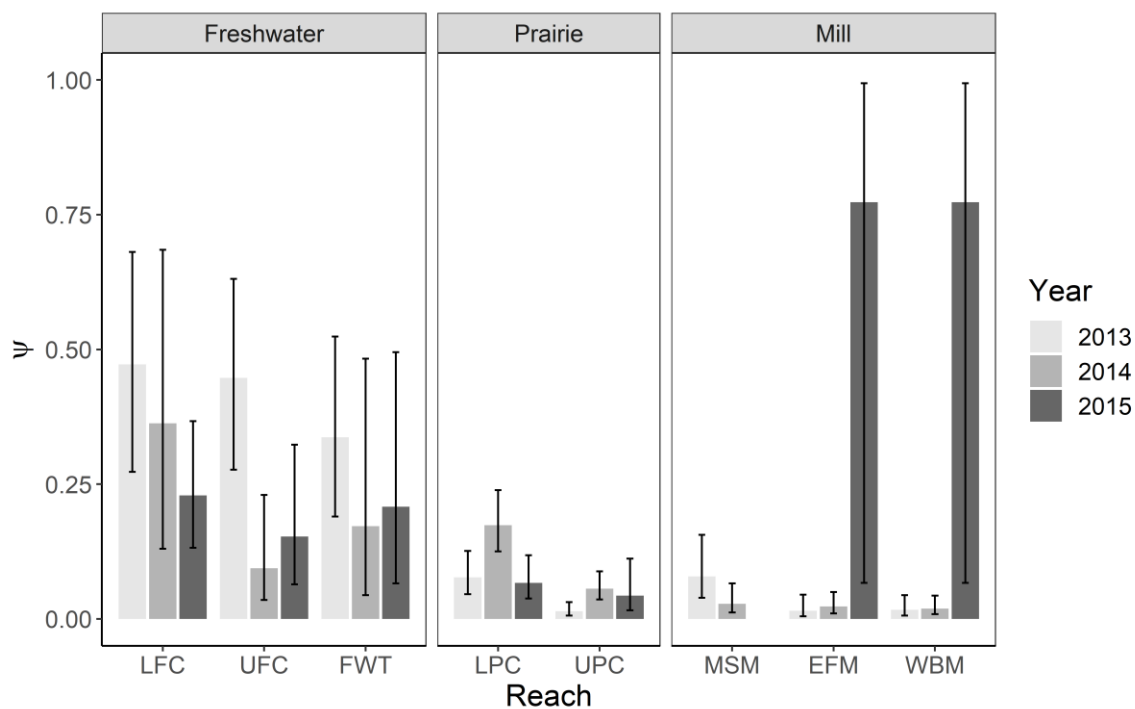
Figure 18. Reach-specific estimates of early emigration (ψ) prior to migrant trap installments in late March of each year with error bars representing 95% CIs, given mean fall fork length values. No fish were marked in Mainstem Mill Creek in 2015; no estimates available. Reach abbreviations are as follows, from left: lower Freshwater Creek (LFC), upper Freshwater Creek (UFC), Freshwater tributaries (FWT), lower Prairie Creek (LPC), upper Prairie Creek (UPC), mainstem Mill Creek (MSM), East Fork Mill Creek (EFM) and West Branch Mill Creek (WBM).
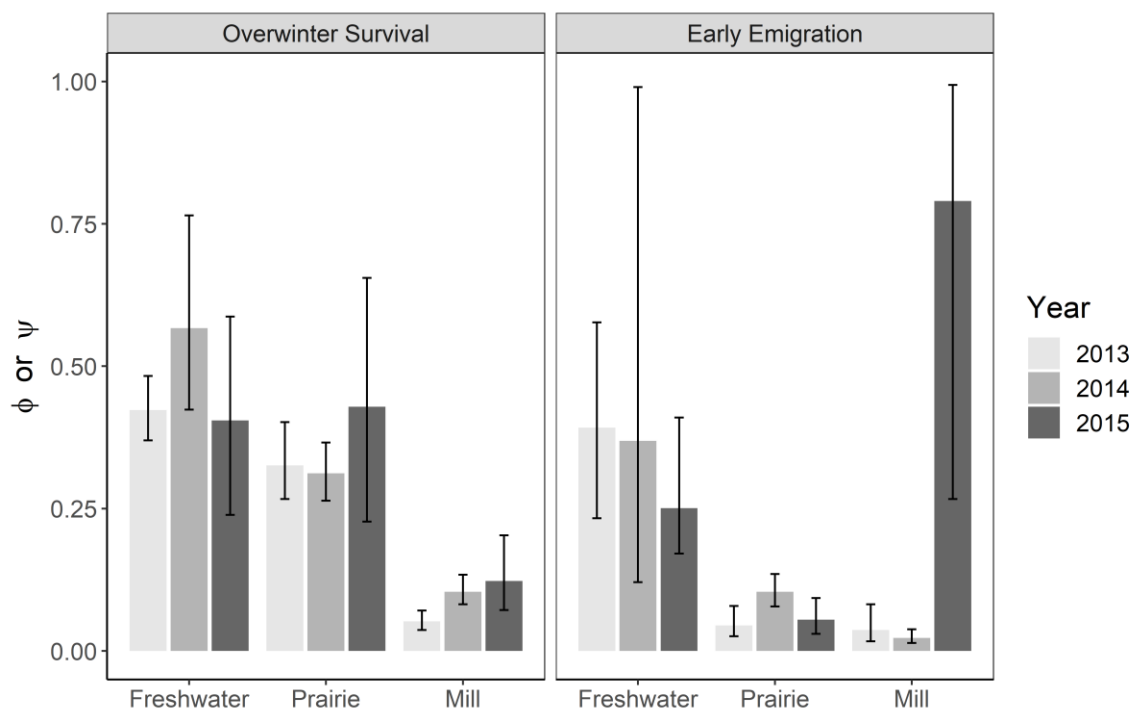
Figure 19. Mean basin-specific parameter estimates and 95% credible intervals of apparent overwinter survival and early emigration rates from the survival and emigration models for each year, given mean fall fork length values. Note that estimates for Mill Creek in 2015 only include the two upstream reaches as no fish were tagged in mainstem Mill Creek that year.

DISCUSSION

This study used a multi-basin modeling approach to answer key questions regarding variations in freshwater habitat used by Coho Salmon populations across a landscape and how the available habitat affects their survival and movement. In contrast to studies that investigate single projects (e.g., sites, reaches or basins) I used mark-recapture modeling and habitat inventories from three basins. This approach provides a means to leverage data from multiple study areas to increase the scope of inference to the region. I formed research questions in hopes to inform stream restoration practices for juvenile Coho Salmon by characterizing their habitat availability, overwinter survival and movement patterns and obtained mixed results. The effects on survival and emigration from the habitat covariates used in the models were not significant and likely muted by other biological or environmental factors. A much clearer picture emerged from evaluating the spatial variability of emigration and survival throughout the study area. This study provides an example of the potential difficulties and successes that can come with such large projects.

Large Woody Debris and Low-Velocity Habitat Effects

Results from this study did not indicate that LWD volume plays a role in apparent overwinter survival or early emigration of juvenile Coho Salmon in northern California streams. Due to the demonstrated effect of LWD on the habitats selected by juvenile Coho Salmon and other stream-dwelling salmonids (Cederholm et al. 1997; Johnson

2005; Roni et al. 2014), it seemed plausible that LWD would have a non-negative effect on survival rates. Although the effects of LWD on stream ecology are numerous and predominantly accepted in the literature as positive, little evidence exists showing positive relationships between LWD and salmonids at a watershed scale (Roni et al. 2014). A recent study by Anderson et al. (2019) showed marked increases in a watershed population due to habitat expansion (i.e., barrier removal), however, only insignificant increases in abundance followed large-scale LWD additions to the stream.

One plausible reason research continues to demonstrate inconsistencies in the value LWD provides to salmonid populations could be that the benefits LWD provides are mostly indirect in nature, such as pool formation (Montgomery et al. 1995), bank/sediment stabilization (Collins et al. 2012), cover from predation (Montgomery et al. 1999), and influences in primary and secondary production (Benke et al. 1985). In these cases, the potential for LWD to benefit a Coho Salmon population would be contingent on other characteristics of the watershed context (i.e., geology, riparian health, predator abundance, or trophic structure). Alternatively, the lack of support for a correlation between LWD and survival in this study could be because instream wood in this area of Northern California was simply not limiting Coho Salmon.

I conducted the LWD surveys in a flexible manner such that the survey results could be categorized in several ways. For example, surveys delivered LWD statistics in number of wood pieces, number of extra-large (XL) wood pieces (i.e., > 60 cm diameter) and volume of wood per km, none of which correlated with another (Figure 7). The XL piece density could have been driven by or correlated to the stream channel size as

suggested by Bilby and Ward (1989), but more likely is due to past land use. Other than in lower Freshwater Creek, the number of pieces per km (minimum size of ≥ 1.0 m long $\times \geq 10$ cm diameter) varied little, largely due to high numbers of small pieces throughout the entire study area. Unsurprisingly, the mean volume per piece was by far the highest in Mainstem Mill Creek and Upper Prairie Creek, the two pristine reaches running through Jedediah Smith Redwoods and Prairie Creek Redwoods State Parks, respectively.

Although I quantified some notable differences in habitat across the study area, the choice of study streams was predicated on the presence of ongoing monitoring programs. It is fair to suggest that the LWD statistics I observed in this study may not accurately reflect the distribution of LWD in Coho Salmon streams in northern California, considering both Mill and Prairie Creek are either pristine or recovering and Freshwater Creek habitat conditions were better than expected. One valuable change to this study would be to include additional basins that support populations of Coho Salmon yet are certain to demonstrate more negatively impacted winter habitat for salmonids. Several other basins in Humboldt Bay have existing Coho populations which could provide a wider range of habitat availability. Including a stream such as Rowdy Creek could be beneficial as a similarly-sized tributary of the Smith River with high intrinsic potential for Coho Salmon that contrasts with its extensive logging history, limited Coho abundance (Walkley and Garwood 2015) and a currently operating anadromous fish hatchery (NMFS 2014). Unfortunately, Coho Salmon populations in streams of this nature are often so suppressed that population monitoring would be more challenging.

LVH and LWD are often functionally linked in that large pieces or accumulations of wood enhance pool formation (Roni and Quinn 2001) and increase channel connectivity to the floodplain via side-channels and backwaters where marginal slack water is common (Collins et al. 2012). However, several other mechanisms also contribute to low-velocity currents such as precipitation patterns, stream gradient, boulder/bedrock protrusions and debris dams. Results from LVH surveys showed that greater areas of slow water were present in each basin's lower reaches while Prairie and Freshwater provided a larger overall proportion of slow water than Mill at velocities $\leq$ 0.1 m•sec^{-1} (Figure 8). The availability of off-channel slow water habitat was highest overall in Mill Creek while lower reaches had larger backwaters than higher reaches.

While the lack of observed LWD effects on Coho Salmon could be due to a limited range of LWD in the study area, it seems likelier that I did not see an effect of LVH due to the data collection methods. For LVH to have an observable effect on Coho survival, or emigration, the velocities at which the data were collected (25th – 50th quartile) would need to be flows at which the habitat limiting factor was experienced. If juvenile Coho are unaffected by the 'typical' winter flows exhibited during data collection, observing no effect would make sense. This could be especially true in reaches like mainstem Mill Creek that are characterized by a narrow valley width and a U-shaped channel. Throughout the majority of mainstem Mill Creek, some of the largest slow-water pools (exceeding 200 m long) during low flows become refugia-less torrents from bank to bank at peak discharge—conditions which may leave rearing Coho little choice but to vacate. Models designed to estimate shorter-term survival over a wide range

of water velocity or discharge would provide valuable information for prescribing future restoration techniques or recovery strategies.

Spatial Variation in Survival and Emigration

I estimated apparent overwinter survival and early emigration by reach to assess the variability in survival and emigration throughout the study area. In previous studies on Prairie Creek (Drobny 2016) and Freshwater Creek (Hauer 2013; Rebenack et al 2015), higher survival occurred in upstream reaches compared to downstream reaches, but this was not observed in my study. Rebenack et al. (2015) also observed higher early emigration from lower Freshwater Creek reaches in some years. I observed a similar pattern in this study, although the posterior credible intervals showed considerable overlap among reaches (Figure 19).

While the variation observed within basins in apparent overwinter survival and emigration was expected, the variability among basins was much more surprising. Throughout the study, Mill Creek exhibited significantly reduced apparent survival estimates (3.6–15.4%) compared to Prairie (22.8–44.9%) and Freshwater Creek (23.1–61.6%). Although apparent overwinter survival has never been estimated for Coho Salmon in Mill Creek, previous survival rates estimated at 36% (Brakensiek and Hankin 2007), 39% (Moore 2014) and 35% (Drobny 2016) in Prairie Creek and from 13-49% (Rebenack et al. 2015) in Freshwater Creek fit within a similar range. Given the number of previous studies suggesting some populations of juvenile Coho Salmon are limited by winter habitat (e.g., Nickelson et al. 1992, Solazzi et al. 2000; Gallagher et al. 2012), it is

possible Coho in this study were limited by certain habitat features not documented during LWD and LVH surveys (e.g., habitat complexity, off-channel rearing access). Alternatively, low apparent survival in Mill Creek (as well as high early migration) could be partly due to biological responses (e.g., limited food sources, density dependence), ecological pressures (e.g., predation) or fluvial geomorphic conditions (e.g., discharge, stream gradient). However, since mortality and emigration are confounded in the CJS models, low apparent survival in Mill Creek could instead be biased low, especially given the exceptionally high early emigration rates observed.

Since apparent survival estimates are based on the joint probability that an individual does not emigrate early and survives the winter period, the consistently low survival estimates from Mill Creek suggests either (1) juvenile Coho Salmon mortality in Mill Creek was higher during winter, (2) more fish in Mill Creek emigrated early or (3) a combination of both. Knowing undetected early emigrants can bias apparent overwinter survival estimates low, the surprisingly low survival estimates from Mill Creek in year 1 and 2 motivated expectations of high early emigration rates from the basin. Yet, this was not the case, as shown by the estimated mean emigration rates of 1.5–7.9% in Mill Creek—easily the lowest rates from any basin. The low apparent overwinter survival and early emigration estimates obtained from the same years in Mill Creek were peculiar outcomes when examined together. Coho Salmon populations which already endure low ocean survival rates must have a reasonable outmigrant population to maintain independent existence. Additional antennas installed before year 3 were necessary to uncover bias from year 1 and 2.

In year 3, two new antennas were installed approximately 7 and 10 miles downstream from the mouth of Mill Creek in two small tributaries to the lower Smith River. The detection results from these antennas were overwhelming. 96 of the 821 (11.7%) total Coho Salmon marked in Mill Creek in the fall of 2015 were detected on the additional antennas during fall and winter, of which only 2 were previously detected on the original Mill Creek antennas. Because these new antennas were in small tributaries outside of Mill Creek, it seems likely the antennas detected only a small subsample of tagged fish. The importance of these findings was invaluable in evaluating the early emigration and survival biases in Mill Creek during the first two study years.

Adding the new antennas provided greater independence between capture occasions than the previous method of separating one antenna array into two capture occasions, increasing confidence and reducing bias in the early emigration estimates. This change was partially due to a sharp increase in detection probability at the new antennas. The extreme caution exercised in interpreting early emigration results from Mill Creek in the first two years could be relaxed in 2016. Utilizing the new antennas as a final capture occasion in the early emigration model also resulted in the model estimating a much higher early emigration probability (77.3%) in Mill Creek in 2015 compared with 2013 (3.7%) and 2014 (2.3%). This suggests that antenna performance in Mill Creek during years 2013 and 2014 either (1) failed the assumption of independence among capture occasions at the original antennas (occasions 2 and 3 in the early emigration model), (2) failed to detect marked fish at a high enough rate to estimate parameters accurately, or (3) a combination of both. Future researchers planning to use multiple PIT

tag antennas in CJS or multistate mark-recapture models should ensure that any two antennas forming consecutive capture occasions are far enough apart that detection of tags by each antenna is independent of one another.

Additional antennas were located in Mill Creek (Figure 2), Prairie Creek (Figure 3) and Freshwater Creek (Figure 4) at the downstream end of each reach, which detected individuals emigrating from their original tagging reach. Due to the upstream locations of these antennas and their inconsistent placement among basins, their detections could not be incorporated into the CJS model structure. Nonetheless, a comparison of early versus spring detections as proportions of total individuals detected revealed a similar pattern across reaches and watersheds each year. Coho Salmon reach fidelity in Mill Creek appeared lower than Prairie and Freshwater Creeks every year suggesting Mill fish were consistently more likely to leave their tagging locations before spring (Table 9).

Parish and Garwood (2016) detected juvenile Coho Salmon from Mill Creek using off-channel habitats along the mainstem Smith River during winter and spring. One explanation for this pattern could be that fish traveling a greater distance from natal rearing grounds to the ocean (approx. 24 km) must depart earlier to ensure a timely ocean arrival. Conversely, Prairie Creek is just over three miles from the ocean with minimal off-channel rearing opportunities in lower Redwood Creek. Freshwater Creek is more difficult to define in distance from the ocean as tidal surges from Humboldt Bay push into the lower watershed, yet, juveniles still must travel more than 12 miles through brackish sloughs and the bay to reach the open ocean. My hypothesis that habitat availability in natal rearing areas is a primary driver for early emigration (or fidelity) is

Table 9. Comparison of juvenile Coho Salmon counts by basin and reach detected leaving their tagging reach each year before March 15th (n_e) or during spring (n_s). Values for early detection greater than 50% indicate more individuals were detected leaving their tagging reach early than during spring. Note that percentages were calculated from raw detections and do not account for survival or detection probabilities.

Year	BASIN Reach	Fall Tagged Coho	Early Detections (n_e)	Spring Detections (n_s)	% Early Detection $n_e/(n_e+n_s)$
2013	MILL CREEK	1431	102	69	59.6%
	East Fork Mill	472	24	33	42.1%
	West Branch Mill	491	37	27	57.8%
	Mainstem Mill	468	41	9	82.0%
	PRAIRIE CREEK	637	95	215	30.6%
	Upper Prairie Creek	447	80	193	29.3%
	Lower Prairie Creek	190	15	22	40.5%
	FRESHWATER CREEK	705	182	232	44.0%
	Freshwater Tributaries	191	47	87	35.1%
	Upper Freshwater	293	82	78	51.3%
	Lower Freshwater	221	53	67	44.2%
2014	MILL CREEK	1385	73	83	46.8%
	East Fork Mill	467	31	34	47.7%
	West Branch Mill	550	30	41	42.3%
	Mainstem Mill	368	12	8	60.0%
	PRAIRIE CREEK	718	126	149	45.8%
	Upper Prairie Creek	441	78	107	42.2%
	Lower Prairie Creek	277	48	42	53.3%
	FRESHWATER CREEK	500	98	181	35.1%
	Freshwater Tributaries	105	13	41	24.1%
	Upper Freshwater	170	35	66	34.7%
	Lower Freshwater	225	50	74	40.3%
2015	MILL CREEK	821	112	81	58.0%
	East Fork Mill	415	69	32	68.3%
	West Branch Mill	406	43	49	46.7%
	Mainstem Mill	0	N/A	N/A	N/A
	PRAIRIE CREEK	504	38	94	28.8%
	Upper Prairie Creek	241	9	66	12.0%
	Lower Prairie Creek	263	29	28	50.9%
	FRESHWATER CREEK	329	61	61	50.0%
	Freshwater Tributaries	61	10	12	45.5%
	Upper Freshwater	107	17	25	40.5%
	Lower Freshwater	161	34	24	58.6%

not disputed by the results in this study. However, it is unclear if fish are more likely to emigrate in response to adverse conditions in their natal rearing habitat (e.g. stream channelization, limited high flow refuge, poor habitat complexity, etc.) or following a predisposition to rear elsewhere.

Other studies on juvenile Coho Salmon movement suggest early emigration could be a response to a suite of conditions (Koski 2009) including fish density (Chapman 1962), fish size (Rebenack 2015), food availability (Mason 1976), habitat preference (Kahler et al. 2001) and fish location within the watershed (Roni et al. 2012; Rebenack 2015). The variation of emigration rates in this study was partly explained by size (i.e., fork length) at tagging in 2015 (Figure 14) while relationships with LWD and LVH were not detected. Taking into account the correlation fish size had with early emigration while considering the previously observed relationship between early emigration and reach (Hauer 2013) with supporting evidence from this study, the results suggest that the farthest downstream and smallest juvenile Coho Salmon are most likely to emigrate early. This evidence supports other recent research in Freshwater Creek, where VanVleet (2019) observed a strong negative relationship between Coho Salmon fall fork length and early migration using a multistate model. While a lot remains to be learned regarding how habitat affects the migratory behavior of Coho Salmon in California, the variability in basin-specific emigration I observed underscores the importance of using a multi-basin study design. In this case, analyzing survival or emigration by reach in only Mill Creek would have produced merely incidental or irrelative results. With a few exceptions, the three coastal watersheds included in this study exhibit relatively similar physical

conditions. They range from 92.3 to 103 km^2 in watershed area and span only 75 miles of latitude from Mill Creek to Freshwater Creek, making it somewhat surprising to observe such variable apparent survival and early emigration rates. One difference that I observed was that the natal rearing habitat data collected throughout each basin shows a smaller proportion of low-velocity rearing area in Mill Creek than in Prairie Creek and Freshwater Creek. Not only is this difference apparent at the basin levels (Figure 8), but the pattern persists within reaches as well (Figure 9). This is one potential explanation for the lower survival and higher early emigration rates observed in Mill Creek, but further research is necessary to determine if other differences exist between these three basins that may also contribute to increased mortality and movement. For example, Coho Salmon in Mill Creek may be driven out of natal rearing habitats or experience poorer survival due to interspecific competition with higher densities of juvenile Chinook Salmon in the fall. Chinook Salmon occupied pools in West Branch (49% occupancy), East Fork (25%) and mainstem Mill Creek (45%) during CDFW snorkel surveys from June to September in 2014 (Walkley and Garwood 2015) while Upper Prairie Creek was unoccupied (0% occupancy) by Chinook the same year (Moore and Wilzbach 2016) and Freshwater rarely sees more than a handful of Chinook spawners each winter (Ricker and Anderson, 2011). Identifying the factors that drive the lower survival and earlier emigration in Mill Creek may guide managers on what aspects of rearing habitat are most important for restoration in the southern range of Coho Salmon.

Connecting Apparent Overwinter Survival and Early Emigration

While the apparent overwinter survival and early emigration models were analyzed independently, the two processes remain fundamentally linked. Given that fish which choose to emigrate early inherently negate themselves as 'apparent survivors', apparent overwinter survival can be described as function of early emigration. For this reason, it is important to emphasize the shortcomings of estimating apparent overwinter survival before using it as a tool for research or species management.

First, the estimate for overwinter survival is inherently biased low because the death or emigration of individuals cannot be estimated separately. In other words, if early emigration is substantial and the early emigrants survive, apparent survival will be biased low. For example, the estimate for apparent overwinter survival from this study in 2015 for Mill Creek was 12.3% (95% CI: 7.2-20.3%). It can safely be expected that true survival was no less than the lower credible interval 7.2%, but we cannot say with certainty what proportion of the remaining 91.8% of fish died or emigrated.

Using the same data, the early emigration model for Mill Creek in 2015 estimated 77.3% (95% CI: 26.7-99.4%) of fish emigrated early. In this model, the confounded parameters change, where instead, mortality is confounded with not emigrating (i.e., staying). In this case, whether fish that stay live or die has no bearing on the "early" emigration process, making early emigration unbiased with respect to movement and survival. Knowing this, useful suggestions can still be made such as "approximately 89.6% of fish survived to emigrate early (77.3%) or in the spring (12.3%) while the

remaining 10.4% perished at some point during the study." The main drawback in this formulation is that the survival of the 77.3% early emigrants is unknown and can only be estimated with additional capture occasions after spring. This weakness may be problematic for certain study designs which raises an important question: How can we best untangle Coho Salmon survival and emigration when their migratory behavior differs so variably in time and in space?

The answer depends how one wants to define overwinter survival. If the interest is in the number of juveniles that make it out of the basin alive, simply adding the survival and emigration rates together could be sufficient, as done by Roni et al. (2012) and Hauer (2013). If the research interests are in the survivorship of only fish that stay until spring (i.e., do not emigrate early) the use of a multi-state model could aid in estimating emigration as a transition probability while simultaneously estimating overwinter survival. Under this model construct, overwinter survival and early emigration can be uncoupled by including the additional parameter, transition probability, yielding an estimate of 'true' survival (Cooch and White 2014), yet this method does not come without drawbacks. Multi-state models intrinsically require more data to estimate a greater number of parameters, especially in cases with low probabilities of detection (Kéry and Schaub 2012) like in Mill Creek. Unfortunately, increasing detection probability can be very costly, requiring more detection points (e.g., PIT tag antennas, migrant traps, etc.) or more rigorous sampling designs (e.g., repeat sampling throughout the winter period). Adding these components to multi-basin studies may further reduce

feasibility by requiring multiple monitoring groups to meet (or afford) certain fish monitoring standards.

Another way to estimate overwinter survival of spring emigrants could be by (1) generating early emigration estimates as done with a CJS model in this study, (2) removing a proportion of fish from the overwinter survival capture history equal to the estimated probability of early emigration, and (3) running the CJS model to estimate survival with the reduced capture history. This method could provide a feasible and cost-effective way to estimate survival of the fish overwintering in freshwater for anyone that has the minimum infrastructure necessary (e.g., two year-round PIT tag antennas and one spring migrant trap). In the end, maybe the most appropriate way to report estimates is to simply provide apparent overwinter survival and early emigration estimates separately for each cohort, giving the reader the freedom to choose a method for interpretation that best suits their needs.

This study demonstrates several advantages gained by incorporating multiple basins into Coho Salmon population studies which include providing a relative scale for evaluating population demographics and extending inference outside of the study area. While the spatial variability in "true" overwinter survival remains unclear, the variability in emigration timing that exists in California Coho Salmon populations appears to be significant. Nevertheless, more research is needed to determine whether early emigration is due to forced displacement from high flows, a life history trait, a density dependent choice or multiple factors. It is also not clear how outmigration timing affects marine survival and escapement.

In the end, my findings regarding inter-basin variability in Coho Salmon survival and movement suggest that the scale of management currently used for California populations could be too broad. Given that Coho Salmon populations in such close proximity can exhibit drastic differences in life histories patterns, additional research with multi-basin components may help determine how to plan restoration more effectively from local to regional scales.

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APPENDIX A

Appendix A: Geometric mean volumes for each size class of large woody debris collected in Mill, Prairie and Freshwater Creeks in summer 2014. Geometric mean volumes were estimated from measurements of more than 75,000 pieces of large woody debris collected by the U.S. Forest Service in Oregon and Washington. The volume formula developed by Rentmeester (2014) calculates the geometric mean cylindrical volume of LWD pieces within each size class.

Size class (diameter-length)	Diameter (cm)	Length (m)	Geometric mean[a] volume (m^3)
Small-small	10-15cm	1-3m	0.02035
Small-medium	10-15cm	3-6m	0.04878
Small-large	10-15cm	6-15m	0.10758
Medium-small	15-30cm	1-3m	0.05981
Medium-medium	15-30cm	3-6m	0.15101
Medium-large	15-30cm	6-15m	0.40012
Large-small	30-60cm	1-3m	0.22887
Large-medium	30-60cm	3-6m	0.57739
Large-large	30-60cm	6-15m	1.72582

APPENDIX B
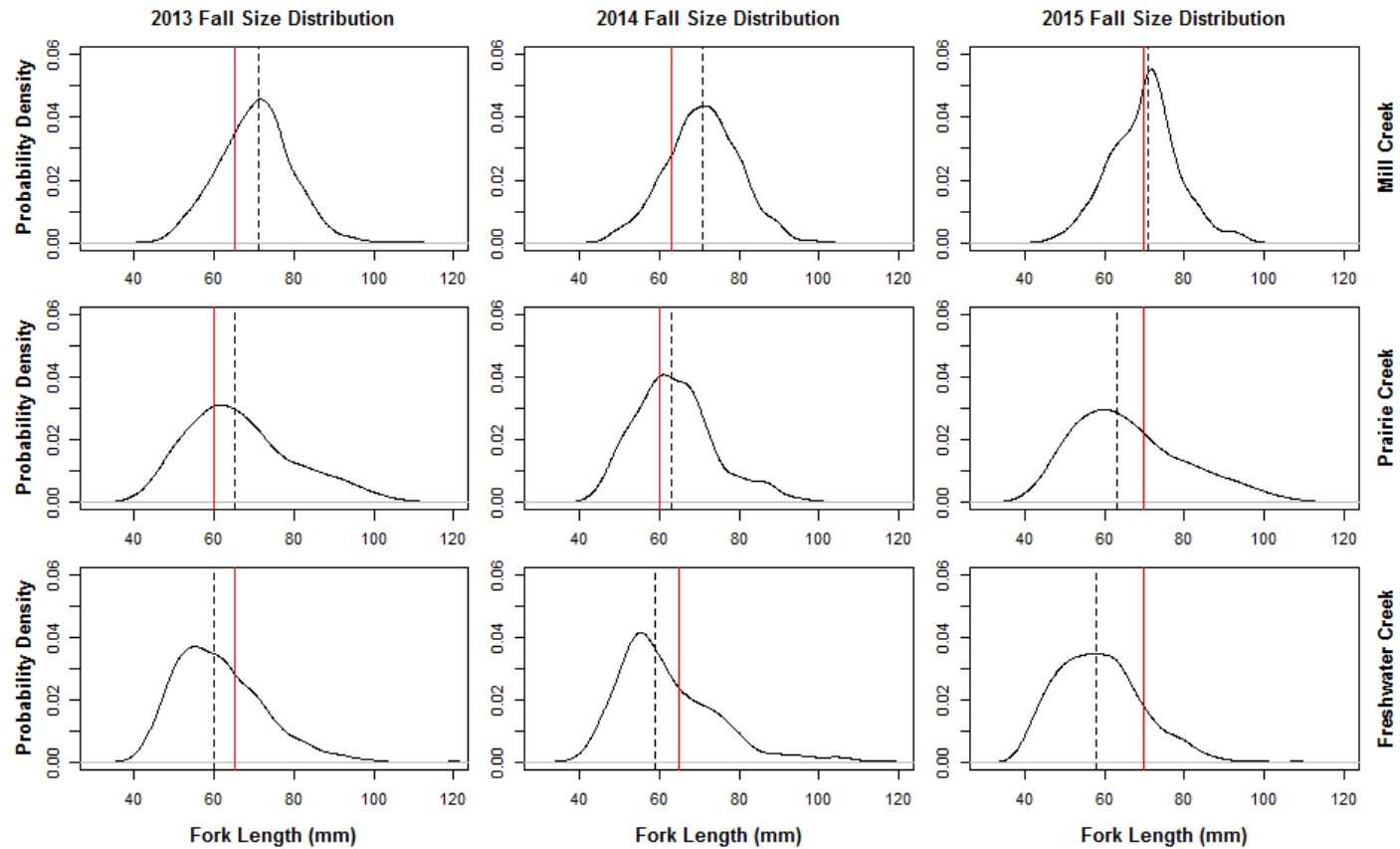
Appendix B: Probability density distributions of fork length for Coho Salmon populations based on random sampling during fall tagging for each year in each basin. Years are labeled at the top of each column. Basins are labeled at the far right of each row. The dotted black line shows the mean fish size. The solid red line shows the lower size limit for tagging Coho Salmon each season.

APPENDIX C

Appendix C: M-array table of data used for apparent overwinter survival model showing number of fish tagged and recaptured by occasion, basin (in bold) and reach during the 2013 season.

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| Release Occasion | Tag Origin | Number Released (R_i) | Recapture Occasions | | Total Recaptured (r_i) | Never Recaptured ($R_i - r_i$) |
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
Fall Tagging (Occasion 1)	**Mill Creek**	**1442**	**43**	**64**	**88**	**1354**
	East Fork Mill	472	19	22	31	441
	West Branch Mill	493	19	17	28	465
	Mainstem Mill	477	5	25	29	448
	Prairie Creek	**639**	**113**	**102**	**169**	**470**
	Upper Prairie	447	89	67	122	325
	Lower Prairie	192	24	35	47	145
	Freshwater Creek	**705**	**152**	**275**	**343**	**362**
	Freshwater Tribs	191	43	83	100	91
	Upper Freshwater	293	57	101	127	166
	Lower Freshwater	221	52	91	116	105
Antenna Array (Occasion 2)	**Mill Creek**	**43**		**19**	**19**	**24**
	East Fork Mill	19		10	10	9
	West Branch Mill	19		8	8	11
	Mainstem Mill	5		1	1	4
	Prairie Creek	**113**		**46**	**46**	**67**
	Upper Prairie	89		34	34	55

Release Occasion	Tag Origin	Number Released (R_i)	Recapture Occasions		Total Recaptured (r_i)	Never Recaptured ($R_i - r_i$)
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
	Lower Prairie	24		12	12	12
	Freshwater Creek	**152**		**84**	**84**	**68**
	Freshwater Tribs	43		26	26	17
	Upper Freshwater	57		31	31	26
	Lower Freshwater	52		27	27	25

APPENDIX D

Appendix D: M-array table of data used for apparent overwinter survival model showing number of fish tagged and recaptured by occasion, basin (in bold) and reach during the 2014 season.

| Release Occasion | Tag Origin | Number Released (R_i) | Recapture Occasion | | Total Recaptured (r_i) | Never Recaptured ($R_i - r_i$) |
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
Fall Tagging (Occasion 1)	**Mill Creek**	**1385**	**86**	**73**	**129**	**1256**
	East Fork Mill	467	42	32	58	409
	West Branch Mill	550	37	27	53	497
	Mainstem Mill	368	7	14	18	350
	Prairie Creek	**718**	**102**	**181**	**220**	**498**
	Upper Prairie	441	50	99	120	321
	Lower Prairie	227	52	82	100	127
	Freshwater Creek	**500**	**92**	**117**	**182**	**318**
	Freshwater Tribs	105	23	24	41	64
	Upper Freshwater	170	33	36	59	111
	Lower Freshwater	225	36	57	82	143
Antenna Array (Occasion 2)	**Mill Creek**	**86**		**30**	**30**	**56**
	East Fork Mill	42		16	16	26
	West Branch Mill	37		11	11	26
	Mainstem Mill	7		3	3	4
	Prairie Creek	**102**		**63**	**63**	**39**

Release Occasion	Tag Origin	Number Released (R_i)	Recapture Occasion		Total Recaptured (r_i)	Never Recaptured ($R_i - r_i$)
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
	Upper Prairie	50		29	29	21
	Lower Prairie	52		34	34	18
	Freshwater Creek	**92**		**27**	**27**	**65**
	Freshwater Tribs	23		6	6	17
	Upper Freshwater	33		10	10	23
	Lower Freshwater	36		11	11	25

APPENDIX E

Appendix E: M-array table of data used for apparent overwinter survival model showing number of fish tagged and recaptured by occasion, basin (in bold) and reach during the 2015 season.

| Release Occasion | Tag Origin | Number Released (R_i) | Recapture Occasion | | Total Recaptured (r_i) | Never Recaptured ($R_i - r_i$) |
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
Fall Tagging	**Mill Creek**	**821**	**43**	**36**	**69**	**752**
(Occasion 1)	East Fork Mill	415	19	21	33	382
	West Branch Mill	406	24	15	36	370
	Mainstem Mill	0	0	0	0	0
	Prairie Creek	**504**	**36**	**87**	**110**	**394**
	Upper Prairie	241	14	49	57	184
	Lower Prairie	263	22	38	53	210
	Freshwater Creek	**329**	**43**	**99**	**117**	**212**
	Freshwater Tribs	61	16	18	25	36
	Upper Freshwater	107	12	33	39	68
	Lower Freshwater	161	15	48	53	108
Antenna Array	**Mill Creek**	**43**		**10**	**10**	**33**
(Occasion 2)	East Fork Mill	19		7	7	12
	West Branch Mill	24		3	3	21
	Mainstem Mill	0		0	0	0
	Prairie Creek	**36**		**13**	**13**	**23**

| Release Occasion | Tag Origin | Number Released (R_i) | Recapture Occasion | | Total Recaptured (r_i) | Never Recaptured ($R_i - r_i$) |
			Antenna Detection (Occasion 2)	Migrant Trap (Occasion 3)		
	Upper Prairie	14		6	6	8
	Lower Prairie	22		7	7	15
	Freshwater Creek	**43**		**25**	**25**	**18**
	Freshwater Tribs	16		9	9	7
	Upper Freshwater	12		6	6	6
	Lower Freshwater	15		10	10	5