INFLUENCE OF BODY SIZE, INTRA-AND INTER- SPECIFIC SALMONID

DENSITIES, AND HABITAT ON OVERWINTER SURVIVAL OF JUVENILE COHO

SALMON (*ONCORHYNCHUS KISUTCH*) IN PRAIRIE CREEK, CALIFORNIA

By

Peter Drobny

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Fisheries

Committee Membership

Dr. Margaret Wilzbach, Committee Chair

Dr. Darren Ward, Committee Member

Dr. Nicholas Som, Committee Member

Dr. Bret Harvey, Committee Member

Dr. Alison O'Dowd, Graduate Coordinator

May 2016

ABSTRACT

INFLUENCE OF BODY SIZE, INTRA-AND INTER- SPECIFIC SALMONID
DENSITIES, AND HABITAT ON OVERWINTER SURVIVAL OF JUVENILE COHO
SALMON (*ONCORHYNCHUS KISUTCH*) IN PRAIRIE CREEK, CALIFORNIA

Peter Yale Drobny

I evaluated the effects of fish length, habitat attributes, and densities of Coho
Salmon and trout on overwinter survival of juvenile Coho Salmon in Prairie Creek,
California. Survival of PIT tagged juvenile Coho Salmon was estimated using a
Cormack-Jolly-Seber Model based on mark-recapture data from seine net captures, PIT
tag antenna detections, and a rotary screw trap. A zero inflated Poisson binomial model,
based on a 2-pass snorkeling methodology, estimated pool-specific abundance of juvenile
Coho Salmon while accounting for variable snorkeler detection efficiency as well as
estimating the effect of habitat attributes on density. Trout densities were obtained using
raw snorkel counts.

Overwinter survival of PIT tagged juvenile Coho Salmon during 2014-2015 was
estimated to be 0.35 (95% CI 0.30-0.40), similar to survival estimates for Prairie Creek in
previous years. Survival increased with fish length and decreased with intraspecific
density. There was no evidence that density of small (<150 mm) trout, large (>150 mm)
trout, or habitat attributes influenced survival. Estimated density of juvenile Coho
Salmon in pools averaged 0.5 fish/m^2 (n= 159) and ranged from 0- 2.2 fish/m^2, consistent

with regional density values within the Pacific Northwest. Juvenile Coho Salmon density estimates declined with cover complexity and watershed area, and increased with pool depth. Probability of detecting a fish while snorkeling varied with habitat features and among observers; estimated probability of detection averaged 0.63 (n=318) and ranged from 0.19 to 0.96 across snorkel passes.

This study not only continued valuable monitoring of juvenile Coho Salmon overwinter survival in the southern portion of their range, but also determined factors that may be contributing to survival rates. In addition, this study successfully applied a relatively new hierarchical modeling technique (N-mixture model) to estimate juvenile Coho Salmon densities using non-invasive methods.

ACKNOWLEDGEMENTS

Scheer, Justin Alverez, Sam Rizza, and others. I would also like to thank my wonderful

girlfriend, parents, and sister for all their support during this time.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Overwinter survival of juvenile Coho Salmon (*Oncorhynchus kisutch*) in fresh

water is believed to play a crucial role in affecting their abundance in the Pacific

Northwest (NRC 1996, Nickelson and Lawson 1998, Brakensiek and Hankin 2007,

Gallagher et al. 2012). While ocean conditions have been assumed to more strongly

drive variability in population abundance of Coho Salmon than does the freshwater

environment (Gallagher et al. 2012), freshwater conditions may be more critical in setting

the upper bound of population abundance if freshwater survival is density dependent.

Although summer water temperatures and habitat volume during summer low flows can

limit production of juvenile Coho Salmon (e.g. Lawson et al. 2004), several studies in

coastal Oregon streams presented experimental evidence that a shortage of slow-water

habitat during winter high flows posed a particular bottleneck, resulting in juvenile

mortality (Nickelson et al. 1992a, Solazzi et al. 2000, Johnson et al. 2005).

Understanding the factors that drive overwinter survival and growth across the

Coho Salmon range is important for making conservation and restoration decisions.

Among the environmental variables that may affect survival and growth of Coho Salmon

parr in streams are water temperature (Giannico and Hitch 2003), discharge (Gallagher et

al. 2012), turbidity (Gregory and Levings 1998); habitat characteristics that provide cover

from predation and/or velocity refuges (Pess et al. 2011, Gallagher et al. 2012) and food

availability (Rosenfeld et al. 2005, Pess et al. 2011). In many watersheds across the

range of Coho Salmon, historical land use practices have led to a significant reduction in

winter habitat (Brown et al. 1994, Katz et al. 2013). Slow-water refuge habitat during winter floods, often associated with habitat complexity (Fausch and Northcote 1992, Crispin et al. 1993), is thought to be a large driver of survival (Quinn and Peterson 1996, Nickelson and Lawson 1998, NMFS 2014). Some examples of winter refuge habitat include alcoves, side channels, floodplain ponds, back waters, beaver ponds, and deep rootwad-formed pools. Slow-water habitat is thought to provide shelter from high discharge events which have been suggested to increase mortality in high flows (Erman et al. 1988, Bell et al. 2001, Gallagher et al. 2012). Bell et al. (2001) showed increased use of winter refuge habitat in Prairie Creek, California during high flow events. There is evidence that higher flows can cause fish displacement (Bell et al. 2001), increase energetic costs (Piccolo et al. 2008), and cause direct mortality through physical crushing by bed load transport (Erman et al. 1988).

In undisturbed streams a better understanding of the relative importance of different causal factors potentially affecting salmon productivity is a key step towards an appropriate management response to current and potential future declines in productivity (Ly et al. 2011). The creation of slow water habitat through the use of large woody debris (LWD) structures is in large use across the Pacific Northwest to restore fish habitat in historically degraded streams (Roni and Quinn 2001, Bernhardt et al. 2005, NMFS 2014). In historically degraded Washington and Oregon streams, large wood and other structure has been shown to increase the quantity and depth of pool habitats (Roni and Quinn 2001, Sharma and Hilborn 2001). Both LWD and pool habitat has been associated with higher densities and increased survival of Coho Salmon (Solazzi et al. 2000,

Johnson et al. 2005, Pess et al. 2011, Roni et al. 2012). In more pristine streams such as

Prairie Creek in Northern California it may be that creation of more winter habitat

through the addition of large wood or other structures would not be beneficial, as

historical habitat degradation in the watershed is relatively low. Because of this, other

factors may be limiting to Coho Salmon such as inter- or intra- density dependent

processes for food availability or predation risk. Although extensive studies have

documented the need for increased habitat complexity in systems with historic resource

exploitation (e.g. logging, mining, etc.), it may be that habitat characteristics play a less

critical role on survival variability in more pristine and intact systems.

As in other locations within the Pacific Northwest (Quinn and Peterson 1996,

Ebersole et al. 2006, Pess et al. 2011), overwinter survival of juvenile Coho Salmon in

Prairie Creek has been found to increase with body size in late summer and fall

(Brakensiek 2002, Brakensiek and Hankin 2007, Moore 2014, Sparkman et al. 2015).

Size survival relationships can be driven by both density dependent or non-density

dependent processes. Body size could be related to survival through size-selective

predation (Parker 1971, Duffy and Beauchamp 2008), because large fish have higher

energy reserves (Simpkins et al. 2004), because small fish aren't as strong of swimmers

(Bainbridge 1958) and get washed out in floods, and other non-competitive mechanisms.

Both size of fish and density of fish have been shown to influence survival and at times

fish size and fish density are linked as well (Roni and Quinn 2001) suggesting the

possibility of complex interactions between fish size, density, and survival. It has been

documented that juvenile salmonids generally avoid sharing shelter with conspecifics

(Cunjak 1988; Gregory and Griffith 1996; Armstrong and Griffiths 2001). In the presence of conspecific competitors, the smallest fish are often displaced from structure or shelter by the largest fish (Harwood et al. 2002; Orpwood et al. 2003). This could explain the commonly observed positive size-survival trends (Moore 2014, Sparkman et al. 2015) if displacement (Bell et al. 2001) or predation (Dolloff 1993) consistently caused mortality for smaller fish that were not able to associate with structure. Similarly, because juvenile Coho Salmon are drift feeders, competition for feeding zones may be size dependent as smaller fish may be pushed to the margins through territorial and aggressive behavior of larger dominant fish (Rosenfeld et al. 2005). This exclusion from quality feeding zones could lead to a lack of growth opportunities and decrease their ability to compete as higher growth of juvenile Coho Salmon has been observed in dominant territorial individuals relative to non-territorial individuals (Martel 1996).

Several studies have suggested an effect of intra-specific density dependence on growth (Rosenfeld et al. 2005), habitat use (Young 2004, Rosenfeld et al. 2005, Roni et al. 2012) and survival (Gallagher et al. 2012, Wright et al. 2012) of rearing juvenile Coho Salmon. Density dependence is created through negative feedback mechanisms that regulate abundance through competition for resources. Although it can be difficult to identify exact density dependent mechanisms within a specific stream, feeding behavior (Glova 1986), movement patterns (Roni et al. 2012), predator avoidance behavior (Achord et al. 2003), habitat use (Young 2004, Rosenfeld et al. 2005, Roni et al. 2012), and fish growth (Rosenfeld et al. 2005) are some examples of density dependent processes that may arise. Density dependent disease and parasitism of juvenile salmonids

have also been known to decrease growth and survival (Urawa 1995). Even in streams with reduced carrying capacity due to degraded habitat, density dependent processes may be the mechanism which drive the observed trends between habitat and survival (Achord et al. 2003).

Densities of other juvenile salmonid species may affect growth and survival of juvenile Coho Salmon through competition (e.g. Fraser 1969, Harvey and Nakamoto 1996, Young 2004). However, in reviewing the literature, Milner et al. (2003) found more frequent evidence for intraspecific than interspecific effects on Atlantic Salmon, and concluded that the niche separation among juvenile salmonid species is often sufficient to reduce interspecific competition relative to intraspecific competition.

While inter-specific density competition may be low relative to intra-specific competition, predation by larger trout on juvenile Coho Salmon has been observed (Nowak et al. 2004, Duffy and Beauchamp 2008, Duffy et al. 2011). Studies have shown that larger, predatory Cutthroat Trout *O. clarkii* select deeper habitats with more cover (Heggenes et al. 1991) usually associated with preferred Coho Salmon winter rearing habitat. Direct interaction, predation or competitive risk can alter behavior patterns such as habitat use and feeding behavior (Rosenfeld et al. 2005) which could indirectly effect growth and mortality rates.

The objectives of my study are to: 1) Estimate salmonid densities within pools in late summer and evaluate the relationship between habitat attributes and fish density; 2) estimate late summer and overwinter growth of juvenile Coho Salmon; and 3) estimate juvenile Coho Salmon overwinter survival and evaluate the contributing effect of body

size of juvenile Coho Salmon, habitat features (pool depth, cover complexity, abundance

of LWD, and watershed area), and late summer densities of conspecifics and trout.

STUDY SITE

Prairie Creek drains a 102.5-km^2 watershed situated almost entirely within the boundaries of Redwood National and State Parks in coastal northern California (Cannata et al. 2006). Prairie Creek flows into Redwood Creek near the town of Orick, CA. Much of the upper watershed of Prairie Creek is forested by pristine old growth coast redwood *Sequoia sempervirens* and Sitka spruce *Picea sitchensis*. The lower watershed has been protected from anthropogenic land uses since the expansion of Redwood National Park boundaries in 1978, but was impacted by unregulated logging, road-building, and agricultural activities prior to that time. Extensive restoration to revegetate denuded slopes and remove logging roads in the lower watershed has been on-going since 1978. Riparian tree species common to the entire watershed include tanoak *Lithocarpus densiflorus*, big-leaf maple *Acer macrophyllum*, Douglas-fir *Pseudotsuga menziesii,* and red alder *Alnus rubra*.

The watershed supports four species of salmonids including Chinook salmon *O. tshawytscha*, Coho Salmon, steelhead trout *O. mykiss*, and Cutthroat Trout. All but Cutthroat Trout within the watershed are federally listed as threatened (NOAA 2011). Other fish species present in the watershed include Sacramento Sucker *Catostomus occidentalis,* Threespine Stickleback *Gasterosteus aculeatus,* Prickly Sculpin *Cottus asper,* Coastrange Sculpin *C. aleuticus*, Pacific Lamprey *Lampetra tridentata,* and Pacific Brook Lamprey *L. richardsoni* (Brakensiek and Hankin 2007).

The climate of the study area is characterized by dry, foggy summers and rainy winters with average annual rainfall of 177 cm. Mild climate and stable temperatures are maintained due to the close proximity of the Pacific Ocean (Janda et al. 1975). In this study period the prolonged drought continued with peak flow of 254 cms in Redwood Creek near Orick (USGS 2016). From the mid-1970s through water year 2015, peak discharge has exceeded the discharge of a 5-year recurrence interval (906 cms) only once, in 1997 (Wilzbach 2016). Elevation of the watershed ranges from 8-692 m elevation. Streams are primarily of low gradient.

In addition to approximately 18 km of the main stem of Prairie Creek, I sampled parts of Prairie Creek tributaries including Lost Man Creek, Streelow Creek, Boyes Creek, and Godwood Creek (Figure 1).
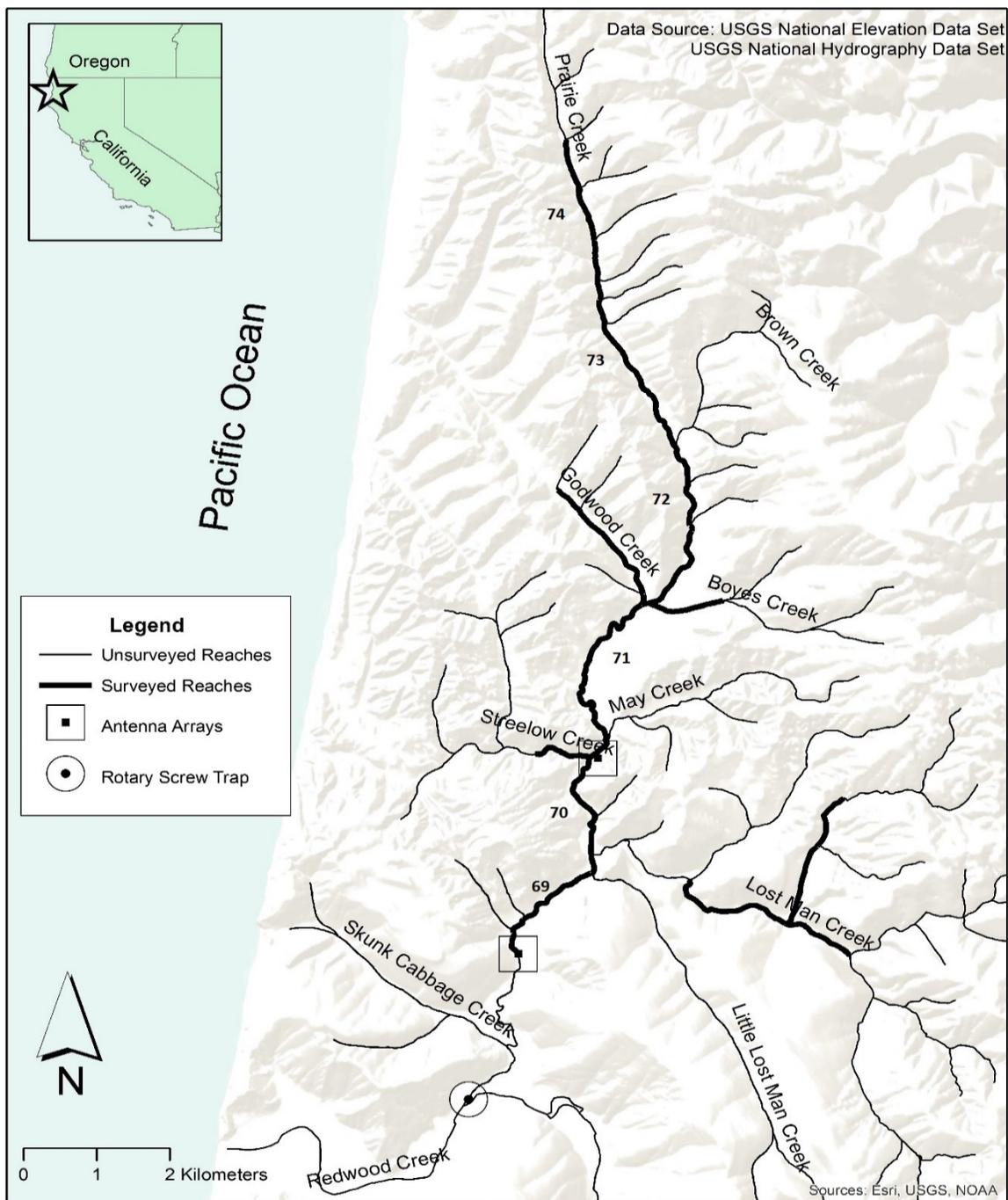
Figure 1. Map of the Prairie Creek watershed in northwestern California (USA). Sampling was conducted on approximately 18 km of the main stem of Prairie Creek. Reach numbers are indicated. In addition, portions of four tributaries were sampled including Lost Man, Streelow, Boyes, and Godwood creeks. Survey locations, PIT tag antenna arrays, and screw trap location are shown.

MATERIALS AND METHODS

Data Collection

Sampling of fish and habitat features was restricted to pools, which constitute the preferred habitat of juvenile Coho Salmon (Bisson et al. 1988, Nickelson et al. 1992b, Lau 1994). All pools within Prairie, Lost Man, Streelow, Boyes, and Godwood creeks that met pool selection criteria were sampled in a spatially balanced way. Pool selection criteria and habitat attribute collection were chosen to conform with regional California Department of Fish and Wildlife (CDFW) juvenile Coho Salmon monitoring protocols (S. Ricker and J. Garwood, pers. Comm., 2014). Reach distinctions within Prairie Creek were based on boundaries previously established by the California Department of Fish and Wildlife for long-term salmon spawner surveys, based on geomorphic breaks in gradient and landform (Table 1).

For a pool to be included as a potential sampling unit, the minimum depth criteria had to be met. Depth criteria varied with stream size to avoid excessive sampling in marginal quality habitats in larger stream reaches. Minimum depth of pools in streams with summer base flows <0.1 $m^3 \cdot s^{-1}$ was 25 cm; in streams with flows of 0.1-1.0 $m^3 \cdot s^{-1}$ depth was 30 cm; in streams with flows of 1.0-1.5 $m^3 \cdot s^{-1}$ depth was 40 cm; and streams with flows >1.5 $m^3 \cdot s^{-1}$, minimum depth was 50 cm. Additional criteria for pool selection included having a width of at least one-half the wetted channel width. For stream reaches with wetted widths > 3 m minimum pool surface area was 6 m^2, and for streams with a

wetted channel width < 3 m minimum pool surface area was 3 m^2. Backwater pools were not required to equal at least one-half the channel width to be selected, but still had to have a minimum surface area of at least 3 m^2. Selected side channel units required a minimum depth of 30 cm and surface areas of 3 m^2 with a width of at least one-half the wetted channel. Pool boundaries were identified based on hydrologic and geomorphic breaks or obstructions that could impede fish from passing from one unit to the next between dive passes.

Snorkel counts were made and habitat attributes were measured in each selected pool (159 total). All but 51 of these pools were subsequently seined to capture fish for tagging and measurement of fish length (reduced sample size reflected permit restrictions); in 9 of the 108 seined pools, fish were not captured (Table 1). To obtain pool-specific fish densities a 2-pass snorkeling count was made in each pool by independent sequential observers, prior to habitat measurement or seining. Snorkelers started all snorkel passes on the downstream end and moved upstream, and all fish were counted including those in the shallow margins. Flashlights were used in all dives to better observe fish and mechanical counters were used to help keep track of fish counted. The number of fish counted were recorded onto data sheets immediately following a snorkel pass. Fish in each pool were visually identified to species, enumerated, and trout were binned into size classes (less than or larger than 150mm). Steelhead and Cutthroat Trout were counted together as "trout" because of difficulties in distinguishing species. The two snorkeling passes in each pool were conducted within 24 hours of each other; the vast majority of pools were sampled on a second pass 5 - 15 minutes following the

first snorkel pass, after allowing the water to settle. First and second snorkel passes

within a pool were always conducted by different individuals to maintain the abundance

model assumption of independent sampling.

Table 1. Geographic coordinates (NAD 83, UTM, zone 10T), sampling strategy and
sample size of pools selected for snorkel/habitat surveys and for fish tagging in
each reach or tributary location of Prairie Creek.

Location	Lowest Coordinate	Upper Coordinate	Sampling Strategy	# of Pools Snorkeled	# of Pools with tagged Coho Salmon
Prairie Creek Reach 69	0412688 E 4574613 N	0413706 E 4575816 N	Every 4th pool	7	7
Prairie Creek Reach 70	0413706 E 4575816 N	0413779 E 4577510 N	Every 4th pool	7	7
Prairie Creek Reach 71	0413779 E 4577510 N	0414580 E 4579737 N	Every 6th pool	15	14
Prairie Creek Reach 72	0414573 E 4579725 N	0414743 E 4582238 N	Every 6th pool	16	13
Prairie Creek Reach 73	0414743 E 4582238 N	0413831 E 4584578 N	Every 6th pool	26	21
Prairie Creek Reach 74	0413831 E 4584578 N	0413831 E 4586645 N	Every 6th pool	15	11
Boyes Creek	0414575 E 4579736 N	0415461 E 4579825 N	Every 4th pool	13	12
Streelow Creek	0413657 E 4577529 N	0412943 E 4577568 N	Every 4th pool	14	14
Lost Man Creek	0415059 E 4575731 N	0416930 E 4574781 N	Every 8th pool	8	0
Lost Man Creek Tributary	0416306 E 4575129 N	0417176 E 4576890 N	Every 8th pool	17	0
Godwood Creek	0414394 E 4579796 N	0413246 E 4581396 N	Every 8th pool	21	0
Total:				159	99

Habitat measurements were made in concert with snorkel surveys from Godwood

and Lost Man creeks from June 24th to July 24th 2015 for inclusion in the abundance

model. All other habitat data and snorkel surveys were collected starting July 25th 2014

and extended through August 30th 2014 and were included in both the abundance model

and survival model. This distinction is important because the Godwood and Lost Man

Creek reaches were not included in the overwinter survival model. Habitat data collected in each pool included maximum pool length (nearest 0.1 m), average pool width (nearest 0.1 m), residual pool depth (nearest cm), large woody debris (LWD) counts (see Table 5 or Table 6 for definition of LWD criteria), cover complexity, and watershed area (nearest 0.1 km^2). Cover complexity was visually assessed and rated on a scale of 1-5 (Table 2), and included any features within the pool or suspended less than 1 meter above the pool that were available refugia for juvenile salmonids including undercut banks and boulders, woody debris, overhanging vegetation, bubble curtains, and aquatic vegetation. Pool area (nearest 0.1 m^2) was estimated using maximum pool length and average pool width. Watershed area (km^2) above a given pool was estimated using ARC GIS (J. Wartella, pers. comm., 2015). Habitat attributes are summarized in Table 3.

Table 2. Rating descriptions for cover complexity.

Cover Rating	Cover Description
1	*None*: Unit was void of fish cover
2	*Poor*: Unit was lacking significant fish cover and complexity. Unit contained at least one of the following features in limited availability: LWD, small woody debris (SWD), boulders, root masses, undercut bank, submerged vegetation, overhanging vegetation, bubble curtain;
3	*Average*: unit generally provided fish cover, but lacked complexity, containing at least two of the following features in moderate availability: LWD, SWD, boulders, root masses, undercut bank, submerged vegetation, overhanging vegetation, bubble curtain;
4	*Good*: unit provided extensive quality fish cover for up to 50% of the area from at least three of the following complex features: > 1 LWD, > 2 SWD, deep undercut bank, large root mass, extensive aquatic vegetation/ submerged branches, >4 undercut boulders, dense submerged overhanging vegetation
5	*Excellent*: unit had excellent fish cover usually dominating >40% of the pool area with at least four complex cover features (each available in extensive amounts). Unit must have included >2 LWD and numerous SWD. Unit was difficult to navigate and survey

Table 3. Number of pools sampled, mean of pool area, depth, cover rating, large woody debris (LWD) counts, and watershed area of sampled reached and tributaries of Prairie Creek. Standard errors are shown in parentheses.

Location	n	Pool Area (m^2)	Pool Depth (cm)	Cover Rating	LWD Count	Watershed Area (km^2)
Prairie Creek 69	7	318.4 (45.9)	100 (22.8)	3.1 (0.4)	13 (5.4)	93.0 (0.7)
Prairie Creek 70	7	303.7 (43.5)	117.6 (15.2)	3 (0.4)	9.1(1.9)	52.1 (4.6)
Prairie Creek 71	15	223.8 (62.5)	89.4 (7.6)	2.8 (0.2)	3.6 (1.0)	32.6 (0.8)
Prairie Creek 72	16	98.7 (26.5)	61.9 (7.6)	2.8 (0.2)	2.8 (0.6)	20.8 (<0.1)
Prairie Creek 73	26	86.5 (20.5)	58.0 (6.0)	3.0 (0.2)	7.7 (1.3)	16.3 (1.0)
Prairie Creek 74	15	33.0 (3.7)	51.2 (5.2)	2.7 (0.2)	1.7 (0.4)	7.4 (0.6)
Lost Man Creek	8	110.8 (28.6)	91.4 (9.1)	2.6 (0.2)	2.6 (0.4)	23.1 (1.4)
Lost Man Creek Trib.	17	17.3 (2.7)	42.8 (3.0)	2.5 (0.2)	1 (0.3)	5.2 (0.2)
Streelow Creek	14	53.1 (10.3)	50.4 (3.9)	3.0 (0.2)	7.1 (1.6)	7.3 (<0.1)
Godwood Creek	21	23.4 (2.7)	43.0 (3.1)	3.1 (0.2)	1.1 (0.3)	3.9 (0.2)
Boyes Creek	13	27.4 (3.3)	49.9 (4.0)	2.8 (0.3)	1.4 (0.5)	4.8 (<0.1)
Mainstem Prairie Cr.	86	140.0 (17.4)	71.3 (4.1)	2.9 (0.1)	5.6 (0.7)	27.6(2.5)
Tributaries Only	73	38.0 (5.0)	50.9 (2.5)	2.8 (0.1)	2.5 (0.4)	7.1 (0.7)
Entire Watershed	159	93.1 (10.5)	61.9 (2.6)	2.9 (0.1)	4.1 (0.5)	18.2 (1.6)

Fish sampling and handling procedures were approved under Humboldt State University Institutional Animal Care and Use Committee (IACUC) protocols (No. 12/13.F.74-A and 13/14.F.125-A). Fish were captured in each sampled pool using a seine net during late summer/fall low flows of 2014. Captured fish were sedated in a 40 mg/L solution of tricaine methane sulfonate (MS-222) buffered to neutral pH before a representative sample of up to 30 fish per pool were measured for length (± 1 mm) and mass (± 0.1 g). Up to 15 Coho Salmon ≥ 60 mm fork length per pool were implanted with 12 mm passive integrated transponder (PIT) tags. Captured fish were allowed to recover from anesthesia in a bucket of fresh water before being released to the location of capture.

Fish were sampled and tagged in two events. The first event started on July 25th 2014 and extended through August 30th 2014 and was done in tandem with snorkel and habitat surveys. A second sampling event started on October 3rd, 2014 and extended through October 20th, 2014. During the second event, fish were sampled from a combination of previously seined and previously unsampled pools. The second event allowed for recapture of previously tagged fish and capture and tagging of additional fish. The numbers of tags applied per tagging event and number of tags applied per stream reach are given in Table 4.

Table 4. Number of PIT tags applied to juvenile Coho Salmon by reach location and tagging event in Prairie Creek during the summer and fall of 2014.

Location	Tag Event 1 (summer)	Tag Event 2 (fall)	Total Tags
Prairie Creek Reach 69	83	114	197
Prairie Creek Reach 70	0	140	140
Prairie Creek Reach 71	81	97	178
Prairie Creek Reach 72	70	126	196
Prairie Creek Reach 73	0	164	164
Prairie Creek Reach 74	37	25	62
Boyes Creek	27	0	27
Streelow Creek	97	0	97
Lost Man Creek	0	0	0
Lost Man Creek Tributary	0	0	0
Godwood Creek	0	0	0
Total Fish Tagged:	395	666	1061

Emigration of tagged fish from Prairie Creek was detected by two paired radio-frequency identification (RFID) PIT tag antenna arrays in the main stem of Prairie Creek (0413779 E, 4577510 N and 0412688 E, 4574613 N) and from a rotary screw trap at the mouth of Prairie Creek (Figure 1). RFID antenna arrays detected unique tag numbers and date of detection. Antennas were kept running by battery power until July 7, 2015, after fish movement was no longer detected for several weeks. The rotary screw trap was operated by California Department of Fish and Wildlife and California Cooperative Research Unit crews at the mouth of Prairie Creek from February 27th until July 25th, 2015. All Coho Salmon captured at the rotary screw trap were scanned for the presence of a PIT tag, and tagged fish were measured for fork length.

Model Development and Data Analysis

Density Estimation of Coho Salmon and Trout

Developing reliable noninvasive methodologies to estimate abundance of wild populations is desirable particularly for threatened species such as Coho Salmon. Methodologies commonly used to estimate juvenile salmonid abundances in-streams are generally more invasive than snorkel counts and often involve electrofishing or mark-recapture methods. Studies have used snorkel surveys to estimate abundance, but the effects of variable detection rates on snorkel counts is generally not accounted for (Hartman and Brown 1987, Roni and Quinn 2001, Anderson et al. 2008). This study was able to estimate abundance using snorkel counts while accounting for biases brought on by differing detection rates. A benefit of this model is that identification of unique individuals is not required (Kery 2008).

Abundance and density of juvenile Coho Salmon, small juvenile trout (<150 mm), and large trout (>150 mm) were estimated using a zero-inflated Poisson binomial N-mixture model (Royle 2004, Royle and Dorazio 2008). The model accounted for varying detection efficiency associated with spatially replicated counts (observation process), and distinguished between covariates that were correlated with abundance and those which influenced the observation process. The model conceives of observed counts as arising from a hierarchical process. The first level of the hierarchical model represents observed snorkeler counts (y) at a given location(i):

$$y_i = (y_{i1}, y_{i2}, \ldots\ldots, y_{iJ})$$

At each sampling location there were two snorkel passes (J). Each of the J counts at a single location are assumed to be independent, and the true abundance is assumed to be constant over the J sampling occasions.

At the second level of the hierarchy the true abundance (N) at a given location (i) and the probability of detection (p) for all individuals at a given location (i) was estimated. The p_i parameter can vary among pools and by sampling occasion (J), but the probability of detection for all individual fish within a sampling occasion (J) at a given pool was assumed to be homogenous. The model structure of the detection process, conditional on the true abundance at each location (N_i), and the probability of detection for each individual at a given location (p_i) is:

$$p(y_i|N_i, p_i) = \prod_{j=1}^{J} Bin(y_{ij}|N_i, p_i)$$

The third level of hierarchy contained meta-population parameters α and β that drove detection probability and abundance respectively across the study area. Model structure for detection probability is:

$$y_i \sim Bin(N_i, p_i)$$

$$logit(p_i) = \alpha_0 + \alpha_1 z_{1i} + \alpha_2 z_{2i} + \ldots$$

Model structure for abundance is:

$$N_i \sim zero-inflated\ Poission\ (\lambda_i, \pi_i)$$

$$log(\lambda_i) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \ldots + log(Area_i)$$

where λ_i is the mean of the count process (Poisson distribution) and π_i is the probability

of being in the extra zeros group. The $log\ (Area)$ term was added to the linear predictor

to allow covariates to explain variation in fish density instead of abundance (Table 5).

The zero-inflated Poisson distribution was used because the data had more zero

values than expected to occur under a standard Poisson distribution. Zero inflation of the

Poisson distribution is often appropriate for describing the distribution of site abundance

data (Joseph et al. 2009). The zero-inflated Poisson distribution comes from a mixture of

two processes. In the first process, the data are considered as zeros and non-zeros and a

Bernoulli model is used to estimate the probability that a zero value is observed for true

absence versus present but not observed. In the second process, counts are modeled

using a Poisson distribution and includes all non-zero counts and zero counts associated

with true absence since under some covariate conditions a zero value can be observed.

The probability that an observation of the zero-inflation Poisson mixture process equals

zero is:

$$P(Y_i\ =\ 0|\ \lambda_i\ , \pi_i)\ =\ \pi_i +\ (1-\ \pi_i)e^{-\lambda_i}$$

where Y is the population from which observations (y_i) were taken. Additionally, $e^{-\lambda_i}$

is the probability of a Poisson random variable equaling zero, with (i) indicating ability

of the parameter to vary as a function of explanatory variables for each observation.

Similarly, the probability that an observation is greater than zero is:

$$P(Y_i\ =\ y_i|y_i\ >\ 0;\ \lambda_i\ , \pi_i)\ =\ (1-\ \pi_i)\left(\frac{e^{-\lambda_i}\ \lambda_i^{y_i}}{y_i!}\right)$$

Models were run in R (R Core Team 2013) using the package "unmarked" (Fiske and Chandler 2011). For Coho Salmon, distribution of fish fit the model well, however, neither trout model had sufficient goodness-of-fit ($\hat{c} > 5$) to proceed with abundance estimation (goodness of fit test methods shown below). Trout density values were therefore based on maximum snorkel count in a pool, and were uncorrected for variable detection efficiency of snorkelers across sites. Consequently, trout density values represent an index or relative abundance.

To evaluate the association of Coho Salmon density with habitat attributes, candidate model sets for model selection were generated with different combinations of covariates of abundance including watershed area, cover rating, depth, and LWD (Table 5). All candidate models included the same set of detection covariates:

$$logit\ (p_{iJ}) = Intercept\ + \alpha_k * \sum_{k=2}^{6} IT(S_{i,J} = k)\ +\ \alpha_7\ (Cover\ Rating_i)$$

$$+\ \alpha_8\ (Depth_i)\ +\alpha_9\ (LWD_i)$$

where snorkeler 1 was treated as the intercept, $S_{i,j}$ is an individual snorkeler at given sampling location (i) on a given pass (J), and IT is an indicator function. Standard errors of probability of detection estimates for given individual snorkelers were generated using the "deltaMethod" function within the "car" package in R (Fox and Weisberg 2011). Abundance covariates varied among candidate models but the global model was:

$$log\ (\lambda)\ =\ Intercept\ +\ \beta1\ (Watershed\ Area)\ +\ \beta2\ (Cover\ Rating)$$

$$+\ \beta3\ (Depth)\ +\ \beta4\ (LWD)$$

In addition, a $log\ (area)$ term was used in all candidate models of abundance to allow the covariate estimates to explain variation in fish density (fish/m^2) instead of fish abundance across sites. Continuous covariates were standardized into z-scores using a z-transformation (Mudholkar 2006). Correlations were analyzed between covariates to detect multicollinearity. Spearman tests with the R function "cor.test" (R Core Team 2013) were used with a Rho value ≥ 0.6 used as a cutoff for being too highly correlated to include both covariates in the model. Graphical displays were also used to identify correlations between categorical and continuous covariates.

Table 5. Model parameters used in the zero-inflated Poisson binomial N-mixture model to estimate Coho Salmon density and detection probability in Prairie Creek. The superscript d represents a covariate of density and a superscript p represents a covariate of probability of detection.

Model Parameter	Parameter Description
Area^d	Measured by multiplying maximum pool length by average pool width. Pool area (m^2) was used to allow other density covariates to relate to fish density instead of fish abundance.
Depth^{p,d}	The residual pool depth (± 1 cm) determined by subtracting the maximum depth of the riffle crest exiting the pool from the maximum pool depth of the sample unit.
LWD^{p,d}	The number of logs greater than 30 cm in diameter and greater than 2 m in length occurring in (or suspended ≤ 1 meter directly above) the wetted area of the sampled unit.
Cover Rating^{p,d}	The ranking of cover complexity scaled from 1 (cover absent) – 5 (highly complex cover) based on a visual assessment of cover available to salmonids in relation to the total pool volume.
Watershed Area^d	The amount of watershed area above a given pool (km^2).
Snorkeler^p	Categorical covariate to idenify different snorkelers.

The appropriate K value for the model set (the integer upper index of integration for the model, set so as to not influence parameter estimates [Fiske and Chandler 2011])

was identified by running the global model with K values increasing from 50 in
increments of 50 until model parameter estimates stabilized and remained unchanged
with additional K increases. The K value was identified using the global model and then
held constant for other models in the model set. A goodness of fit test was run on the
global model using the "Nmix.gof.test" function from the R package "AICcmodavg"
(Mazerolle 2015) using 2000 simulated bootstrapped samples. This test gives an estimate
of the overdispersion parameter (ĉ) which is a measure of how much extra variation
exists in the fit of the data to the specified model. A ĉ =1 means that no extra variation
exists in the fit of the data to the specified model and according to Lebreton et al. (1992)
models with a ĉ > 3 do not have good fit and cannot be corrected effectively using $QAIC_c$
model selection. Model selection used Quasi-Akaike's Information Criterion corrected
for sample size ($QAIC_c$), as follows (Amstrup et al. 2005):

$$QAIC_c = \frac{-2log_e(L\,(\hat{\theta})\,|x)}{\hat{c}} + 2K + \frac{2K\,(K\,+\,1)}{n\,-\,K\,-\,1}$$

where $L(\hat{\theta})|x$ is a likelihood function given the data x that indicates lack of model fit, K
is the number of estimable parameters, and n is the effective sample size. The term
$\frac{2K(K+1)}{n-K-1}$ is suggested by Amstrup et al. (2005) and is a correction for a finite sample size.
For this study, the best models were considered to be the simplist model within
approximately four $QAIC_c$ values of the best fitting model (Burnham and Anderson
2002).

Growth of Juvenile Coho Salmon

Summer growth was estimated from PIT tagged Coho Salmon tagged in the summer tagging event and recaptured in the fall tagging event. Overwinter growth was estimated from PIT tagged Coho Salmon tagged or captured in October until recaptured at the screw trap. Absolute growth rate (AGR) was determined as:

$$AGR = \frac{l_{t2} - l_{t1}}{t_2 - t_1}$$

and specific growth rate (SGR) was determined as:

$$SGR = \frac{ln\,(l_{t2}) - ln\,(l_{t1})}{t_2 - t_1} * 100$$

where l_{t2} is the final fork length, l_{t1} is the initial fork length, t_2 is the time in days at final measurement, and t_1 is the time at initial measurement.

Overwinter Survival of Juvenile Coho Salmon

A Cormack-Jolly-Seber (CJS) model run in Program MARK (Cooch and White 2014) was used to estimate capture probability at recapture points and estimate apparent survival based on maximum-likelihood estimation (Horton and Letcher 2008, White and Burnham 1999). Estimated survival rates were considered apparent rather than actual because death and undetected emigration could not be differentiated (White and Burnham 1999).

This CJS model had five occasions; the first two occasions were the summer and fall tagging events. Fish were either marked on the first capture occasion in summer or the second occasion in fall. The 3rd, 4th, and 5th encounter occasions included detection at

the upper antenna array, lower antenna array, and capture in the rotary screw trap respectively. A capture history was compiled for each tagged fish and recorded as a sequence of 0's and 1's to indicate whether a fish was captured or detected at each detection point or occasion (two tagging events, two antenna arrays, and a rotary screw trap). A 1 represented detection and a 0 represented absence of detection in each possible period. For example, a capture history of 11111 would represent an individual marked on occasion 1 (i.e. summer tagging event) and resighted on occasions 2,3,4, and 5 while 01001 would mean the individual was not observed on occasion 1, marked on occasion 2 (i.e. fall tagging event), not resighted on occasion 3 or 4 (i.e. two antenna arrays), and recaptured on occasion 5 (i.e. rotary screw trap). A fish that was not detected at an occasion either did not survive to that occasion or was alive but not detected.

In the model, apparent survival rates between capture occasions are represented by φ, and recapture rates are represented by p. Using the design matrix within MARK, recapture efficiency (p) was allowed to vary for each capture occasion (ie.seining,each antenna detection, and screw trap capture), and survival (φ) was allowed to vary for each interval between capture occasions. For example, φ_1 would be the survival rate between the first and second capture occasions, while p_2 would be the recapture rate at the second capture occasion. The survival and recapture rates were used to calculate the probability of an encounter history (Cooch and White 2014). The model is based on the following assumptions (Amstrup et al. 2005):

1. All fish in the population alive at the time of sampling have equal probability of detection except as accounted for by covariates;

2. All fish in the population have equal survival for a given interval except as accounted for by covariates;

3. No errors are associated with PIT tagging (i.e. no tag loss, misread tags, or tag mortality);

4. Sampling is instantaneous;

5. All emigration from the population is permanent; and

6. The fate of each fish is independent of any other fish.

Because of the limitation posed by the timeframe of operation of the screw trap (February – July 2015), only antenna detections from February to July 2015 were included in the analysis. This excluded 67 individuals detected at the lower antenna prior to screw trap operation. A more detailed description of assumption violations is given in the discussion section.

In CJS models, the last φ and p parameters are are not separately identifiable (Lebreton et al. 1992). Because the last φ and p are confounded, the detection efficiency of the screw trap (p_5) was fixed to 0.55, based on an independent estimate of the Prairie Creek screw trap capture efficiency for juvenile Coho Salmon (Sparkman et al. 2016). To estimate trap efficiency throughout the season a subset of captured juvenile Coho Salmon were marked and held for upstream release. Efficiency estimates were then obtained using mark-recapture methods described in Carlson et al. (1998).

The φ for the period between the fall occasion and detection at the upstream antenna array represents the overwinter apparent survival rate for all fish, both those tagged above the upstream array (Prairie Creek reaches 71-74, Boyes Creek, and

Streelow Creek) and those tagged below (Prairie Creek reaches 69-70). Although fish

tagged in reaches 69 and 70 were not as likely to be encountered at the upstream array

during outmigration, they could still potentially be detected at recapture points

subsequent to the upstream antenna array occasion, i.e. at the lower antenna array (=

fourth recapture occasion) and rotary screw trap (= fifth recapture occasion). Thus these

fish were considered to be overwinter survivors. Since the CJS model assumes an equal

probability of recapture for all individuals and fish tagged in reaches 69 and 70 were not

as likely to be detected at the upper antenna array, recapture efficiency estimation of the

upstream antenna array could be biased. To account for this potential bias, a grouping

variable was applied to the recapture model, based on whether a fish was tagged above or

below the upstream antenna array to allow the recapture efficiency of the upstream array

(p_3) to be estimated separately for fish tagged above and below the antenna array. In

addition, not all pools sampled on occasion 1 were revisited on occasion 2. For this

reason, another grouping variable was applied that allowed recapture efficiency of fall

seining (p_2) to vary based on whether a fish was tagged in a pool that was revisited on

occasion 2 or not. This was done because recapturing a fish originally tagged in a pool

only sampled on occasion 1 required movement of the fish.

The overdispersion parameter ($\hat{c}$) was estimated using the median $\hat{c}$ method in

MARK with lower and upper bounds conservatively set at 1 and 10 respectively. The

upper bound is generally set just above the observed deviance $\hat{c}$ (Cooch and White 2014).

Again to be conservative, 500 intermediate points between lower and upper bounds and

500 replicates at each design point were used. Because this test in program MARK is

unable to handle models containing individual covariates, the general starting model was used to assess general goodness of fit. Although this model doesn't include continuous covariates, it does include the grouping variables and p and φ interval parameterization built into the MARK design matrix. The ĉ value was then used to account for any over-dispersion in the data using $QAIC_c$ model selection as given in the abundance model methodology above. The effect of body length, Coho Salmon and trout densities, location, and habitat attributes on overwinter survival were evaluated using model selection (Table 6). The logit link function was used for all models, restricting survival and recapture rate estimates to the interval (0,1) (Lebreton et al. 1992). The general model for apparent survival (φ) was:

$$logit\,(\varphi_i) = Intercept + \delta_2\,IT_{1i} \ + \delta_3\,IT_{3i} + \delta_4\,IT_{4i}$$

where IT_x is an indicator function that equals 1 in time x and 0 otherwise. The intercept is the indicator function for time 2. The general model for recapture efficiency (p) was:

$$logit(p_i) \ = \ \Theta_1\,(IT_{2i_{same}}) \ + \ \Theta_2\,(IT_{2i_{new}}) \ + \ \Theta_3\,(IT_{3i_{above}}) \ + \ \Theta_4\,(IT_{3i_{below}})$$

$$+ \ \Theta_5\,(IT_{4i}) \ + \ \Theta_6\,(IT_{5i})$$

where no intercept was specified for p. In time two, "same" indicates fish tagged in a pool on occasion one that were resampled again on occasion two. "new" indicates fish tagged in a pool on occasion one not resampled on occasion two. In time three, above and below indicate location in relation to the upper antenna array.

Table 6. Model parameters used in the overwinter survival model for juvenile Coho
Salmon in Prairie Creek.

Model Parameter	Parameter Description
Area	Measured by multiplying maximum pool length by average pool width.
Length	The fork length of fish in fall. For fish which were only measured in summer, length was adjusted for summer growth using the average growth rate (mm) so that fish length was comparable between fish tagged in the summer and fall events. Average length after adjustment was 71 mm (n=1061, SD = 9.8).
Depth	The residual pool depth (± 1 cm) determined by subtracting the maximum depth of the riffle crest exiting the pool from the maximum pool depth of the sample unit.
LWD	The number of logs greater than 30 cm in diameter and greater than 2 m in length occurring in (or suspended ≤ 1 meter directly above) the wetted area of the sampled unit.
Cover Rating	The ranking of cover complexity scaled from 1 (cover absent) – 5 (highly complex cover) based on a visual assessment of cover available to salmonids in relation to the total pool volume.
Watershed Area	The amount of watershed area above a given pool.
Small.trout	The number of trout <150 mm counted divided by the pool area.
Large.trout	The number of trout >150 mm counted divided by the pool area.
Coho	N-mixture model pool abundance estimates of juvenile Coho Salmon divided by pool area.

Because fish less than 60 mm were not tagged, inference can only be made on fish

60 mm or larger and not on the population as a whole. The proportion of fish in the

population that were large enough for tagging (≥60 mm) during the study was determined

through representative length measurements at each sampled pool. The proportion of the

population that the overwinter survival estimate represents (P_{OWS}) was calculated by:

$$P_{OWS} = \frac{(T_s * P_s) + (T_f * P_f)}{T_s + T_f}$$

where T_s is the number of tagged fish in summer, T_f is the number of tagged fish in fall,

P_s is the proportion of fish ≥ 60 mm in the summer, and P_f is the proportion of fish ≥ 60

mm in the fall.

RESULTS

Hierarchical Modeling for Coho Salmon Density

Density point estimates of juvenile Coho Salmon in Prairie Creek, generated from the top model using the zero-inflated Poisson binomial model averaged 0.52 fish/m^2 (n= 159) and ranged from 0-2.21 fish/m^2. Average abundance was estimated at 45.1 fish per pool (n= 159) and ranged from 0-571 fish per pool. The probability of detecting a juvenile Coho Salmon across the 318 snorkel passes ranged from 0.19 to 0.96, as a function of habitat and snorkeler identity. The range among snorkelers in probability of detecting a Coho Salmon was 0.47 (SE=0.02) – 0.80 (SE=0.05), assuming average covariate values from the best model.

A goodness of fit test gave an overdispersion parameter (ĉ) of 2.73. Because overdispersion was < 3, I proceeded with $QAIC_c$ model selection to correct for overdispersion (Lebreton et al. 1992) (Table 7).

Table 7. $QAIC_c$ Model selection for abundance covariates in zero-inflated Poisson
binomial N-mixture model. Detection covariates were held constant in each
model as: (Snorkeler [categorical] + Cover Rating + Depth + LWD). The null
model contained mean-only detection and abundance parameters. Back
transformed zero-inflation parameter (π_i) estimates ranged from 0.077-0.087.

Model	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ Weights	Num. Par.
Cover Rating+Depth+Watershed Area+log(Area)	1060.1	0	0.674	15
Cover Rating+Depth+LWD+Watershed Area+ log(Area)	1061.7	1.57	0.307	16
Depth+LWD+Watershed Area+ log(Area)	1068.0	7.96	0.013	15
Cover Rating+Watershed Area+ log(Area)	1071.4	11.36	0.002	14
Depth+Watershed Area+ log(Area)	1071.6	11.48	0.002	14
Cover Rating+LWD+Watershed Area+ log(Area)	1072.2	12.12	0.002	15
Watershed.Area+ log(Area)	1076.5	16.46	<0.001	13
LWD+Watershed Area+ log(Area)	1078.4	18.36	<0.001	14
Null	2252.2	1192.1	0	3

In the top model, density was best predicted as a function of cover complexity,

depth, and watershed area. Probability of fish detection varied as a function of snorkeler

identity, cover complexity, depth, and LWD abundance. The probability of being in the

extra zeros group (π_i) was estimated as 0.078 for the top model (Table 8).

Table 8. N-mixture Coho Salmon model results for top model. Coefficients are the raw
model output. Abundance coefficients are on the log scale. Detection
coefficients and the zero-inflation coefficient are on the logit scale. The 95%
confidence intervals were constructed using standard errors corrected for
overdispersion.

Global Model	Coefficient	Estimate	95% CI Lower	95% CI Upper
Abundance	Intercept	3.3	3.1	3.4
(Density due to	Cover Rating	-0.25	-0.38	-0.11
Area covariate)	Depth	0.21	0.08	0.33
	Watershed Area	-0.22	-0.27	-0.17
Detection	Snork1(intercept)	0.68	0.31	1.05
	Snork2	0.68	-0.21	1.57
	Snork3	-0.12	-0.42	0.17
	Snork4	-0.08	-0.32	0.16
	Snork5	-0.31	-0.59	-0.03
	Snork6	-0.80	-1.04	-0.56
	Snork7	0.60	-0.19	1.40
	Cover Rating	0.71	0.48	0.95
	Depth	-0.25	-0.46	-0.05
	LWD	-0.16	-0.31	-0.02
Zero-Inflation		-2.47	-3.48	-1.46

Coho Salmon density declined as the rating of cover complexity (from 1-5)

increased; for a one standard-deviation increase in cover (0.9 cover units), estimated

density decreased by 21.7% (95% CI 10.6-31.4%), after accounting for the effects of pool

depth and watershed area. Coho Salmon density increased as pool depth increased; for a

one standard-deviation increase in pool depth (33 cm), estimated density increased by

22.9% (95% CI 8.1-39.6%), after accounting for the effects of cover complexity and

watershed area. Coho Salmon density declined as watershed area (km^2) increased; for a

one standard-deviation increase in watershed area (20 km^2), estimated density decreased

by 19.8% (95% CI 15.7-23.8%), after accounting for the effects of complexity rating and pool depth.

Habitat covariates affected odds of detection of juvenile Coho Salmon in pools. Odds of detection increased as the rating of cover complexity (from 1-5) increased; for a one standard-deviation increase in cover (0.9 cover units), estimated odds of detection increased by 104.4% (95% CI 61.9-158.0%), after accounting for the effects of pool depth, LWD, and individual snorkeler. Odds of detection declined as LWD increased; for a one standard-deviation increase in LWD count (5.7), estimated odds of detection decreased by 14.9% (95% CI 1.5-26.4%), after accounting for the effects of pool depth, cover complexity, and individual snorkeler. Odds of detection declined as pool depth (cm) increased; for a one standard-deviation increase in pool depth (33 cm), estimated odds of detection decreased by 22.3% (95% CI 4.6-36.7%), after accounting for the effects of cover complexity, LWD, and individual snorkeler.

Trout Snorkel Counts and Density

Snorkel counts of large trout averaged 1.0 fish per pool (SD=1.4, SE=0.1, n=159) and ranged from 0-8. Densities of large trout averaged 0.02 fish/m^2 (SD=0.05, SE=0.004, n=159) and ranged from 0-0.5 fish/m^2. Counts of small trout averaged 12.7 fish per pool (SD=15.5, SE=1.2, n=159) and ranged from 0 to 79. Densities of small trout averaged 0.2 fish/m^2 (SD=0.2, SE= 0.02, n=159) and ranged from 0-2.0 fish/m^2. Snorkel counts and densities for both size classes of trout were not corrected for detection efficiency.

Summer and Overwinter Growth of Juvenile Coho Salmon

Absolute growth rate of juvenile Coho Salmon over the summer averaged 0.16 mm/d (n = 52 fish, SD = 0.13). Time from first tagging to second tagging events ranged from 43 - 67 days, and averaged 51 days (n=52 fish, SD=9.49). Specific growth rate averaged 0.21 % /d during the summer (n=52 fish, SD = 0.17). Average growth rate between the summer and fall tagging events was 7.2 mm (n=52 fish, SD=5.5).

Absolute growth rate of juvenile Coho Salmon over the winter averaged 0.14 mm/d (n = 103 fish, SD = 0.05). Time from October measurement to trap capture ranged from 155 – 250 days, and averaged 204 days (n = 103 fish, SD = 19.0). Specific growth rate averaged 0.16 % /d during the winter (n=103 fish, SD = .06). Average growth between October and spring screw trap capture was 28.9 mm (n=103 fish, SD= 10.7). Size at time of trap capture ranged from 76 – 121 mm FL, and averaged 102.4 mm (n = 103 fish, SD =9.7).

Apparent Overwinter Survival Analysis

A total of 395 juvenile Coho Salmon were tagged in the summer tagging event; during the fall tagging event, 666 individuals were newly tagged, and 52 of the 395 fish tagged in the summer were recaptured. During the spring migration (starting February 27th) 142 fish were detected at the upper antenna array, 159 fish were detected at the lower antenna array, and 168 fish were captured at the rotary screw trap (Table 9).

Table 9. M-array table showing number of fish tagged and recaptured by occasion. An additional 67 fish (excluded from this analysis) were detected at the lower antenna array prior to trap installation. However, 8 of those 67 were detected in spring at the screw trap. Occasions 1-5 are tagging event 1, tagging event 2, upper antenna array, lower antenna array, and screw trap respectively.

Releases	Number Released (R_i)		Occasion 2	Occasion 3	Occasion 4	Occasion 5	Total Recap. for first time (r_i)	Never Recaptured (R_i-r_i)
Tag event 1	**395**		52	50	35	16	**153**	**242**
Tag event 2	**718**							
		[11]	52	10	5	6	21	31
		[01]	666	82	53	29	164	502
			718				**185**	**533**
Upper Antenna Array	**142**							
		[101]	50	23	13		36	14
		[111]	10	6	4		10	0
		[011]	82	37	17		54	28
			142				**100**	**42**
Lower Antenna Array	**159**							
		[1001]	35	21			21	14
		[1101]	5	2			2	3
		[1011]	23	15			15	8
		[1111]	6	4			4	2
		[0101]	53	26			26	27
		[0111]	37	15			15	22
			159				**83**	**76**

Although ĉ was estimated to be 1.1, I decided to be conservative, and opted to proceed

with $QAIC_c$ model selection to estimate the continuous covariates that best predicted

survival (Table 10).

Table 10. $QAIC_c$ model selection results table for continuous covariates of juvenile Coho Salmon overwinter survival. A full description of each term is given in Table 6. All models contained p and φ parameterization and grouping variables (general model given in methods), except the null model. Only continuous covariates of survival are shown and were evaluated for model selection. The "none" model was the general model which lacked continuous covariates.

Continues Covariates	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ Weights	Num. Par	QDeviance
Length+Watershed Area	2204.05	0	0.293	12	2179.83
Length+Watershed Area+Coho	2205.50	1.446	0.142	13	2179.24
Length+Watershed Area+Large.trout	2205.90	1.846	0.116	13	2179.64
Length+Watershed Area+Small.trout	2206.00	1.954	0.110	13	2179.74
Length+Watershed Area+Coho+Large.trout	2207.29	3.236	0.058	14	2178.99
Length+Watershed Area+Coho+Small.trout	2207.33	3.283	0.057	14	2179.03
Length+Watershed Area+Small.trout+Large.trout	2207.88	3.831	0.043	14	2179.58
Length+Watershed Area+Coho+Depth+LWD+Cover Rating	2207.94	3.893	0.042	16	2175.55
Length+Watershed Area+Depth+LWD+Cover Rating	2208.33	4.278	0.034	15	2177.99
Length+Watershed Area+Coho+Small.trout+Large.trout	2209.17	5.121	0.023	15	2178.83
Length+Watershed Area+Coho+Large.trout+Depth+LWD+Cover Rating	2209.41	5.356	0.020	17	2174.97
Length+Watershed Area+Coho+Small.trout+Depth+LWD+Cover Rating	2209.42	5.368	0.020	17	2174.98
Length+Watershed Area+Large.trout+Depth+LWD+Cover Rating	2210.03	5.978	0.015	16	2177.64
Length+Watershed Area+Small.trout+Depth+LWD+Cover Rating	2210.37	6.323	0.012	16	2177.98
Length+Watershed Area+Coho+Small.trout+Large.trout+Depth+LWD+Cover Rating	2211.04	6.990	0.009	18	2174.55
Length+Watershed Area+Small.trout+Large.trout+Depth+LWD+Cover Rating	2212.07	8.021	0.005	17	2177.63
None	2250.05	46.00	0	10	2229.89
Null	2553.02	348.97	0	2	2549.01

Survival was estimated for four separate intervals. The first interval (φ_1) was between the summer tagging event and fall tagging event and is interpreted as summer survival. In the top model, summer survival was estimated to be 0.80 (95% CI 0.63-0.90). The second interval (φ_2) was between the fall tagging event and the upper antenna array and represents overwinter survival. In the top model, overwinter survival was estimated as 0.35 (95% CI 0.30-0.40) for the average covariate values of fish length and watershed area. The third and fourth intervals (φ_3 and φ_4) represented the intervals between the upper antenna array and lower antenna array and between the lower antenna array and rotary screw trap. Survival during the 3rd and 4th intervals was nearly 100% (Table 11). For this study I did not include these intervals in the overwinter survival estimate because the majority of overwinter loss occurred during φ2. Additionally, any fish that survived φ3 or φ4 also had to have survived overwinter (φ2). For example, a fish that was tagged on the first occasion and not detected again until the last occasion still survived the winter, even though it was not detected at the antenna arrays. A similar model structure and interpretation was used in estimating overwinter survival of juvenile Coho Salmon in Prairie Creek during 2012-2013 (Moore 2014) and 2013-2014 (Sparkman et al. 2015).

Table 11. Estimates, standard errors (SE), and 95% confidence intervals of apparent survival and detection of juvenile Coho Salmon in Prairie Creek, 2014-2015, based on a Cormack-Jolly-Seber model. Recapture rate at the rotary screw trap (p_5) was fixed.

Estimated Parameters	Description	Estimate	SE	95% CI Lower	95% CI Upper
φ_1	Survival rate between summer and fall tagging occasions (summer survival).	0.80	0.07	0.63	0.90
φ_2	Survival rate between fall tagging and upstream antenna arrays (overwinter survival).	0.35	0.03	0.30	0.40
φ_3	Survival rate between upper and lower antenna arrays.	0.93	.07	0.63	0.99
φ_4	Survival rate between the lower antenna array and the rotary screw trap.	0.95	0.08	0.47	1.0
p_2(same habitat)	Recapture rate for fish in fall tagging occasion where tagging occurred in same pool in summer tag event.	0.33	.05	0.24	0.43
p_2(new habitat)	Recapture rate for fish in fall tagging occasion where tagging did not occur in same pool in summer.	0.03	0.01	0.01	0.08
p_3(above)	Recapture rate at the upstream antenna array for fish tagged above the upstream antenna.	0.69	0.04	0.60	0.76
p_3(below)	Recapture rate at the upstream antenna array for fish tagged below the upstream antenna.	0.05	0.02	0.03	0.11
p_4	Recapture rate at the lower antenna array.	0.50	0.04	0.42	0.58
p_5	Recapture rate at the rotary screw trap.	0.55	-	-	-

In the top model, apparent overwinter survival was predicted as a function of fish length and watershed area (Table 10). Overwinter survival increased as fish length increased; for a one standard-deviation increase in fish length (11 mm), estimated overwinter survival increased by a factor of 2.0 (95% CI 1.6 - 2.5), after accounting for the effects of watershed area (Figure 2). Overwinter survival declined as watershed area increased; for a one standard-deviation increase in watershed area (30 km^2), estimated overwinter survival was reduced by a factor of 0.93 (95% CI 0.77-1.11), after accounting for the effects of fish length (Figure 3). Watershed area was in all models including the top model, however the estimated effect on survival appears to be not biologically significant because the estimated effect was so low and the confidence intervals are large. Although Coho Salmon density was not in the top model, there was marginal evidence for an effect as it was in half the models with a delta $QAIC_c$ less than 4, and had a $QAIC_c$ weight totaling 0.30. Overwinter survival declined as Coho Salmon density increased; for a one standard-deviation increase in Coho Salmon density (0.3 fish/m^2), estimated overwinter survival was reduced by a factor of 0.92 (95% CI 0.77-1.13), after accounting for the effects of fish length and watershed area (Figure 4). Other covariates were not estimated to contribute to prediction of survival.

Table 12. Coefficient estimates (δ and Θ) for the top model. Coefficient estimates are on the logit scale. The 95% confidence intervals were not corrected for overdispersion because ĉ was estimated to be low.

Global Model	Parameter	Coefficient Estimate	SE	95% CI Lower	95% CI Upper
φ Coefficients	Length	0.70	0.12	0.47	0.93
	Watershed Area	-0.07	0.09	-0.26	0.11
	Intercept (Time 2)	-0.62	0.11	-0.84	-0.40
	Time 1	1.98	0.49	1.02	2.95
	Time 3	3.27	1.12	1.08	5.46
	Time 4	3.55	1.57	0.47	6.62
p Coefficients	Time 2 (same)	-0.72	0.23	-1.16	-0.28
	Time 2 (new)	-3.33	0.45	-4.21	-2.46
	Time 3 (above)	0.79	0.19	0.41	1.17
	Time 3 (below)	-2.86	0.39	-3.62	-2.10
	Time 4	-0.01	0.16	-0.33	0.31
	Time 5	-0.10	0.00	-0.10	-0.10
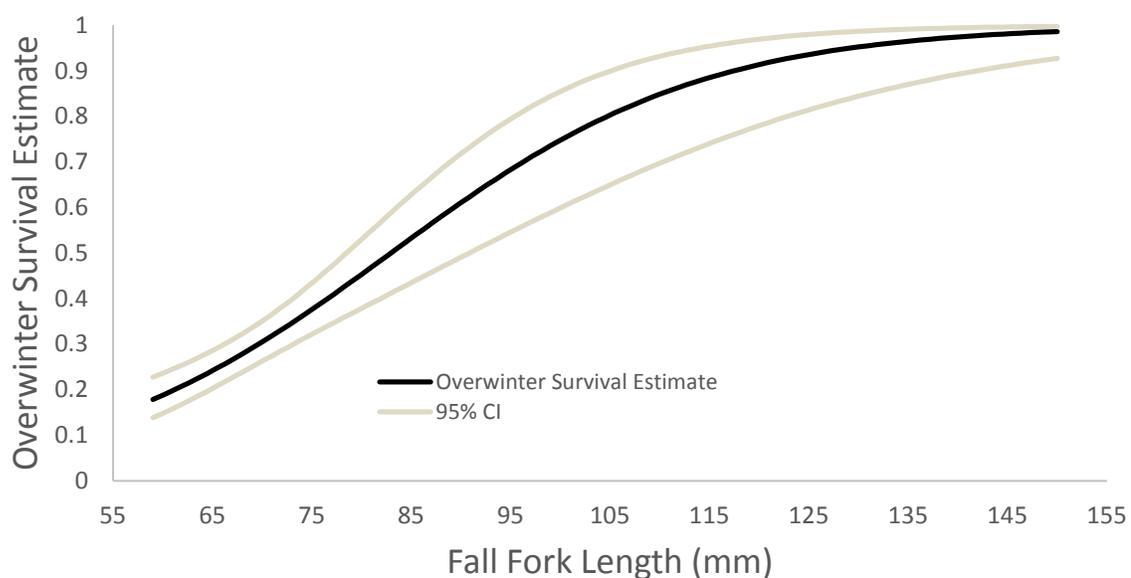
Figure 2. Estimated overwinter survival relationship with fall fork length (mm), taken from the top model containing length and watershed area as predictors. Survival estimates are for the average watershed area value. The 95% confidence interval were generated by MARK using the delta method.
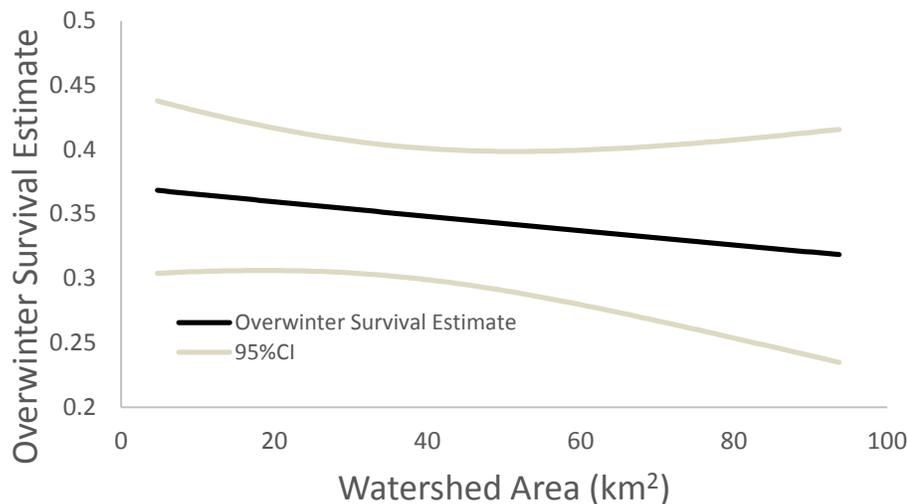
Figure 3. Estimated overwinter survival relationship with watershed area, taken from the top model containing length and watershed area as predictors. Survival estimates are for the average fish length value. The 95% confidence interval were generated by MARK using the delta method.
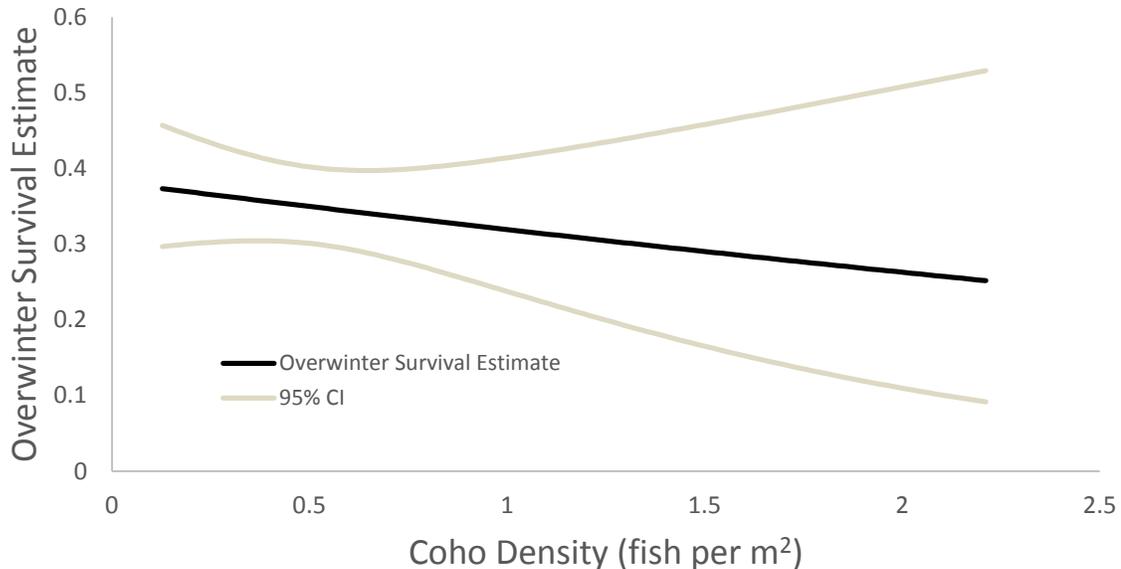
Figure 4. Estimated overwinter survival relationship with Coho Salmon density, taken from the model containing length, watershed area, and coho as predictors. Survival estimates are for the average length and watershed area values. The 95% confidence interval were generated by MARK using the delta method.

In the summer, the proportion of fish 60 mm or larger was 0.35 (n= 2088), while in the fall the proportion was 0.65 (n=374) (Figure 5). The estimated proportion of the population that were large enough for tagging (≥60 mm) relative to the single estimated overwinter survival represented 0.54 of the population.
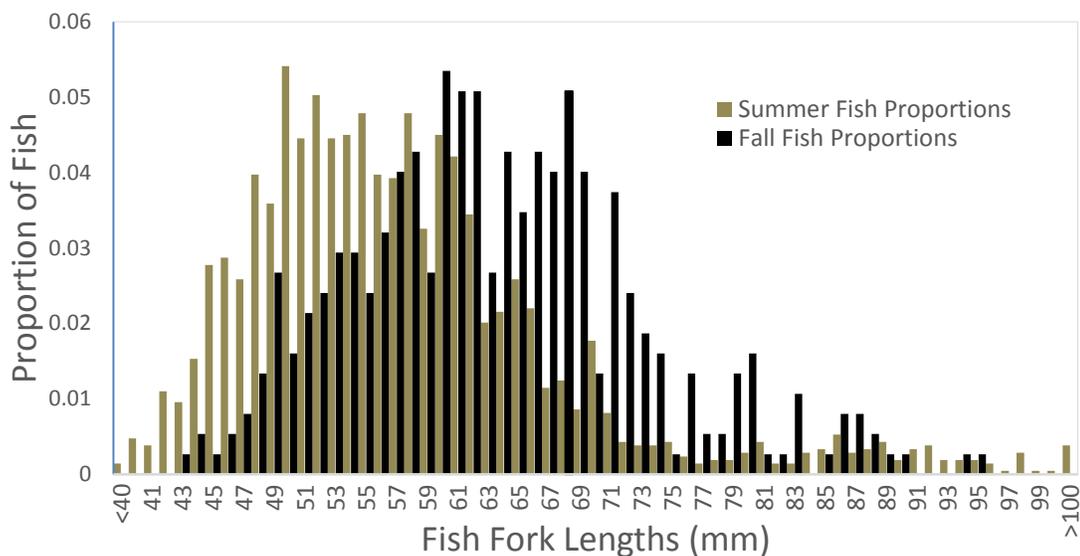
Figure 5. Size distribution of Coho Salmon throughout all tagging locations in summer and fall tagging events. Sample size for summer lengths = 2088 and sample size of fall sizes = 374. Size distribution is distinguished for summer and fall measured fish to illustrate seasonal differences in size distribution. The long right skew is likely composed of 1+ juveniles.

DISCUSSION

Density Estimation

The estimated density of juvenile Coho Salmon (0.52 fish/m^2) from pools in 2-4th order streams, is well within the range of average summer densities of juvenile Coho Salmon (0.135 fish/m^2 to 1.064 fish/m^2) summarized by Duffy (2012) from data collected annually from 1998-2010 within the Prairie Creek watershed in pool and run habitat (e.g. Gonzalez 2006, Ransom 2007). In a more northern region, Roni et al. (2012) estimated mean Coho Salmon density across 3 years within the East and West Twin Rivers, Washington. Mean Coho Salmon density estimates in pool and run habitat ranged from 0.37 – 1.94 fish/m^2. This studies mean density estimate is at the lower end of this range, and Prairie Creek densities from previous years overlap but appear to be slightly lower than these streams in Washington.

The estimated effects of model covariates on density were not entirely consistent with findings from previous studies. While I found that increased cover complexity was associated with decreased juvenile Coho Salmon density, several studies have documented increased density and abundance associated with cover following restoration-related increases in cover (e.g. Nickelson et al.1992a, Solazzi et al. 2000, Roni and Quinn 2001). Increased density of juvenile Coho Salmon has been associated with natural stream cover not associated with restoration (Webster et al. 2008), although a lack of an effect has been observed when looking at natural densities relative to

available cover (Rosenfeld et al. 2000). It is difficult to explain why cover would reduce Coho Salmon density. However, this may suggest that higher cover is associated with some other unaccounted for factor that fish are actively selecting against such as predation pressure, food access, or foraging efficiency. After rains begin fish may redistribute into pools with higher cover and shelter from high flows as suggested by Bell et al. (2001). The effect of increased cover is generally measured in recently restored or degraded systems that previously lacked pool structure and habitat. In a pristine system, the trend of increased density in areas with more cover may not hold. The finding that LWD did not affect fish density is inconsistent with Roni and Quinn (2001) who observed a significant increase in juvenile Coho Salmon density following addition of LWD. However, in a more pristine watershed perhaps availability of LWD does not drive density patterns. The finding that fish density increased with pool depth is consistent with previous research (e.g. Nickelson et al. 1992b). The decrease in mean density associated with larger watershed area is also consistent with the findings from previous studies. Although overall abundance may increase, fish density generally declines with greater stream order and channel width (Rosenfeld et al. 2000).

The relationships between model covariates and odds of detection by a snorkeler were not in accordance with my expectations. The finding that LWD decreased the odds of detection is consistent with previous studies (Thurow et al. 2006). The negative effect of depth on snorkel efficiency is also consistent with previous work (Schill and Griffith 1984) and personal experience, as observing fish in deeper and darker habitat can be more difficult. However, the strong positive relationship found between cover and odds

of detection was unexpected. This may suggest problems with my assessment of cover, which included structures such as vegetation up to a meter above the surface. A better method of measuring cover that directly influences snorkeler detection rates may be needed. In particular, distinguishing between types of cover may be important as odds of detection as well as fish behavior may vary with cover type. Fish hiding in loose cover such as debris, brush, or cut banks may actually be easier to detect since snorkelers are consciously targeting these spots within pools, and spotting a juvenile Coho Salmon or group of Coho Salmon is certainly possible in looser cover. In contrast, when fish hide under or inside dense cover it may be much more difficult for divers to observe them consistently.

Growth Estimation

The overwinter growth estimate of 0.16 % /day is slightly higher than found in previous years and streams. Moore (2014) observed growth of 0.13 % /day from fall 2012 to spring 2013. In the 2013-2014 year growth from initial tagging to spring was 0.15 % /day (Sparkman et al. 2015). These overwinter growth rates are similar to observed rates in Pudding Creek, California (~0.1 - ~0.16 % /day) from 2006-2010 (Wright et al. 2012). Duffy (2012) observed average growth of 19.1 mm from October to May in Prairie Creek (Duffy 2012). This is in contrast to the 28.9 mm growth observed from October to spring this year.

Survival Estimation

The overwinter survival estimate of 0.35 I generated was within a broad range of overwinter survival estimates (15.3-82.3 %) for Prairie Creek, CA since 1999 (Gonzales 2006, Brakensiek and Hankin 2007, Duffy 2012, Moore 2014, Sparkman et al. 2015), and is within the wide range of overwinter survival estimates for other coastal streams throughout their range (5– 80 %) (e.g. Ebersole et al. 2006, Wright et al. 2012, Rebenack et al. 2015). Although Prairie Creek is a relatively pristine system, overwinter survival of juvenile Coho Salmon is not substantially higher than has been found for other northern California streams which have been disturbed to a greater extent, such as nearby Freshwater Creek (Rebenack et al. 2015). Studies of survival in Prairie Creek and other Pacific Northwest streams have been primarily conducted during a prolonged drought when slow water habitat in the winter may be less limiting. During years of higher flows, overwinter survival might be higher in Prairie Creek than in disturbed regional streams because of the greater availability of slow water habitat. Currently, data are not available to explore this hypothesis, but continuing to monitor overwinter survival during high water years may give insights into the benefits of a pristine stream.

Early fall migration has not been well monitored in Prairie Creek so survival estimates may be biased low. Juvenile Coho Salmon that migrated prior to the operation of the screw trap in February 2015 were not accounted for in this study. The overwinter survival estimate may thus be lower than true survival. I used the lower antenna detections (without excluding captures before screw trap operation) to assess the extent of

migration unaccounted for in the CJS model. The antenna array was located approximately 3.5 km upstream of the mouth of Prairie Creek. At the lower antenna array 159 individuals were detected in spring while 67 were detected before spring (i.e. before screw trap operation). From this, detections prior to trap installation represented 30% of the lower antenna array detections over the season. This method may underestimate the importance of early migrants if the antenna efficiency was lower in winter than spring due to flow differences. However, of the 67 early migrants 8 fish were still detected at the trap leaving in the spring meaning they were not true early migrants out of Prairie Creek and likely reared in lower Prairie Creek between the lower antenna and screw trap. Additionally, this overestimates the importance of the early migrant population because these individuals were not yet subjected to the overwinter survival period. Insights into overwinter survival of early migrating juvenile Coho Salmon is lacking but may be low relative to spring migrants, particularly in Prairie Creek where the lower estuary has been hugely degraded and transformed (Ricks 1995). In the past, early migrating juvenile Coho Salmon have been assumed to be displaced in high flows. However, Bennett et al. (2014) showed that early migrants can be a significant portion of the migrating population and contribute to the returning adults. Rebeneck et al. (2014) also showed that in a nearby coastal stream early migrants in some years outnumber spring migrants.

The two year life history of extended freshwater rearing is not accounted for in this study. Using fish scales Moore (2014) estimated that the average size of 1+ parr in fall 2012 (two-year freshwater resident) was 86 mm (SD = 7) in Prairie Creek, and that the percentage

of parr exhibiting this life history was only 1.4%. Age classes overlapped somewhat; the largest age 0 fish was 82 mm and the smallest age 1+ fish was 74 mm. The finding of a low percentage of the 1+ life history suggests that it likely did not significantly impact the overwinter survival estimate in this study.   However, in one year (2000), Bell and Duffy (2007) found that 28% of out migrating Coho Salmon were 2 year old fish in Prairie Creek. Studies have shown that the expression of this life history varies between years, and other studies have reported variable percentages of a 2-year life history among years (Ransom 2007,Gallagher et al. 2012) so the extent that this assumption is being violated is not clear. In Prairie Creek, of 400 juvenile Coho Salmon tagged in fall 2012, one was detected in spring 2014, and of 809 juvenile Coho Salmon tagged in fall 2013, nine were detected in spring 2015 at the antennas or captured in the screw trap. This suggests that indeed some portion of the fish do stay and survive through a second year although it appears to only be a small fraction. The only insight into the proportion of two year olds in Prairie Creek for the 2014/2015 is shown in Figure 5 which shows the size distribution of captured fish throughout the stream in summer and fall 2014. There is a clear right skew to the data which is probably driven by the larger two year olds.

Limited fish movement is an important assumption of this study because a fish tagged in a given pool is assumed to be subjected to the conditions in that pool. Because I measured covariates at the pool scale, findings from this study do not take into account observations by Bell et al. (2001) that juveniles in upper Prairie Creek had low habitat unit fidelity over winter - a mean of 16% in both years surveyed. However, their study occurred in years with much higher flows and so their finding may not be applicable to

this study. Moore (2014) suggested that some juvenile Coho Salmon in upper Prairie

Creek may move into the lower reaches prior to the spring migration. Rodriguez (2002)

studied 6 salmonid species across 27 populations and found that the proportion of mobile

individuals in the dry season was low in most populations and that displacement was

typically less than 50 meters. Of the 52 fish tagged in summer and recaptured in fall from

this study, 42 were recaptured in the same pool, and no fish were recaptured in a different

reach than it was tagged in. Kahler et al. (2001) found that as many as half the juvenile Coho

Salmon moved one habitat unit or more over the summer. However, movement was more

likely in lower quality habitat (smaller and shallower pools) and less likely in higher quality

habitat (larger and deeper pools). If fish in Prairie Creek do change habitat associations

seasonally, my findings are still useful in identifying covariate effects on survival. For

example, if pool depth increases pool fidelity and pool fidelity increases survival probability

then the estimated effect of pool depth on survival would still be useful. However, the

association of pool depth with a specific movement pattern that drives the survival

relationship would be obscured. If low quality habitat causes movement and fish that move

more have lower survival, then it is still true that the low quality habitat lowers survival,

although the mechanism of movement is obscured.

The CJS model presented here assumes that detection efficiency remains

consistent throughout the season at each detection point. This may be problematic

because antenna efficiency and trap efficiency can vary to an unknown degree based on

water conditions (Aymes and Rives 2009) and operator maintenance.   In some cases,

detection efficiency was brought to zero when antenna arrays could not operate in high

flows. When interpreting covariates of survival, the effect of a covariate is confounded in respect to the effect on survival and detection efficiency. In particular, my model has shown that survival increases for larger fish. However, this trend may be confounded by the effect of fish length on detection. Fish swimming behavior has been shown to affect detection efficiency of PIT tag antennas (Aymes and Rives 2009). For example, if smaller fish generally travel along the stream edge and this causes higher detection rates for larger fish at a given location, this would cause the model to increase survival estimates for larger fish.

This study did not account for any potential PIT tag mortality or tag loss which has been shown in some cases to be size dependent (Brakensiek and Hankin 2007). However, Rebenack et al. (2015) found no PIT tag mortality and PIT tag loss in nearby Freshwater Creek using identical tagging procedures. In addition, other similar studies have shown zero mortality after holding fish for 24 hours (Bennett et al. 2011). Most PIT tag studies of juvenile salmonids have reported a tag shed rate of less than 5% (Ombredane et al. 1998; Bell et al. 2001; Gries and Letcher 2002; Brakensiek and Hankin 2007; Sloat et al. 2011).

Measured habitat attributes were not found to influence survival in this study. Study findings that pool depth did not influence survival probability is consistent with past findings in Prairie Creek (Moore 2014) and other systems (Quinn and Peterson 1996, Roni et al. 2012). Watershed area was not associated with survival, and even though it was in the top model the relationship between survival and watershed area was not biologically significant. In the 2012/2013 season in Prairie Creek, Moore (2014) found

that overwinter survival of fish low in the watershed had a negative relationship with fish length in fall, while overwinter survival of fish high in the watershed had a positive relationship with fish length in fall. Findings from 2013/2014 showed that apparent survival was higher in the upper reaches of main stem Prairie Creek than in the lower reaches (Sparkman et al. 2015). Study estimates are inconsistent with these past findings in Prairie Creek, however, research suggests that watershed scale survival can be highly variable spatially and temporally (Ebersole et al. 2009, Roni et al. 2012). Watershed area may not account for differences in past land use as the pristine headwaters of Prairie Creek were grouped with historically logged tributaries because of similar small watershed area sizes. Within the mainstem, the upper reaches are pristine while the lower reaches have been relatively degraded. This may confound the effects of historical land use and the effects of watershed area on survival.

Results from this study suggesting that LWD did not influence survival were consistent with earlier findings in Prairie Creek. Moore (2014) suggested that measuring volume as well as density of LWD may be appropriate in Prairie Creek, because much of the large wood is composed of very large, slowly decomposing old-growth redwood trees. In addition to measuring LWD volume, taking into account LWD position in the stream could be important to distinguish between variable functions of LWD such as pool formation (Cederholm et al. 1997, Rosenfeld and Huato 2003), high flow refuge (Roni and Quinn 2001), feeding habitat (Piccolo et al. 2008, Rosenfeld and Raeburn 2009), etc. In Prairie Creek, particularly in a drought year, survival trends may not be dictated by availability of LWD.

The absence of a relationship between survival and cover was unexpected as cover is thought to provide refuge from high flows and increasing stream cover is a common restoration practice (e.g. Nickelson et al.1992a, Solazzi et al. 2000, Roni and Quinn 2001). Similar to LWD discussed above, it may be that cover complexity associated with more high flow refugia is not critical in a drought year. Additionally, the study methodology for measuring cover may not have taken into account all of the variable functions often associated with different types of cover such as refugia from high flows (Roni and Quinn 2001), refugia from predators, optimal foraging habitat, and food production.

Study results that trout density did not influence survival rates is consistent with other studies in experimental stream channels (Fraser 1969, Rosenfeld et al. 2005) and field experiments in relatively degraded habitat (Harvey and Nakamoto 1996). Studies have shown that increasing trout densities can reduce juvenile Coho Salmon growth (Harvey and Nakamoto 1996) and can have effects on habitat selection (Young 2004). However, in anthropogenically-simplified habitat, the opportunity for different species to avoid competition with one another through habitat segregation is often reduced (Young 2004). In Prairie Creek, the higher availability of complex habitat may buffer against the potential for strong interspecific interactions to affect survival of juvenile Coho Salmon. It should be noted, however, that the estimates of trout densities may be biased, as these were based only on raw counts uncorrected for detection efficiency. In addition, as small trout likely exhibit higher movement among pool and riffle habitats (Bisson et al. 1988,

Bugert and Bjornn 1991), the trout density covariates may have only weakly represented the true densities to which pool-dwelling Coho Salmon were exposed.

The marginal evidence that increased Coho Salmon density decreased survival is an important and interesting finding. Density dependent survival has been previously detected in Prairie, Streelow, and Boyes creeks in summer (Ransom 2007), and in more degraded systems in Northern California (Gallagher et al. 2012 and Wright et al. 2012). This could have potential important implications for effective restoration and conservation. Depending on the particular resources which may be limiting survival, restoration practices such as the addition of large woody debris, may or may not be effective in increasing survival or population viability. This study did not measure food availability or habitat features that may affect predation risk, or other potentially limiting resources.

Other time periods such as summer could be limiting and influential in Prairie Creek. The study estimate of late summer survival was 0.80 (95% CI 0.63-0.90) which is consistent with similar summer survival estimates from the Prairie Creek watershed in previous years. From 1998 to 2010 survival of juvenile Coho Salmon between July and October among years ranged from 72% to 87% (Duffy 2012). Ransom (2007) estimated survival for Prairie (86-93%), Streelow (53- 88%), and Boyes Creeks (70 – 105 %) from July to October 2000-2002. These survival estimates were obtained by comparing density in July to October and were calculated for each stream separately which may explain the larger range of survival estimates. When summer and winter survival estimates are converted to monthly survival rates there does not appear to be a difference

between the two seasons, with summer survival of 88 %/month and winter survival of 86 %/month. The strong effect of fish size in summer/fall on winter survival could suggest that conditions and growth prior to the winter are really what drives a fish's ability to survive the winter. Given that California has remained in a prolonged drought and that Prairie Creek has relatively high levels of winter habitat, perhaps population limitations are not currently during the wet season, but during the dry season. Determining what limits survival and growth in summer may be useful for understanding the larger picture of limitations on smolt export out of Prairie Creek in the face of climate change and potential drought.

LITERATURE CITED

Achord, S, P S Levin, and R W Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past. *Ecology Letters* 6(4): 335-342.

Amstrup, S C, T L McDonald, and B F J Manly. 2005. Handbook of capture-recapture analysis. Princeton University Press, New Jersey.

Anderson, J H, P M Kiffney , G R Pess and T P Quinn. 2008. Summer Distribution and Growth of Juvenile Coho Salmon during Colonization of Newly Accessible Habitat, *Transactions of the American Fisheries Society* 137(3): 772-781.

Armstrong, J D, and S W Griffiths. 2001. Density-dependent refuge use among overwintering wild Atlantic salmon juveniles. *J. Fish Biol*. 58: 1524–1530.

Aymes J C, J Rives. 2009. Detection efficiency of multiplexed Passive Integrated Transponder antennas is influenced by environmental conditions and fish swimming behavior. *Ecology of Freshwater Fish* 18: 507–513.

Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *Journal of Experimental Biology* 35.

Bell, E and W G Duffy. 2007. Previously Undocumented Two-Year Freshwater Residency of Juvenile Coho Salmon in Prairie Creek, California, *Transactions of the American Fisheries Society* 136(4): 966-970.

Bell, E, W G Duffy and T D Roelofs. 2001. Fidelity and survival of juvenile Coho Salmon in response to a flood. *Transactions of the American Fisheries Society* 130(3): 450-458.

Bennett, T R, P Roni, K, Denton, M McHenry, and R Moses. 2014. Nomads no more: early juvenile coho salmon migrants contribute to the adult return. *Ecology of Freshwater Fish* 24(2): 264-275.

Bennett, T R, R Wissmar, and P Roni. 2011. Fall and spring emigration timing of juvenile coho salmon from East Twin River, Washington. *Northwest Science* 85:562–570.

Bernhardt, E S, M A Palmer, J D Allan, G Alexander, K Barnas, S Brooks, J Carr, S Clayton, C Dahm, J Follstad-Shah, D Galat, S Gloss, P Goodwin, D Hart, B Hassett, R Jenkinson, S Katz, G M Kondolf, P S Lake, R Lave, J L Meyer, T K

O'Donnell, L Pagano, B Powell, and E Sudduth. 2005. Synthesizing U.S. river restoration efforts. *Science* 308:636–637.

Bisson, P A, K Sullivan and J L Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile Coho Salmon, steelhead, and cutthroat trout in streams. *Transactions of the American Fisheries Society* 117(3): 262-273.

Brakensiek, K E. 2002. Abundance and survival rates of juvenile Coho Salmon (Oncorhynchus kisutch) in Prairie Creek, Redwood National Park. MS Thesis. Humboldt State University. CA.

Brakensiek, K E, and D G Hankin. 2007. Estimating overwinter survival of juvenile Coho Salmon in a northern California stream: accounting for effects of passive integrated transponder tagging mortality and size-dependent survival. *American Fisheries Society. Transactions* 136(5):1423–37.

Brown, L R, P B Moyle and R M Yoshiyama. 1994. Historical decline and current status of Coho Salmon in California. *North American Journal of Fisheries Management* 14(2): 237-261.

Bugert, R M, T C Bjornn. 1991. Habitat use by steelhead and Coho Salmon and their responses to predator and cover in laboratory streams. *Transactions of the American Fisheries Society* 120: 486-493.

Burnham, K P, and D R Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Bustard, D R and D W Narver. 1975. Aspects of the winter ecology of juvenile Coho Salmon and Steelhead Trout. *Canada. Fisheries Research Board. Journal* 32(5): 667-680.

Cannata, S, R Henly, J Erler, J Falls, D McGuire and J Sunahara. 2006. Redwood Creek Watershed Assessment Report. Coastal Watershed Planning and Assessment Program and North Coast Watershed Assessment Program. California Resources Agency and California Environmental Protection Agency, Sacramento California.

Carlson, S R, L G Coggins Jr., and C O Swanton. 1998. A simple stratified design for mark-recapture estimation of salmon smolt abundance. *Alaska Fishery Research Bulletin* 5(2):88-102.

Cederholm C J, R E Bilby , P A Bisson , T W Bumstead , B R Fransen , W J Scarlett and J W Ward. 1997. Response of juvenile Coho Salmon and steelhead to placement

of large woody debris in a coastal Washington stream. *North American Journal of Fisheries Management* 17(4): 947-963.

Cooch, E and G White. 2014. Program MARK: a gentle introduction, 13th edition. Colorado State University, Fort Collins, Colorado. http://www.phidot.org/software/mark/docs/book/.

Crispin, V, R House, and D Roberts. 1993. Changes in instream habitat, large woody debris, and salmon habitat after the restructuring of a coastal Oregon stream. *North American Journal of Fisheries Management* 13: 96-102.

Cunjak, R A. 1988. Behavior and microhabitat of young Atlantic salmon during winter. *Can. J. Fish. Aquat. Sci.* 45: 2156–2160.

Dolloff, C A. 1993. Predation by river otters (*Lutra canadensis*) on juvenile Coho Salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) in Southeast Alaska. *Can. J. Fish. Aquat. Sci.* 50: 312–315.

Duffy, E J and D A Beauchamp. 2008. Seasonal patterns of predation on juvenile Pacific salmon by anadromous Cutthroat Trout in Puget Sound. *Transactions of the American Fisheries Society* 137(1): 165-181.

Duffy, W G. 2012. Prairie creek sub-basin life cycle monitoring project. Report to the Fisheries Restoration Grants Program of the State of California Department of Fish and Wildlife. 80 pp. available at http://www.humboldt.edu/cuca/documents/reports/Final%20Report%20Prairie%20Creek%202014.pdf.

Duffy, W G, E P Bjorkstedt and C S Ellings. 2011. Predation on juvenile Pacific salmon Oncorhynchus spp. in downstream migrant traps in Prairie Creek, California, *North American Journal of Fisheries Management* 31(1): 151-164.

Ebersole, J L , M E Colvin , P J Wigington Jr. , S G Leibowitz , J P Baker , M. R Church, J E Compton, B A Miller, M A Cairns, B P Hansen and H R La Vigne. 2009. Modeling stream network-scale variation in Coho Salmon overwinter survival and smolt size. *Transactions of the American Fisheries Society* 138(3): 564-580.

Ebersole, J L, P J Wigington, J P Baker, M A Cairns, M R Church, B P Hansen, B A Miller, H R Lavigne, J E Compton, and S G Leibowitz. 2006. Juvenile Coho Salmon growth and survival across stream network seasonal habitats. *Transactions of the American Fisheries Society* 135(6): 1681–97.

Fausch, K D, T G Northcote. 1992. Large Woody Debris and Salmonid Habitat in a Small Coastal British Columbia Stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49(4): 682-693.

Fiske, I, and R B Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43(10): 1-23. URL http://www.jstatsoft.org/v43/i10/.

Fox, J and S Weisberg. 2011. An {R} companion to applied regression, second edition. Thousand Oaks CA: Sage. URL http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Fraser, F J. 1969. Population density effects on survival and growth of juvenile Coho Salmon and Steelhead trout in experimental stream-channels. *Fish, Fisheries & Aquatic Biodiversity Worldwide.* 253-266.

Gallagher, S P, S Thompson, and D W Wright. 2012. Identifying factors limiting Coho salmon to inform stream restoration in coastal Northern California. *California Fish and Game 98*(4): 185-201.

Giannico, G R., and S G Hinch. 2003. The effect of wood and temperature on juvenile Coho Salmon winter movement, growth, density and survival in side-channels. *River Research and Applications* 19(3): 219–31.

Glova, G J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon and coastal cutthroat trout in a laboratory stream. *Hydrobiologia* 132: 155-168.

Gonzales, E J. Diet and prey consumption of juvenile Coho Salmon in three Northern California Streams. MS thesis. Humboldt State University, CA, 2006.

Gregory, J S, and J S Griffith. 1996. Aggressive behavior of under yearling rainbow trout in simulated winter concealment habitat. *J. Fish Biol.* 49: 237–245.

Gregory, R S, and C D Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* 127(2): 275–85.

Gries, G and B H Letcher. 2002. Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management* 22:219–222.

Hartman, G F and T G Brown. 1987. Use of small, temporary, floodplain tributaries by juveniles salmonids in a west coast rain-forest drainage basin, Carnation Creek,

British Columbia. *Canadian journal of fisheries and aquatic sciences* 44: 262-270.

Harwood, A J, N B Metcalfe, S W Griffiths, and J C Armstrong. 2002. Intra- and inter-specific competition for winter concealment in juvenile salmonids. *Can. J. Fish. Aquat. Sci.* 59:1515–1523.

Harvey, B C, and R J Nakamoto. 1996. Effects of steelhead density on growth of Coho Salmon in a small coastal California stream. *Transactions of the American Fisheries Society* 125:237-243.

Hauer, Jennifer. Overwinter survival and growth of juvenile Coho Salmon in Freshwater Creek, California. MS thesis. Humboldt State University, CA, 2013.

Heggenes, J, T G Northcote, and A Peter. 1991. Seasonal habitat selection and preferences by cutthroat trout in a small, coastal stream. *Can. J. Fish. Aquat. Sci.* 48: 1364-1370.

Hillman, T W, J W Mullan and J S Griffith. 1992. Accuracy of Underwater Counts of Juvenile Chinook Salmon, Coho Salmon, and Steelhead. *North American Journal of Fisheries Management* 12(3): 598-603.

Horton, G E, B H Letcher. 2008. Movement patterns and study area boundaries: influences on survival estimation in capture-mark-recapture studies. *Oikos* 117: 1131-1142.

Janda, R J, K M Nolan, D R Harden, and S M Colman. 1975. Watershed conditions in the drainage basin of Redwood Creek, Humboldt County, California as of 1973, United States Geological Survey, Open-File Report 75-568, Menlo Park, California.

Johnson, S L, J D Rodgers, M F Solazzi, and T E Nickelson. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus spp.)* in an Oregon coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 412–4.

Joseph, L N, C Elkin, T G Martin, and H P Possingham. 2009. Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. *Ecological Applications* 19(3): 631-642.

Kahler, T H. 1999. Summer movement and growth of individually marked juvenile salmonids in western Washington streams. M.S. thesis, University of Washington, Seattle, Wash.

Kahler, T H, P Roni, and T P Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1947–1956.

Katz, J, P B Moyle, R M Quiñones, J Israel, and S Purdy. 2013. Impending extinction of Salmon, Steelhead, and Trout (*Salmonidae*) in California. *Environmental Biology of Fishes* 96(10-11):1169–86.

Kery, M. 2008. Estimating abundance from bird counts: binomial mixture models uncover complex covariate relationships. *The American Ornithologists Union* 125(2): 336-345.

Lau, M R. Habitat utilization, density, and growth of steelhead trout, Coho Salmon, and Pacific giant salamander in relation to habitat types in a small coastal redwood stream. MS Thesis. University of California, Davis, 1994.

Lawson, P W, Logerwell, E A, Mantua, N J, Francis, R C, and Agostini, V N. 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest Coho Salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 61(3): 360-373.

Lebreton J, K P Burnham, J Clobert, and D R Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.

Ly, J, Z Ruddy, A Garrett, I Lagomarsino, and C Winger. 2011. Southern Oregon/northern California coast recovery domain: 5-year review: summary and evaluation of southern Oregon/northern California coast coho salmon ESU. National Marine Fisheries Service, Long Beach, California.

Martel, G. 1996. Growth rate and influence of predation risk on territoriality in juvenile Coho Salmon. *Can. J. Fish. Aquat. Sci*. 53: 660-669.

Mazerolle, M J. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. http://CRAN.Rproject.org/package=AICcmodavg.

Milner, N J, J M Elliott, J D Armstrong, R Gardiner, J S Welton, and M Ladle. 2003. The natural control of salmon and trout populations in streams. *Fisheries Research* 62:111–125.

Moore, T. Overwinter survival and redistribution of juvenile Coho Salmon, *Oncorhynchus kisutch*, in Prairie Creek, California. MS thesis. Humboldt State University, CA, 2014.

Mudholkar, G S. 2006. Fisher's z-transformation. Encyclopedia of Statistical Sciences. 4.

Nickelson, T E, M F Solazzi, S L Johnson, and J D Rogers. 1992a. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile Coho Salmon (*Oncorhynchus Kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences 49*(4): 790-794.

Nickelson, T E, and P W Lawson. 1998. Population viability of Coho Salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. *Canadian Journal of Fisheries and Aquatic Sciences* 55(11): 2383–2392.

Nickelson, T E, J D Rogers, S L Johnson, and M F Solazzi. 1992b. Seasonal Changes in Habitat use by juvenile Coho Salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49(4): 783-789.

NMFS (National Marine Fisheries Service). 2014. Final recovery plan for the Southern Oregon/Northern California coast evolutionarily significant unit of Coho Salmon (*Oncorhynchus kisutch*). National Marine Fisheries Service. Arcata, CA.

NOAA (National Oceanic and Atmospheric Association). National Marine Fisheries Service. 2011. ESA salmon listings. http://www.nwr.noaa.gov/ESA-Salmon-Listings/.

Nowak, G M , R A Tabor , E J Warner , K L Fresh , T P Quinn. 2004. Ontogenetic shifts in habitat and diet of Cutthroat Trout in Lake Washington, Washington. *North American Journal of Fisheries Management* 24(2): 624-635.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Ombredane, D, J L Bagliniere, and F Marchand. 1998. The effects of passive integrated transponder tags on survival and growth of juvenile brown trout (*Salmo trutta L.*) and their use for studying movement in a small river. *Hydrobiologia* 371/372: 99-106.

Orpwood, J E, Griffiths, S W, and Armstrong, J D. 2003. Effects of body size on sympatric shelter use in over-wintering juvenile salmonids. *J. Fish Biol.* 63: 166–173.

Parker, R R. 1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *Journal of the Fisheries Research Board of Canada* 28(10): 1503-1510.

Pess, G R, P M Kiffney, M C Liermann, T R Bennett, J H Anderson, and T P Quinn. 2011. The influences of body size, habitat quality, and competition on the movement and survival of juvenile Coho Salmon during the early stages of stream recolonization. *Transactions of the American Fisheries Society* 140(4): 883–97.

Piccolo, J J, N F Hughes, M D Bryant. 2008. Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon and steelhead. *Can. J. Fish. Aquat. Sci.* 65: 266-275.

Quinn, T P, N P Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile Coho Salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 53(7):1555-1564.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Ransom, B O. 2007. Extended freshwater rearing of juvenile Coho Salmon in Northern California streams. MS thesis. Humboldt State University, CA, 2007.

Rebenack J J, S Ricker, C Anderson, M Wallace and D M Ward. 2015. Early emigration of juvenile Coho Salmon: implications for population monitoring. *Transactions of the American Fisheries Society* 144(1): 163-172.

Ricks, L C. 1995. Effects of channelization on sediment distribution and aquatic habitat at the mouth of Redwood Creek, Northwestern California. Geomorphic processes and aquatic habitat in the Redwood Creek Basin, Northwestern California. United States Geological Survey Professional Paper 1454-Q.

Rodriguez, M A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* 83(1): 1-13.

Roni, P, K Hanson, and T Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat and rehabilitation techniques. *North American Journal of Fisheries Management* 28: 856-890.

Roni, P, T Bennett, R Holland, G Pess, K Hanson, R Moses, M McHenry, and J Walter. 2012. Factors affecting migration timing, growth, and survival of juvenile Coho Salmon in two coastal Washington watersheds. *Transactions of the American Fisheries Society* 141(4): 890-906.

Roni, P, and T P Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58(2): 282-292.

Rosenfeld, J S, M Porter, and E Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout and coho salmon. *Can. J. Fish Aquat. Sci.* 57: 766-774.

Rosenfeld, J S, and L Huato. 2003. Relationship between large woody debris characteristics and pool formation in small coastal British Columbia streams. *North American Journal of Fisheries Management* 23(3): 928-938.

Rosenfeld, J S, T Leiter, G Lindner, and L Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile Coho Salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 62(8): 1691–1701.

Rosenfeld J S, E Raeburn. 2009. Effects of habitat and internal prey subsidies on juvenile coho salmon growth: implications for stream productive capacity. *Ecology of Freshwater Fish* 18: 572–584.

Royle, J A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108-115.

Royle, J A, and R M Dorazio. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities. 1st ed. London: Academic, 127-155. Print.

Sandercock, F K. 1991. Life history of Coho Salmon. Pages 419-424 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia.

Schill, D J, and J S Griffith. 1984. Use of underwater observations to estimate cutthroat trout abundance in the Yellowstone River. *North American Journal of Fisheries Management* 4: 479-487.

Sharma, R and R Hilborn. 2001. Empirical relationships between watershed characteristics and Coho Salmon (*Oncorhynchus kisutch*) smolt abundance in 14 western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1453–1463.

Simpkins, D G, W A Hubert, C Martinez Del Rio, and D C Rule. 2004. Constraints of body size and swimming velocity on the ability of juvenile rainbow trout to endure periods without food. *Journal of Fish Biology* 65(2): 530-544.

Sloat, M R, P F Baker and F K Ligon. 2011. Estimating habitat-specific abundances of PIT-tagged juvenile salmonids using mobile antennas: a comparison with standard electrofishing techniques in a small stream. *North American Journal of Fisheries Management* 31:986-993.

Solazzi, M F, T E Nickelson, S L Johnson, and J D Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. *Canadian Journal of Fisheries and Aquatic Sciences* 57(5): 906-914.

Sparkman, M D, M A Wilzbach, P Y Drobny, M E Gordon, and C M G Boone. 2015. Prairie Creek Monitoring Project, 2014 Season: a report to the Fisheries Restoration Grants Program of the State of California Department of Fish and Wildlife. 79 pp. (Project No. P1210321). available at: http://www2.humboldt.edu/cuca/documents/reports/prairiecreek2014annualrreport.pdf

Sparkman, M D, P Y Drobny, M A Wilzbach, M E Gordon, and C M G Boone. 2016. Prairie Creek Monitoring Project, 2015 Season: a report to the Fisheries Restoration Grants Program (Project No. P1210321).

Thurow, R F, J T Peterson and J W Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating Bull Trout abundance in first- to third-order streams. *North American Journal of Fisheries Management* 26(1): 217-232.

Urawa, Shigehiko. 1995. Effects of rearing conditions on growth and mortality of juvenile chum salmon infected with Ichthyobodo necator. *Can J. Fish. Aquat. Sci.* 52(1):18-23.

United States Geological Survey. 2016. Surface water for USA: peak streamflow. http://nwis.waterdata.usgs.gov/nwis/peak?. (Feb., 9 2016).

Webster, R A, K H Pollock, S K Ghosh and D G Hankin. 2008. Bayesian Spatial Modeling of Data from Unit-Count Surveys of Fish in Streams. *Transactions of the American Fisheries Society* 137(2): 438-453.

White, G C and K P Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120-139.

Whiteway, S L, P M Biron, A Zimmerman, O Venter, and J W A Grant. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 831-841.

Wilzbach, M A. 2016. State of the fisheries and aquatic resources of Prairie Creek: final report to Redwood National and State Parks (Cooperative Agreement Number P13AC00848, Task Agreement Number P14AC01284).

Wright, D W, S P Gallagher, and C J Hannon. 2012. Proceedings of coast redwood forests in a changing California: a symposium for scientists and managers. General Technical Report PSW-GTR-238. Pages 459-470.

Young, K A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology* 85(1): 134–49.

APPENDIX A

Appendix A: Relationship between average juvenile Coho Salmon fork length and juvenile Coho Salmon density. Both average juvenile Coho Salmon fork length and density are for a given pool. Fish length is across 95 pools and includes 2064 fish length measurements. A pool had to have 5 or more length measurements to be included in analysis. Coho Salmon density were derived from the N-mixture abundance model.