BEAVER BANK LODGE USE, DISTRIBUTION AND INFLUENCE ON SALMONID REARING HABITATS IN THE SMITH RIVER, CALIFORNIA

By

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ABSTRACT

BEAVER BANK LODGE USE, DISTRIBUTION AND INFLUENCE ON SALMONID REARING HABITAT IN THE SMITH RIVER, CALIFORNIA
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Anthropogenic activities in the coastal plain of the Smith River have reduced the quality and quantity of productive salmonid rearing habitat. Consequently, restoration is needed to aid in the recovery of the threatened Smith River Coho salmon (*Oncorhynchus kisutch*) population. The ecological engineering activities of the North American beaver (*Castor canadensis*) have been shown to provide beneficial salmonid habitat. However, data showing beaver importance in coastal rivers where they are unable to create dams is lacking. A substantial beaver population resides in and utilizes bank lodges in the mainstem and coastal tributaries of the Smith River basin in Northern California. This distribution overlaps almost entirely with the current Coho salmon distribution in the Smith River. I conducted surveys during the summer 2014 and winter 2014-15 with two objectives: (1) to assess the influence of hydraulic control structures and bank height on beaver bank lodge site selection, and (2) to evaluate multi-season occupancy parameters of juvenile Coho salmon at non-natal rearing habitats with and without beaver activity. Presence of a hydraulic control feature and increased bank height were found to have a significant positive influence on beaver bank lodge site selection. Volume of fish cover created by beavers was found to have a positive influence on juvenile Coho salmon occupancy during summer rearing. Volume of cover created by beavers was a better predictor of Coho salmon occupancy than other habitat variables commonly used in restoration, such as large woody debris. These data suggest that beaver enhance juvenile Coho salmon non-natal rearing habitat in a large river system, even where beavers are unable to create channel spanning dams. Management and restoration decisions should consider beaver distribution and abundance in large river systems to better assess where and how beavers can be utilized to provide and enhance rearing habitat for juvenile salmonids in coastal rivers and streams, as well as how to improve habitat to support a robust beaver population.

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INTRODUCTION

North American beavers (*Castor canadensis*) are ecological engineers because their activity modifies the resources available to other species (Jones et al. 1994). Research has shown beaver dams provide many ecosystem services by raising the level of ground water, increasing riparian habitat, instream habitat, and retention of organic matter (Johnston and Naiman 1987, Naiman et al. 1988), as well as improving water quality (Balodis 1994). Dams elevate organic matter and soil retention resulting in increased nitrogen fixation and microbial activity (Collen and Gibson 2001). Increased salmonid growth and productivity have been shown in streams with beaver dams when compared to streams without (Bustard and Narver 1975). Furthermore, beaver activity has been shown to increase biodiversity of all taxa at the landscape scale (Collen and Gibson 2001, Wright and Jones 2002, Müller-Schwarze, and Sun. 2003). Restoration mimicking and encouraging beaver damming has illustrated that beaver dams can successfully restore incised streams in central Oregon through channel aggradation, raising the water table and increasing riparian vegetation (Pollock et al. 2007).

These past findings and restoration efforts have been primarily focused on small (2^{nd} – 4^{th} order) streams or lakes and have not investigated the impacts of beaver's non-damming activities, such as creation and use of bank lodges on large coastal mainstem rivers. Data are lacking in coastal streams along coastal California where beavers utilize streams with frequent fluctuations in flow (Tappe 1942, Yocom et al. 1956), including in the mainstem and tributaries downstream of the Forks of the Smith River in Northern

California, where a substantial beaver population resides. These beavers generally do not construct dams but rather build lodges along river banks where water has sufficient depths to provide safe movement into and out of their lodge. In the Smith River, beaver distribution almost entirely overlaps with current Coho salmon (*Oncorhynchus kisutch*) distribution (Garwood and Larson 2014, Parish and Garwood 2015). Thus, beavers may provide ecosystem services for this endangered species.

The Coho salmon population in the Smith River has low abundance and productivity, which puts them at risk of extinction (Garwood and Larson 2014). This species is listed as threatened under both federal (ESA) and state (CESA) endangered species acts (Federal Register 1997, CDFG 2002). The survival and viability of this population is limited due to the lack of floodplain connectivity and complex instream and off-channel habitat in the Smith River. These vital rearing habitats have proved to be productive for Coho salmon, as well as other salmonid species, in fry, juvenile and smolt stages (Wissmar and Simenstad 1998, Wallace and Allen 2009, NMFS 2014). Improvement of channel-complexity, floodplain connectivity and overall health of the riparian forest are needed to increase juvenile Coho salmon survival, productivity and recovery of the population (NMFS 2014).

Beavers likely have a significant role in creating and maintaining salmonid rearing habitat in the Smith River coastal plain and may present restoration opportunities to improve salmonid habitat, thereby aiding in recovery of the Coho salmon population and viability of all salmonid species within the basin. To fill the data gaps on beaver habitat use and influence in a large river system I conducted this research with two objectives. The first objective was to describe beaver distribution, suitable habitat, and lodge site selection in the mainstem Smith River and its tributaries (Chapter 1). The second objective was to document and analyze juvenile salmonid use of beaver-influenced vs. non-beaver-influenced off-channel and backwater habitats for summer and winter rearing (Chapter 2). Together these two objectives were used to evaluate the influence beavers have on juvenile salmonid non-natal rearing habitat in a mainstem coastal river and the potential of using beavers as a restoration tool in similar systems.

CHAPTER 1 – BEAVER BANK LODGE SITE SELECTION

Introduction

Within their territory, beavers use engineering skills to build lodges and sometimes dams and food caches. There are two main types of lodges, hut lodges and bank lodges. Hut lodges are built out of wood and mud and are surrounded by water in a stream, lake or pond. Bank lodges, also known as bank burrows, are built by burrowing into the bank, and sticks may or may not be added on top to create a nest chamber (Bradt 1938). A single beaver colony shares a territory that may contain multiple active and inactive lodges (Bradt 1938, Baker and Hill 2003). Dams built with wood, mud and rock impound water by entirely or partially spanning a river to maintain deep water, which is required to provide safe movement to and from lodges, as well as access to and transportation of food sources (Bradt 1938, Müller-Schwarze and Sun 2003). Food caches are harvested food items (e.g., willow) secured under water for winter food supply; however, these are uncommon in riverine and ice-free inhabited areas (Robel and Fox 1993, Baker and Hill 2003). Beavers' engineering activities create favorable habitat by providing predator protection and a food supply for the colony to survive throughout the year (Baker and Hill 2003).

A colony is a single territorial family group, which typically consists of a monogamous adult breeding pair, yearlings or sub-adults (12-24 months old), and young of the year or kits (< 12 months old) (Bradt 1938, Baker and Hill 2003). On average a single colony has approximately 5 individuals, however as many as 15 individuals in a colony have been reported (Bradt 1938, Yocom et al. 1956, Müller-Schwarze and Sun 2003). Yearlings disperse in the spring or summer in search of a mate and a new territory, typically before a new litter is born (Van Deelen and Pletscher 1996, Müller-Schwarze and Sun 2003). Dispersal distance can vary widely, ranging from 0.2 to 81.6 km along the stream (Beer 1955, Van Deelen and Pletscher 1996, Müller-Schwarze and Sun 2003). Due to diverse habitat conditions, the home range of a colony living along a river or stream has been reported to range from 0.5 km (Semyonoff 1951) to 2.4 km (Robel and Fox 1993) with a density of 0.08 – 1.40 colonies/km (Robel and Fox 1993). The territory size and actively used area vary seasonally due to parental care, weather, and stream flow conditions (Baker and Hill 2003) and are typically larger during the summer than the winter months. An unused neutral area of stream commonly occurs between territories (Bradt 1938, Semyonoff 1951, Robel and Fox 1993).

Beavers' ability to modify the landscape allows them to utilize a wide range of habitats. While beavers prefer wider streams (>8 m) they are able to utilize narrower creeks as well (2.4 m) (Beier and Barrett 1987, McComb et al. 1990). Their distribution is further increased because they are generalist herbivores and can exploit a wide variety of vegetation types (Müller-Schwarze and Sun 2003). Their preferred food sources include aspens and cottonwoods (*Populus* sp.) and willows (*Salix* sp.). These fast growing plants have soft wood and are easy for beavers to chop and peel away bark. Beavers can also survive on hardwoods including maples (*Acer* sp.), alders (*Alnus* sp.), beech (*Fagus* sp.), ash (*Fraxinus* sp.) and, while they are least preferred, pines (*Pinus* sp.)

and spruce (*Picea* sp.) (Müller-Schwarze and Sun 2003). During the spring and summer beavers consume non-woody vegetation including pond lilies (*Nymphaeaceae* sp.), ferns (*Leptosporangia* sp.), grasses (*Poeceae* sp.) and sedges (*Cyperaceae* sp.) (Svendsen 1980, Müller-Schwarze and Sun 2003). Movement across land is awkward for beavers and exposes them to predation, so food sources are required within close proximity to water (within 30 m). However, beavers have been documented traveling long distances (>200 m) across land to reach desirable food sources (Müller-Schwarze and Sun 2003).

Habitat suitability models have been used to predict beaver colony density and territory selection on small streams where beaver dams can be constructed (Slough and Sadleir 1977, Allen 1983, Howard and Larson 1985). These models suggest beavers prefer seasonably stable water levels, and that large rivers and lakes where water depth cannot be controlled are partially or wholly unsuitable for beavers (Allen 1983). However, these findings don't encompass all possible beaver habitats. Optimal beaver habitats are not restricted to montane riparian, valley foothill riparian, and fresh emergent wetlands. Beavers also utilize and thrive in riverine and lacustrine habitats (Zeiner et al. 1990). Furthermore, higher beaver lodge densities were found in the tidal channels of the Skagit Delta in Washington than have been recorded in non-tidal streams (Hood 2012). Throughout the coastal plain of the Smith River basin in Northern California a significant beaver population currently resides (Parish and Garwood 2015), where stream flow and depth fluctuate greatly throughout the year in response to rainfall. Understanding the features beaver select when choosing lodge locations in areas where dams are not constructed, such as in the Smith River, could help to inform restoration and management decisions.

On the Big Sioux River in South Dakota, Dieter and McCabe (1989) found the slope of the river bank, density of overhanging vegetation, and water depth 1 m from the bank to be significant variables influencing beaver lodge site selection. Additionally, Fustec et al. (2003) also found increased canopy cover and the lack of a sandbank to be good predictors of lodge habitat selection. Typically a lodge has multiple entrances, and to ensure safe movement into and out of the lodge, at least one entrance must remain under water (Müller-Schwarze and Sun 2003). Because large streams and rivers experience extreme flow fluctuations, an inconspicuous lodge on a steep bank may offer space to construct chambers above water while also providing deep water for the maintenance of a constant underwater entrance (Dieter and McCabe 1989, Fustec et al. 2003). Beavers will also burrow into the root systems of large trees, which add stability and prevent the lodge chambers from collapsing (Fustec et al. 2003). Smith River beaver lodges identified during snorkel surveys conducted by California Department of Fish and Wildlife (CDFW) are commonly associated with a hydraulic control feature, defined as a slow water area or an eddy created by obstructing points of land, (e.g., bedrock or a vegetated bank) that deflects the current or stabilizes the river bank (pers. obs.). As a result, the reduced velocity area causes deposition of fine substrates and provides protection from fast currents especially during high winter flows. A hydraulic control feature may be fundamental to the persistence of a bank lodge through high flow events.

I tested the hypothesis that the presence of a hydraulic control structure and an increased bank height influence beaver bank lodge site selection. I predicted that a hydraulic control structure would be present and the river bank would be taller at active bank lodges than at paired random sites. Additionally, I documented current beaver distribution and lodge abundance throughout the Smith River downstream from the confluence of the South Fork and Middle Fork. Improved understanding of colony density and bank lodge requirements can help to protect and manage for beavers in a large river system.

Methods

Study Area

The Smith River is the largest coastal undammed river and northern most major coastal watershed in California meeting the Pacific Ocean six km south of the Oregon border. This study focused on the Smith River coastal plain throughout the mainstem, estuary and coastal tributaries downstream of the confluence of the Middle Fork and South Fork (hereafter Smith River) (Figure 1). On average the basin receives an impressive 234.5 cm of rainfall annually, with 84% of annual average rainfall received from October to March during large winter storm events (Gasquet Ranger Station; CDEC 2015). The sparsely vegetated and shallow rocky soils throughout most of the interior basin hold little precipitation and stream flows directly respond to rain events producing highly variable flows. Average annual peak flow from 1932 to 2014 was 82,266 cubic feet per second (cfs) (USGS 2016). Minimum stream flow is reached in September, with

Figure 1. Location of the area surveyed for beaver activity in relation to all anadromous salmonid streams throughout the Smith River basin, Del Norte County, California.

a mean monthly flow of 334 cfs (USGS 2016). As a result, biotic life dependent on the aquatic environment of the Smith River basin, including beavers and salmonids, must be capable of adapting or migrating to suitable habitat based on variation in stream flow throughout the year.

The depth, substrate, width, and channel complexity of the mainstem Smith River vary among three distinct sections, all of which have a low gradient (<1.2 %). The estuary, beginning at the narrow mouth, remains open year-round with a thin strip of shifting sand dunes on the south bank. The channel is deep (>5 m) and wide (>300 m) with a large floodplain dominated by sedges and rushes (*Juncaceae* sp.) with willows found on the margins (Mizuno 1998). Due to the presence of bedrock and poorly vegetated sand banks much of the estuary does not provide suitable burrowing habitats for beavers. Continuing upstream, the river turns east as a single deep (>5 m) channel with a sandy bottom where entire trees, shore pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) commonly fall into the channel providing complex instream habitat. Three major sloughs connect to the Smith River estuary: Tillas, Islas, and Yontocket (Figure 1). Both Tillas and Yontocket sloughs are comprised primarily of silt and have deep (>2 m) pools while Islas Slough is shallow throughout, and contains gravel and cobble as well as silt. All three sloughs have been impacted by anthropogenic activities resulting in a simplified stream channel and loss of riparian vegetation.

Upstream from the mouth of Yontocket Slough, the substrate changes from sand and pebble to predominantly cobble with smaller substrates along the margins. The majority of the floodplain throughout this section is terraced 3 – 5 m above the channel with deep scour pools. A levee along the north bank prevents lateral channel movement and floodplain connectivity. Much of the riparian vegetation is composed of willow, red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) adjacent to cattle pastures lining both north and south banks. Two major tributaries enter the Smith River in this section, Rowdy Creek and Morrison Creek (Figure 1). Rowdy Creek has a levee on its northwestern bank and the banks have been hardened with rip rap in various locations resulting in a simplified and high-energy channel (James 2015). Further upstream, Rowdy Creek meanders throughout its floodplain but has been impacted by historic timber practices. Coast redwood (*Sequoia sempervirens*), willow, red alder and bigleaf maple (*Acer macrophyllum*) dominate the riparian vegetation. Morrison Creek is predominantly surrounded by agriculture land and enters the mainstem through a backwater channel extending ~600 m (Figure 1).

Upstream from Highway 101, the river leaves the coastal plain and the valley width begins to narrow, with the active channel meandering through alluvial point bars and bedrock. Cobble and gravel dominate the substrate throughout much of the channel, with areas of bedrock forming deep pools that collect finer substrates. Multiple tributaries and small seeps are located within this section as well as multiple side channels and backwater features (Figure 1). Willow, red alder, and black cottonwood sprouts growing in the active channel and gravel bars stabilize substrates and provide riparian habitat. Many riparian areas below residential properties have been altered to increase views and access to the river.

Mill Creek, the largest tributary in this study, has two main forks, the East Fork (EF) and the West Branch (WB). These streams, historically managed for timber production, are now protected along with the mainstem Mill Creek within Jedediah Smith Redwoods State Park (Figure 1, Appendix A). Old growth coast redwood dominates the canopy of the mainstem with smaller populations of bigleaf maple, western hemlock (*Tsuga heterophylla*), douglas fir (*Pseudotsuga menziesii*), tan oak (*Notholithocarpus densiflorus*) and California bay laurel (*Umbellularia californica*). The EF and WB have younger forests, with timber harvested throughout most of the basins at least once. Red alder and willow are more common in these tributaries than in the mainstem Mill Creek.

<u>Field Methods</u>

Studies of burrowing animals are typically conducted by identifying signs of fresh tracks, scat and cleared vegetation at the entrance of the burrow. While I utilized these techniques, evidence of beaver activity can be cryptic (Beier & Barrett 1987). From 21 May – 4 June 2014, kayak, bank, and snorkel surveys were used to identify potential lodge locations. When a possible lodge was identified, defined as a location containing an underwater tunnel, a willow fence (described below) and game cameras were placed at the underwater entrances. The following day these same sites were visited to determine if the lodge was currently used by a beaver colony (active) or not.

Beaver are most active at night or near dawn and dusk, leaving their lodges prior to sundown to forage and returning close to sunrise (Müller-Schwarze and Sun 2003). In the afternoon, while beavers were likely in their lodges, I placed a fence made of willow stems across all underwater entrances at a number of identified lodges that could be visited in a single day. Each fence was composed of approximately 8 – 12 willow stems, no greater than 2 cm diameter. Stems were stuck into the substrate 10 – 15 cm apart spanning the width of the underwater entrance. The following morning entrances were surveyed to determine if the fences were removed during the night, substantiating activity within the lodge. At least one underwater game camera was paired with the largest entrance and fence at each potential lodge. Camera use was intended to distinguish beaver use of the potential lodge from other aquatic mammals, such as river otter (*Lontra canadensis*) or muskrat (*Ondatra zibethicus*). Game cameras did not serve as the primary detection method because the waterproof cases reduced sensitivity of the motion sensor. This protocol was followed at each lodge location throughout the mainstem Smith River.

After active lodge sites were identified, a paired control site was randomly selected through five steps. 1) Using Microsoft Excel, I randomly generated a percentage ranging from 30 - 80 for each identified lodge. Percentage range was selected to prevent overlap of the random site with the lodge or the edge of the change in channel characteristics (see step 3). 2) I then randomly selected upstream or downstream of each lodge site. 3) Using ArcMap 10.1 (ESRI, Redlands, CA), I identified stream segments with similar channel characteristics based on the same valley width, stream gradient, and mean annual discharge as each identified lodge, using an intrinsic potential (IP) shapefile created for the National Oceanic Atmospheric Administration (Agrawal et al. 2005). The distance along the river bank from the lodge to the end of the paired stream segment in the randomly selected upstream or downstream direction was then measured using National Agriculture Imaging Program (NAIP) 2012 satellite imagery collected by

United State Department of Agriculture and the measuring tool in ArcMap 10.1. 4) I then multiplied the measured length by the random percentage to determine the distance from the lodge to the paired control site. 5) Lastly, a waypoint of the location was identified by measuring along the bank the determined distance away from the lodge using 2012 NAIP imagery. I navigated to this waypoint in the field with a Garmin 60 CSX Global Positioning System (GPS) to establish the center of the paired control site along the water's edge. To minimize for the strong effect of water depth in modeling, control sites were required to have a minimum depth of 0.3 m at a distance of 3 m from the water's edge. If the control site did not meet this requirement the site was moved to the opposite bank of the river, perpendicular to flow.

During July – August 2014, bank characteristics of each active summer lodge and its paired control site were measured on the same day to remove effects of differences in habitat conditions due to seasonal variation. Measurements were collected based on an established site center. The site center for a lodge was the center of the underwater lodge entrance or the middle entrance when multiple underwater entrances were present. The control site center was determined by the generated waypoint in ArcMap located in the field. Habitat measurements were collected using a 4 m stadia rod, a 50 m measuring tape, a spherical densiometer, and a clinometer (Table 1). All beaver lodge surveys were conducted under Humboldt State University (HSU) Institutional Animal Care and Use Committee (IACUC) No. 13/14.W.101-A approved on 15 April 2014.

Table 1. Habitat covariates collected at all lodge and paired random sites during summer 2014, in the mainstem Smith River, Del Norte County, California.

Parameter	Units	Description	Lodge Only
Hydraulic Control	Presence/Absence and Type	An obstructing points of land, (e.g., bedrock or a vegetated bank) that deflects the current or stabilizes the river bank and creates a slow water area or an eddy.	No
Bank Height	Meters	At site center from the water surface to the top of the river terrace nearest to the water's edge.	No
Average Canopy Cover	Percent	Using a spherical densiometer 3 m from the water's edge at the site center, one reading perpendicular to the bank and two parallel, one upstream and one downstream, were measured and then averaged.	No
Water Depth	Meters	Measured 3 m from the water's edge at the site center.	No
Average Bank Slope	Degrees	With a clinometer the slope of the bank above and below the water was measured. These two measurements were then used to calculate the average of the entire bank.	No
Substrate Type	Categorical	Dominant substrate type within the site was categorized as silt/sand, gravel, cobble, boulder or bedrock.	No
Bank Length	Meters	Average bank length with edges identified by a lack of beaver sign such as trimmings or entrances or by a change in bank direction, substrate type, bank slope, and/or vegetation composition.	No
Underwater Entrances	Count	While snorkeling, the river bank was surveyed to identify and count all entrances into the lodge located underwater.	Yes
Above Water Entrances	Count	While kayaking, the bank was surveyed to identify and count all entrances into the lodge located above the water.	Yes

A further assessment of beaver distribution and activity was conducted throughout Mill Creek and Rowdy Creek from 7 – 13 August 2014. New observations of beaver activity were also noted while conducting fish monitoring surveys during June – August 2014 and January – March 2015. All identified beaver activity was documented with a GPS unit and classified as the specific use type: lodge, dam, feeding activity, tracks, scat, food cache, and individual.

Statistical Methods

Linear distribution and density of beavers were calculated using shapefiles drawn along the deepest point, the thalweg, of the stream channel in ArcMap. Typically the presence of a food cache identifies active beaver colonies; however food caches were rare in the riverine environment of the Smith River, similar to other riverine beaver surveys (Robel and Fox 1993). Instead all observed beaver sign was evaluated to estimate boundaries of individual colonies. Breaks in beaver activity were used to identify separate colonies similar to Robel and Fox (1993). In the lower mainstem, density of lodges was high and contained long segments of continuous beaver sign. When no clear break was present, a minimum distance of 500 m between active lodge sites was used to delineate separate colonies, based on findings of Semyonoff (1951) and Robel and Fox (1993).

To meet their required habitat needs, beavers are likely to build dams in the upper extent of their potential habitat due to low summer flows and shallow water depths. I calculated suitable habitat (stream km) based on optimum valley width and gradient identified in habitat suitability indexes for beavers (Allen 1983, Suzuki and

McComb1998). Using the Smith River IP shapefile (Agrawal et al. 2005), I identified stream segments with a mean stream gradient ≤3% and valley width ≥46 m. Composition of bank substrate, presence of willow, and dry channel segments observed in the field were used to further refine the upstream and downstream extent of suitable habitat during both the summer and winter. Winter suitable habitat represents the maximum suitable habitat while the summer habitat was reduced due to dry stream segments. While this study was conducted in the third year of drought, care was taken to include areas where water would persist throughout the summer on a normal water year. Delineations were designed to be inclusive to prevent underestimation of suitable habitat.

Most lodge variables were non-normal; I therefore employed a non-parametric statistical test, the Wilcoxon paired signed rank test, to evaluate each variables' influence on bank lodge site selection, using Program R (R Core Team 2014), with each habitat characteristic modeled separately as the predictor variable. Multiple habitat variables influence particular species site selection preferences. Due to the landscape scope of resource selection studies, both measured (i.e., presence of hydraulic control) and unmeasured (e.g., distance to food, slope, aspect) variables may influence the results. By pairing the lodge location data, the effect of unmeasured variables such as access to food resources, and distance to disturbance, are accounted for in the analysis. The Wilcoxon paired signed rank test ensures data collected from paired case and control sites were compared only to one another, not to the entire data set, under the assumption that all the paired differences are independent. Either a single or two-tailed test was performed on measured habitat variables of interest based on biological predictions of lodge requirements and findings from past research. Past research has found increased depth, canopy cover, slope, and decreased substrate (Dieter and McCabe 1989, Fustec et al. 2003) influence lodge site selection. Additionally I predicted that increased bank height and presence of a hydraulic control positively influence lodge locations as these features may provide more area to build nesting chambers and protection during elevated flow events. An estimated rather than exact p-value and confidence interval were calculated for some variables due to differences equaling zero and ties in rank present in some variables.

This study was designed to use paired logistic regression. However, due to a lack of convergence for models with hydraulic control as an explanatory variable, a key variable of interest in this study, a priori models were built using binomial Generalized Linear Models with a logit link function in Program R (R Core Team 2014). Multicollinearity was assessed prior to model construction by visually evaluating a pairwise plot and calculating a Spearman correlation test with a pairwise correlation ≥ 0.6 as the cut off. The a priori candidate model set containing 15 models was determined based on assessing the influence hydraulic control features have on the occurrence of bank lodges from previous research (Dieter and McCabe 1989, Fustec et al. 2003). Each of the six variables was individually modeled, then added to hydraulic control to evaluate if accounting for the presence of hydraulic control improved on each individual variable. Four additional models were built to evaluate the influence of hydraulic control on the additive effect of findings from prior research. Models were ranked using Akaike information criterion corrected for small sample size (AICc) and AICc weights were used to evaluate relative importance of the top model (Burnham and Anderson 2002). Before proceeding with inference a drop in deviance test and a condition index cut off of >30 were conducted to ensure multicollinearity was not present between the explanatory variables in the top model.

Results

I surveyed 88.5 km of stream to assess beaver distribution and lodge locations throughout the Smith River. Beaver activity was distributed across 59.9 km during the summer and 41 active lodges were distributed across 49.8 km (Figure 2). During winter fish sampling surveys, three additional lodges were identified that had not been present during summer surveys. These new observations increased distribution to 71.1 km, representing 77.8% of the total estimated suitable stream (Table 2). In some cases lodges were in close proximity (<500 m), which commonly signifies utilization of multiple lodges by a single colony (Bradt 1938, Baker and Hill 2003). While I did not specifically monitor activity of individual colonies, based on observed beaver sign and lodge spacing, my conservative estimate is there are at least 31 beaver colonies in the Smith River (Table 2). Robel and Fox (1993) found colony density to be higher in the mainstem streams compared to smaller streams in riverine habitats of Kansas. Based on observed summer distribution of beaver activity, this trend was not consistent with the observed Smith River population. However, the densities found are within the range of those reported in past literature (Table 3). Based on observed distribution, colony density in the mainstem (0.5/km) was equal to the Mill Creek density (0.5/km) but lower than the

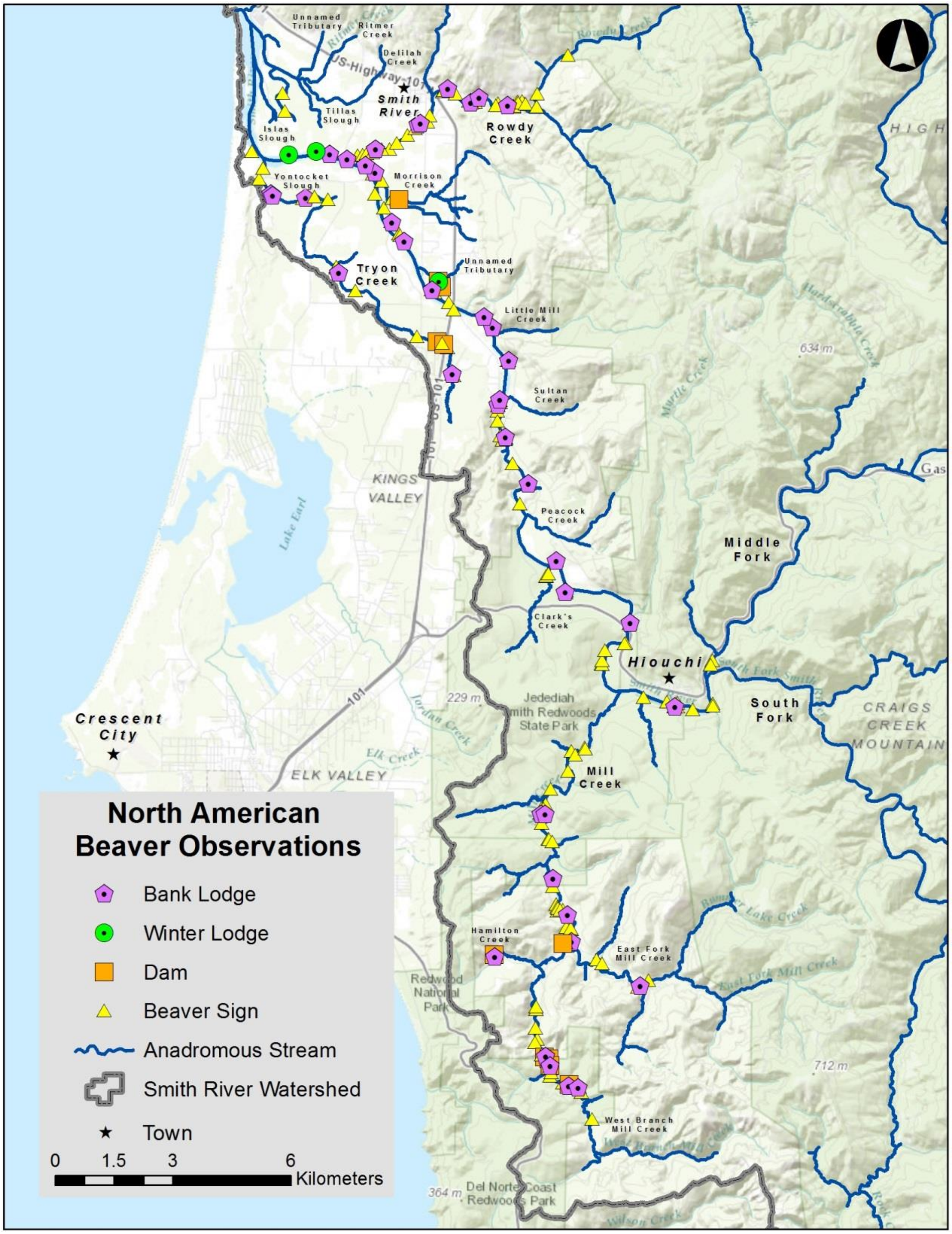

Figure 2. Distribution of North American beaver observations recorded during this study throughout the Smith River mainstem and coastal tributaries, Del Norte County, California. Winter lodges were not present during summer surveys. Beaver sign included browse, feeding debris, bank excavation (not lodge), tracks, scat, and individuals.

Table 2. Summary of observed distribution of beaver activity, measured suitable habitat, and lodge and colony quantities across all surveyed sub basins of the Smith River mainstem and coastal tributaries, Del Norte County, California.

	Tillas Slough	Islas Slough	Tryon Creek/ Yontocket Slough	Rowdy Creek	Morrison Creek	Unnamed Tributary	Mill Creek	Mainstem	Total
SUMMER									
Stream surveyed (km)	8.8	1.6	12.8	8.8	1.8	0.9	24.7	29.1	88.5
Suitable habitat (km)	2.3	0.0	9.0	14.6	1.3	0.0	24.7	26.4	78.3
Beaver distribution (km)	0.0[a]	0.0	2.9	7.4	1.3[a]	0.0	23.0	25.3	59.9
Lodge distribution (km)	0.0	0.0	2.4	5.1	0.4	0.0	21.0	20.9	49.8
Lodges	0	0	5	7	0	0	11	18	41
Lodges/ km	0.0	0.0	1.7	1.0	0.0	0.0	0.5	0.7	0.8
Colonies	0	0	4	5	1[b]	0	8	13	31
Colonies/ km	0.0	0.0	1.4	0.7	0.8	0.0	0.5	0.5	0.5
WINTER									
Suitable habitat (km)	3.4	0.6	12.8	14.8	3.3	1.9	26.2	28.4	91.4
Beaver distribution (km)	1.7[a]	0a	8.8	7.4	1.8[a]	0.9	24.7	25.8	71.1

[a] minimum observed distribution due to lack of property access
[b] based on Ron Rawson, pers. comm.

Table 3. Summary of colony densities reported in past literature and those found in the Smith River during the summer of 2014.

Colonies/km	Location	Source
~1.70[a]	Mad River, CA	Yocom (1956)
1.09	New Brunswick	Nodstrom (1972)
0.40	Birch Creek & Chena River, AK	Boyce (1974)
0.38	Newfoundland	Bergerud and Miller (1977)
0.55 - 0.70	Massachusetts	Hodgdon (1978)
0.58 - 0.80	Sagehen Creek, CA	Busher (1987)
0.08 - 1.40	Kansas	Robel and Fox (1993)
0.50 - 1.40	Smith River, CA	Parish (2016), (this study)

[a] Estimated based on number of colonies and area surveyed reported in literature

density in Rowdy Creek (0.7/km), Tryon Creek (1.4/km), and Morrison Creek (0.8/km) with an average colony density of 0.5/km throughout the basin (Table 2). Portions of Morrison Creek go dry during the summer and no lodges were located within the stream channel. However, recent beaver observations in a pond located on private property adjacent to Morrison Creek (Ron Rawson, pers. comm.) represent a colony that is believed to utilize Morrison Creek during the winter and spring based on beaver sign (trimmings and dam building) in the channel.

Twelve dams were identified during the study in Mill Creek, Morrison Creek, Tryon Creek, and an Unnamed Tributary (Figure 2). Seasonal dams in WB Mill Creek were built during the low flow season and increased water depth near lodges but were destroyed during winter high flow events. Two successive dams were constructed in the winter and spring elevating the water level of an old quarry pond near the confluence of

EF and WB Mill Creek but the pond drained during the summer months. Only one dam occurred year-round and has maintained a pond since 2010 (Justin Garwood, pers. comm.) located on Hamilton Creek, a tributary to the WB Mill Creek (Figure 2). This dam creates the only year-round beaver pond located within the Smith River. The dam in Morrison Creek was small (<0.25 m) and was observed during both the summer and winter surveys but was not associated with a lodge. While the two dams on Tryon Creek were present in the summer, fresh signs of activity were only present during winter surveys. No lodges were identified in this section of Tryon Creek. However, low visibility and dense vegetation hindered detectability and a colony likely utilized this stream section during the winter high flow months. While no current beaver activity was observed in Tillas Slough or its tributaries (Delilah Creek and Ritmar Creek) during the summer, old sign of cutting and burrows were observed. I was unable to survey this area during the winter. It is possible that Tillas Slough and its tributaries were utilized during the winter months.

Throughout the mainstem, 18 active lodges were identified during the summer across 20.9 km (Table 2). Poor water clarity and highly complex dense bank vegetation prevented accurate measurements of one lodge located in an alcove and was excluded from all analyses. A second lodge was excluded because it was abandoned between June and July resulting in sediment deposition and decreased water depth, thereby not representing an active lodge. Habitat measurements (Table 1) were collected at the remaining 16 active summer lodges in the mainstem to assess the influence of habitat variables on lodge site selection and to evaluate lodge characteristics.

Lodges varied greatly with the utilized bank length ranging from 5.1 – 82.4 m, bank height from 1.5 – 2.4 m, average bank slope from 31.0 – 80.5˚, and water depth ranging from 24 – 268 cm. Substrate of lodges was dominantly composed of fine sediment such as silt and sand, and some lodges utilized silt deposited in and around boulders or rip rap. Composition of entrances varied with an average of 1.9 above water entrances per lodge, three lodges having none visible, and a maximum of ten entrances observed at a single lodge. There was an average of 2.8 underwater entrances per lodge, with two lodges having no completely submerged entrances by the end of the summer, and three lodges containing six underwater entrances.

Measurements of many habitat parameters overlapped across the dataset of lodge and random sites (Figure 3). All lodges except one were constructed near a hydraulic control feature. Features included bedrock, trees whose root wads stabilized the bank, and vegetated banks that protruded into the channel causing a redirection of stream flow. The presence of hydraulic control structures was significantly higher at lodge sites than at paired random sites ($V=28$, $p = 0.005$, Table 4) indicating that lodge placement near a hydraulic control feature is not random.

Bank height was initially found not to be significantly different between lodges and paired random sites (Table 4). Upon further review, an outlier was found due to a random site occurring at an unusually tall terrace (>8 m), >3 standard deviations above the mean. The outlier and the matched lodge were removed for a second analysis of bank height. The test on the reduced data set found lodge sites had a positive association with increased bank height (Table 4). Similar to past research I found increased canopy cover

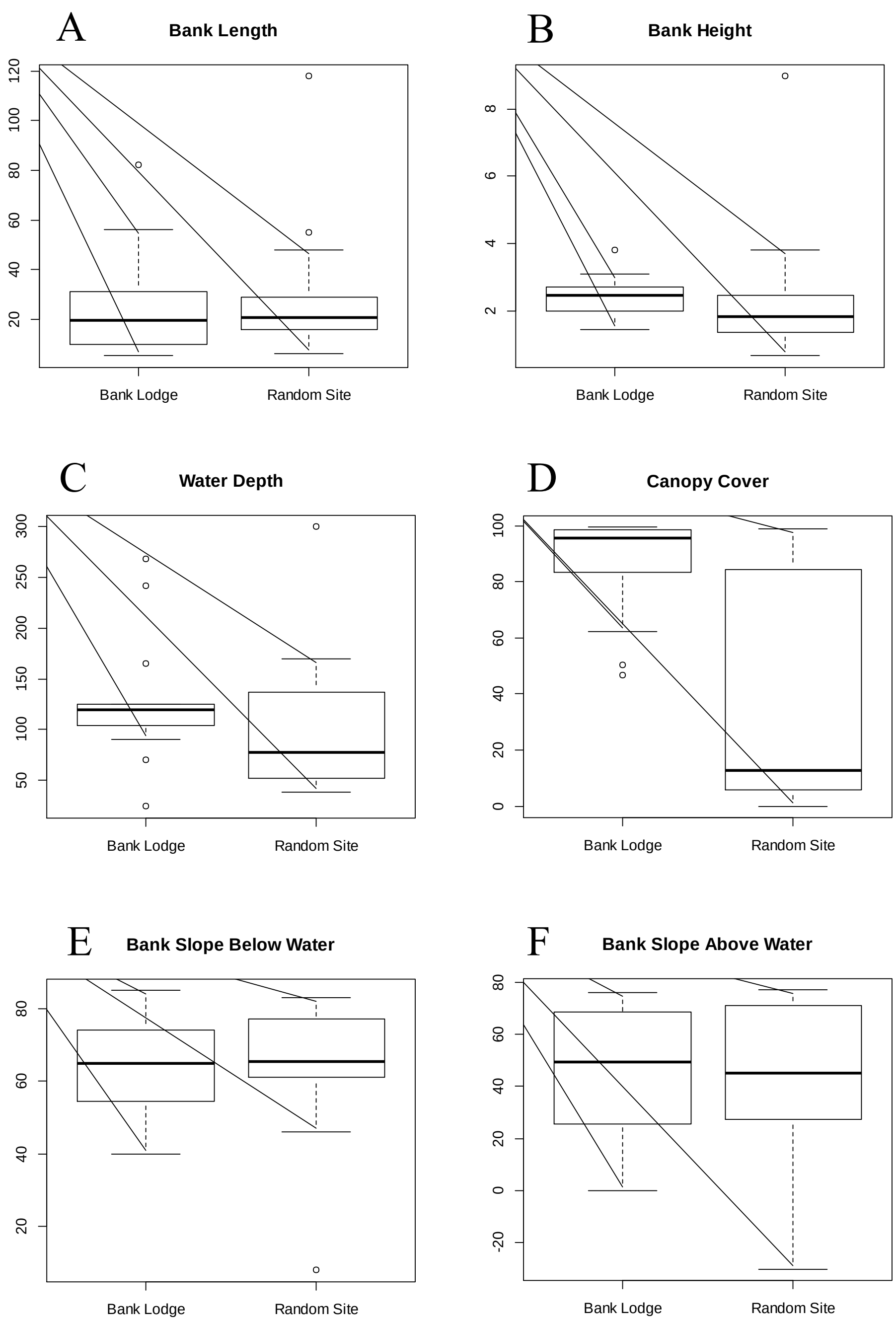

Figure 3. Boxplots comparing bank length (A), bank height (B), water depth (C), canopy cover (D), and bank slope below (E) and above (F) the water surface at beaver bank lodges and random sites.

Table 4. Results from paired Wilcoxon signed rank tests assessing the differences of bank measurements between lodges and paired random sites. An estimated p-value and 95% confidence interval are presented when differences between a lodge and the paired random site equaled zero or ties in rank were present in the dataset.

Variable	Wilcoxon test	Wilcoxon p-value	Test statistic (V)	95% Confidence interval		Estimated or exact p-value & CI
				Lower	Upper	
Hydraulic	Single tail - upper	0.005*	28.0	NA	NA	Estimated
Bank Height	Single tail - upper	0.149	89.0	-0.28	Infinity	Exact
Bank Height - minus outlier	Single tail - upper	0.054*	89.0	-0.05	Infinity	Exact
Canopy Cover	Single tail - upper	0.001*	126.0	27.73	Infinity	Estimated
Depth	Single tail - upper	0.065	98.0	-5.00	Infinity	Exact
Slope Above Water	Single tail - upper	0.398	73.5	-14.00	Infinity	Estimated
Slope Below Water	Single tail - upper	0.463	54.5	-8.50	Infinity	Estimated
Average Slope	Single tail - upper	0.541	66.5	-9.00	Infinity	Estimated
Substrate	Single tail - lower	0.0008*	0.0	-Infinity	-2.00	Estimated
Bank Length	Two tailed	0.130	38.0	-11.45	2.5	Exact

*denotes statistically significant p-value and smaller substrate types (i.e., silt) also significantly associated with lodge sites. No other habitat variable associations with lodge sites were statistically significant.

Visual assessment of the pairwise plots did not reveal any obvious multicollinearity between explanatory variables; however, the spearman correlation test revealed correlation between canopy cover and substrate type (>0.6). The candidate model set was then determined based on this finding and resulted in 15 models (Table 5). Models contained six variables of interest, including hydraulic control presence, bank height, and the four variables shown to be significant in previous research: substrate, canopy cover, bank slope and water depth.

Adding hydraulic control individually to bank height and each of the four variables known to influence lodge site selection resulted in a higher ranked model than modeling the variables individually (Table 5). Substrate with the added effect of hydraulic control ranked as the top model with the lowest AICc, carrying 71% of the weight (Table 5). A drop in deviance test performed on the top model was found to be significant ($p < 0.001$), suggesting strong evidence that the additive effect of substrate size and presence of a hydraulic control structure describes the variation in the data. The condition index for the top model was found to be 28.13 suggesting the explanatory variables in the top model are not strongly correlated with one another. The model estimates the odds of a location being a suitable lodge site increase by a factor of 22.09 (95% CI: 1.52 to 320.16 increase) when a hydraulic control is present, after accounting for substrate type.

Table 5. Candidate model statistics for generalized linear models comparing bank characteristics of beaver bank lodges and random non-lodge sites ranked by Akaike's information criteria corrected for small sample size (AICc). ΔAICc is the difference in AICc value to the top model, AICc *w* is the strength of the model given the candidate set, Cum *w* is the cumulative weight, k is the number of parameters estimated in the model, and LL is the log likelihood.

Models	AICc	ΔAICc	AICc *w*	Cum *w*	k	LL
Substrate + Hydraulic Control	25.67	0	0.71	0.71	3	-9.41
Substrate + Depth + Average Slope + Hydraulic Control	29.11	3.44	0.13	0.83	5	-8.4
Substrate	29.9	4.23	0.08	0.92	2	-12.74
Canopy Cover + Depth + Average Slope + Hydraulic Control	32.25	6.58	0.03	0.94	5	-9.97
Canopy Cover + Hydraulic Control	33.06	7.39	0.02	0.96	3	-13.1
Canopy Cover	33.25	7.58	0.02	0.98	2	-14.42
Substrate + Depth + Average Slope	33.82	8.15	0.01	0.99	4	-12.17
Canopy Cover + Depth + Average Slope	34.45	8.78	0.01	1	4	-12.48
Depth + Hydraulic Control	38.83	13.16	0	1	3	-15.99
Hydraulic Control	40.41	14.74	0	1	2	-18
Height + Hydraulic Control	42.18	16.51	0	1	3	-17.66
Average Slope + Hydraulic Control	42.82	17.15	0	1	3	-17.98
Depth	47.32	21.65	0	1	2	-21.45
Height	48.74	23.07	0	1	2	-22.16
Average Slope	48.78	23.11	0	1	2	-22.18

Discussion

This study found lodge site selection to be influenced by the presence of a hydraulic control structure, banks composed of fine substrate (i.e., silt), and increased canopy cover. Findings also suggest an elevated bank increases a site's suitability for a bank lodge. The results regarding the influence of substrate type and canopy cover are consistent with findings from past research (Dieter and McCabe 1989, Fustec et al. 2003). I believe the composition of these bank conditions influence lodge site selection for various reasons. A hydraulic control protects the bank from the erosive powers of water particularly experienced during high flow events and may cause deposition of fine substrates. Large substrates, such as cobbles, reduce a beaver's ability to excavate and burrow into a bank. Increased canopy cover conceals the lodge and beavers as they move to and from their lodge. Lastly, an elevated river bank provides increased area for lodge nesting chambers; this is particularly important at high flow events, which can flood lodges that lack vertical space for beavers to reside in during these elevated flows. Similar to Dieter and McCabe (1989) I observed above water entrances connected or adjacent to active lodges. These features are likely utilized during high winter flow events.

The beaver population was active throughout the summer and winter, constantly modifying and maintaining lodges. I often observed creation of new lodges and incomplete burrows throughout the summer in the mainstem. In contrast, beaver activity decreased in the mainstem during winter and increased in small tributaries that were dry during the summer months. New dams and lodges were created in these tributaries during the winter and subsequently abandoned during the summer as flows declined. These findings show that beavers dynamically utilize suitable habitat based on seasonal conditions and behaviorally are able to adapt to changing stream conditions.

This study found beaver activity to be prevalent and widely distributed across the Smith River, downstream of the confluence of the Middle Fork and South Fork, with a high proportion of the suitable habitat utilized by beavers. Old beaver chews have been observed outside of the study area incidentally and during CDFW salmon spawner surveys in the Middle Fork Smith River (M. McCain, USFS, pers. comm.) and its tributary, Siskiyou Fork (pers. obs.). While these observations show that beaver exploration extends further upstream, due to the lack of current activity and low frequency of these observations, I do not believe successful colonies currently reside upstream of the mainstem. The increased stream gradient, reduced availability of fine sediment, confided bedrock canyons and high winter flows likely reduce beavers' ability to permanently reside in most of the upper watershed.

In the Smith River, anthropogenic activities have likely reduced the availability of suitable habitat and potentially hinder movement in the coastal plain. Fustec et al. (2003) found the abundance of favorable lodge sites to decease in areas where human activities increased, and beavers tend to settle in quieter places with less human activity. Some areas that were identified as suitable were excluded due to anthropogenic landscape alterations. For example, the levee, tide gate, and agricultural alterations along Tillas and Islas sloughs likely hinder beaver movement and have reduced food and lodge availability. Other non-agriculture activities also likely influence beaver lodge site selection and habitat use. The abandoned lodge I observed was located near a river access trail. This abandoned site may be suitable year round if not disturbed by frequent human presence. Additionally, many private residences along the river remove riparian vegetation resulting in reduced canopy cover, which may limit suitable lodge locations in these areas.

The continuously altered state of river banks utilized by beavers can result in habitat measurements to widely vary depending on the time of year data are collected. Furthermore, habitat measurements along a river can be correlated as river forces continually shape bank slope, vegetation, and flow characteristics. For example, the presence of a hydraulic control structure likely results in deposition of fine sediments and protects the bank and riparian vegetation. Additionally, dense riparian vegetation can also protect the bank and vegetation is more likely to become established in fine substrates compared to areas with large substrate. Care is needed when designing river studies and developing models to minimize multi-collinearity. An increased sample size and a multi-year data analysis would likely strengthen conclusions on beaver bank lodge site selection, particularly on the influence of bank height.

The findings from this study support the need to protect areas with hydraulic control structures including vegetated banks. Protecting and increasing the abundance of large standing trees within the riparian zone, which act as hydraulic control structures, will stabilize banks and increase locations where beaver lodges can persist in an active river channel. Protecting access to the riparian corridor in smaller tributaries should be considered during management decisions in order to provide suitable habitat for beavers during elevated flow events, both natural and as a result of dam releases. Furthermore, vegetated terraces help to stabilize river banks and provide high terraced banks for beavers to utilize during elevated river flow events and help to stabilize and maintain small substrates such as silt.

CHAPTER 2 - JUVENILE SALMONID USE OF NON-NATAL REARING HABITAT CREATED BY BEAVERS

Introduction

Anthropogenic-induced habitat loss negatively affects all salmonid species, especially while rearing as juveniles in fresh water. Coho salmon in particular are heavily impacted due to their wide range of low gradient habitat use and extended rearing time in fresh water. Coho salmon rear for approximately 14-18 months, compared to Chinook salmon (*Oncorhynchus tshawytscha*) who rear for approximately 3-6 months, before they migrate to the ocean throughout the spring – fall (Moyle 2002). While Steelhead trout (*Oncorhynchus mykiss*) also have an extended use of freshwater, rearing for 1-3 years, they are likely more robust to habitat changes because they utilize a wider range of gradients and are iteroparous (Moyle 2002).

Juvenile Coho salmon experience variable survival rates while rearing in freshwater, with estimates ranging from 63 to 91% during the summer months (Spalding et al. 1995) and 25 to 56% during winter months (Quinn and Peterson 1996, Rebenack et al. 2015). Various life history patterns have been observed and described for Coho salmon during the freshwater rearing stage. Some individuals will remain in their natal stream to rear. Others may relocate to non-natal streams as sub-yearlings (age 0+) for summer rearing, or during the fall to low velocity, off-channel and estuarine habitats to overwinter as yearlings (age 1+) (Miller and Sadro 2003, Koski 2009, Bennett et al. 2014, Wallace et al. 2015). The ability for individuals to relocate to non-natal streams increases access to rearing space and food resources, ultimately increasing survival, carrying capacity, and stability of the population (Chapman 1966, Koski 2009, Bennett et al. 2014).

Throughout the Pacific Northwest, habitat use by juvenile Coho salmon varies by season. In the summer, the highest abundance is in pools. In contrast, during the winter, the highest abundance is in low velocity backwaters, off-channel ponds, wetlands, and beaver ponds (Swales and Levings 1989, Nickelson et al. 1992, Henning et al. 2006, Wigington et al. 2006, Wallace and Allen 2009, Wallace et al. 2015). Summer habitat availability is generally limited due to low dissolved oxygen, elevated water temperature, and reduced channel area due to channel drying. Winter habitat is limited by a lack of low velocity habitats such as off-channel habitats including beaver ponds, sloughs, backwaters and tributary habitats, as well as a lack of floodplain connectivity (Beechie et al. 1994, Pollock et al. 2004, NMFS 2014).

The Smith River Coho salmon population is identified as a core population within the Southern Oregon/Northern California Coast Evolutionary Significant Unit (SONCC ESU). Due to low abundance, productivity, and diversity of life history strategies the population is at high risk of extinction (NMFS 2014) and is listed as threatened under both the federal and California Endangered Species Act (Federal Register 1997, CDFG 2002). Due to anthropogenic land and water use throughout the coastal zone of watersheds across the SONCC ESU, the quality and quantity of productive rearing habitats have been reduced and are a leading cause in the decline of Coho salmon populations and the diversity of life history strategies (NMFS 2014). Increased diversity of life history strategies and productive rearing habitats can provide population resiliency to environmental variation and stochastic events thereby aiding in recovery of SONCC Coho salmon populations.

Beavers' activities maintain and increase underwater complexity and as a result improve rearing habitat for salmonids and other fishes. In particular, beaver dams increase productive rearing habitat for juvenile Coho salmon due to increased channel inundation area and depth, low velocity habitat, and abundance of aquatic insects (Bryant 1983, Naiman et al. 1984, 1988, Leidholt-Bruner et al. 1992, Pollock et al. 2007). Streams impounded by beaver dams have been shown to have higher abundance of fish, produce larger individuals, and increase survival of rearing juvenile Coho salmon when compared to un-impounded streams during both summer and winter months (Bustard and Narver 1975, Murphy et al. 1989, Leidholt-Bruner et al. 1992). Tidal beaver ponds had significantly higher densities of juvenile Chinook salmon compared to other tidal channel habitats in the Skagit Delta of Washington state (Hood 2012). However, information about juvenile Coho salmon non-natal seasonal habitat use in large tributaries and mainstem rivers is lacking (Beechie et al. 1994, Pollock et al. 2004). Additionally, salmonid use of beaver altered habitats in streams that lack dams has not been quantified.

Juvenile salmonid snorkel surveys, conducted for CDFW, noted higher quantity and diversity of salmonids around beaver bank lodges than other adjacent sites in the mainstem Smith River (Garwood and Larson 2014). Furthermore, the distribution of beaver and the Coho salmon populations in the Smith River largely overlap in the coastal plain (Parish and Garwood 2015, this study). However, the beaver population in the Smith River almost wholly resides in bank lodges with few beaver dams present year round (Chapter 1, this study), presenting an ideal setting to evaluate the impacts of beaver bank lodges on salmonid non-natal rearing habitat.

I collected data on juvenile salmonid use of beaver lodge and non-lodge habitats in the mainstem Smith River during the summer of 2014 and winter of 2014-15 to examine the influence of beavers on juvenile salmonid non-natal rearing habitat, focusing largely on Coho salmon. I tested the hypothesis that presence of beaver bank lodges and beaver-created habitat influences occupancy of juvenile Coho salmon. I predicted juvenile salmonid occupancy, particularly Coho salmon, is positively influenced by the amount of beaver-created habitat during both the summer and winter seasons.

Materials and Methods

Study Area

As described in Chapter 1, the Smith River experiences the annual high water temperatures, lowest flows, and highest tidal influence during the summer. During low flows the water height can fluctuate by 3 m (Monroe et al. 1975) in the tidal influenced zone, which continues 8.5 km upstream from the mouth (Parish and Garwood 2015). In contrast, winter flow conditions greatly fluctuate throughout the basin due to winter storm events because the basin receives the majority (84%) of its rainfall during the winter months. Like other coastal basins throughout California and the Pacific Northwest, the northern portion of the Smith River estuary is a working landscape (Appendix A) and has been highly modified through the construction of levees, dikes, and drainage ditches for the purpose of flood control and floodplain reclamation for agricultural uses. As a result, off-channel rearing habitats for salmonids have been reduced and many small drainages and sloughs in the northern portion of the estuary (up to the mouth of Rowdy Creek) are filled in and severed from the main estuary channel. In the Smith River this is evident from historic and current aerial imagery illustrating loss of riparian habitat, and the reduced size and channel connection of Islas Slough due to a private levee built in the 1970s for flood control (Figure 4). Similar land alterations across the mainstem and tributaries throughout the coastal plain have led to reduced channel complexity, floodplain connectivity, and loss of quality rearing habitat for juvenile salmonids.

Upstream from Highway 101 to the confluence of the South Fork and Middle Fork, fewer channel alterations have occurred and the active channel naturally meanders through alluvial point bars and bedrock. As a result this area contains side channels and large bends that form off-channel habitats, some of which are only connected to the main channel during high winter flows. Tributaries within this section, including Little Mill Creek, Sultan Creek, Peacock Creek, Clark’s Creek, Mill Creek, and smaller seeps and streams such as Camp 6 Creek (Figure 1), provide cold water inputs during the summer and off-channel rearing habitat for juvenile salmonids during the winter. This study was conducted at these off-channel habitats where juvenile Coho salmon are able to rear during the summer and winter months.

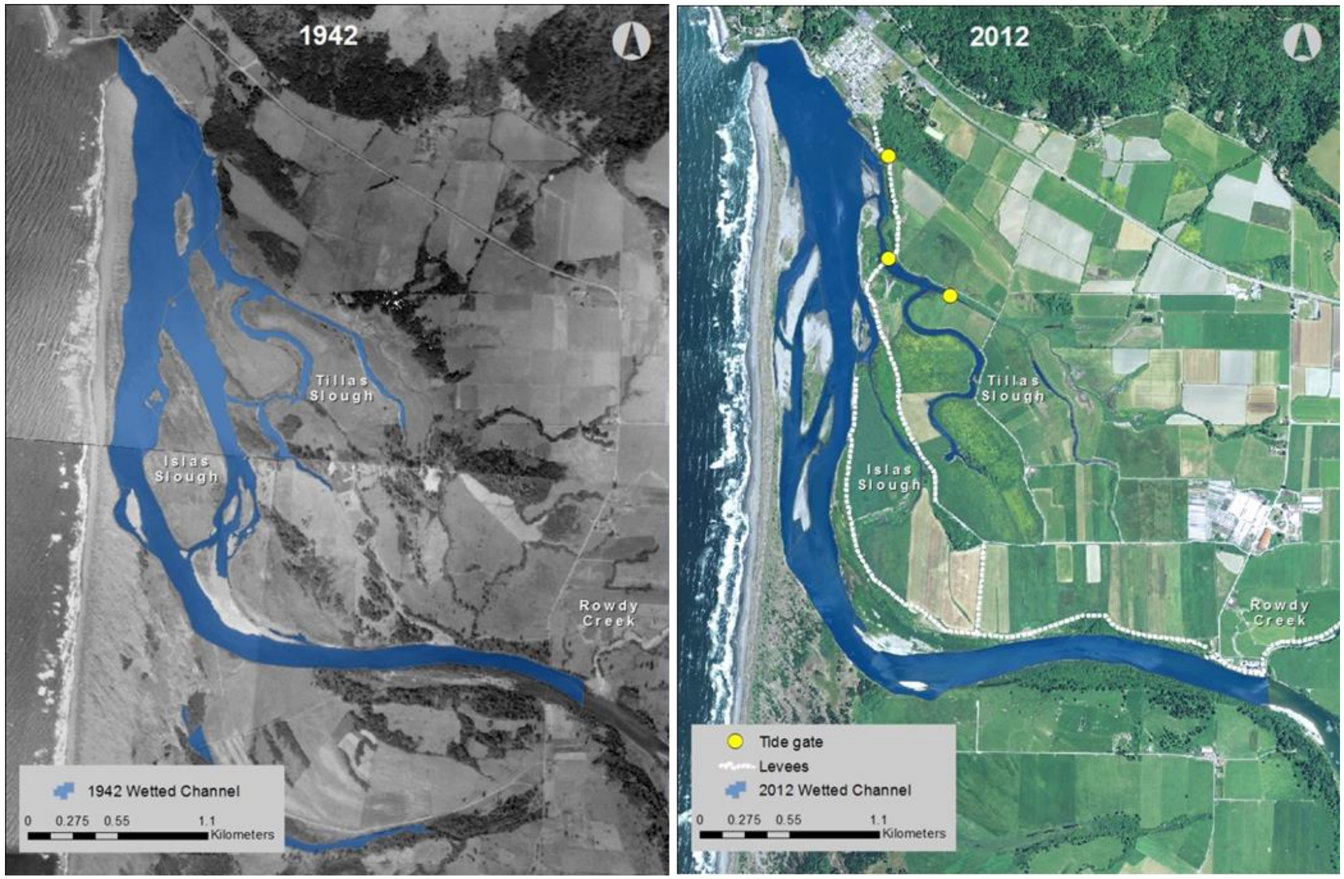

Figure 4. Historic (1942) and current view (2012) of the Smith river plain and estuary, Del Norte County, California. Blue shaded areas in each image depict the estimated active channels at the time the image was collected. The 1942 image shows the presence of small stream and slough channels, identified by dense strips of riparian vegetation between Rowdy Creek and Islas Slough. Also shown is the upper end of Islas Slough connected to the Smith River. Private levees and tide gates, seen in the 2012 image, were built for flood control and land reclamation, resulting in reduced stream and slough channels, were mapped using the 2010 NOAA coastal liDAR dataset.

Field Methods

Based on pre-season surveys and previous data collected throughout the study area by Garwood and Larson (2014) and Garwood et al. (2014), I established 24 unique fish monitoring sites for both the summer and winter salmon rearing periods (Figure 5). Habitats were not selected at random, but were identified based on their high likelihood of persisting throughout the summer or winter rearing periods. Additionally all sites selected were presumed to be suitable for juvenile Coho salmon rearing due to presence of habitat features such as large woody debris (LWD), overhanging vegetation, beaver burrows. Because the summer and winter periods have contrasting available habitats, I selected fish monitoring sites independently for the summer and the winter (Figure 5). However, eight sites were monitored during both the summer and winter seasons. To ensure salinity at all sites would remain within salmon tolerance thresholds throughout the summer sample season, sites were located in areas likely to have salinity levels < 5 ppt, as identified by Mizuno (1998). Sites represented a diverse range of potential salmonid non-natal rearing habitats including backwaters, edge waters, beaver lodges, and cold water seeps. Effort was made for half of the sites to be located at beaver lodges and half lacking lodges.

Multiple primary sampling occasions were conducted to measure temporal occupancy patterns (i.e., extinction and colonization processes) of juvenile salmonids as they relate to beaver-created habitat, as well as water quality throughout a specific season. Surveys at fish monitoring sites were conducted using Pollock’s robust design (Pollock 1982), which has secondary sample occasions within each primary sample

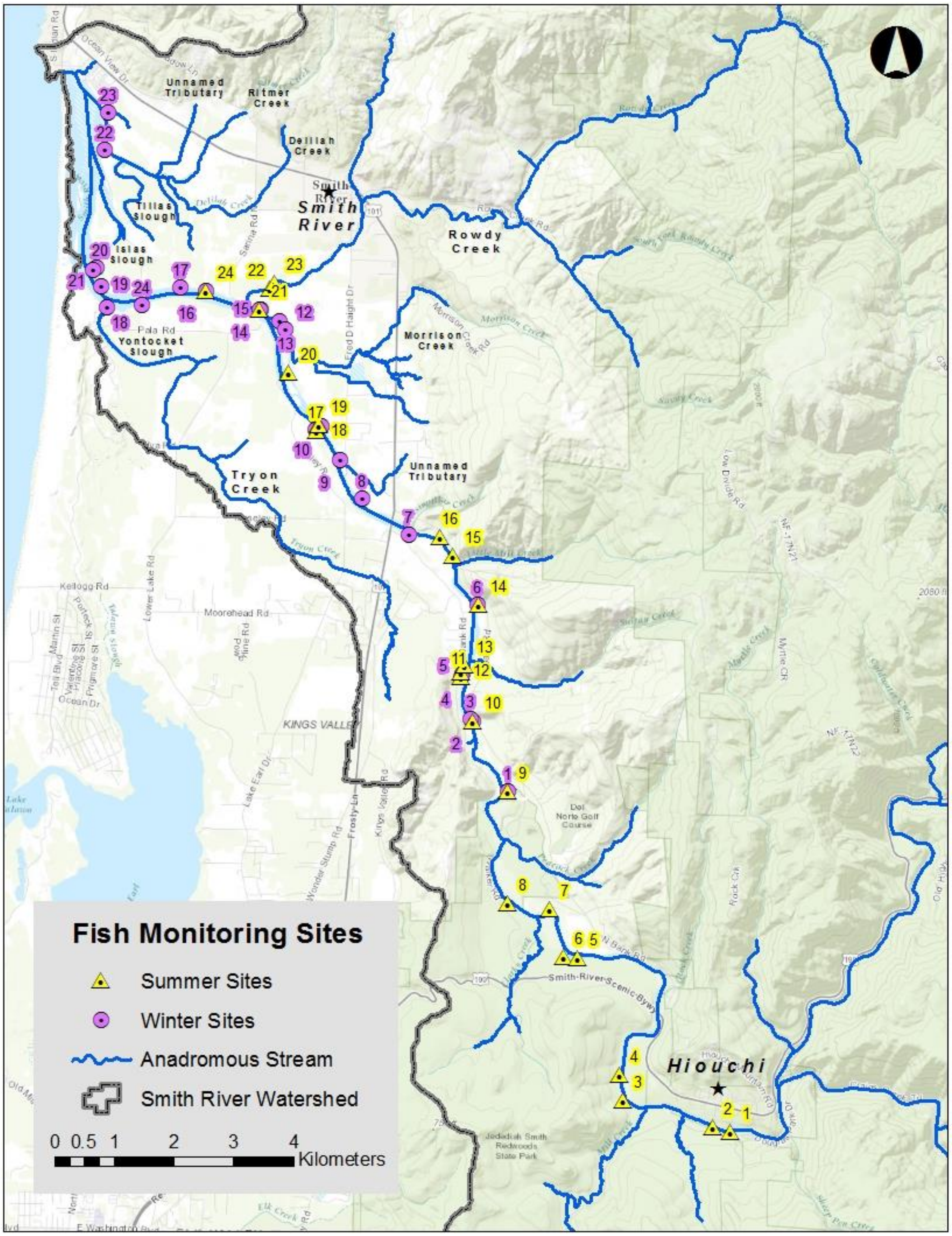

Figure 5. Location of summer 2014 and winter 2014-15 fish monitoring sites across the mainstem Smith River and Rowdy Creek, Del Norte County, California. Summer fish monitoring site locations are represented by light triangles and winter fish monitoring site locations are dark circles. Eight locations were surveyed as both summer and winter sites.

occasion. This design assumes closure while sampling within primary sample occasions (i.e., between secondary sampling occasions, dive passes one and two) but allows for colonization (γ) and extinction (or emigration in this case; ε) of a species between primary sampling occasions (i.e., between summer months) (Figure 6).

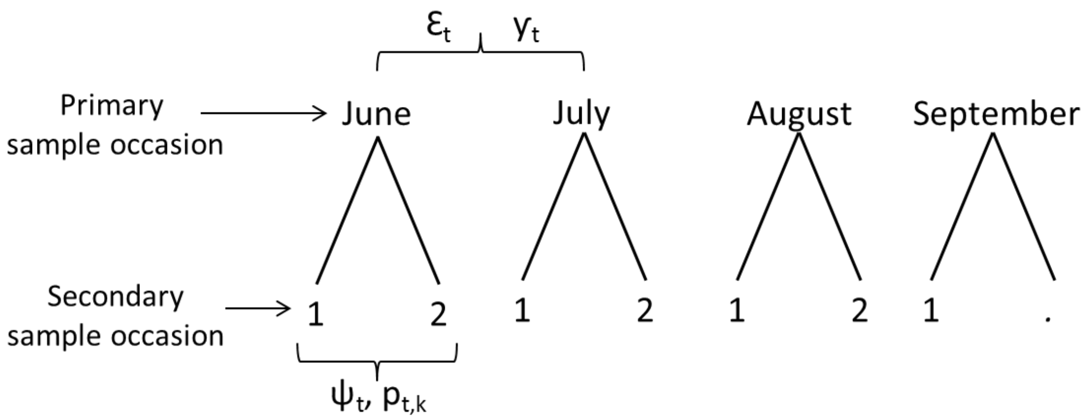

Figure 6. Multi-season occupancy sampling followed Pollock's Robust sampling design where occupancy (ψ_t) and detection probability ($p_{t,}$) can be calculated when closure is assumed between two secondary sampling occasions (i.e., survey events), which occur within each primary sampling occasion. Movement in the form of extinction (ε_t) and colonization (γ_t) probabilities are estimated between primary sampling occasions.

Summer Fish Monitoring Surveys. All 24 summer fish monitoring sites received three primary sampling occasions once per month from 23 June – 21 August 2014, using the spatial structure snorkel survey protocol from Garwood and Ricker (2014) described below. An opportunistic fourth survey was conducted from 15 – 20 September by a single surveyor, while retrieving deployed temperature loggers and therefore does not have a secondary sampling occasion. Most site habitat measurements were based on Garwood and Ricker (2014). However, measurements specific to assessing beaver modifications and water quality parameters were added to explore their potential influence on Coho salmon occupancy (Table 6). Habitat variables were measured during each sampling effort as declining water height resulted in changing habitat conditions. Temperature loggers were deployed at all sites from 27 May – 19 June and recorded water temperature at 0.5 hour intervals throughout the summer (Table 6). Water quality variables including temperature (°C), salinity (ppt), and dissolved oxygen (mg/l) were measured during each sample period; *see* Water Quality Measurements section below for details. No habitat measurements were collected during the fourth survey, with the exception of water quality.

I used snorkel surveys to determine occupancy of aquatic species throughout the study area during the summer months. Each sample unit was surveyed by two independent dive passes, occurring on the same day, to estimate detection probability. Each diver independently identified and counted all fishes and aquatic vertebrates observed at each survey site using hand tally counters. Species and age classes of fish were divided into categories based on size and physical appearance (*see* Fish Processing and Marking Procedures). Prior to the survey season, we completed intensive underwater training on fish identification, quantitative dive counts, and habitat classification in streams of various sizes hosting different assemblages of fish species to maximize inter-observer reliability. Underwater tests on species identification were given to each surveyor to ensure all fish species were correctly identified. Divers used waterproof LED flashlights at all times so shadowed and complex habitats could be inspected thoroughly.

Table 6. Various habitat and water quality metrics collected at fish monitoring sites during summer 2014 and winter 2015 surveys, Smith River, Del Norte County, California.

Parameter	Units	Description	Season
Pool Type	Categorical	Physical description of habitat feature: main channel pool, scour pool, backwater pool, alcove, edge water. Derived from Flosi et al. (1998).	Summer/ Winter
Unit Length	Meters	Maximum length of the site to the nearest 0.1 m, used to calculate site area.	Summer/ Winter
Unit Width	Meters	Average width representative of the site to the nearest 0.1 m, used to calculate site area.	Summer/ Winter
Unit Depth	Centimeters	Depth at the deepest location of the site measured to the nearest cm.	Summer/ Winter
Cover Rating	Category	Rank (1-5) of cover availability and complexity, adopted from Garwood and Ricker (2014).	Summer/ Winter
Total Cover Area	$Meter^2$	Overhead view estimate of available fish cover with a minimum of 0.25 m^2 for any single habitat that is in the water column or within 1 m of the water surface.	Summer/ Winter
Total Cover Volume	$Meter^3$	Quantity of underwater cover volume based on length, width, and average depth of cover features measured to the nearest 0.1 m that is in the water column or within 1 m of the water surface.	Summer
Beaver Cover Area	$Meter^2$	Overhead view estimate of available fish cover created or added to water due to beaver activity (e.g. burrow and feeding debris) that is in the water column or within 1 m of the water surface.	Winter
Beaver Cover Volume	$Meter^3$	Quantity of volume cover created or added to water due to beaver activity, (e.g. burrow and feeding debris) that is in the water column or within 1 m of the water surface.	Summer

Parameter	Units	Description	Season
Canopy Cover	Percentage	Average of three canopy cover readings (one reading facing the bank, facing upstream and facing downstream) measured 3 m from the bank at the center of the site with a densiometer.	Summer
LWD Count	Count	Count of all wood pieces which are greater than 30 cm in diameter and 2 m in length which are in or suspended within 1 m of the water surface of the survey site.	Summer/ Winter
Continuous Water Temperature	Degrees Celsius	Deployed HOBO V2 (Onset Corporation) thermographs at the 24 fish monitoring sites throughout the summer months. Logging interval was set at 0.5 hours and used to calculate Maximum Weekly Maximum Temperature reached throughout the summer months.	Summer
Instantaneous Water Temperature	Degrees Celsius	Water temperature at all sites time of survey at deepest location within the site. Three readings at sites >1 m (i.e., bottom, middle, top), two readings at sites 31 cm – 1m deep (i.e., bottom and surface), and one reading at sites < 31cm deep.	Summer/ Winter
Instantaneous Dissolved Oxygen	Milligrams Per Liter	Dissolved oxygen at all sites during time of survey at deepest location within the site. Three readings at sites >1 m (i.e., bottom, middle, top), two readings at sites 31 cm – 1 m deep (i.e., bottom and surface), and one reading at sites < 31 cm deep.	Summer/ Winter
Instantaneous Salinity	Parts Per Thousand (ppt)	Salt concentration at all sites during time of survey at deepest location within the site. Three readings at sites >1 m (i.e., bottom, middle, top), two readings at sites 31 cm – 1 m deep (i.e., bottom and surface), and one reading at sites < 31 cm deep.	Summer/ Winter
Flow Turbulence	Percent of Surface Area With Turbulence	Percent of total survey unit that exhibited a visibly elevated flow and lacked slow water refuge.	Winter

Winter Fish Monitoring Surveys. All 24 winter fish monitoring sites received four primary sampling occasions from 3 January – 30 March, 2015, using minnow traps to determine salmonid occupancy. Unpredictable stream turbidities made snorkel surveys unreliable, whereas minnow traps could be deployed across wide ranges of flow and turbidity. I used Gee ® brand minnow traps (Cuba Specialty Manufacturing Company, Fillmore, NY) composed of two interlocking inverted cone baskets of 6 mm mesh galvanized steel wire measuring 23 x 44 cm when assembled. An opening measuring 25 mm diameter located on each side of the trap allowed for juvenile fish to enter the trap. Minnow traps were baited with ~4 g (one tbsp) of sterilized salmon roe procured by CDFW from the Trinity River Hatchery. Minnow traps were secured to anchors using parachute cord and deployed in areas having flow refuge with individual traps set for a period between 80 - 120 minutes. To ensure equal survey effort across sites of varying size, a single minnow trap was set for every 10 m of bank habitat. Fish sites were sampled twice over two days using the same number of traps and same approximate trap soak times to account for detection probability that is <1.0.

To prevent trapping in areas having poor water quality for salmonids, I measured water quality at each sampling location prior to setting minnow traps. Thresholds for deploying traps were defined as dissolved oxygen >3.5 mg/L, salinity <5 ppt, and temperature <17 ˚C following studies by Ruggerone (2000) and Wallace and Allen (2009). Habitat variables were only measured once at fish monitoring sites during the winter. We adjusted monthly sampling to occur during similar river discharges so physical conditions of each station were comparable between primary sampling occasions. During the winter water temperatures typically do not limit the available habitat and underwater cover was difficult to accurately measure due to elevated turbidity. Therefore, I did not collect continuous water temperature data or cover volume during the winter.

Fish Processing and Marking Procedures. Salmonids captured during the winter surveys were identified to species (Chinook salmon, Coho salmon, trout spp. [*Oncorhynchus* sp.], coastal cutthroat trout [*Oncorhynchus clarki clarki*]), migrant stage (young-of-year, parr, smolt, adult), counted, and measured (Garwood and Ricker 2014). Juvenile trout were not identified to species and coastal cutthroat trout were only identified when lacking parr marks, indicating a sexually mature adult. All fork lengths of juvenile salmonids were measured to the nearest mm. All Coho salmon captures were scanned for Passive Integrated Transponder (PIT) tags to determine if any of the 1380 individuals marked by CDFW during the fall of 2014 in the Mill Creek sub-basin had emigrated to the lower basin and estuary prior to smolting. To explore relative site abundances and possible trap effects on back-to-back capture rates (e.g., trap happy or shy), I marked subsets of Coho salmon, steelhead, and juvenile trout (*spp.*) with a batch fin clip. Clips were applied on the first trapping day of each primary sample occasion at winter sites by removing approximately 3 mm^2 of the upper caudal fin with small sharp scissors. All fish surveys and handling procedures were conducted under HSU IACUC No.13/14.W102-A approved on 22 May 2014.

Water Quality Measurements. Water quality was measured at all fish monitoring sites during each primary sampling occasion during both the summer and winter sampling efforts (Table 6) with a Yellow Springs Instrument® Professional Plus multi-parameter meter. Parameters measured included water temperature (°C) accuracy of ± 0.2°, dissolved oxygen (mg/L) accuracy of ± 0.2 mg/L, and salinity (ppt) accuracy of ± 0.1 ppt. Three readings were collected at the maximum depth within the site (i.e., bottom, middle, surface) at sites >1 m deep, two readings (i.e., bottom and surface) at sites 31 cm – 1 m deep, and one reading (middle) at sites < 31 cm deep. The minimum, maximum, and average of each parameter was determined for each site. Additionally, I deployed water temperature data loggers at all sites during the summer of 2014 from early June to mid-September with logging intervals set at every 0.5 hour to evaluate the influence of stream temperature on occupancy parameters. I used HOBO© water temperature pro v2 data loggers- U22-001 (Onset Computer Corporation, USA) with an accuracy of ± 0.21°C. To prevent solar radiation from influencing temperature readings, care was taken to place loggers under submerged large wood, undercut banks and root wads. Perforated PVC piping was used as a shield where suitable locations presented the possibility of direct sunlight at some time during the survey season. The maximum and average for each day, with 24 hours of temperature recordings, and the previous 6 days were averaged, to calculate the maximum weekly maximum temperature (MWMT) and maximum weekly average temperature (MWAT), respectively.

Statistical Methods

Summer and winter surveys were conducted at 24 fish monitoring sites using Pollock's robust design (Pollock 1982) as described previously (Figure 6). A multi-season occupancy model developed by MacKenzie et al. (2003) was then used to evaluate the significance of habitat and water quality variables on rearing tenure of juvenile salmonids using the logit link function. Fish monitoring sites were surveyed with four primary sample occasions (*t*) during both the summer and winter sampling seasons. To account for detection probability that is <1.0, two secondary survey occasions were conducted with two independent snorkel surveys on the same day during the summer months; minnow traps deployed for 80-120 minutes on two back-to-back days were used during the winter months.

Dynamic changes in occupancy were modeled as a first order Markov process to account for temporal autocorrelation where the probability of a site being occupied in a single primary occasion (*t*) is dependent upon whether or not the site was occupied in the previous primary occasion (*t* - 1), and:

ψ_1 = probability a station was occupied in season 1

γ_t = probability a station became occupied between season *t* and *t*+1

ε_t = probability a station became unoccupied between season *t* and *t*+1

$p_{t,j}$ = probability that a salmonid was detected at a site in a survey *j* of season *t* (given presence).

This structure results in a real estimate of occupancy for the first primary occasion (ψ_1) and real estimates of colonization and extinction between each primary occasion. These estimates were then used to derive estimates of ψ for all subsequent primary occasions by incorporating a mechanistic process for how occupancy at each site changed between primary sampling occasions (MacKenzie et al. 2006).

The occupancy model assumes there is closure within a single primary sample occasion, species detection is independent across all fish sites and between sample occasions (i.e., any one site being occupied does not influence the occupancy of any other site), and the target species are correctly identified. Due to time constraints and low dissolved oxygen, some sites had missing observation data for both seasons. The flexible unconditional model developed by MacKenzie et al. (2003) allowed for these sites to remain in the analysis under the assumption that the probability of occupancy was equal between surveyed and un-surveyed sites.

I used an information theoretic approach to model selection (Burnham and Anderson 2002). Site-level habitat and water temperature covariates were selected *a priori* for multi-season occupancy modeling in program MARK (Cooch and White 2014). The candidate model set was ranked using Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) and Akaike weights (*w*) were used to evaluate model support. Models with a ΔAIC <2 were considered to be competing models (Burnham and Anderson 1998). The candidate model set was aimed at answering questions regarding habitat and water quality parameters' relationship to ψ and ε. Prior to analysis, total cover and beaver-created cover were transformed using natural log, and temperature and canopy cover were standardized by subtracting the mean and dividing by the standard deviation, using the whole number nearest to the true standard deviation. Counts of LWD were not transformed.

During the summer, I examined model sets hierarchically to test multiple hypotheses about the relationship between Coho salmon occupancy, habitat, and water quality parameters. 1) I hypothesized Coho salmon occupancy was best explained by habitat conditions at sites and the maximum weekly maximum temperature (MWMT) reached prior to the first primary sampling occasion (June). 2) Due to high stream temperatures during the summer sampling season, I hypothesized extinction at a given site varied by season and was explained by variations in MWMT. 3) Lastly, I explored the hypothesis that the highest ranked habitat variable would explain Coho salmon occupancy better than stream temperature after accounting for seasonally varied extinction rates explained by MWMT.

I aimed to model occupancy for the winter similar to the summer; however, due to low detection and occupancy, models with habitat covariates either could not converge on a maximum likelihood estimate or produced extremely large confidence intervals, reducing model strength and inference. Alternatively, a univariate comparison of habitat measurements collected at sites where Coho salmon were and were not detected was assessed. I used a Welch t-test because variances of habitat variables at sites with and without Coho salmon were not equal (Ruxton 2006), with α level of 0.05. Additionally, occupancy parameters were calculated using the simplest model with occupancy as a function of no covariates.

Species Diversity

Snorkel surveys allowed for detection of multiple aquatic species. Species diversity was assessed at fish monitoring sites surveyed during the summer season to evaluate the ecosystem services of beaver’s non-damming activities. Both a species count and abundance metrics were evaluated to compare between the two site types.

Results

Summer

Selected fish monitoring sites were distributed across 22.5 km, beginning 5.84 km upstream from the mouth (Figure 5). I surveyed fish monitoring sites on four occasions, from June - September, with 18 – 27 days between each primary sample occasion. On average, primary sampling occasions required 4 days to survey all 24 sites. Flows ranged from 230 – 783 cfs during the sampling season reaching the minimum on September 14.

Beaver sign was observed in June at 20 of the 24 sites even though only 12 were located at lodges. A single lodge was abandoned between the June and July sample occasions and beaver sign was no longer observed at this site throughout the summer. Interestingly, juvenile Coho salmon and Chinook salmon were observed at this site during the June sample occasion but were not observed again during any subsequent summer surveys. Overall there was no significant difference in beaver created cover at lodge and non-lodge sites (Table 7). Furthermore, there was no significant difference of measured habitat variables between lodge and non-lodge sites, as was hoped to ensure all sites provided suitable habitat for rearing juvenile salmonids. Water temperatures were high throughout the summer survey period; MWMT ranged from 19.4 to 23.9 °C and was reached at all sites from 10 July to 15 September, with the majority occurring on 2 and 3 August (Appendix B).

I documented the presence of juvenile salmonids, including Coho salmon and unidentified trout sp., and beaver lodge in June. The site was abandoned by beavers

Table 7. The average, range, p-value, and t statistic from a Welch two sample t-test comparing habitat parameters measured at lodge and non-lodge fish monitoring sites during the summer of 2014.

	Non-lodge		Lodge		T-test	
	Average	Range	Average	Range	p-value	t
Maximum Length (m)	18.7	(2.1 - 35.8)	21.7	(6.7 - 60.5)	0.33	-0.98
Average Width (m)	4.7	(2.3 - 7.2)	4.9	(1.3 - 10.5)	0.75	-0.31
Total Area (m^2)	93.1	(13.0 - 250.6)	123.5	(9.1 - 490.4)	0.23	-1.22
Depth (cm)	166.8	(33 - 335)	172.2	(71 - 372)	0.77	-0.29
Volume Cover (m^3)	22.6	(0.3 - 110)	24.7	(0.3 - 207.5)	0.78	-0.29
Volume Cover created by Beaver (m^3)	9.9	(0 - 110)	12.4	(0.1 - 189.5)	0.71	-0.37
LWD	2.3	(0 - 7)	2.5	(0 - 10)	0.89	-0.14
Canopy Cover (%)	90.6	(66.9 - 99.2)	92.5	(62.4 - 99.5)	0.67	-0.43
MWMT (°C)	22.2	(19.4 - 23.6)	22.7	(21.0 - 23.9)	0.32	-1.47

between June and July, and salmonids were not detected there again. This observation suggests rearing habitat was reduced once beavers and salmonids either emigrated from the site or were no longer able to survive in the location, further highlighting the benefits of active beavers present in a large river. Furthermore, as summer flows decreased I observed a loss in habitat complexity due to loss of inundated overhanging vegetation, LWD, and undercut bank features. However, beaver activity maintained and increased underwater complexity and fish cover at lodge and non-lodge sites throughout the summer.

Coho Salmon Occupancy. Coho salmon were consistently detected at 17 of the 24 sites (Figure 7, Appendix B) during summer sampling, with eight sites having a change in occupancy status: six with extinction and two with colonization. Four of these changes in occupancy status occurred between the last two primary sampling occasions (Appendix B). These low observed site transition rates produced low estimates of overall colonization at 0.14 (SE=0.1) and extinction at 0.08 (SE=0.04) (Table 8A). Coho salmon occupancy remained relatively consistent throughout the summer ranging from 0.80 in June to 0.72 in September (Table 8A) based on the model with no covariates. Low extinction and colonization coupled with high and stable occupancy indicates most fish sites provided rearing habitats throughout the majority of the summer period. MWMT at sites occupied by Coho salmon averaged 22.5 °C (19.4 – 23.9 °C) and MWAT averaged 21.4 °C (19.3 – 21.9 °C) (Appendix B). Average salinity equaled 0.07 ppt (0.03 – 0.08 ppt) and average dissolved oxygen equaled 7.66 mg/L (4.17 – 10.93 mg/L) (Appendix B) both within acceptable thresholds previously defined for Coho salmon.

In the candidate model set, Beaver created cover out ranked all other habitat variables and MWMT reached prior to the sampling period, all of which were individually modeled on Coho salmon occupancy during the first sampling occasion (i.e., June) (Table 9). Beaver created cover produced a positive maximum likelihood estimate on the log scale (2.51, 95% CI: 0.61 to 10.34) (Table 10). This model was further

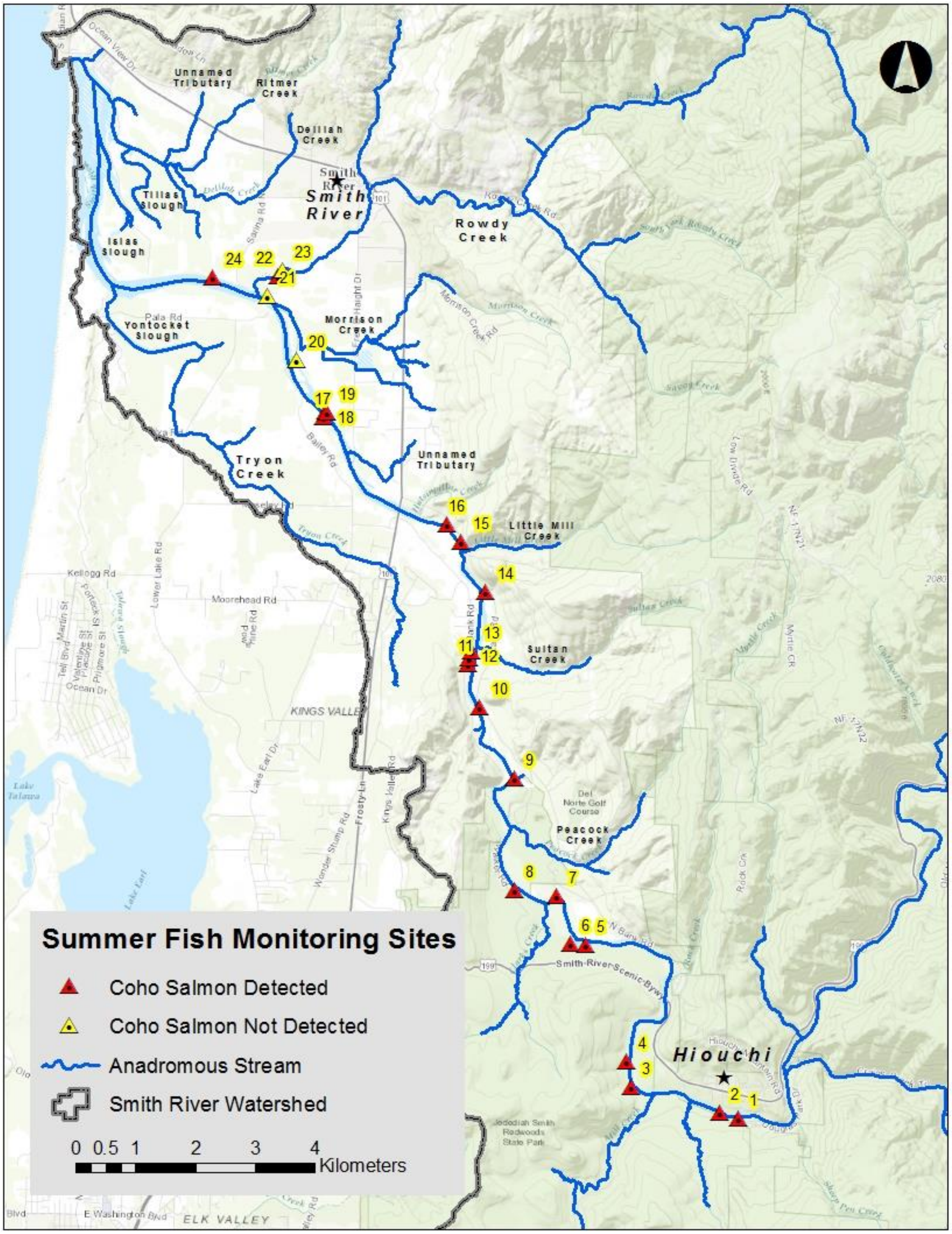

Figure 7. Coho salmon (*Oncorhynchus kisutch*) detections during summer 2014 surveys at fish monitoring sites across the mainstem Smith River and Rowdy Creek, Del Norte County, California.

Table 8. Estimates (Est) of multi-season occupancy parameters for all salmonids detected at fish monitoring sites by snorkeling during the summer (A) 2014, and with minnow traps during winter (B) 2014-15, based on the dot model. Occupancy is reported ± standard error (SE) with 95% confidence interval (CI) in ( ) below.

A

Species	Occupancy (ψ)				Colonization (γ)			Extinction (ε)			Detection (*p*)		
	June	July	August	September	Est	SE	95% CI	Est	SE	95% CI	Est	SE	95% CI
Coho Salmon	0.80 ± 0.08 (0.59 - 0.92)	0.76 ± 0.08 (0.62 - 0.91)	0.74 ± 0.09 (0.57 - 0.91)	0.72 ± 0.10 (0.52 - 0.92)	0.14	0.1	0.03 - 0.44	0.08	0.04	0.02 - 0.21	0.9 3	0.03	0.86 - 0.96
Chinook Salmon	0.88 ± 0.07 (0.68 - 0.96)	0.69 ± 0.08 (0.54 - 0.84)	0.55 ± 0.10 (0.36 - 0.74)	0.44 ± 0.11 (0.23 - 0.65)	0.03	0.06	<0.01 - 0.83	0.22	0.07	0.11 - 0.38	0.8 9	0.04	0.80 - 0.94
Trout Spp.	0.88 ± 0.07 (0.67 - 0.97)	0.83 ± 0.06 (0.72 - 0.93)	0.80 ± 0.7 (0.67 - 0.94)	0.80 ± 0.08 (0.64 - 0.95)	0.51	0.18	0.20 - 0.81	0.13	0.05	0.06 - 0.27	0.9 0	0.03	0.83 - 0.95
Coastal Cutthroat Trout	0.15 ± 0.08 (0.05 - 0.38)	0.28 ± 0.08 (0.12 - 0.44)	0.38 ± 0.11 (0.17 - 0.59)	0.45 ± 0.14 (0.17 - 0.73)	0.17	0.06	0.08 - 0.32	0.09	0.14	<0.01 - 0.73	0.6 0	0.11	0.38 - 0.79

B

Species	Occupancy (ψ)				Colonization (γ)			Extinction (ε)			Detection (*p*)		
	Early Jan	Late Jan	Mid-Feb	Mid-March	Est	SE	95% CI	Est	SE	95% CI	Est	SE	95% CI
Coho Salmon	0.19 ± 0.11 (0.05 - 0.50)	0.20 ± 0.08 (0.04 – 0.36)	0.20 ± 0.09 (0.03 - 0.38)	0.20 ± 0.10 (0.01 - 0.40)	0.11	0.06	0.04 - 0.28	0.42	0.25	0.09 - 0.84	0.44	0. 15	0.19 - 0.72
Trout Spp.	0.13[a]	0.21[a]	0.08[a]	0.08[a]	-	-	-	-	-	-	-	-	-

[a] Naïve estimates

Table 9. Candidate model set for multi-season occupancy models evaluating habitat and temperature covariates ability to explain Coho salmon occupancy at fish monitoring sites during the summer 2014, ranked with Akaike information criterion corrected for small sample size (AICc). ΔAICc is the difference in AICc value to the top model, AICc *w* is the strength of the model given the candidate set, and k is the number of parameters estimated in the model.

Model*		AICc	ΔAICc	AICc *w*	Model Likelihood	k
1)	ψ(BEAVVOL), ε(MWMT + season), γ(.), *p*(.)	127.08	0	0.47	1	8
2)	ψ(.), ε(MWMT + season), γ(.), *p*(.)	127.69	0.61	0.35	0.74	7
3)	ψ(BEAVVOL), ε(.), γ(.), *p*(.)	131.44	4.36	0.05	0.11	5
4)	ψ(.), ε(.), γ(.), *p*(.)}	132.21	5.13	0.04	0.08	4
5)	ψ(MWMT-June), ε(.), γ(.), *p*(.)	133.39	6.31	0.02	0.04	5
6)	ψ(CC), ε(.), γ(.), *p*(.)	133.67	6.59	0.02	0.04	5
7)	ψ(VOLCOV), ε(.), γ(.), *p*(.)	133.67	6.59	0.02	0.04	5
8)	ψ(LWD), ε (.), γ(.), *p*(.)	134.09	7.01	0.01	0.03	5
9)	ψ(LODGE), ε(.), γ(.), *p*(.)	134.24	7.16	0.01	0.03	5
10)	ψ(.), ε(season), γ(.), *p*(.)	134.98	7.90	0.01	0.02	6

*Occupancy (ψ) was modeled to be constant (.) or to vary on covariates including volume cover created by beaver (BEAVVOL, m^3), maximum weekly maximum temperature measured in June (MWMT- June), total volume cover (VOLCOV, m^3), canopy cover (CC), large woody debris count (LWD), and presence or absence of a beaver lodge (LODGE). Extinction (ε) was either constant (.), varied by season (season), or varied by season with the added effect of monthly MWMT (MWMT + season). Colonization (γ) and detection (p), held constant in all models.

Table 10. Covariate beta estimates, standard errors (SE), 95% Confidence Interval, and the transformed real estimates for variables individually modeled on occupancy of Coho salmon during the first primary sample occasion at fish monitoring sites during the summer 2014.

Covariate	Beta Estimate	SE	95% Confidence Interval Lower	95% Confidence Interval Upper	Transformed Real Estimate
Volume Beaver cover	0.921	0.722	-0.87	1.87	2.51[a]
June - MWMT	0.389	0.370	-0.34	1.11	4.37
Canopy cover	-0.528	0.882	-2.26	1.20	1.80
Total volume cover	0.366	0.427	-0.47	1.20	1.44[a]
Large woody debris	0.124	0.223	-0.31	0.56	3.10
Lodge	0.469	1.038	-1.57	2.50	4.95

[a]: transformed real estimate reported on the log scale

improved by allowing for extinction to vary by season with the added effect of the monthly MWMT, which was the best model with 47% of the AICc weight (Table 9). The model that only accounts for seasonally varying extinction with the added effect of monthly MWMT is a competing model with a ΔAICc <2. These results suggest that the presence of beaver created cover positively influences the likelihood that Coho salmon will occupy a summer rearing site.

Seasonally varying extinction was the lowest ranking model (Table 9). However, the model with an additive effect of MWMT and season on extinction performed substantially better in explaining extinction alone (Table 9) despite the parameter estimate being low overall (ε= 0.08, SE 0.04) (Table 8A). This model had low extinction probabilities between the first and second primary sampling occasions (i.e., from June through August) with increased extinction probability between the third and fourth primary occasions, after peak MWMT was reached at the majority of the sites. Biologically speaking, as stream temperature increased in the mainstem, there was little movement from a currently occupied rearing location. However, once the stream temperature began to decrease, fish movement began to increase.

Other Salmonids. Juvenile Chinook salmon occupancy declined consistently throughout the summer (Table 8A), which was expected given their common life history of migrating to the ocean during spring through their first fall. However, their occupancy was estimated to be 0.44 (SE 0.11) in September, indicating Chinook salmon in the Smith River have an extended stream rearing period, potentially due to the high water quality and cold head water streams. Similar to Coho salmon, occupancy of juvenile trout was generally high (0.80 – 0.88) and remained stable throughout the summer (Table 8A). Coastal cutthroat trout occupancy rates increased substantially through time from 0.15 in June to 0.45 in September (Table 8A).

Species diversity

During summer snorkel surveys, multiple aquatic species were detected including three-spined stickleback (*Gasterosteus aculeatus*), unidentified sculpin species (*Cottoidea* spp.), Klamath smallscale sucker (*Catostomus rimiculus*), rough-skinned newt (*Taricha granulosa*), western toad (*Anaxyrus boreas*), foothill yellow legged frog (*Rana boylii*), aquatic garter snake (*Thamnophis atratus*), unidentified crayfish (*Astacoidea* spp.), and western pearlshell mussel (*Margaritifera falcata*). Species richness at lodge and non-lodge sites was not significantly different (p= 0.91) with an average of 4.98 and 5.02 species observed, respectively. Nor was there a significant difference in maximum count between lodge and non-lodge sites (p= 0.18). On average lodge sites had a maximum count of 105 (2 – 764) aquatic individuals observed while non-lodge sites had 72 (1 – 247).

Western toads were detected at four monitoring sites, all of which were lodge sites, throughout the summer: three in June, one in July and one in August. Aquatic garter snake was observed only once in July at a lodge site. Rough skinned newts were observed during all four primary sampling occasions at both lodge and non-lodge sites. Overall, I found a diverse community of salmonids and other vertebrate species using most fish monitoring sites.

Winter

Winter sites were distributed across 15.8 km, beginning 0.97 km upstream from the mouth (Figure 5), eight of which were also surveyed in summer. On average, each primary sampling occasion required four days to survey all 24 sites. I surveyed sites on four occasions, from January – March, with 18-23 days between each sample occasion. Flows ranged from 1,130 – 38,400 cfs during the sampling season with a storm event producing a rise in flows between each primary sampling occasion (Figure 8). The peak winter flow was 59,100 cfs on 21 December 2014. Due to sampling constraints only eight of the 24 sites were located at lodges, though beaver activity was present at 14 of the sites. Habitat conditions at lodge and non-lodge sites were fairly similar with only amount of cover created by beavers ($p = 0.046$), maximum depth ($p=<0.001$), and dissolved oxygen ($p=0.006$) found to be significantly different between lodge and non-lodge sites (Table 11). Lodge sites had more beaver created cover, had greater water depths, and had higher dissolved oxygen. Overall elevated winter flows reduced the variation of habitat conditions at lodge and non-lodge sites and beaver activity was less prevalent in the mainstem during winter compared to summer.

Coho Salmon Occupancy. Based on the model with no covariates, estimated Coho salmon occupancy was low (0.20, SE= 0.09) and remained consistent (0.19 – 0.20) throughout the winter sampling season (Table 8B). A moderate detection rate was estimated for minnow traps (p= 0.44, SE=0.15), though was similar to those reported in other studies (Bryant 2000, Sethi 2013). No individual Coho salmon was captured during both days within a single primary sample occasion, determined by fin clips applied on

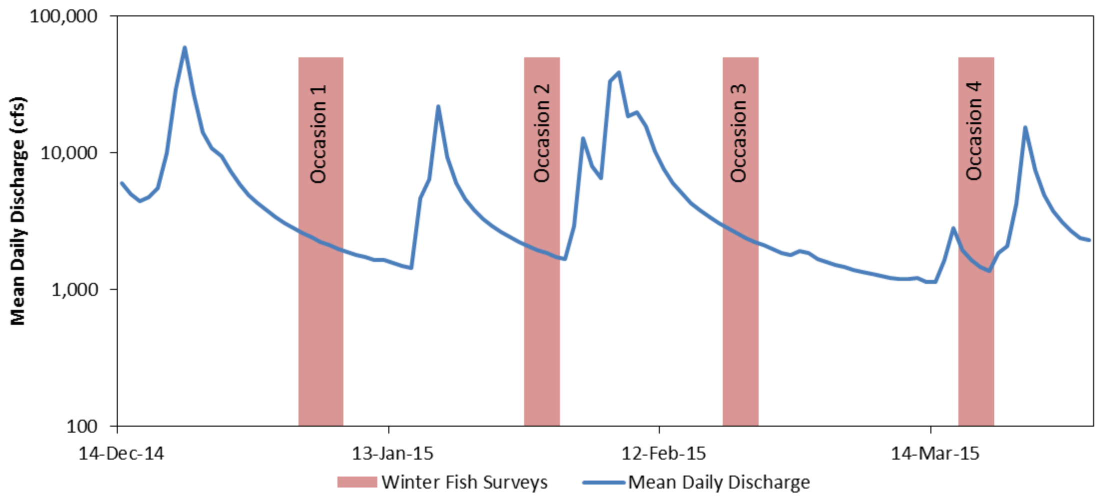

Figure 8. Daily average winter discharge and timing of winter sample surveys conducted at winter fish monitoring sites from January – March 2015. Flow measured and recorded by the USGS Jed Smith stream gauge (11532500) located on the Smith River 25.97 km upstream from the mouth near Hiouchi, California.

day 1 of sampling during each primary sampling occasion. These findings suggest a lack of independence between the two days of sampling. This apparent ‘trap shy’ behavior likely resulted in the large confidence interval for detection probability. Extinction and colonization were estimated to be 0.42 and 0.11, respectively (Table 8B). Standard errors for both colonization and extinction estimates were large, likely due to the small number of occupied sites coupled with the moderate detection probability (Table 8B).

Coho salmon were detected at eight of the 24 fish stations (Figure 9) but were present at only one location consistently throughout the winter (Site 8; Appendix C). Site 8 also had the highest number of individual Coho salmon detections during any single trapping occasion. This location is a large alcove formed from a remnant gravel harvest pit that is connected intermittently to the mainstem river during high winter flows. In addition, this location is heavily used by beavers, with multiple separate groups of lodge entrances within the 150 m long pool. The water quality at this site did not vary greatly from other sites; however it did maintain the highest mean water temperature of all locations (Appendix C). Sites where Coho salmon were and were not detected were not significantly different in size, total cover, or with cover created by beaver (Table 12). Maximum depth was the only habitat variable found to be significantly different between sites, with deeper water where Coho salmon were detected as opposed to not detected (Table 12).

Table 11. The average, range, p-value, and t statistic from a Welch two sample t-test comparing habitat parameters measured at lodge and non-lodge fish monitoring sites during the winter of 2014-15.

	Non-Lodge		Lodge		t-test	
	Average	Range	Average	Range	p-value	t
Maximum Length (m)	23.0	(3.0 - 58.0)	37.8	(6.7 - 145.0)	0.424	-0.84
Average Width (m)	5.4	(2.5 - 16.0)	6.2	(3.0 - 12.5)	0.542	-0.62
Total Area	138.5	(7.5 - 720.0)	351.0	(27.0 - 1812.5)	0.367	-0.96
Maximum Depth (cm)	121	(25 - 240)	238	(197 - 320)	< 0.001*	-5.19
Total Cover Area (m^2)	27.00	(0.00 - 118.00)	128.5	(11.00 - 531.00)	0.153	-1.60
Area Cover created by Beaver (m^2)	1.00	(0.00 - 5.25)	36.7	(4.00 - 106.25)	0.046*	-2.42
LWD	2.00	(0 - 9)	2.9	(1 - 9)	0.478	-0.73
Dissolved Oxygen (mg/l)	7.42	(1.1 - 10.9)	9.9	(7.16 - 11.15)	0.006*	-3.03
Temperature (°C)	12.2	(6.8 - 14.7)	12.1	(6.6 - 13.8)	0.750	0.32
Salinity (ppt)	0.63	(0.05 - 5.31)	0.06	(0.05 - 0.09)	0.115	-1.68

*denotes statistically significant p-value

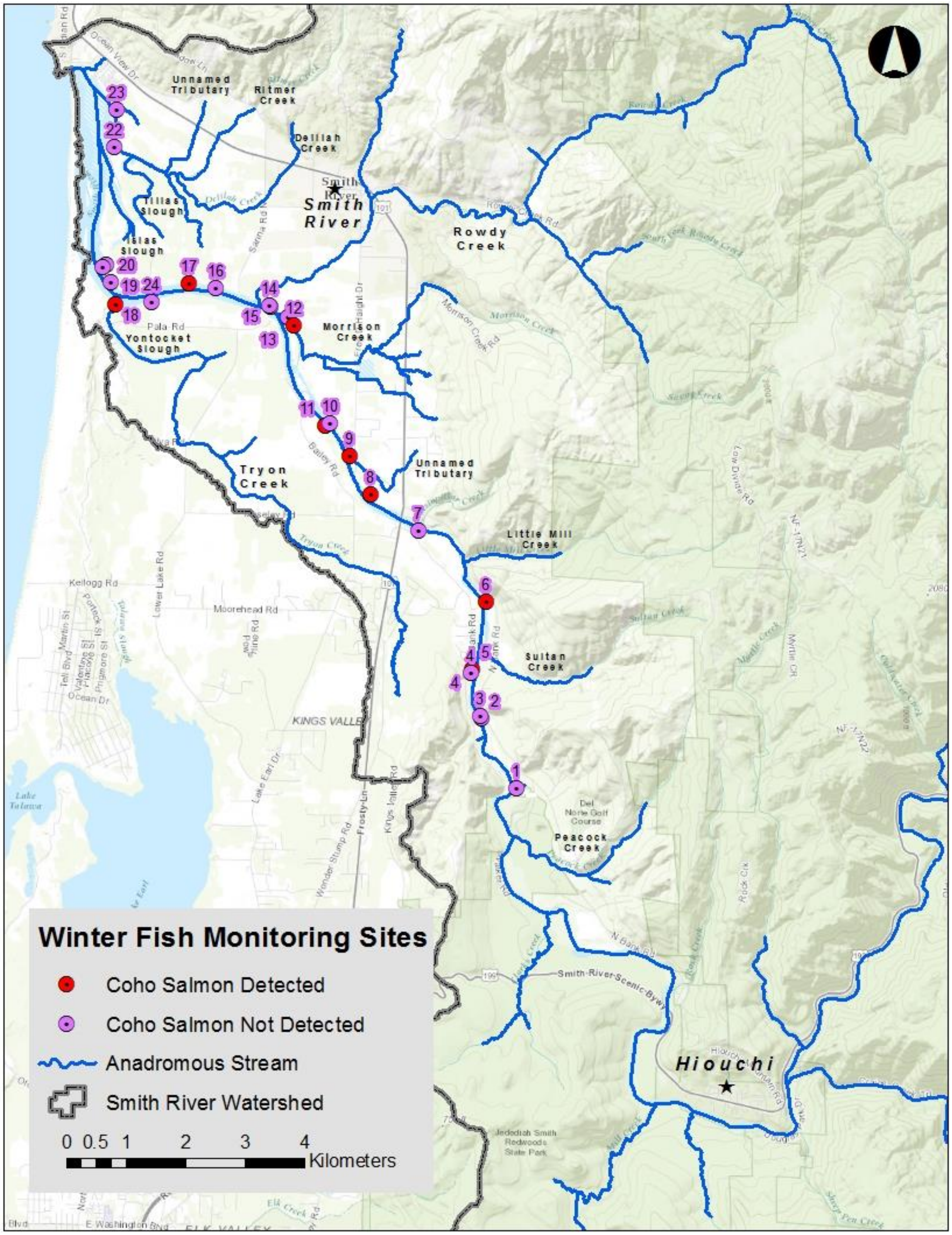

Figure 9. Coho salmon (*Oncorhynchus kisutch*) detections during winter 2014-15 surveys at fish monitoring sites across the mainstem Smith River, Del Norte County, California.

Table 12. The average, range, p-value, and t statistic from a Welch two sample t-test comparing habitat parameters measured fish monitoring sites during the winter of 2014-15 where Coho salmon were and were not detected.

	Coho Salmon not detected		Coho Salmon detected		t-test	
	Average	Range	Average	Range	p-value	t
Maximum Length (m)	19.0	(3.0 - 58.0)	46	(6.7 - 145.0)	0.133	-1.67
Average Width (m)	4.6	(2.5 - 10.0)	7.73	(3.7 - 16)	0.084	-1.96
Total Area (m^2)	86.5	(7.5 - 232.0)	454.94	(37.52 - 1812.5)	0.127	-1.73
Maximum Depth (cm)	137	(25 - 320)	206.63	(130 - 258)	0.015*	-2.63
Total Cover Area (m^2)	20.33	(0.00 - 92.00)	141.88	(23 - 531)	0.086	-1.99
Area Cover created by Beaver (m^2)	2.81	(0.00 - 13.75)	33.08	(0.00 - 106.25)	0.096	-1.92
Large Woody Debris	2.31	(0 - 9)	2.25	(0 - 9)	0.96	0.05
Lodge	0.25	-	0.5	-	0.277	-1.14
Minimum Dissolved Oxygen (mg/L)	7.86	(1.09 - 11.15)	9.05	(5.95 - 10.96)	0.225	-3.18
Maximum Temperature (˚C)	12.0	(9.6 - 14.7)	12.5	(11.4 - 13.8)	0.219	-1.28
Minimum Temperature (˚C)	8.2	(6.6 - 9.7)	9.7	(6.9 - 12.6)	0.082	-1.95
Maximum Salinity (ppt)	0.63	(0.05 - 5.31)	0.06	(0.05 - 0.10)	0.121	1.65

*denotes statistically significant p-value

Through PIT tag scanning, I detected three individuals in Site 8 originally marked in Mill Creek during the previous fall (2014), on the 28th of January. On average these fish grew 20.6 mm and traveled a minimum of 26.9 km with 123 days between capture events. These fish demonstrate that individuals captured at the mainstem fish monitoring sites exhibited an early emigration life history into non-natal rearing locations during the winter months.

Other Salmonids. One Chinook salmon was detected during the first January sampling occasion at Site 8 but was not detected again. Due to the limited data, and typical life history of juvenile Chinook salmon not present in the river during the winter months, no occupancy parameters were assessed for Chinook salmon. Detections of unidentified trout and steelhead were also rare with only 15 individuals at seven sites across all four primary sampling occasions. As a result, occupancy parameters were not stable in occupancy models and could not be accurately estimated. Therefore only naïve estimates are reported and were found to vary between 0.08 and 0.21 (Table 8B). Coastal cutthroat trout were not detected with minnow traps at winter sites, likely due to trap entrances being too small for much of the adult cutthroat population.

Discussion

Salmonid Occupancy

All four salmonids species found in the Smith River basin were observed occupying rearing habitats across the mainstem throughout the summer months. Chinook salmon were detected throughout the summer months with occupancy steadily declining form June - September. Coastal cutthroat trout occupancy steadily increased during this same time period. Coho salmon and unidentified trout both had high and stable occupancy during the summer sampling months. I found Coho salmon occupancy in the mainstem Smith River to be higher during the summer months than winter months and was relatively stable throughout both seasons. Juvenile Coho salmon use of seasonally varying habitats in the stream estuary ecotone has been documented across numerous

Pacific Northwest basins (Miller and Sadro 2003, Koski 2009, Jones et al. 2014, Wallace et al. 2015). During winter sampling I detected juvenile Coho salmon in the mainstem Smith River that had been individually marked with PIT tags during the fall of 2014 in Mill Creek. These individuals confirm juvenile Coho salmon express life history diversity in the Smith River by migrating in the fall or winter to non-natal rearing habitats.

All habitat variables modeled on Coho salmon occupancy during the summer months resulted in large standard errors relative to the covariate estimates (Table 10) and are likely a function of the site selection protocol. Fish monitoring sites were selected based on their inferred high habitat quality resulting in a lack of variation in habitat conditions. Furthermore sites were selected due to their high likelihood to be used by salmonids for non-natal rearing. Overall the summer dataset lacked variation and very few sites lacked Coho salmon detections. All 95% confidence intervals overlapped zero, though only by a small margin. I believe a larger dataset which includes a wider variety of habitat conditions would help to reduce standard errors and help to highlight the importance of summer non-natal rearing habitats characterized with underwater cover features. Also, the analysis of how habitat conditions influence Coho salmon occupancy during the winter would likely have been improved with increased detection probability, which could be achieved with a third day of sampling during each primary sampling occasion or potentially by containing the bait. Coho salmon habitat use seasonally varies, with use of small tributaries and intermittent streams increasing during the winter months (Miller and Sadro 2003, Parish and Garwood 2015, Wallace et al. 2015). Including winter sample sites in these areas would improve understanding of juvenile Coho salmon winter habitat use and distribution.

Stream temperature appeared to explain seasonal Coho salmon extinction rates and is likely a limiting factor to non-natal summer rearing habitat has been shown in other Pacific Northwest Streams (Welsh et al. 2001, Madej et al. 2006). Surprisingly, I documented Coho salmon to consistently occupy sites with MWMT >23 °C (Appendix 2), indicating Coho salmon were rearing in temperatures above those reported in another Northern California stream (Welsh et al. 2001). However these findings support the Coho salmon tolerance threshold of a 95% of MWAT value of 23.4 °C reported by Eaton et al. (1995). Fluctuations in temperature occurred daily and at various water depths. These fluctuations likely play a role in allowing for juvenile Coho salmon to survive peak summer water temperatures and individuals may behaviorally adapt to daily variation as has been shown in the Klamath River (Witmore 2014). Restoration and habitat enhancement projects for summer habitats should focus efforts in areas having cold water seeps, confluences with cold water tributaries, or sites with water depths >1 m throughout the summer, and encourage dense overhanging cover to provide shade and cooler water temperatures.

This study was conducted during the third consecutive year of drought producing low summer flows with water temperatures higher than normal. While Coho salmon spatial and temporal use of non-natal rearing habitats in the Smith River basin has been shown to seasonally vary (Parish and Garwood 2015), further data collection during various flow conditions and salmon abundance would aid in addressing the range of beaver bank lodge use by Coho salmon and other aquatic species. Additionally, estimates of the adult spawning population preceding this study was low (Garwood et al. 2014), potentially resulting in a lower propensity for non-natal rearing by juvenile Coho salmon (Rebenack et al. 2015, Wallace et al. 2015) during this study.

Beaver Influence on Non-natal Salmonid Rearing Habitat

North American beaver bank lodges and activity were prevalent throughout the study area (Figure 2). All four salmonids species present in the Smith River basin were observed occupying beaver bank lodges and utilizing beaver-created habitat throughout the summer months. Using Coho salmon as the focal species, I found beaver-created cover modeled on Coho salmon occupancy during the first primary sample occasion of the summer out ranked all other habitat parameters, including habitat variables known to provide beneficial salmonid rearing habitat. Variables included large woody debris and overhanging vegetation (canopy cover), both of which are commonly used in fish habitat enhancement and restoration designs. Beavers were found to create and maintain habitat complexity, particularly in the summer, but also in small intermittent streams during the winter. Some habitat features (backwaters) would have become isolated from the mainstem if not for beavers' continued excavation activities during the summer months.

During the summer, locations with beaver activity had higher habitat complexity and shade with the addition of small woody debris, through food caching and feeding activities, as well as by creation of new burrows and sites without beaver activity were uncommon in the study area. Coho salmon and other salmonids were commonly observed utilizing burrows and woody debris piles created by beavers. The model rankings and field observations made during this research support my prediction that Coho salmon occupancy is higher at sites with increased beaver activity during summer rearing. Due to beaver prevalence throughout the mainstem during the summer, these findings would be strengthened with control sites where beaver activity could be excluded.

The lack of significant variation in beaver-created cover at sites with and without Coho during the winter does not provide support for my prediction that Coho occupancy increases at sites with increased beaver activity. Low detection probability and a lack of independence between the first and second day of minnow trapping likely contributed to my inconclusive results (Pollock 1982, MacKenzie et al. 2003) and inability to model beaver influence on Coho salmon occupancy at mainstem non-natal rearing sites during winter months. High flow conditions during the winter inundated habitat and increased underwater complexity, while low velocity habitats were lacking. These stream conditions likely reduce the influence of beaver activity and bank lodge presence on Coho salmon. The increase in winter beaver activity in small intermittent tributaries during winter highlights the dynamic nature of the species in a coastal watershed. These seasonal movements, which mimic juvenile Coho salmon movement (Parish and Garwood 2015), highlight additional ways in which beavers likely improve habitat conditions for juvenile salmonids in coastal watersheds during the winter months.

CONCLUSION

Beaver activity was found to be widely distributed and to be an important component in creating and maintaining habitat availability and complexity for salmonids rearing in the Smith River coastal plain, where rearing habitat loss in the basin has been highest (NMFS 2014). Beavers created and maintained complex underwater habitat that did not impede flow during both the summer and winter sampling seasons. These habitats throughout the mainstem were heavily utilized by multiple juvenile salmonids species during the summer months and less in the winter months. Beaver use of the coastal plain was found to be seasonally dynamic and mimicked the seasonal movement of juvenile Coho salmon (Parish and Garwood 2015). On average, beaver activity and sign was more abundant in the mainstem during the summer months than the winter months, with increased beaver activity in intermittent streams that contained flowing water during the winter months. Juvenile Coho salmon were also found to use the mainstem more heavily during the summer and have been shown to utilize small tributaries and intermittent streams in the winter (Parish and Garwood 2015), a seasonal trend found in other coastal California streams (Wallace et al. 2015). This seasonal variation and the fact that my fish surveys were focused in the mainstem likely impacted my strong findings of beaver's positive influence on summer non-natal rearing habitat compared to the winter.

Increasing beaver abundance is listed as a recovery strategy for Coho salmon in the Smith River Basin (NMFS 2014). Beaver presence and lodges have also been observed in the Tolowa Dunes State Park (C. Appel, pers. comm.). This area may aid in beaver population recruitment and resilience during the winter months when activity in the mainstem decreases. Restoration mimicking and encouraging beaver damming, such as beaver dam analogs (BDAs), have illustrated beaver dams can successfully restore incised streams in central Oregon through channel aggradation, raising the water table and increasing riparian vegetation (Pollock et al. 2007), thereby improving fish habitat. Areas to incorporate BDAs are limited in the Smith River coastal plain due to the hydrologic regime; however, they likely could be used to recruit and increase beaver activity in intermittent summer streams. Beaver activity in these streams may also limit the extent of invasive Reed canary grass (*Phalaris arundinacea*) due to beavers creating and maintaining channels and increasing water depth. However, established Reed canary grass likely limits suitable beaver habitat in small streams, as the plant species increases sedimentation and displacing native vegetation (DiTomaso and Healy 2007). Alternatively, beaver bank lodges may present potential restoration opportunities in larger rivers. Furthermore, protection and management of the beaver population will encourage the continued construction and maintenance of bank lodges, the dominant way beavers alter and create fish habitat in the Smith River.

Coho salmon were found to have high occupancy at non-natal rearing sites in the mainstem during the summer rearing months. These same areas are where human land use is highest in the Smith River basin. Therefore, during their freshwater life stages, Coho salmon are likely vulnerable to anthropogenic alterations, including loss and alteration of stream habitat and removal of riparian vegetation. Variations in life history strategies likely buffers negative impacts of environmental and population stochasticity on Coho salmon and adds resilience to the population as has been documented for other salmonid species (Hilborn et al. 2003; Greene et al. 2010). Protection and enhancement of non-natal rearing habitat should be the focus of restoration and conservation efforts in the basin for the benefit of all salmonid species.

Annual variation in flow and river conditions requires beavers and salmon to constantly adapt to a changing environment. A multi-year study throughout all seasons assessing beaver habitat use and suitability would strengthen understanding of the species' behavioral movements and lodge requirements in a large river system. These data would lead to more informed management and restoration decisions on how and where beavers can be utilized to naturally enhance and maintain rearing habitat for juvenile salmonids in coastal rivers and streams as well as how to improve habitat to support a robust beaver population.

Beaver presence was once prevalent and widespread across California (Lanman et al. 2012, 2013). Recent work has been done highlighting ways to keep beavers on the landscape while minimizing the possible negative impacts of their land alteration activities (Lundquist and Dolman 2016). Research showing the landscape-scale benefits and positive effects on salmonid populations when using beavers and BDAs as restoration tools (Bouwes et al. 2016) further highlights the importance of having beavers on the landscape. Beaver habitat needs should be taken under consideration when making restoration and management decisions particularly regarding juvenile salmonid habitat enhancement.

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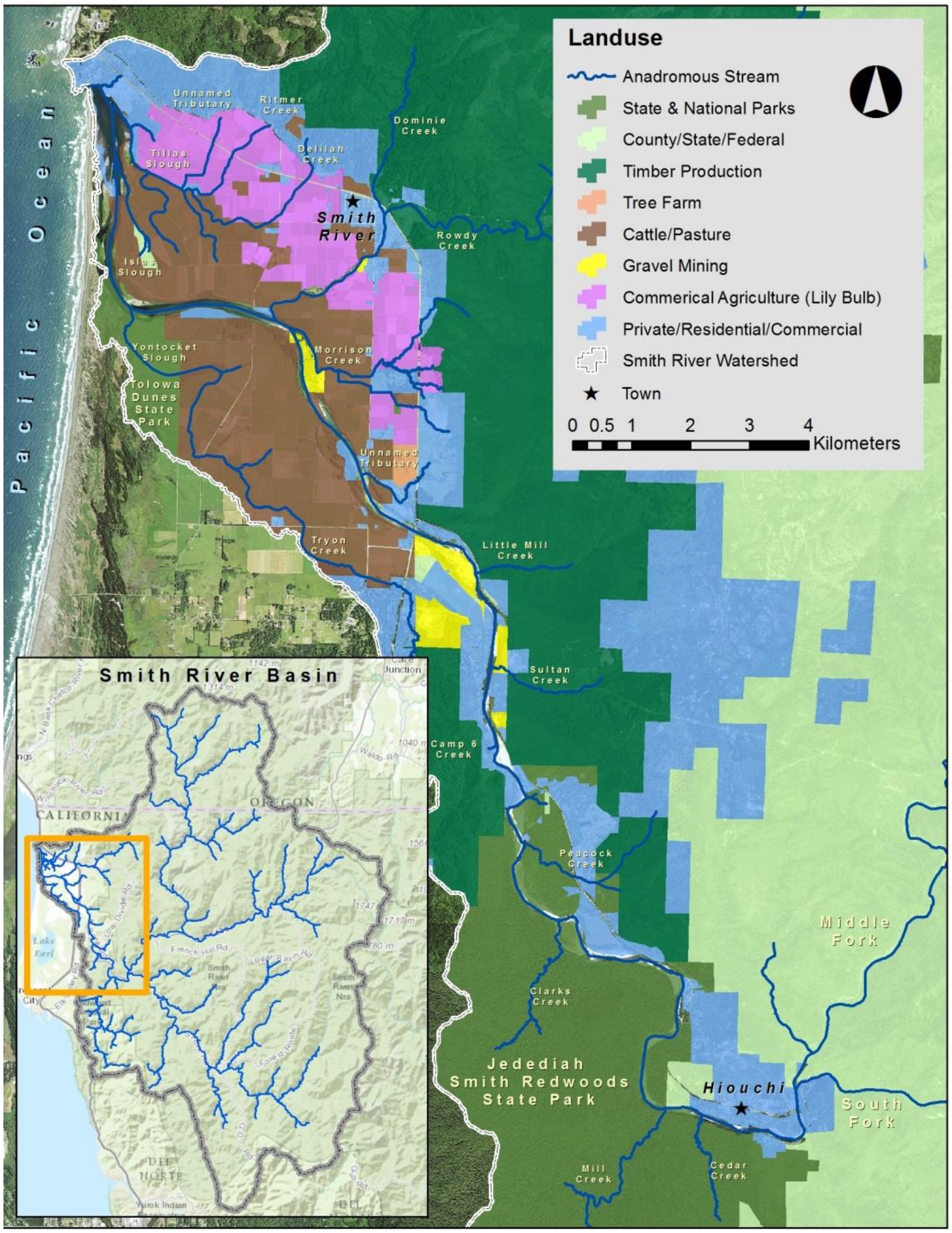
APPENDICES



Appendix A. Map of general land use and ownership throughout the Smith River mainstem and coastal tributaries, Del Norte County, California. The general study area extends downstream from the main river forks in Hiouchi to the mouth and includes major tributaries in the coastal plain: Morrison Creek, Rowdy Creek, Tryon Creek, Yontocket Slough, Tillas Slough, Islas Slough, and various unnamed streams below HWY 101.

Appendix B. Combined two pass detection history of juvenile Coho salmon and water quality conditions including maximum weekly average temperature (MWAT), maximum weekly maximum temperature (MWMT), mean daily range (MDR), dissolved oxygen (DO), and salinity at fish monitoring sites during the summer 2014. A (-) denotes that the site was not surveyed during that occasion.

Site	Occupancy				MWAT (°C)	MWAT Date	MWMT (°C)	MWMT Date	MDR (°C)	MDR Date	Mean DO (mg/L)	DO Range (mg/L)	Mean Salinity (ppt)	Salinity Range (ppt)
	Jun	Jul	Aug	Sep										
1	Y	Y	Y	Y	21.21	3-Aug	22.22	3-Aug	2.03	28-Jul	6.77	(5.36 - 8.36)	0.07	(0.07 - 0.08)
2	Y	Y	Y	N	21.76	3-Aug	22.79	3-Aug	2.00	14-Jul	8.88	(7.51 - 9.90)	0.07	(0.06 - 0.08)
3	Y	Y	Y	Y	21.61	3-Aug	22.79	2-Aug	2.60	26-Jul	8.54	(7.52 - 9.45)	0.07	(0.06 - 0.08)
4	Y	Y	Y	Y	19.29	4-Aug	19.44	3-Aug	1.86	9-Jul	8.06	(6.03 - 10.93)	0.06	(0.03 - 0.08)
5	Y	Y	Y	Y	20.47	3-Aug	22.07	10-Jul	4.05	30-Jun	7.01	(5.34 - 8.66)	0.06	(0.04 - 0.08)
6	Y	Y	Y	Y	20.16	2-Aug	21.21	2-Aug	2.93	18-Jun	6.61	(5.06 - 7.91)	0.08	(0.07 - 0.08)
7	Y	Y	Y	-	21.96	3-Aug	22.95	2-Aug	7.08	10-Oct	7.73	(6.54 - 9.42)	0.07	(0.06 - 0.08)
8	Y	Y	Y	Y	21.30	3-Aug	21.98	2-Aug	3.62	30-Jun	6.84	(4.17 - 8.89)	0.07	(0.06 - 0.08)
9	Y	Y	Y	Y	22.02	3-Aug	22.80	3-Aug	3.52	30-Jun	8.51	(6.56 - 9.91)	0.07	(0.06 - 0.08)
10	Y	Y	Y	Y	21.92	3-Aug	22.70	3-Aug	3.43	30-Jun	8.41	(6.50 - 9.80)	0.07	(0.06 - 0.08)
11	Y	Y	Y	Y	19.72	3-Aug	20.14	3-Aug	3.45	24-Jul	6.29	(4.81 - 7.89)	0.07	(0.06 - 0.08)
12	Y	Y	Y	N	21.98	3-Aug	23.41	3-Aug	3.31	5-Jun	7.08	(5.87 - 8.35)	0.07	(0.06 - 0.08)
13	Y	Y	Y	Y	22.00	3-Aug	22.94	2-Aug	2.74	29-Jun	8.24	(6.52 - 9.73)	0.07	(0.06 - 0.08)
14	Y	Y	Y	-	22.04	3-Aug	23.89	2-Aug	5.40	11-Jun	8.08	(6.24 - 9.39)	0.07	(0.06 - 0.08)
15	Y	N	N	-	-	-	-	-	-	-	8.73	(7.21 - 9.64)	0.07	(0.06 - 0.07)
16	Y	Y	Y	-	21.86	3-Aug	23.37	2-Aug	8.35	11-Jun	8.91	(7.34 - 9.72)	0.07	(0.06 - 0.07)
17	Y	Y	Y	N	22.08	2-Aug	23.59	2-Aug	4.17	24-Jul	7.36	(5.28 - 9.63)	0.07	(0.06 - 0.08)
18	Y	Y	Y	N	21.89	2-Aug	23.30	31-Jul	3.94	25-Jul	7.01	(5.41 - 8.95)	0.07	(0.06 - 0.08)
19	N	N	Y	Y	21.74	3-Aug	22.95	1-Aug	3.57	24-Jul	7.55	(6.11 - 9.11)	0.07	(0.06 - 0.08)
20	N	N	N	N	21.96	2-Aug	23.28	31-Jul	3.90	25-Jul	8.61	(7.73 - 9.52)	0.07	(0.06 - 0.08)
21	N	N	N	N	21.84	2-Aug	22.68	31-Jul	3.50	30-Jun	6.91	(0.59 - 9.75)	1.80	(0.06 - 9.70)
22	N	Y	Y	Y	17.73	26-Aug	20.80	25-Aug	7.16	24-Jul	7.87	(4.29 - 10.87)	0.05	(0.04 - 0.06)
23	N	N	N	N	18.81	4-Sep	21.00	15-Sep	6.96	10-Sep	8.79	(4.69 - 12.49)	0.05	(0.04 - 0.07)
24	Y	Y	N	N	21.72	26-Aug	23.36	26-Aug	3.75	5-Sep	8.00	(6.38 - 9.17)	3.88	(0.06 - 17.21)
Overall Average & Full Range					21.18	-	22.42	-	4.06	-	7.78	(0.59 – 12.49)	0.30	(0.03 - 17.21)

Appendix C. Combined two day detection history of juvenile Coho salmon and water quality conditions including, temperature (Temp), dissolved oxygen (DO), and salinity at fish monitoring sites during the winter 2014-15. A (-) denotes that the site was not surveyed during that specific occasion.

	Coho Salmon Occupancy				Mean Temp (°C)	Temp Range (°C)	Mean DO (mg/L)	DO Range (mg/L)	Mean Salinity (ppt)	Salinity Range (ppt)
Site	1	2	3	4						
1	N	N	N	N	9.07	(6.6 - 11.6)	12.38	(11.15 - 13.16)	0.05	(0.05 - 0.05)
2	N	N	N	N	9.09	(6.6 - 11.7)	12.07	(10.55 - 13.09)	0.05	(0.05 - 0.05)
3	N	N	N	N	9.15	(6.9 - 11.6)	10.77	(6.35 - 12.5)	0.05	(0.05 - 0.06)
4	N	N	N	N	9.42	(6.9 - 11.8)	10.11	(6.21 - 11.78)	0.05	(0.05 - 0.06)
5	N	N	Y	N	9.78	(6.9 - 11.9)	11.22	(10.11 - 12.98)	0.05	(0.05 - 0.05)
6	N	N	Y	N	9.92	(7.5 - 12)	10.66	(8.95 - 11.76)	0.05	(0.02 - 0.05)
7	N	N	N	N	10.99	(8.8 - 12.6)	8.72	(6.65 - 10.08)	0.09	(0.07 - 0.13)
8	Y	Y	Y	Y	12.98	(12.6 - 13.8)	8.37	(7.16 - 10.48)	0.08	(0.06 - 0.09)
9	Y	N	Y	N	12.70	(12.2 - 13.3)	6.78	(5.95 - 7.32)	0.07	(0.06 - 0.10)
10	N	N	N	N	10.41	(8.4 - 12.5)	10.97	(9.97 - 12.18)	0.05	(0.05 - 0.05)
11	N	Y	Y	N	10.88	(9.0 - 13.0)	11.22	(10.38 - 11.94)	0.05	(0.05 - 0.05)
12	Y	N	N	N	11.33	(10.5 - 13.2)	9.89	(8.74 - 10.38)	0.04	(0.04 - 0.06)
13	N	N	N	N	11.18	(9.7 - 12.4)	10.26	(9.51 - 11.08)	0.05	(0.03 - 0.06)
14	N	N	N	N	10.41	(9.3 - 11.7)	11.63	(10.89 - 12.12)	0.05	(0.05 - 0.05)
15	N	N	N	N	10.28	(9.3 - 11.7)	11.54	(11.1 - 12.13)	0.05	(0.05 - 0.05)
16	N	N	N	N	10.25	(9.3 - 11.4)	11.54	(10.96 - 12.19)	0.05	(0.05 - 0.05)
17	N	N	N	Y	10.42	(9.9 - 11.4)	11.15	(10.18 - 11.85)	0.05	(0.05 - 0.05)
18	N	Y	N	N	9.52	(8.0 - 11.6)	6.72	(3.74 - 10.75)	0.10	(0.06 - 0.14)
19	N	N	N	N	10.72	(9.6 - 11.6)	8.78	(5.94 - 10.8)	0.24	(0.09 - 0.37)
20	N	N	N	N	10.26	(8.9 - 11.9)	11.78	(10.29 - 14.16)	0.14	(0.06 - 0.53)
21	N	N	N	N	11.08	(9.3 - 14.7)	10.17	(8.29 - 11.39)	0.19	(0.06 - 0.41)
22	N	N	N	N	10.60	(8.6 - 12.0)	9.07	(5.86 - 10.99)	1.48	(0.42 - 2.43)
23	N	N	N	N	9.71	(8.1 - 12.5)	9.46	(8.17 - 10.82)	1.48	(0.07 - 5.31)
24	N	N	N	N	8.27	(6.8 - 9.6)	3.34	(1.09 - 5.24)	0.18	(0.11 - 0.33)
Overall Average & Full Range					10.35	(6.6 - 14.7)	9.94	(1.09 - 14.16)	0.20	(0.02 - 5.31)