SEASONAL GROWTH, RETENTION, AND MOVEMENT OF JUVENILE COHO SALMON IN NATURAL AND CONSTRUCTED HABITATS OF THE MID-KLAMATH RIVER

by

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ABSTRACT

Seasonal growth, retention, and movement of juvenile coho salmon in natural and constructed habitats of mid-Klamath River

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Juvenile coho salmon (*Onchorynchus kisutch*) in the Klamath River basin often move long distances when natal streams become inhospitable due to high summer temperatures and high winter flows. Therefore, non-natal rearing sites such as tributaries and off- channel ponds are potentially important to the survival of juvenile coho salmon. This study evaluated the potential benefit to juvenile coho salmon of different types of non-natal rearing habitats in the mid-Klamath watershed including tributaries, beaver-influenced ponds, and constructed off-channel ponds. These sites represent different types of seasonal refugia habitat. Juvenile coho salmon were PIT tagged and measured in ten study sites to evaluate their growth, retention within the habitats, and seasonal movement patterns. Few relationships were found between type of site and growth rate, retention rate, or abundance. However, growth rate of fish which reared year-round in the same site was greater in beaver-influenced sites than in other habitat types. Depth, water temperature, volume of habitat, and percent riparian cover were not correlated with growth rates of coho salmon rearing in those sites. However, because I found significant differences in growth rates of fish across individual sites, there may be other habitat characteristics not measured as part of this study that influence growth. Retention rate was positively correlated with average maximum depth; however the summer retention rate of juvenile salmon at the sites was not correlated with salmon growth at the sites. I observed three seasonal movement patterns of juvenile coho salmon: spring redistribution of fry; fall redistribution associated with initial high flows, and outmigration of smolts during the following spring. A diurnal movement pattern was also detected at the mouths of Tom Martin Creek and Caltrans Pond in which juvenile coho salmon left the study site in the evening and returned in the early morning. This exploratory study showed that not only do juvenile coho salmon in the mid-Klamath display several different migratory patterns; choosing different types of off-channel habitats to rear, but the growth and retention rates of those fish depend on complex and site specific characteristics rather than type of habitat.

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INTRODUCTION

Many streams in the Western United States and the Klamath Basin have been altered from human activities which have reduced or degraded habitat for salmonid fishes (Hicks et al 1991). Due to habitat destruction, over fishing, hatcheries, dams, and climate change, the range and abundance of coho salmon (*Oncorhynchus kisutch*) have been greatly reduced, resulting in the federal listing of many coho salmon populations as threatened or endangered (Nehlsen et al. 1991, CDFG 2002). Of particular concern are populations at the southern end of their range, including the Southern Oregon/Northern California (SONCC) coho salmon Evolutionarily Significant Unit (ESU), which encompasses the Klamath Basin. For this project, I compared seasonal habitat use, growth, and movement of juvenile coho salmon between natural habitats and habitats created specifically to enhance coho salmon populations in the mid-Klamath Basin. The overall goal of this study was to collect information to help guide habitat improvement projects that target coho salmon recovery.

In the Upper Klamath, severe hydrologic alteration has been occurring for more than 100 years to support irrigation and hydropower. Five dams and hundreds of miles of canals and pumps support significant water withdrawals, diversions, and transfers throughout the Upper Klamath. Historic mining, logging, and road building practices have contributed to significant environmental degradation in the mid-Klamath and Lower Klamath sub basins (NMFS 2012). Because of these alterations, many streams are now much warmer, shallower, less complex, and have more riffle habitat than they did a century ago (Chamberlin et al. 1991; Hicks et al. 1991). These habitat changes have significant implications for production of juvenile coho salmon.

Coho salmon typically have a 3-year life cycle. Fry emerge from the gravel in the early spring, rear for one year in freshwater, and migrate to the ocean as smolts in the spring. Two growing seasons are usually spent in the ocean before fish return to their natal streams to spawn and die as three year olds. Studies of habitat use and movement patterns in juvenile coho salmon have indicated two major movement events prior to seaward migration: dispersal of fry following emergence in the spring/early summer (Kahler et al 2001) and movement of parr to low velocity or off-channel rearing areas in the fall and winter (Hartman and Brown 1987). In summer, fry movement may be a response to poor habitat conditions such as a declining stream discharge, increasing water temperature, low levels of prey availability, or high population density (Bilby and Bisson 1987, Bjornn 1971, Wilzbach 1985, Rosenfeld 2005). In winter, movement is likely a response to increasing water velocities (Nickelson et al. 1992a, Giannico and Healy 1998). Coho salmon from locations in the Shasta River sub-basin of the Klamath River basin have been found to exhibit seasonal movement in both summer and winter (Adams 2013).

In summer, the main stem Klamath River and major tributaries of the mid-Klamath suffer from high water temperatures and low flows (Lynch and Risley 2003) which can negatively affect juvenile salmonids. High water temperatures have been shown to limit the distribution of salmonids within streams (Meisner 1990), reduce abundance (Ebersole et al. 2001), and fragment populations within a watershed (Matthews and Zimmerman 1990). Preferred temperature ranges for juvenile coho salmon rearing have been reported from 11.4 - 14.6 ºC (Beschta et al 1987, Coutant 1977, Brett 1952) with lethal temperatures occurring at 25.8 ºC (Beschta et al 1987) and cessation of growth at a temperature of 20.3 ºC (Reiser and Bjornn 1979, Brett 1952). In the Seiad Valley region of the Klamath River, main stem temperatures can range from 21 – 27 ºC in July and August with daily extremes as high as 29.5 ºC (Bartholow 2005, Belchik 1997). Besides directly causing physiological stress, elevated water temperatures in the Klamath River are correlated with prevalence of diseases including *Ceratomyxa shasta* that cause mortality in Klamath River coho salmon (Ray et al 2012).

Given warm summer conditions that can occur in the main stem Klamath River and major tributaries, many juvenile coho salmon born in these locations disperse and seek suitable thermal habitat for summer rearing. The fate of juvenile coho salmon that emigrate from natal habitats in response to summer habitat change is not known. Jeffres and Moyle (2012) suggest that juvenile coho salmon that emigrate from the Shasta River (a major Klamath tributary) in response to increasing water temperatures in the lower Shasta River in spring are likely to perish from high temperatures and harsh conditions they encounter in the main stem Klamath River. However, small tributaries and natural reservoirs such as off- channel ponds and beaver ponds often interact with ground water, and are potential sources of cool water through the summer (Knowles et al. 2006, Kiparsky and Gleick 2003). Such habitats are available in many small tributaries of the mid-Klamath, potentially allowing for survival of emigrating juvenile coho salmon.

In winter, the same natural reservoir features that can function as cool water storage sites in the summer may also provide refuge from high winter flows for juvenile coho salmon. Availability of slow water habitats is important to growth and survival of coho salmon during the winter. Multiple studies show that off-channel ponds on the floodplain play a major role in the life history of juvenile coho salmon during their winter rearing period (Peterson 1982, Pollock et al. 2004, Tschaplinski and Hartman 1983). The number of juveniles found in main stem habitat declines significantly as flow increases in the fall, while the number of individuals increases in off-channel ponds, around large wood structures, and undercut banks (McMahon and Hartman 1989, Tschaplinksi and Hartman 1983). Nickelson et al. (1992a) concluded that if spawning escapement was adequate, production of wild coho salmon smolts in most streams on the Oregon Coast would probably be limited by availability of adequate winter habitat. However, considering the severity of water quality stressors in the Klamath River basin (Bartholomew 2005, NMFS 2012), summer conditions may present a threat of direct mortality, independent of density.

Human activities in the Klamath River basin have reduced the amount of summer and winter rearing habitat available to juvenile coho salmon, contributing to the decline of local salmon populations and triggering restoration efforts for habitat improvement. Many stream reaches in the basin have been straightened, diked and leveed to allow for urbanization, road building, and agriculture (NRC 2008). These activities result in channelization, channel simplification, acceleration of water velocity, and reduction in the extent and accessibility of off-channel habitats for juvenile coho salmon (Bilby and Bisson 1987; Lawson et al. 2004). Due to these past human activities, the principle stresses to coho salmon in this stretch of the river are believed to be impaired water quality (high water temperature) and lack of floodplain and channel structure (NMFS 2012).

Restoration actions that increase habitat complexity (i.e. LWD, off-channel habitat) have been shown to increase the abundance of coho salmon occupying the site and increase their overwinter survival (Solazzi et al. 2000). However, in-stream restoration techniques used to create complex habitat can have varying results depending on how and where the habitats are created. Cooperman et al (2006) found that engineered off-channel ponds were most effective in supporting juvenile coho salmon use when they were connected to a ground water source and if they received regular maintenance. Morley et al. (2005) found that constructed channels supported equal or higher densities of juvenile coho salmon than the natural side channels. It is not clear from previous studies whether habitat improvement efforts intended to provide winter refugia also provide suitable sites for summer rearing of juvenile coho salmon.

As restoration activities continue to focus on the construction of off-channel habitats for winter and summer rearing, it is important to understand what habitat characteristics contribute to growth and survival of juvenile coho salmon. Smaller-scale habitat associations of fish are commonly defined in terms of preference for or use of discrete habitat types (e.g., pools versus riffles; Nickelson et al. 1992a) or microhabitats defined in terms of velocity, depth, and substrate (Moyle and Baltz 1985). Inferring habitat requirements or identifying limiting habitats from such approaches is challenging (Rosenfeld 2003). However, field investigations of fish presence, abundance, and growth across habitats is often the only way to get information about how fish performance is related to habitat characteristics. Using this approach, Nickelson et al (1992b) examined the use of constructed and natural habitats by juvenile coho salmon and concluded that the construction of off-channel habitats has the greatest potential to increase production of coho salmon smolts.

In this study, I compared the seasonal movement and growth of juvenile coho salmon occupying three different types of summer and winter habitats in the mid-Klamath watershed: constructed off- channel ponds, beaver- influenced sites, and small tributaries. I sampled these site types in order to determine if off-channel ponds constructed during habitat restoration and improvement efforts are able to support coho salmon growth and abundance at levels comparable to natural tributary and beaver-influenced habitats. I had three specific research questions: 1) do coho salmon abundance, growth, or retention rates differ among the three types of habitats? 2) Is coho abundance, growth, and retention rate associated with biotic and abiotic habitat characteristics (e.g., pool depth, volume of habitat, water temperature, and population density) measured at the sites? 3) What are the patterns of coho salmon movement at the sites? I hypothesized that fish would be more abundant, grow faster, and stay longer in the slow water habitats than the tributary sites. Further, I expected to see higher growth rates in deeper pools, larger habitats, and cooler water temperatures. Knowing that Klamath River coho salmon are highly migratory, I expected to see a spring and fall redistribution of juvenile coho salmon when seeking summer and winter rearing habitats.

Study Area

The Klamath River is located in Southern Oregon and Northern California, draining a basin encompassing almost 41,440 square kilometers. The river flows for approximately 423 kilometers and has been referred to as the “upside down river” because of its geography (Rymer 2009). Typical rivers originate high in the mountains, with steep gradients and are relatively undeveloped until they reach valleys where gradients are lower, temperatures are warmer, and there is an increased level of urbanization. The Klamath River originates in the arid deserts of eastern Oregon, which contain a considerable amount of urbanization and agriculture. Low gradients and large reservoirs are present in the upstream reaches of the Klamath watershed. However, the lower reaches of the river run through the temperate rainforests of California and remain relatively undisturbed with mostly tribal and federal land ownership.

Hydropower dams were constructed in the upper reaches of the Klamath basin in the early to mid-1900’s and continue to alter main stem flows. Operations of the upstream Iron Gate, Copco 1 and 2, JC Boyle, and Keno dams significantly alter flow regimes resulting in low summer flows, elevated temperatures, and impaired water quality downstream of the dams (NRC 2008, Stocking and Bartholomew 2007).

The mid-Klamath subbasin is comprised of the portion of the Klamath River watershed between Iron Gate Dam (river mile 190.1) and the Trinity River confluence (river mile 43.4) excluding the major tributaries, Shasta, Scott, and Salmon Rivers. Nearly this entire region is in the northern California counties of Siskiyou and Humboldt, with a very small amount of the subbasin in southern Oregon's Jackson County.

Ten sites in the mid-Klamath River basin were selected for study (Table 1). Sites included a mix of natural and constructed habitats. All sites are located in the mid-Klamath subbasin and are known from previous sampling efforts (pers. comm., Soto) to provide seasonal habitat for coho salmon. Other aquatic species may be found at the sites, particularly Caltrans pond which has the highest densities of non-native species. However, in most locations coho salmon are the primary species captured.

Table 1. Selected study sites in the mid-Klamath basin, California.

Study Site Name	**Site Type**	**Natal vs Non-Natal[1]**	**Distance from Confluence of Main Stem Klamath (km)[2]**
Tom Martin Creek	Tributary	Non-Natal	0
West Grider Pond	Constructed Pond	Non-Natal[3]	0.4
Alexander Pond	Constructed Pond	Natal	3.0
Seiad Creek Beaver Pond	Beaver-influenced	Natal	1.4
Caltrans Pond	Constructed Pond	Non-Natal	0.4
China Creek	Tributary	Non-Natal[3]	0
Cade Creek	Tributary	Non-Natal	0
Titus Creek	Tributary	Non-Natal[3]	0
Sandy Bar	Beaver-influenced	Non-Natal	0
Stanshaw	Beaver-influenced	Non-Natal	0

[1] Natal streams are those in which adult coho salmon have spawned. Juvenile coho salmon sampled in these sites may have been born there. Non-natal streams are those which adult coho salmon do not spawn and any juvenile coho salmon sampled there immigrated from other habitats.

[2] Tributaries habitats were sampled starting at the confluence of the main stem Klamath River. Ponds were typically situated in tributaries a short distance from the confluence with the main stem Klamath River.

[3] Spawners have been documented in some years; however redd success was estimated to be zero during the spring of 2012 after no coho salmon fry were detected during spring dive surveys, suggesting that all fish captured during the summer in the study site were non-natal

The ten study sites are located in the mid-Klamath watershed and geographically range from near Somes Bar, upstream to the confluence of the Scott River (Figure 1). The off-channel ponds were constructed by Mid-Klamath Watershed Council (MKWC) and the Karuk Tribe for the purpose of providing winter rearing habitat, however fish may occupy the sites in the summer season as well. Of the three beaver-influenced sites, one (Seiad Creek beaver pond) contains a channel-spanning dam, while the other two are natural off-channel water features at the confluence of small streams and the Klamath River. The Seiad Creek beaver pond is likely the only beaver-influenced site with natal fish rearing in the mid-Klamath River. The four small tributaries (0.05-0.25 m^3/sec summer base flow) selected for the study flow into the mid-Klamath River and each support non-natal juvenile coho salmon. These tributaries provide cool water refugia from the warmer water temperatures of the mid-Klamath River; however they do not contain significant complex or off-channel habitat. In each of these streams, the sampling reach extended from the confluence with the main stem Klamath River upstream far enough to allow the capture of the majority of non natal fish. Sampling reaches extended from 55 meters (Tom Martin Creek) where a barrier blocked upstream migration, to 195 meters (Titus Creek) where the stream gradient became steeper and pools were less frequent.

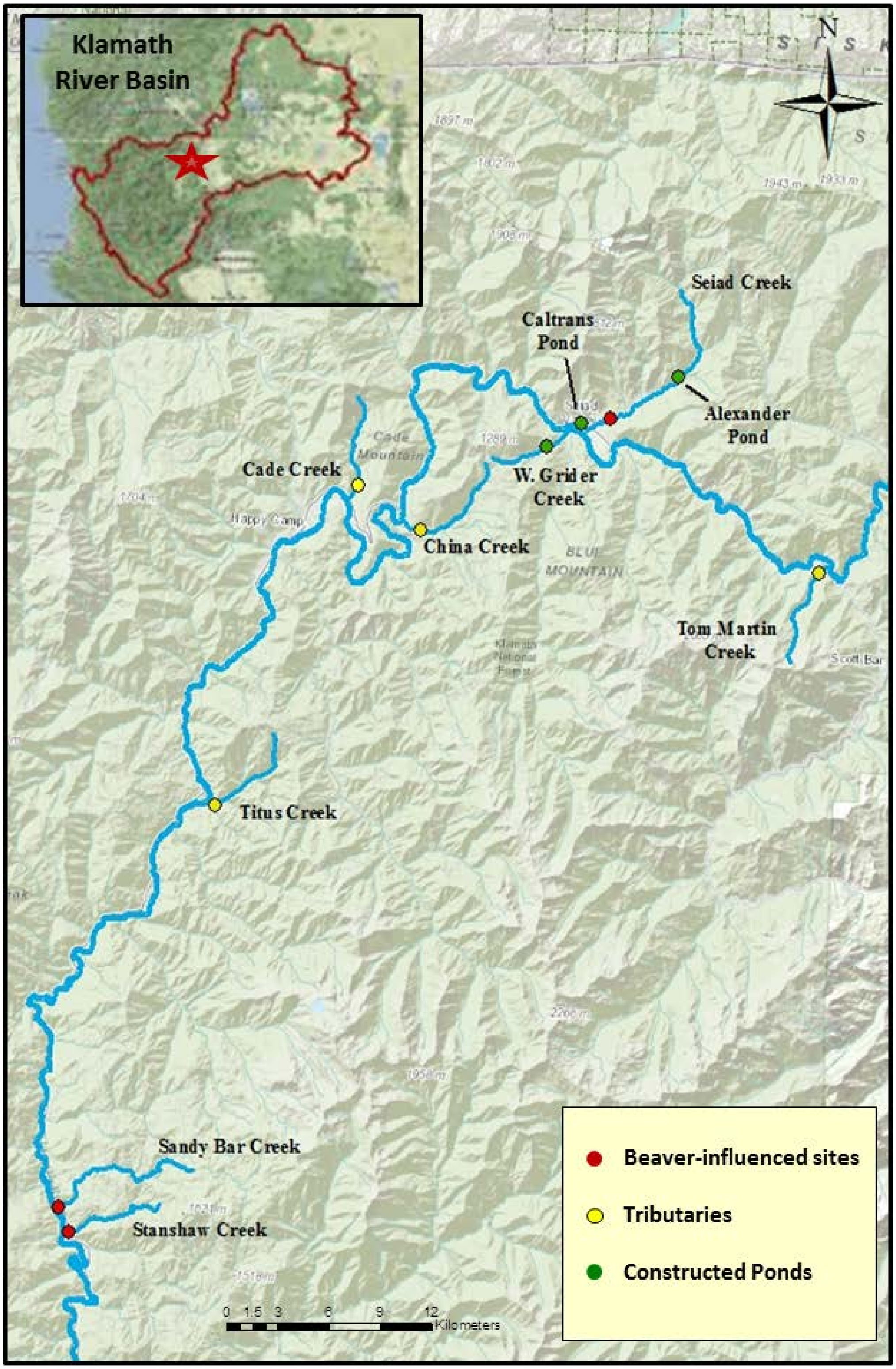


Figure 1. Study site locations in the mid-Klamath watershed of northern California.

METHODS

Capture and Tagging Methods

Fish capture, handling and tagging procedures were approved through Humboldt State University Institutional Animal Care and Use Permit 11/12.F.71-A. To determine the growth and movement patterns of individual fish, a mark and recapture program using PIT tags was used, and was similar to that previously used by the Karuk Tribe. The Karuk Tribe helped develop the sampling protocol and assisted during each sampling event. Fish were captured in each of the ten study sites using seine nets and fyke traps, depending on the time of year and depth of water. The summer sampling season began May 30th 2012 and continued through November 2012. The winter sampling season occurred from December 2012 through March 2013. A presence/absence snorkeling survey was completed at each site during the first week of sampling, and weekly thereafter until presence of juvenile coho salmon was confirmed and sampling could begin. Initially, sampling efforts aimed to sample each site at least two times per month in order to tag as many fish as possible. As main stem temperatures increased, additional fish immigrated into the cool water habitats, providing new opportunities for tagging. Sampling frequency declined to once per month in October. Captured juvenile coho salmon were tagged (see marking techniques below), fork length (nearest mm) and weight (nearest 0.1g) were measured and recorded, and fish were returned to the habitat where initially captured. Recaptured fish were measured, weighed, and released. In addition to recapturing fish at the study sites, fish were also detected as they passed PIT tag antennas or were recaptured as part of other studies which are spread throughout the Klamath River basin (Figure 2).

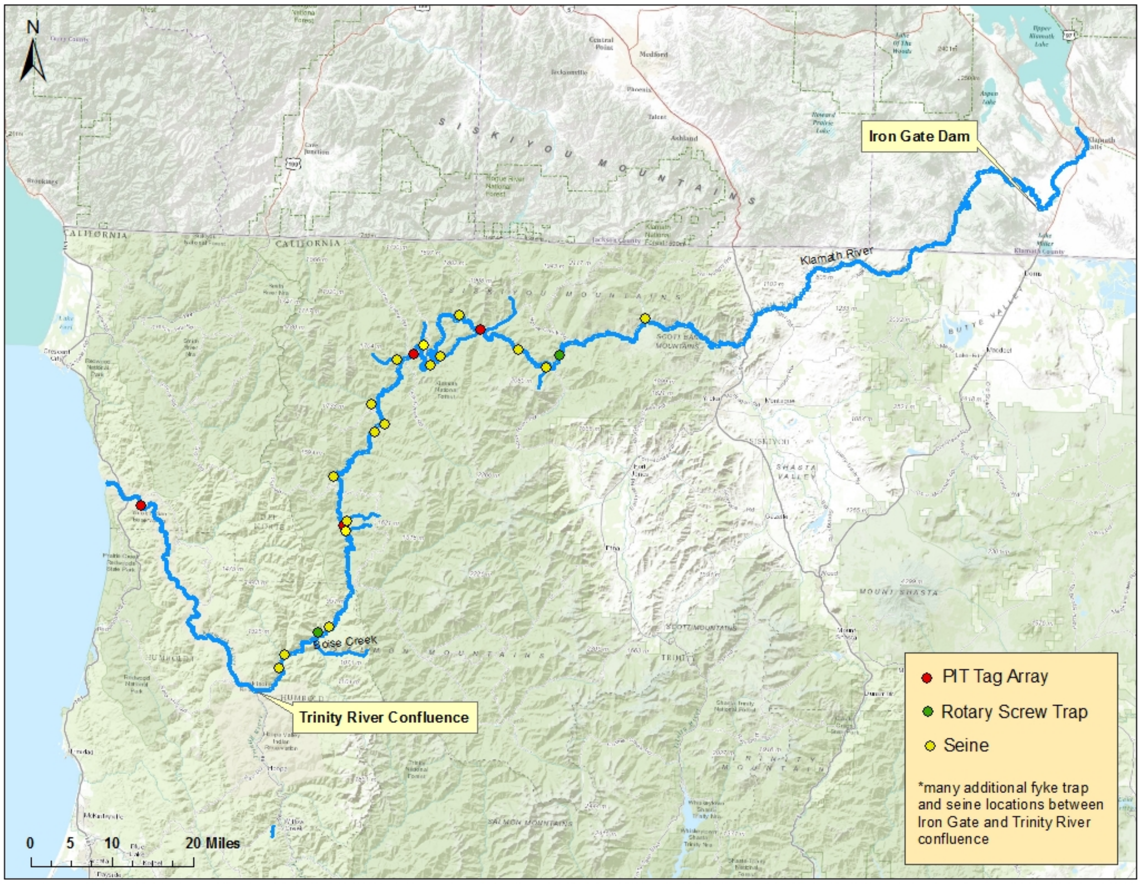


Figure 2. Potential recapture sites in the Klamath River. Fish captured at seine and trapping sites are scanned for PIT tags

A mobile PIT tag array, consisting of several deep cycle 12 volt batteries and a hand-held scanner was set up temporarily at several of the sites, including the outlets of Caltrans Pond (July 13 –July 22nd, 2012) and Tom Martin Creek (August 14 – September 14, 2012).

Marking Techniques

All captured juvenile coho salmon greater than 65 mm fork length (FL) were marked using a PIT tag (Biomark, Inc., Boise, Idaho; full-duplex, 12mm long). The percentage of captured fish large enough to tag increased with time, from 36% in May up to 100% by January (

Table 2). PIT tags were inserted into the body cavity anterior to the pectoral fin using a sterile syringe. Juvenile coho salmon selected for marking were first anesthetized with MS-222 (tricaine methanesulfonate) and fork length and wet weight were recorded.

Table 2. Proportion of captured juvenile coho salmon from mid-Klamath River study sites which were large enough to PIT tag, using a 65 mm threshold size.

Month	**No. Fish <65mm**	**No. Fish ≥65mm**	**Proportion of Taggable Fish**
May	156	88	0.36
June	265	187	0.41
July	403	1092	0.73
August	127	996	0.89
September	7	316	0.98
October	18	736	0.98
November	11	323	0.97
December	1	176	0.99
January	0	449	1.00
February	0	137	1.00
March	0	389	1.00
April	0	62	1.00

Habitat

Physical habitat parameters of each of the study sites were measured so that differences in growth, abundance, and residence time of fish utilizing those habitats could be correlated with site characteristics. Each of the sites was measured two times; once in the summer low flow season, and once in the winter during high flows. The majority of the measurements were made in the summer when access was safer. Measurements during the summer included water temperature, width-to-depth ratio, volume, area, riparian vegetation type/stand age, percent area with overhanging vegetation, and percent cutbanks. A Level II Stream Survey (USFS 2012) was used to characterize the habitat in a consistent format. Percent overhead cover from riparian vegetation was determined using a spherical densiometer, and data were averaged for each site using three sampling points spaced evenly through the reach. During the winter only the basic parameters temperature and volume were recorded. Seasonal volume measurements at each site were critical for calculating densities of fish occupying each habitat. Dissolved oxygen data for a subset of sites were obtained from mid-Klamath Watershed Council who used a YSI meter to monitor the constructed ponds.

Water temperatures at each of the sites were recorded continuously throughout the study. Data were gathered by the US Forest Service Happy Camp Ranger District, the Karuk Tribe, and the mid- Klamath Watershed Council. In the sites not monitored by others, temperature monitors (Onset Water Temp Pro v2) were placed in June 2012 and collected March 2013.

Abundance

Population abundance was estimated using a mark-recapture approach. Separate population estimates were made for each site in summer and winter seasons. I conducted population estimates during seasonal periods with maximum fish occupancy at each site by sampling after seasonal redistribution movement events. In summer, population estimates occurred in late August and early September after the spring redistribution event and after the Klamath River warmed enough to reduce most movement. In the winter, population estimates were made in January after the initial high flows and winter redistribution period. The Lincoln-Petersen Method (Krebs 1998) was used to estimate population size, requiring two sampling events for each density estimate. Because this method assumes a closed system, the two sampling efforts occurred on consecutive days to limit the number of individuals that would die, move out of, or move into the study site. Population estimates are calculated as follows:

$$\widehat{N} = \frac{MC}{R}$$

Where:

$\widehat{N}$ = Estimate of total population size

M = Total number of animals captured and marked on the first visit

C = Total number of animals captured on the second visit

R = Number of animals captured on the first visit that were then recaptured on the second visit

Population density of juvenile coho salmon at each site was estimated using number of fish occupying a habitat divided by the volume of that habitat. I used density per volume of water instead of area because many of the study sites include deep pools where fish were distributed throughout the water column.

Growth

Summer and winter daily growth rates (g/g/day) for tagged juvenile coho salmon were calculated at each of the study sites. Weight was used as a measure of growth instead of length as it appeared to be a better indicator for the condition of the fish; some individuals lost mass but not length over time. For each individual, a daily growth rate was calculated as follows: (ln(final mass/initial mass)/number of days passed)), where final mass and initial mass are the size at the first and last capture during summer or winter. The daily growth rate of all individuals in each of the sites was averaged for each season. Additionally, overall daily growth rates over both seasons were calculated for sites where the same marked individuals were captured in both the summer and winter sampling events.

Retention

Seasonal retention at each of the sites was calculated using a Cormack Jolly Seber Model (CJS) in Program MARK (Cooch and White 2011). The CJS model estimates apparent survival phi (φ) and recapture probability (*p*). Because fish move in and out of the habitat, treating φ as an estimate of survival may be misleading. I treated φ as an estimate of retention, the proportion of tagged fish present in the site at the beginning of the season that are still alive and present at the site at the end of the season. Low retention at a site could be due to low survival or to high rates of emigration from the site. Retention could only be calculated for the summer (May-November) when capture events were more frequent and sample sizes were larger. The timing and number of capture events varied greatly depending on the site and timing of fish immigration (

Table 3). For example, the beaver dam on Seiad Creek was not constructed until August and was washed out in November during high flows, allowing only three sampling efforts in that period. Also, sampling began in May 2012 in the sites already occupied by natal fish, whereas sites relying on non natal recruits often had no fish captured until mid-July when the main stem Klamath River warmed. Because of the variation in the timing and number of sampling events, I combined the φ estimates for each site into a single estimate of overall retention over the summer, combining sample dates so that the interval was as similar as possible across sites (

Table 3). I estimated the standard error of the overall retention estimate using 5000 bootstrapped iterations. To avoid unrealistic estimates (e.g. $\varphi > 1$), bootstrapping was performed on logit-transformed estimates and then back-transformed. Sampling intensity varied across sites, which may confound estimates of retention if recapture probability increases with the number of sample events. However, I found no relationship between number of sampling events and the estimated rate of retention ($F_{1,8} = 0.7679$, $p < 0.406$).

Table 3. Number of capture events and the stop and start sampling dates of juvenile coho salmon in each study site used in the Cormack Jolly Seber analysis for retention rate

Site	**Start/Stop Dates**[1]	**Number of Capture Events**
Caltrans	5/30/12 – 11/7/12	10
Alexander	6/1/12 – 11/28/12	7
W. Grider	7/23/12 – 11/7/12	5
Seiad Cr Beaver Pond	8/1/12 – 8/14/12	3
Sandy Bar	6/4/12 - 10/23/12	8
Stanshaw	6/26/12 – 9/10/12	8
Titus	7/3/12 – 8/9/12	5
Cade	7/10/12 - 8/21/12	6
China	7/3/12 – 8/15/12	4
Tom Martin	7/10/12 – 10/9/12	5

[1] In some circumstances capture events were combined to increase sample size

Movement

The remote PIT tag antenna array at the mouth of Seiad Creek provided an opportunity to document outmigration timing of juvenile coho salmon that were tagged in the sites of the Seiad Creek drainage (Alexander Pond, Seiad Creek Beaver Pond, Caltrans Pond). Additionally, fish initially tagged in upstream locations were discovered entering the mouth of Seiad Creek. Other antenna arrays spread throughout the Klamath River basin were also able to detect fish tagged in many of the ten study sites.

Data Analysis

Although data were collected throughout summer and winter seasons, most statistical analyses were confined to the summer data. Adverse weather conditions, high flows, and changes in sampling crews throughout the winter resulted in inconsistent sampling efforts, technique, and low sample sizes which violated many assumptions of the analyses performed.

Comparison of habitat types

I used a one-way analysis of variance (ANOVA) to evaluate the biological responses (i.e., seasonal density, average growth, and retention of juvenile coho salmon) by habitat type (tributary, constructed ponds, beaver ponds) (Table 4). This analysis tests the hypothesis the habitat types differ, but does not test whether sampling captured significant differences in individual growth across sites, so I use a separate ANOVA to determine if individual growth rate differed significantly across sites, using individual fish as the unit of observation. A two-way ANOVA was used to determine if an interaction occurred between type of site and season, resulting in seasonal changes to abundance of juvenile coho salmon.

Correlations with habitat characteristics

To answer the second question regarding the relationship between coho abundance, retention, growth and biotic and abiotic variables, regression analyses were used. I compared relationships between density, growth rate, and retention (response variables) and the biotic and abiotic factors, mean weekly average temperature, habitat volume, and average maximum depth, density of fish, and growth rate (predictor variables). Additional variables (substrate, percent cover, and unstable banks) were measured, however were associated with the type of habitat and would be further investigated only if habitat type proved to be significant. This is an exploratory analysis to identify the strongest relationships and generate hypotheses for future studies. The p-values for the regressions are presented as indicators only and they have not been corrected for multiple comparisons; they should not be treated as estimates of statistical significance. I also tested the specific hypothesis that retention would be higher at sites where average growth rate was higher.

Identifying patterns in movement

To answer the third question regarding patterns of fish movement, I qualitatively explored movement patterns using graphs. Excel was used to graph counts of moving fish using recorded PIT tag detections at permanent and mobile antenna arrays. Arrays at the mouth of Tom Martin Creek and Caltrans Pond provided an opportunity to look at diurnal movement in and out of the habitat, while the array at the mouth of Seiad Creek showed timing and patterns of spring outmigration and immigration to Seiad Creek.

RESULTS

Capture/PIT tagging

Juvenile coho salmon were initially found only in Caltrans Pond, Alexander Pond, and Sandy Bar. As Klamath main stem water temperatures warmed later in the season, juvenile coho salmon were observed moving into the study sites where water temperatures were cooler (Figure 3). Over the course of a two week period (June 24 - July 8) water temperature in the main stem Klamath River rose from approximately 18 ºC to 23 ºC. During this period the level of fish occupancy among study sites increased from 40 to 70 percent. By the end of July, the occupancy rate was 90 percent. The only site not sampled at this time was Seiad Creek Beaver Pond, where the beaver dam had not yet been constructed. Because seasonal occupancy was variable across sites, number and timing of sampling efforts varied considerably (

Table 4,

Table 5). Across all sites, 1831 coho salmon were tagged in summer with a seasonal recapture rate of 36 percent. During the winter, there were 716 tagged fish (a portion of which were initially tagged during the summer) with a recapture rate of 28 percent.

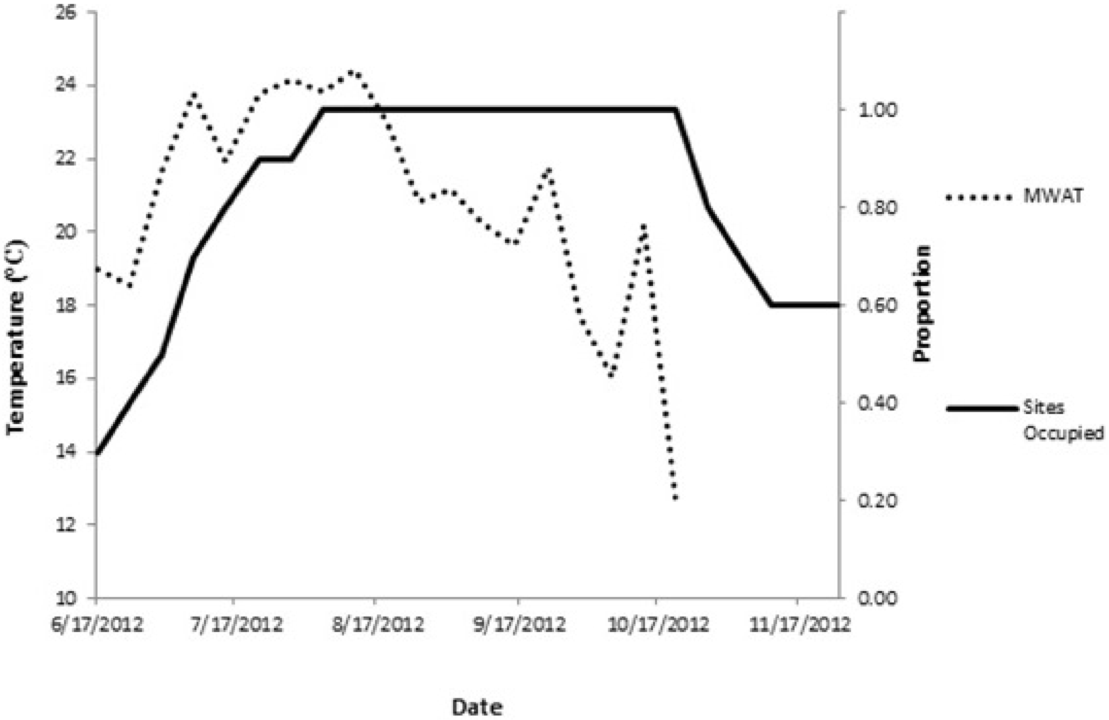


Figure 3. Proportion of study sites occupied in relation to main stem Klamath River maximum weekly average temperature (MWAT), upstream of Indian Creek (at the town of Happy Camp). The left axis has been rescaled

Table 4. Juvenile coho salmon tagging summary for the summer sampling season (May 2012 - November 2012) at the ten study sites, including number of sampling events, number of fish tagged, and number of fish subsequently recaptured

Habitat Type	**Study Site**	**No. Sampling Efforts**	**Total No. Tagged**	**Total No. Recaptured (1 or more times)**
Constructed Ponds	W. Grider Pond	5	98	47
	Alexander Pond	7	221	29
	Caltrans Pond	10	527	141
Beaver-influenced	Seiad Cr. Beaver Pond	3	283	93
	Sandy Bar	8	238	124
	Stanshaw	8	108	57
Tributaries	China Creek	4	92	54
	Cade Creek	6	70	45
	Titus Creek	5	194	74
	Tom Martin	5	432	147
	Total	*56*	*1831*	*664*
	Rate of Recapture			*0.36*

Table 5. Juvenile coho salmon tagging summary during the winter sampling season (November 2012 - March 2013) at the ten study sites, including number of sampling events, number of fish tagged, and number of fish subsequently recaptured.

Habitat Type	Study Site	No. Sampling Efforts	Total No. Tagged	Total No. Recaptured (1 or more times)
Constructed Ponds	W. Grider Pond	5	116	46
	Alexander Pond	4	224	36
	Caltrans Pond	5	206	32
Beaver-influenced	Seiad Cr. Beaver Pond	0	0	0
	Sandy Bar	5	107	75
	Stanshaw	5	63	15
Tributaries	China Creek	0	0	0
	Cade Creek	0	0	0
	Titus Creek	0	0	0
	Tom Martin	4	124	32
	Total	*28*	*716*	*204*
	Rate of Recapture			*0.28*

Habitat

Physical habitat parameters varied greatly across study sites (

Table 6). During the summer, average maximum pool depths were deepest in the constructed ponds with an average maximum depth of 1.47 meters; beaver-influenced sites averaged 1.07 meters and tributaries had an average of just 0.15 meters. Volume of habitat ranged dramatically across sites and within habitat types. The site with the greatest volume was Sandy Bar at 1,121 m^3 while Seiad Creek Beaver Pond had the least volume at 231 m^3. Types of substrate varied across habitat types. Because each of the constructed ponds was recently excavated using heavy equipment, they each had 100 percent unstable banks with perched sediment within the bankfull range. The tributaries had a minimal amount of unstable banks, while the beaver-influenced sites each had zero. The constructed ponds were dominated by silt substrate, beaver-influenced sites were mixed with both silt and gravel substrate dominating, and tributaries were dominated by larger substrate such as cobble, boulders, and bedrock. Tributaries had the highest amount of riparian overhead cover, averaging 81 percent, followed by constructed pond with 46 percent, and beaver-influenced sites with 42 percent cover.

Water temperatures remained cooler in the study sites than in the main stem Klamath River (Figure 4). Among the study sites, Caltrans Pond and Alexander Pond had the warmest water temperatures throughout the summer. Dissolved oxygen levels measured at the constructed ponds showed variability but no clear temporal pattern (Table 7).

Table 6. Physical habitat data summary representing summer conditions during 2012 for each study site.

Habitat Type	Study Site	Average Maximum Pool Depth (m)	Average Pool Tail Crest (m)	Average Residual Depth (m)	Volume (m^3)	Percent Unstable Banks	Dominant Substrate	Second Dominant Substrate	Percent Cover	Maximum MWAT °C[2]
Constructed Ponds	W. Grider Pond	1.37	0.15	1.22	467	100	silt	gravel	79	15
	Alexander Pond	1.98	0.00	1.98	1284	100	silt	silt	42	17
	Caltrans Pond	1.05	0.00	1.05	576	100	silt	gravel	16	18
Beaver-influenced	Seiad Cr. Beaver Pond	0.94	0.00	0.94	231	0	gravel	silt/cobble	16	16
	Sandy Bar	0.66	0.09	0.56	1121	0	sand/silt	cobble	78	
	Stanshaw	1.62	0.06	1.55	766	0	silt	gravel	32	16
Tributaries	China	0.49	0.11	0.38	21	1	cobble	gravel	98	16
	Cade Creek	0.40	0.10	0.30	43	7	cobble	gravel	91	15
	Titus Creek	0.59	0.18	0.41	134	1	cobble	boulder	98[1]	15
	Tom Martin	0.46	0.13	0.33	47	0	bedrock	boulder	38	16

[1] Two distinct habitat types occurred in the sampling reach for Titus Creek; forested tributary habitat and an open mixing zone at the confluence on the main stem Klamath River with only 2% overhead cover occurring there. For this study, 98% was used to represent the habitat where most fish captures occurred in the forested reach since and average would not be representative of either habitat type.

[2] Temperature data from Sandy Bar was not included due to data logger lost at the study site.

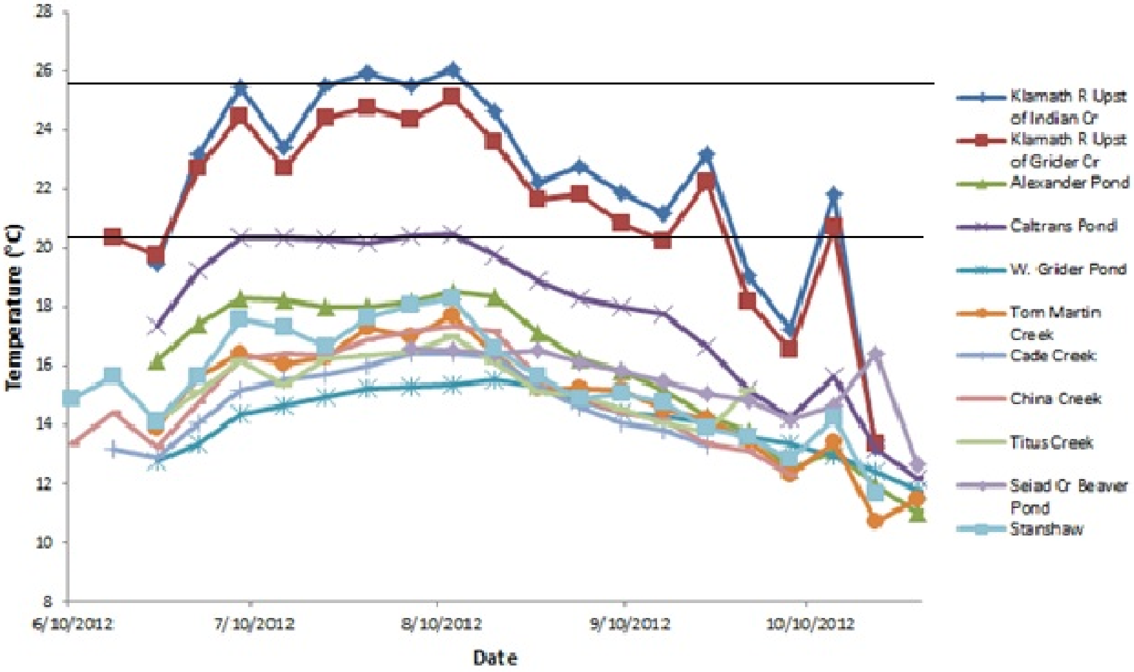


Figure 4. Mean weekly maximum temperatures during summer 2012 in the main stem Klamath River (Grunbaum 2012) and for study sites. Horizontal line at 25.8 °C represents potentially lethal temperature (Beschta et al 1987) and at 20.3° C represents potential cessation of growth (Brett 1952)

Table 7. Minimum and maximum recorded dissolved oxygen levels (mg/l) for constructed ponds (W. Harling pers. comm., 2013). Dissolved Oxygen measured in the morning

Min/Max Dissolved Oxygen (mg/l)						
	May	June	July	Aug	Sept	Jan
Caltrans Pond	6.4 / 8.9	3.3 / 8.2	6.6 / 10.1	8.8 / 10.0		
W. Grider Pond	5.4 / 6.1	3.6 / 4.7	2.0 / 4.7	2.5 / 3.2	1.6 / 3.6	4.6 / 7.8
Alexander Pond			5.2 / 7.1	5.0 / 7.2		

Population Abundance and Density

All study sites were occupied by juvenile coho salmon during the summer season. Conversely, only six of the ten study sites were occupied during the winter season. There was not a significant statistical difference in abundance across site types and season (full model p-value: 0.2279). However, population estimates and densities (Table 8, Table 9) show that although occupied during the summer, constructed ponds had similar or larger numbers of fish utilizing them during the winter. Increased densities in these ponds were a function of greater population sizes as the volume did not change substantially. In contrast, the beaver-influenced sites and tributaries had a substantial decrease in fish abundance during the winter. The habitat predictors tested were not significantly related to population density (

Table 10).

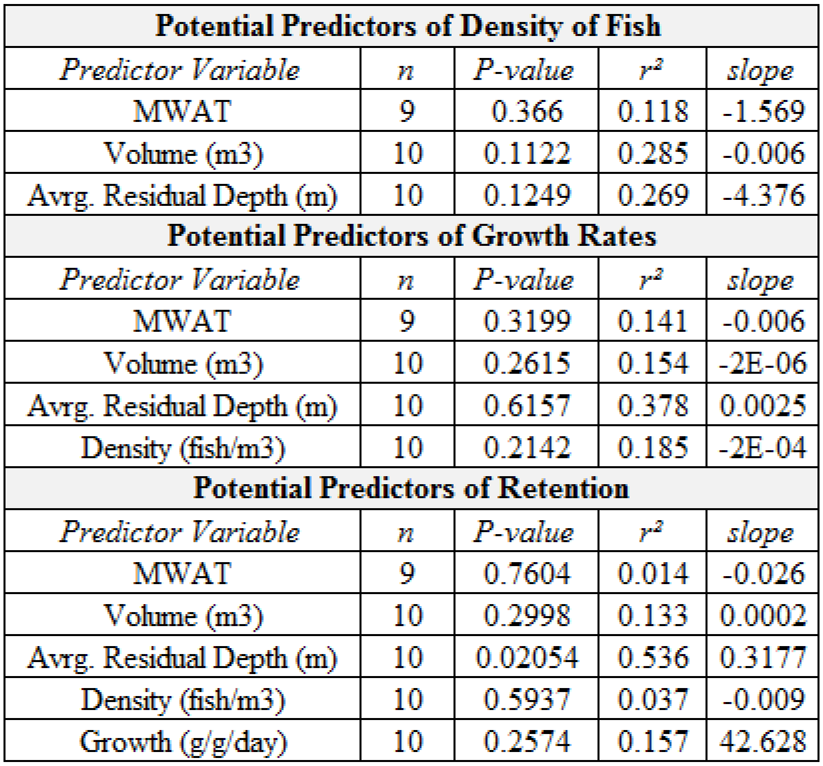
Table 8. Summer (May 2012 - November 2012) and winter (November 2012 - March 2013) population estimates and densities of juvenile coho salmon in each of the study sites.

Habitat Type	*Location*	*Summer Population Estimate*	*Winter Population Estimate*	*Summer Density (fish/m^3)*	*Winter Density (fish/m^3)*
Constructed Ponds	W. Grider Pond	98	156	0.21	0.86
	Alexander Pond	154	862	0.12	1.30
	Caltrans Pond	387	299	0.67	0.48
Beaver-influenced	Stanshaw	140	28	0.18	0.02
	Seiad Cr. Beaver Pond	390	0	1.69	0.00
	Sandy Bar	326	64	0.29	0.05
Tributaries	Tom Martin Creek	748	136	15.96	3.24
	Titus Creek	106	0	0.79	0.00
	Cade Creek	51	0	1.19	0.00
	China Creek	98	0	4.61	0.00

Table 9. Average densities, seasonal growth rates, and rates of retention of juvenile coho salmon with standard error at each site. Retention was not estimated for the winter season

Study Site	**Habitat Type**	**Density (fish/m^3)**		**Growth (g/g/day)**		**Retention (ϕ)**
		Summer	*Winter*	*Summer*	*Winter*	
Alexander Pond	Constructed Pond	0.12	1.30	0.006 ±0.0007	0.005 ±0.0005	0.891 ±0.072
Caltrans Pond	Constructed Pond	0.67	0.48	0.006 ±0.0003	0.003 ±0.0007	0.230 ±0.084
W. Grider Pond	Constructed Pond	0.21	0.86	0.005 ±0.0007	0.000 ±0.0002	0.793 ±0.020
Seiad Beaver Pond	Beaver-influenced	1.69	N/A	0.002 ±0.0006	N/A	0.795 ±0.035
Sandy Bar	Beaver-influenced	0.29	0.05	0.002 ±0.0003	0.008 ±0.0004	0.423 ±0.073
Stanshaw	Beaver-influenced	0.18	0.02	0.004 ±0.0005	0.005 ±0.0007	0.806 ±0.050
Tom Martin Creek	Tributary	15.96	3.24	0.001 ±0.0003	0.001 ±0.0003	0.456 ±0.078
Titus Creek	Tributary	0.79	N/A	0.003 ±0.0005	N/A	0.426 ±0.046
China Creek	Tributary	4.61	N/A	0.006 ±0.0007	N/A	0.565 ±0.088
Cade Creek	Tributary	1.19	N/A	0.000 ±0.0005	N/A	0.302 ±0.081

Table 10. Test statistics for various response and predictor variables across the study sites. P-values are not corrected for multiple comparisons



Potential Predictors of Density of Fish

Predictor Variable	*n*	*P-value*	*r^2*	*slope*
MWAT	9	0.366	0.118	-1.569
Volume (m3)	10	0.1122	0.285	-0.006
Avrg. Residual Depth (m)	10	0.1249	0.269	-4.376

Potential Predictors of Growth Rates

Predictor Variable	*n*	*P-value*	*r^2*	*slope*
MWAT	9	0.3199	0.141	-0.006
Volume (m3)	10	0.2615	0.154	-2E-06
Avrg. Residual Depth (m)	10	0.6157	0.378	0.0025
Density (fish/m3)	10	0.2142	0.185	-2E-04

Potential Predictors of Retention

Predictor Variable	*n*	*P-value*	*r^2*	*slope*
MWAT	9	0.7604	0.014	-0.026
Volume (m3)	10	0.2998	0.133	0.0002
Avrg. Residual Depth (m)	10	0.02054	0.536	0.3177
Density (fish/m3)	10	0.5937	0.037	-0.009
Growth (g/g/day)	10	0.2574	0.157	42.628

Growth

Summer growth rates of juvenile coho salmon varied significantly among the study sites ($F_{9,787} = 22.43$, $P < 0.001$, site means range from 0.0004 – 0.006 g/g/day); however summer growth rates did not differ among habitat types ($F_{2,7} = 2.641$, $P = 0.140$, habitat type means range from 0.002 – 0.005 g/g/day). During the summer, the constructed ponds each had similarly high growth rates (Figure 5). Variability in summer growth rates was greatest in tributary sites; China Creek fish had the highest growth rate among all study sites, and fish from Cade and Tom Martin Creeks had the lowest growth rates. The beaver-influenced sites had intermediate summer growth rates.

Winter growth rates of juvenile coho salmon varied significantly across the six study sites occupied in the winter ($F_{5,226} = 46.312$, $P < 0.001$, means range from 0.0002 – 0.008 g/g/day), however there was no significant difference in growth rates across the habitat types ($F_{2,3} = 2.66$, $P < 0.216$, means range from 0.0007 – 0.006 g/g/day). During the winter, both Caltrans and Alexander Pond fish continued to display high rates of growth, but West Grider Pond fish showed the lowest growth rates among all sites sampled during the winter (Figure 6). In the two remaining beaver-influenced sites, Sandy Bar and Stanshaw, fish were observed to have the highest rates of growth among all sites at 0.008 g/g/day and 0.005 g/g/day, respectively. The average winter growth rate observed at Sandy Bar was higher than the average growth rates at all sites during the summer.

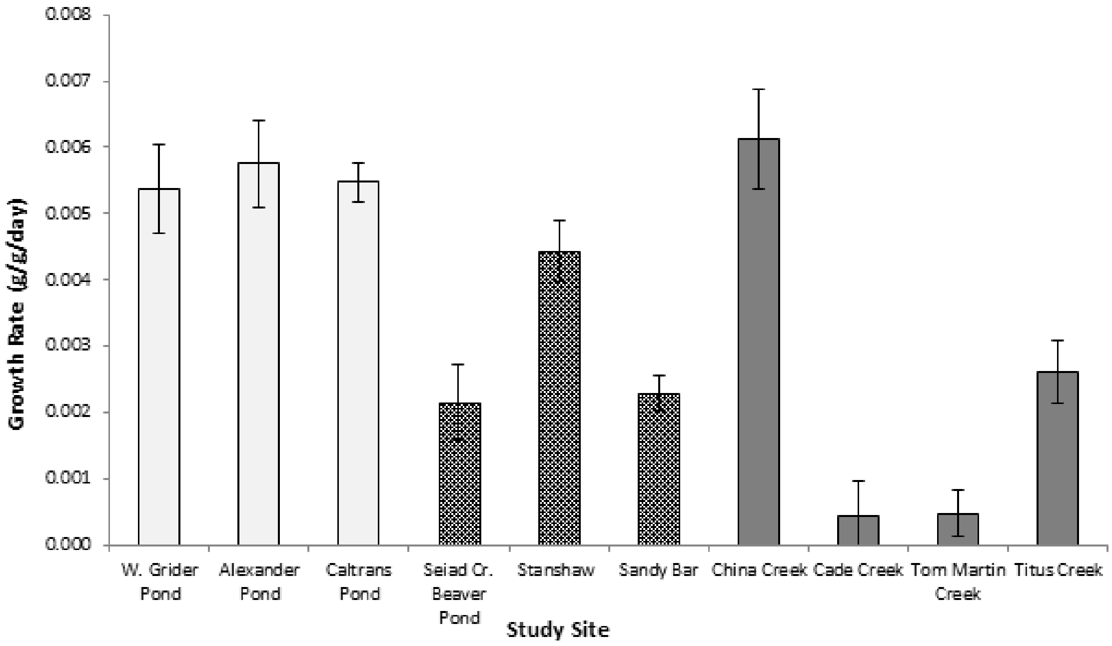


Figure 5. Average (+/- standard error) summer growth rates of juvenile coho salmon at each study site, with constructed ponds shown in white, beaver-influenced sites shown as textured, and tributaries shown as gray

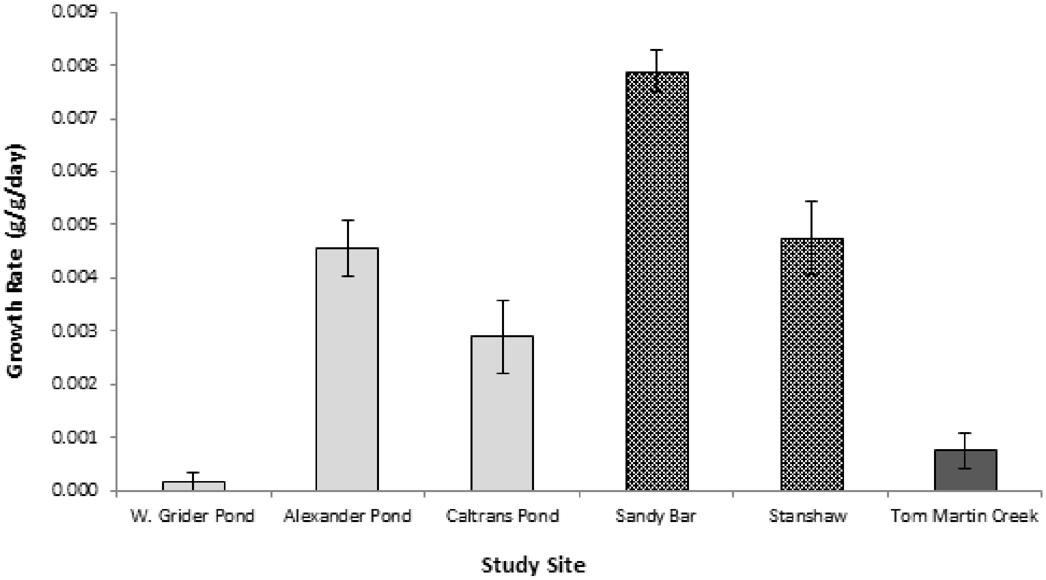


Figure 6. Average winter growth rates (+/- standard error) of juvenile coho salmon at each study site with constructed ponds shown in white, beaver-influenced sites shown as textured, and tributaries shown in gray.

A proportion of fish tagged in the summer remained in the study site during the winter season as well (Table 11). For the sites that were occupied continuously by the same individual fish throughout the summer and winter season, growth rates were averaged and compared. Growth rates were highest in beaver ponds followed by constructed ponds (Figure 7). Overall growth rates of juvenile coho salmon varied significantly across the study sites ($F_{3,62} = 42.973$, $P < 0.001$) and showed a significant difference in growth rates between habitat types ($F_{2,3} = 11.368$, $P < 0.0398$) (Figure 8). Despite generally high growth rates in the constructed ponds, fish that continuously occupied beaver-influenced sites had the highest overall rates of growth. The fish that were found to continuously occupy Tom Martin Creek had the lowest rate of growth of 0.002 g/g/day.

Table 11. Total number of fish tagged at each study site having both summer and winter occupancy, and the proportion of tagged fish that remained both seasons.

Study Site	Total No. Tagged	Total No. Captured Summer & Winter	Proportion Retained Both Seasons
W. Grider Pond	155	45	29%
Alexander Pond	400	52	13%
Caltrans Pond	669	13	2%
Stanshaw	135	13	10%
Sandy Bar	322	6	2%
Tom Martin Creek	450	37	8%

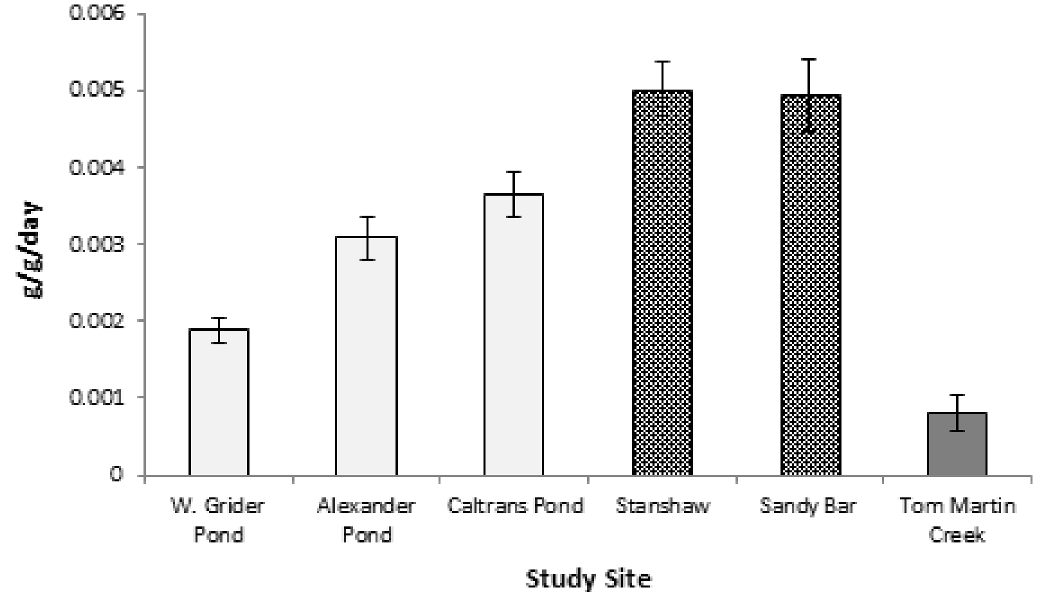


Figure 7. Average growth rates (+/- standard error) for individual juvenile coho salmon occupying the same habitat both in the summer and winter. Constructed ponds are shown in white, beaver-influenced sites are shown as patterned, and tributaries are shown in gray.

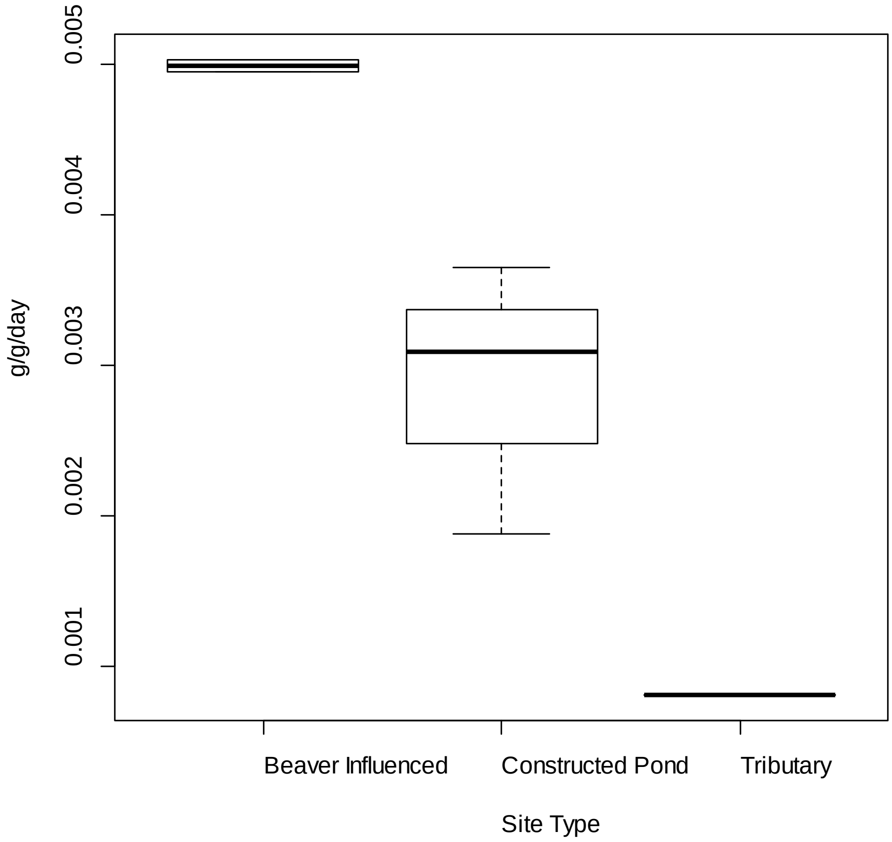


Figure 8. Average growth rates of fish in habitat types which remained at a site in both summer and winter seasons, with mean and standard error shown.

There were no strong correlations between growth rate of fish and the density of conspecifics or the measured habitat variables including water temperature (MWAT), volume, or average maximum water depth (Table 10).

Retention

Summer retention rate of juvenile coho salmon was greatest in Alexander Pond and lowest at Caltrans Pond (Figure 11). No significant correlation occurred between retention and growth rate (

Table 10). The lack of correlation is counter to the hypothesis that fish would remain in habitats where they experienced the highest rates of growth. Retention was not related to temperature, population density, or growth rates, but it was positively related to average maximum pool depth (

Table 10).

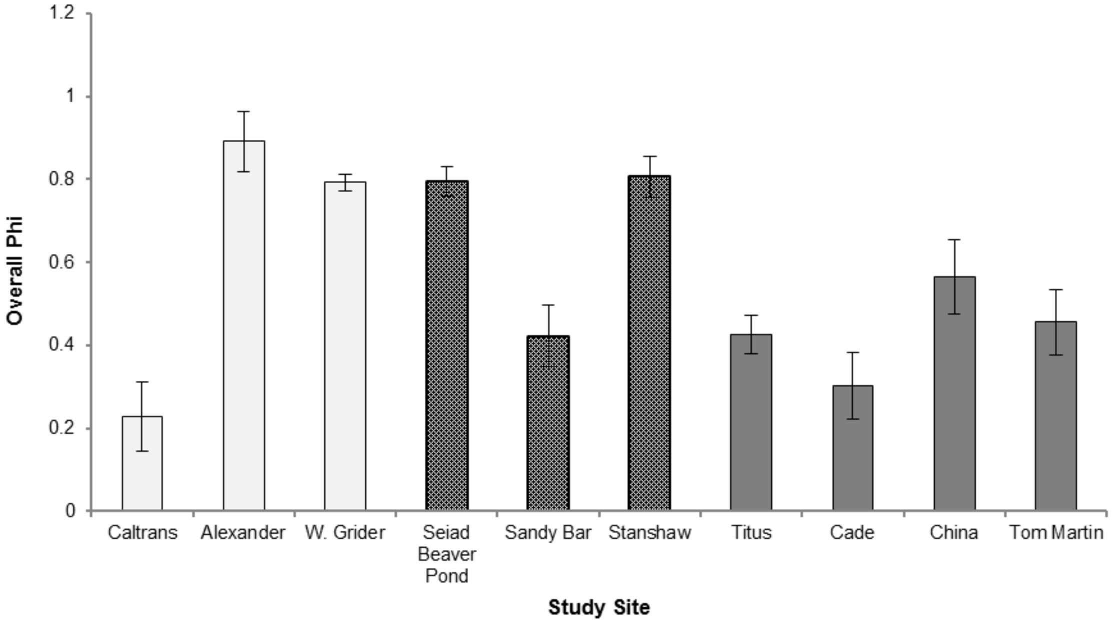


Figure 9. Retention rate (overall ϕ) and standard error of juvenile coho salmon at each study site. Constructed ponds are shown as white, beaver ponds are patterned, and tributaries are gray

Movement

Diurnal movement of juvenile coho salmon was detected at the mouth of Tom Martin Creek and at the outlet of Caltrans Pond in Seiad Creek. Detections indicated juvenile coho salmon exited the study sites to feed in the main stem Klamath River or Seiad Creek. Number of detections was greatest around sunrise and sunset (Figure 10, Figure 11). Coho salmon appeared to move in relation to light rather than water temperature, occupying the Klamath River or Seiad Creek during the darkest periods of the day rather than during the coolest water temperatures.

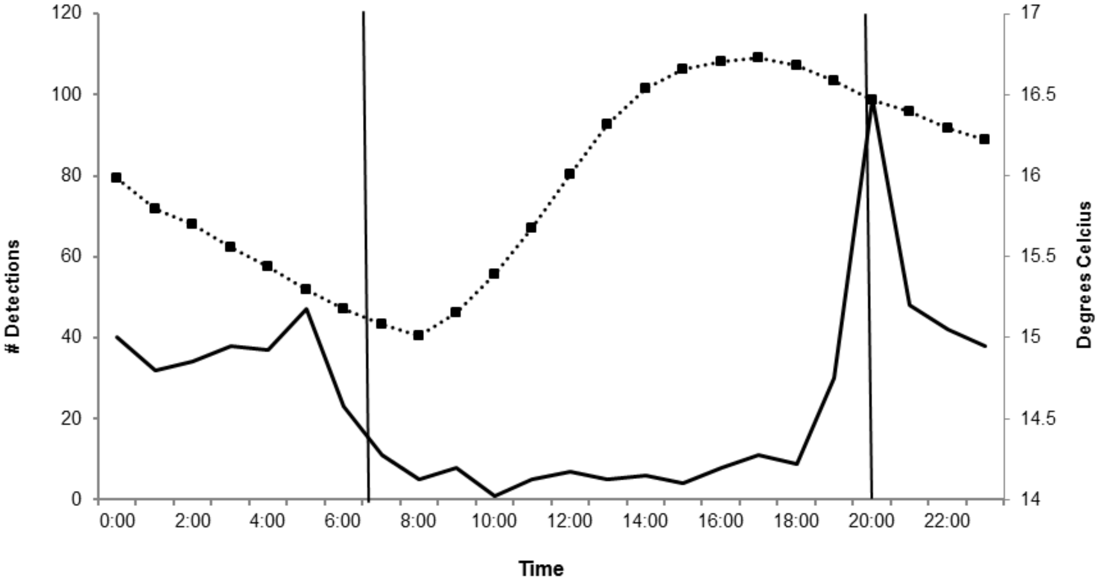


Figure 10. Diurnal movement of juvenile coho salmon at the mouth of Tom Martin Creek from August 14th - September 14th 2012. Solid line represents the number of juvenile coho salmon detected at the mouth of Tom Martin Creek. Dashed line represents the water temperature at the confluence. Vertical lines represent time of sunrise and sunset (Sept. 1).

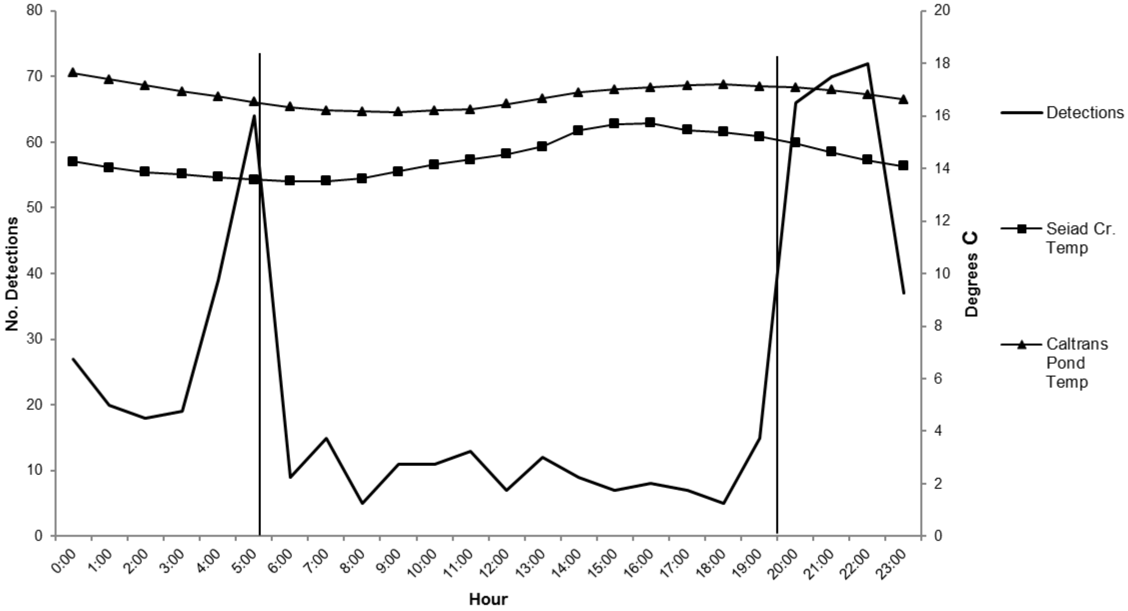


Figure 11. Diurnal movement of juvenile coho salmon in Seiad Creek at the mouth of Caltrans Pond from July 14th - July 22nd 2012. Solid line represents number of juvenile coho salmon detected at the outlet of Caltrans Pond. Box and triangle marked lines represent temperature in Seiad Creek and Caltrans Pond respectively. Two vertical lines represent time of sunrise and sunset (July 18).

Tagged fish from most of the study sites were detected at downstream PIT tag antennas during winter or spring. Seventeen of the 432 fish tagged during the summer in Tom Martin Creek were detected as they entered Seiad Creek; one of those fish was even captured in Caltrans Pond (Table 12). Fish were also detected utilizing over-winter habitats near the mouth of the Klamath River such as McGarvey Alcove and Lower Panther Pond (Table 12).

Three seasonal movement events were documented: during summer when most fish migrated into non natal study sites where they were initially tagged; during fall and early winter when high flows instigated movement, and spring outmigration (Table 13). During the fall-winter redistribution event, most fish moved out of or were displaced from the tributary sites as evidenced during the population estimates. During this same period, an apparent immigration event occurred at the constructed ponds and beaver-influenced sites. The median fork length of captured fish dropped during the winter (Figure 12). If the same fish were being captured each month, an increase in fork length would be expected. Instead, I assume the decrease is an indication of smaller fish, presumably those rearing in the stream during the summer, immigrating into the ponds to rear for the winter season. A drop in median fork length of fish was not observed in Tom Martin Creek, the only tributary with winter rearing fish; instead fork length exhibited a plateauing trend during the winter months (Figure 12).

Table 12. Detection of tagged fish found in locations other than where tagged

Location First Tagged	Date Last Seen in 1st Loc	Location of 2nd Sighting	Date 1st Detected at 2nd Loc	Location of 3rd Sighting	Date 1st Detected at 3rd Loc	Location of 4th Sighting	Date 1st Detected at 4th Loc
Alexander	10/31/2012	Sandy Bar	1/24/2013				
Alexander	10/31/2012	Bulk Plant	12/6/2012				
Alexander	10/31/2012	Bulk Plant	12/7/2012				
Cade	10/23/2012	Bulk Plant	12/4/2012				
Cade	7/23/2012	Bulk Plant	12/3/2012				
Cade	10/23/2012	Bulk Plant	12/4/2012				
Cade	8/8/2012	Bulk Plant	12/8/2012				
Caltrans	11/7/2012	Bulk Plant	12/14/2012				
Caltrans	9/12/2012	Bulk Plant	12/14/2012				
Caltrans	11/7/2012	Bulk Plant	12/12/2012				
Caltrans	9/12/2012	Bulk Plant	12/16/2012				
Caltrans	9/12/2012	Bulk Plant	12/18/2012				
Caltrans	10/10/2012	Bulk Plant	12/13/2012				
Caltrans	7/23/2012	Bulk Plant	12/17/2012				
Caltrans	9/12/2012	Bulk Plant	1/15/2013				
China	10/30/2012	L.McGarvey Alcove	1/29/2013				
Sandy Bar	6/12/2012	L. Salt Creek	7/11/2012				
Seiad Cr Beaver Pond	10/24/2012	Caltrans	1/15/2013	L. Seiad Creek	4/19/2013		
Seiad Cr Beaver Pond	8/14/2012	L. Panther Pond	3/7/2013				
Stanshaw	7/17/2012	L. Panther Pond	3/26/2013				
Titus	11/5/2012	Sandy Bar	12/1/2012				
Titus	9/5/2012	Sandy Bar	11/29/2012				
Titus	7/3/2012	Sandy Bar	12/4/2012				
Titus	7/3/2012	Sandy Bar	12/4/2012				
Tom Martin	8/6/2012	L. Seiad Creek	11/23/2012	Bulk Plant	12/4/2012		
Tom Martin	8/6/2012	L. Seiad Creek	11/25/2012				
Tom Martin	10/9/2012	L. Seiad Creek	11/10/2012				
Tom Martin	8/6/2012	L. Seiad Creek	5/9/2013				
Tom Martin	10/9/2012	Bulk Plant	12/6/2012				
Tom Martin	8/23/2012	L. Seiad Creek	4/10/2013				
Tom Martin	7/23/2012	L. Seiad Creek	3/16/2013				
Tom Martin	8/6/2012	L. Seiad Creek	11/21/2012	Bulk Plant	12/7/2012		
Tom Martin	10/9/2012	L. Seiad Creek	11/23/2012				
Tom Martin	10/9/2012	L. Seiad Creek	11/23/2012				
Tom Martin	8/18/2012	L. Seiad Creek	11/25/2012				
Tom Martin	8/6/2012	L. Seiad Creek	11/11/2012				

Location First Tagged	Date Last Seen in 1st Loc	Location of 2nd Sighting	Date 1st Detected at 2nd Loc	Location of 3rd Sighting	Date 1st Detected at 3rd Loc	Location of 4th Sighting	Date 1st Detected at 4th Loc
Tom Martin	7/23/2012	L. Seiad Creek	7/28/2012	Caltrans	10/10/2012	L. Seiad Creek	4/21/2013
Tom Martin	7/23/2012	L. Seiad Creek	10/19/2012				
Tom Martin	10/9/2012	L. Seiad Creek	4/29/2013				
Tom Martin	1/17/2013	L. Seiad Creek	4/17/2013				
Tom Martin	8/18/2012	Sandy Bar	11/30/2012				
Tom Martin	7/10/2012	L. Seiad Creek	8/10/2012				
Tom Martin	8/15/2012	L. Seiad Creek	11/15/2012				
W. Grider	1/15/2013	L. Seiad Creek	5/1/2013				
W. Grider	3/27/2013	L. Seiad Creek	5/13/2013				

Table 13. Summary of movement events documented when tagged fish were detected in locations other than where initially tagged. Most fish were tagged in non-natal streams, suggesting that they had already moved at the time of initial capture

Movement Event	No. Fish Detected
Summer Re-distribution (5/12 - 9/12)	3
Fall/Winter Re-distribution (10/12 -2/13)	33
Spring Outmigration (3/13 - 5/13)	9

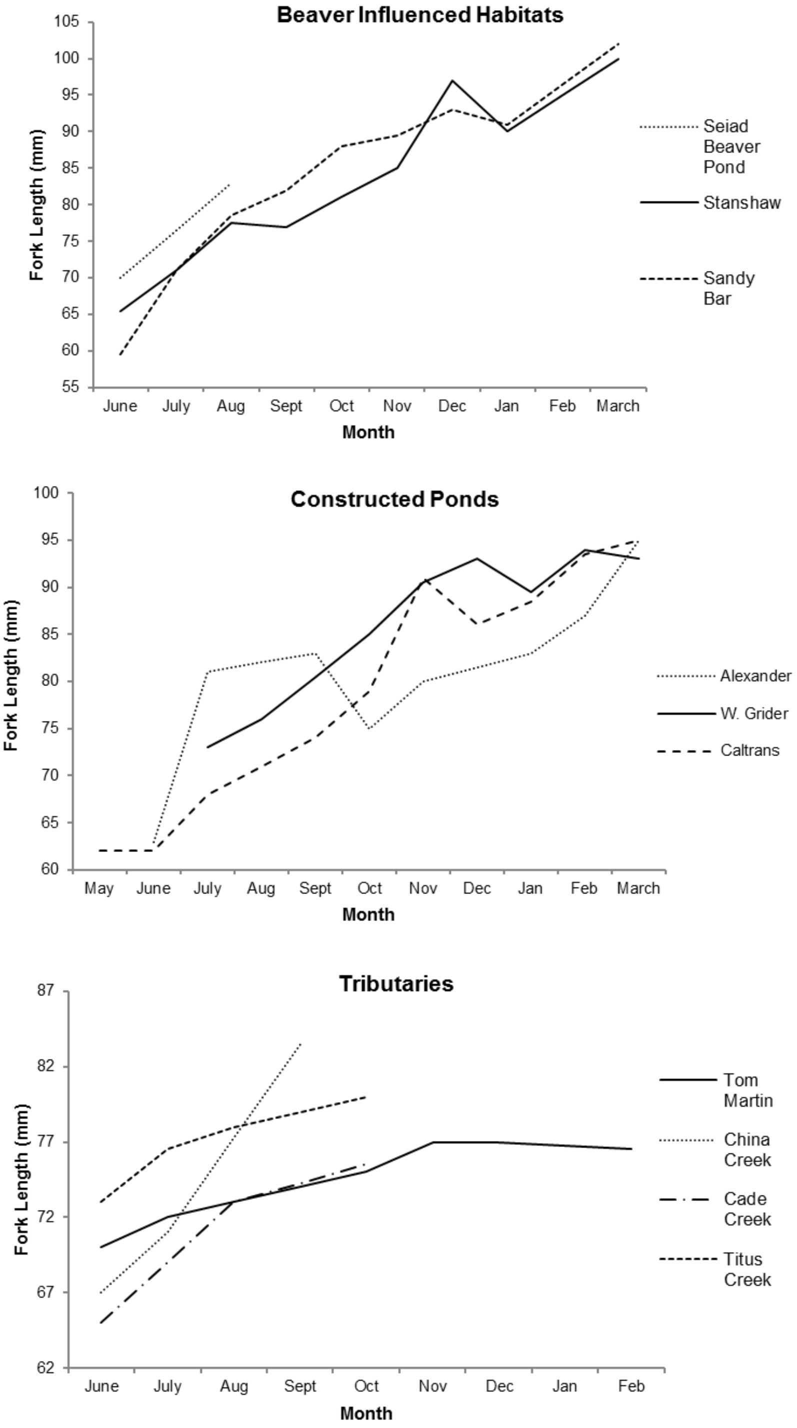


Figure 12. Median fork length of juvenile coho salmon over time at each type of habitat. Dips in the fall for most sites suggest a winter redistribution event where smaller fish emigrated from the stream

Timing of spring outmigration within the Seiad Creek drainage with suggested by PIT tag detections at an antenna array placed at the mouth of Seiad Creek. Fifty-one percent of the fish tagged in Alexander Pond over the course of the project were detected at the mouth of Seiad Creek, 28 percent of the tagged Caltrans fish were detected at the mouth, and 18 percent of the tagged fish from Seiad Creek Beaver pond were detected. Likely, most of the tagged fish from the Seiad Creek study sites out-migrated. However, the PIT tag antenna array was not functioning December 1st through January 17th 2013 due to high flows, which likely corresponds to a large outmigration event.

Using data from the Seiad Creek PIT tag antenna, I determined the frequency of outmigration by date for each of the Seiad Creek study sites in 2013 (Figure 13). There appeared to be little difference in the timing of outmigration among sites in Seiad Creek. The median outmigration dates were estimated from detections that occurred between February 20th and May 31st to avoid including movement associated with the winter redistribution event which occurred earlier in the year (Figure 13). The median date for outmigration of fish in Alexander Pond, Caltrans Pond, and Seiad Creek beaver pond were April 7, April 12, and April 16, respectively in the spring of 2013. The frequency of detections at the mouth of Seiad Creek correlates to spring flow events in the Klamath River.

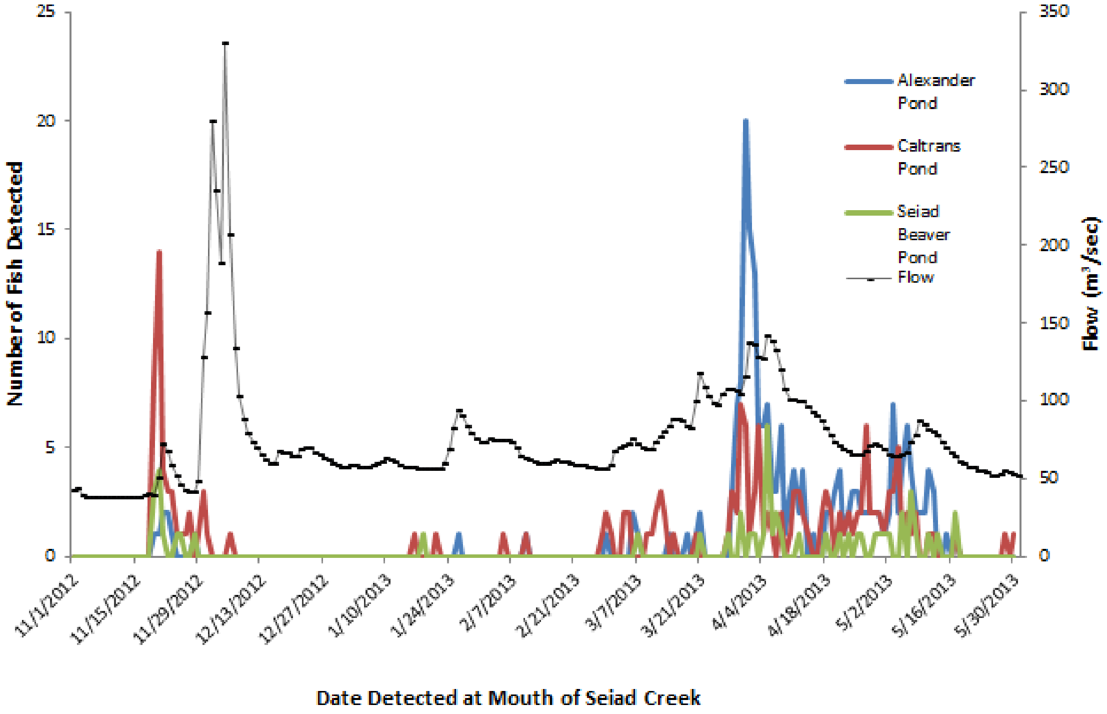


Figure 13. Number of tagged fish from each study site in the Seiad Creek watershed are shown over time as they were detected at the mouth of Seiad Creek. Peaks in detection events represent movement events relative to the flow (m^3/sec) of the Klamath River at Seiad Valley. Flow data were used from the USGS gauging station 11520500 for the Klamath River near Seiad Valley, CA

I calculated the relative proportion of fish that were tagged during the summer and subsequently detected at the mouth of Seiad Creek during different movement events (Figure 14). Summer movement was characterized as detections recorded prior to November 1st, 2012. The winter redistribution included detections from November 1st 2012 – February 20th, 2013 and the spring outmigration event includes detections after February 20th, 2013. Movement was equally distributed throughout the year for those fish tagged in Caltrans Pond as opposed to the other sites where the majority of movement occurred during the spring outmigration, suggesting that fish rearing in the beaver pond and Alexander Pond remained in the system for longer periods. Due to high flows during the winter redistribution period, the PIT tag array at the mouth of Seiad Creek was not operational for approximately two weeks. It is likely that the number of fish moving out of the system during this time was higher than the numbers detected

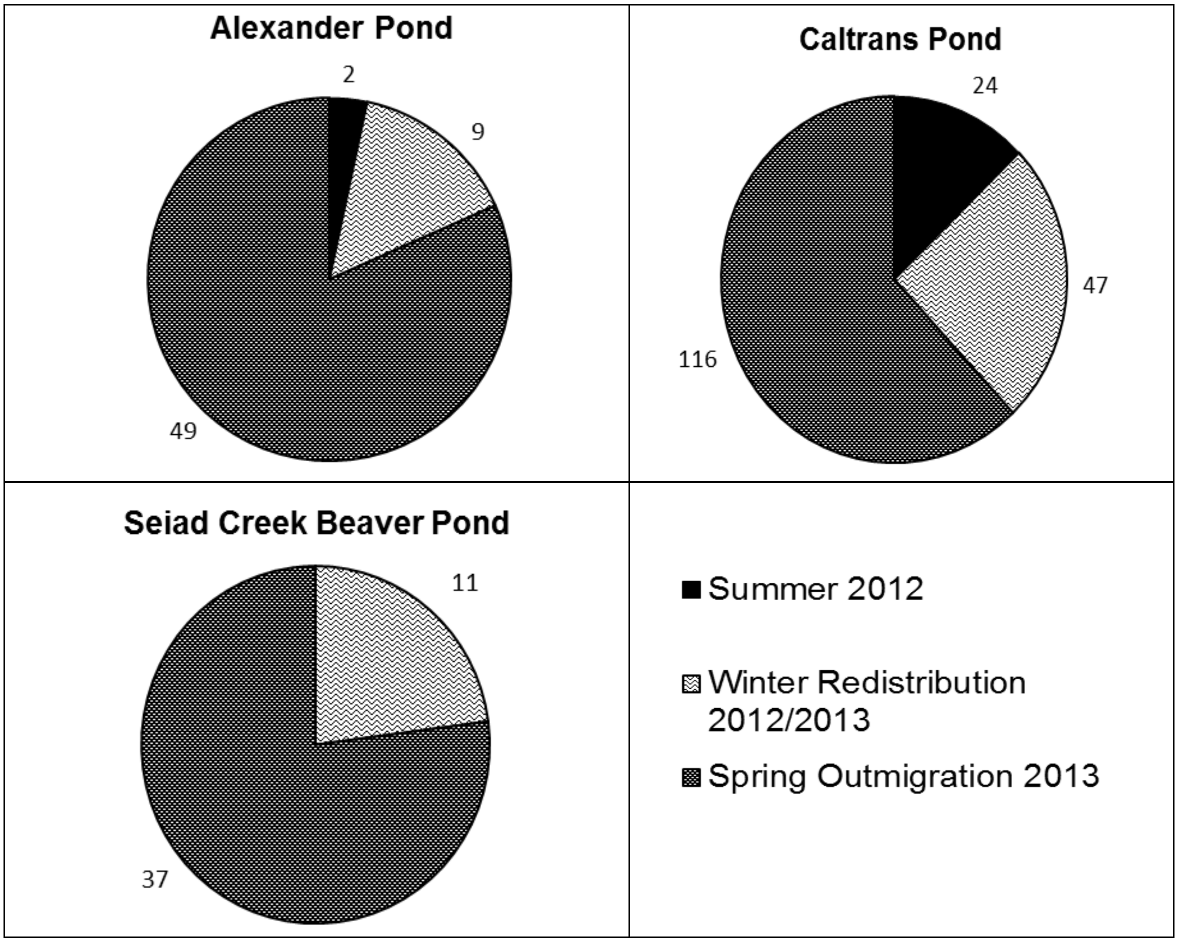


Figure 14. The proportion of fish tagged in Alexander, Caltrans, and Seiad Creek Beaver pond during the summer (May - November 2012) which were detected moving out of Seiad Creek during different movement events.

DISCUSSION

I hypothesized that type of habitat (constructed, beaver influenced, tributary) would influence biological responses. However, most responses did not differ across habitat types. This was not because coho salmon abundance, growth, and retention were similar at all sites. Rather, there were large differences in these responses across sites, but these differences were not consistent within types. This pattern suggests that the characteristics of individual sites likely have a greater influence on factors such as growth, residence time, and density of fish than whether the site is constructed, beaver-influenced, or a tributary. However, few significant relationships could be identified with the site characteristics I chose to assess for this study. Nonetheless, I did find that retention rate was higher at deeper sites and those individuals that reared year round in beaver-influenced sites had the highest rates of growth.

Several reasons may explain why this study could not detect a relationship between habitat variables and density or growth rates of juvenile coho salmon. Perhaps there is no relationship between the predictor variables and biological responses I chose to investigate. Or perhaps there was too much error in the measurements to detect the relationship. However, I think the most likely explanation has to do with the small sample size used for this study and possible complex interactions between predictor variables. My observations in the field, lead me to believe there is too much variability within site type categories to find a correlation between those categories of habitat and growth or density of fish. I do, however, believe that there may be a relationship between growth rates and habitat characteristics which I was unable to detect due to my small sample size and potential interactions between habitat parameters. Had I gathered data from a larger number of study sites, I could have used additional covariates to determine interactions between habitat parameters. For example, perhaps the combination of deep pools and cold water would result in high growth rates.

Alternative Habitat Parameters that May Explain Biological Responses

Because there was a significant difference in growth rates and retention across individual study sites, other habitat characteristics not measured as part of my study likely play a role in determining growth rate of coho salmon at these sites. For example, productivity and available food resources play a role in determining growth rates of juvenile coho salmon. Ward et al (2009) showed prey biomass alone accounted for a significant variation in juvenile Atlantic salmon growth rates, while Wilzbach (1985) found in laboratory experiments that food abundance was more important than cover in determining abundance and distribution of cutthroat trout. Thus, difference in productivity or prey availability across sites may explain the differences in growth rate or densities of fish. However, directly comparing prey availability across the habitat types will be a substantial challenge. Due to their recent construction and circular shape the constructed ponds had little overhead cover while three of the four tributaries had a dense canopy. Therefore, fish in the ponds were likely more reliant on autochthonous production whereas the fish in tributaries were likely more reliant on allochthonous inputs. Further, fish in constructed and beaver ponds likely had access to some food resources not available in the tributaries, such as mosquito larvae and amphibian eggs present in standing water. In a comparison of autochthonous and allocthonous resources in logged and forested stream reaches in Washington, Bilby and Bisson (1992) found fish populations appeared to depend upon food derived from autotrophic pathways during spring and summer in the presence or absence of forest canopy. Their results indicated that increased canopy cover would not benefit growth of fish during spring and summer. Romaniszyn et al (2007) shows that peak food availability occurs in the spring and is derived from aquatic insect larvae, however in the fall overall food availability decreases but is dominated by terrestrial inputs which can prove more difficult for juvenile fish to eat. Bilby and Bisson (1992) did not take into account the difference in energy expenditure of fish residing in standing water compared to flowing water. In reference to previous studies, it appears that the pond habitats in my study may provide preferable food resources during the spring and summer when compared to the tributaries, especially under the additional consideration that pond fish may be expending less energy than stream rearing fish that are in constant flowing water.

The idea presented by Rosenfeld (2008), that a combination of flowing and standing water is ideal, may explain the high growth rates measured in Stanshaw, Sandy Bar, Caltrans Pond, and China Creek. During the winter, the growth rates of juvenile coho salmon were much higher in Stanshaw and Sandy Bar sites than any measured growth rate during the summer. Geomorphically, these sites are similar in the fact that they are somewhat isolated from main stem flows during the summer, with cool tributary water filling the pools in the secondary channel of the main stem Klamath River. However, during the winter, main stem waters flow through the secondary channel. Perhaps, the influence of the main stem provides additional nutrients or the ideal combination of flowing and standing water. The increase in growth rates from summer to winter may be related to the change in habitat from isolated from the main stem to connected to the main stem. Similarly, the high summer growth rates in Caltrans Pond may be attributable to the documented movement of fish between the standing pond water and the flowing stream water. High summer growth rates in China Creek may be a result of fish occupying the very deep pool near the mouth of the tributary, yet receiving inputs from upstream flowing water. Or perhaps, the fish of China Creek move into the main stem of Klamath as documented at Tom Martin Creek, taking advantage of different flow patterns and food resources.

Movement Patterns and Strategies

The access to and location of a study site within a watershed seemed to influence movement. I hypothesized that fish would reside longer in habitats where growth rates were the highest, such as the constructed ponds. The retention analysis however, showed that residence time was shortest in Caltrans Pond and longest in Alexander Pond; both constructed ponds in the same watershed and both having fish with similarly high rates of growth. The primary difference between the two ponds is access and location in the watershed. I suspect that the high turnover rate in Caltrans Pond has to do with the deep outlet channel draining into a glide-like reach of Seiad Creek. The lower reach of Seiad Creek, where Caltrans Pond is located has a very high number of natal and non natal juvenile coho salmon and is characterized by a low gradient, sinuous stretch of stream with lots of deep pool habitat. It appears the fish move freely between the pond and stream habitat. In fact, at one point during the summer, a beaver dam was constructed just downstream of the Caltrans Pond outlet, increasing the water level in Caltrans Pond and providing further connection between stream and pond. I saw similar proportions of fish moving out of Caltrans during each season. Alexander pond, on the other hand, is several miles upstream where the gradient of Seiad Creek increases and few coho salmon rear in the stream channel. The outlet of Alexander Pond is very shallow and may even completely close during a short period during the summer. I found that more than three quarters of the fish from Alexander Pond did not move out until the spring outmigration event. Additionally, the largest number of 1+ juvenile coho salmon was found in Alexander Pond (Appendix A); another indication that fish may stay longer at that site. Similar to Alexander Pond, West Grider Pond is located high in a watershed with more difficult access and the fish there showed a high rate of retention.

Seventeen of the fish tagged in Tom Martin Creek were detected in other locations, and can be described as having three differing strategies in migration timing. First, two of the tagged fish were detected elsewhere during the summer of 2012 prior to lethal main stem temperatures, indicating an exploratory movement pattern as documented by Kahler et al (2001). Second, twelve of the fish detected elsewhere were found during the fall redistribution period, primarily in Lower Seiad Creek. And thirdly, five individuals were not detected until the spring of 2013 presumably as outmigrating smolts, indicating they stayed through the winter season in Tom Martin Creek. Three of the fish tagged in Tom Martin Creek were detected in two additional locations proving they occupied at least four different off-channel habitats (because Tom Martin is a non natal stream) during their freshwater rearing period.

At a shorter temporal scale, the diurnal migration pattern of juvenile coho salmon that was documented at Tom Martin Creek and Caltrans Pond seems to be related to daylight as suggested by other studies. Scheuerell and Schindler (2003) examined a diel vertical migration pattern by juvenile sockeye salmon and found a correlation between depth and amount of light on the lake surface. They suggest the timing of migration is associated with an anti-predation window. Metcalf et al (1999) discusses the nocturnal vs. diurnal foraging trade-off in juvenile Atlantic salmon and showed that winter diel activity patterns in salmon were dependent on food availability. A change in food density led to a parallel change in time spent in the refuge, but the effect was greatest at the time of day with the least favorable ratio of predation cost to feeding benefit. Similarly, I observed the greatest number of fish migrating at night when risk of predation was minimized.

Future Research

Though this study provides evidence to support the value of off-channel restoration sites, additional research could further improve our understanding of what factors influence growth and survival of juvenile coho salmon and how best to maximize these responses in restoration efforts. I found consistently high growth rates during the summer and winter in Caltrans and Alexander Ponds, but oddly found extremely low growth rates in West Grider Creek Pond during the winter. Because West Grider Creek Pond was constructed with the purpose to provide high quality over-winter habitat, it is important to conduct follow up research to determine the reason for low winter growth rates. Dissolved oxygen may be a factor. During the winter, the pond is mostly fed by ground water and overland flow. West Grider Creek Pond is surrounded more by deciduous trees than Alexander and Caltrans ponds and likely has more decomposing organic material in and around it. Because this decomposing material in the winter may reduce the concentrations of dissolved oxygen, a more systematic monitoring approach is necessary. A grid-like sampling design that measures dissolved oxygen at differing locations and depths at the same time every day, repeated throughout the season, would increase our understanding of the role dissolved oxygen may play in growth rates of coho salmon. If in fact dissolved oxygen levels are low in the winter, new design elements could improve the function of West Grider Pond and could be incorporated into future projects. In constructing off-channel habitats in the Lower Klamath River with the Yurok Tribe, Rocco Fiori (Fiori Geosciences) designs “infiltration galleries” to facilitate surface and ground water exchange to enrich dissolved oxygen levels during the winter.

Future studies could investigate the reasons for differences in growth rates further, using more standardized sampling of habitat characteristics and larger sample sizes (i.e. number of habitats within each category) and look at different variables such as production and availability of food resources in a site as discussed above. Perhaps there is a relationship between allocthonous versus authochthonous production and growth rates; perhaps this relationship changes seasonally.

Future studies may also want to broaden the spatial scope beyond the sites themselves, including variables such as “opportunity” or “access” that account for the habitat matrix surrounding the focal sites. Because I found that juvenile coho salmon in the mid-Klamath watershed have high rates of seasonal movement and non-natal rearing, it is important that they can find non natal rearing sites. It is particularly important to understand the role of opportunity and access when designing future off-channel restoration sites.   In my study, fish were observed very early in the season at non-natal sites that were best connected to the main stem Klamath River and had good mixing zones (i.e., Titus Creek, Sandy Bar, Stanshaw, Tom Martin Creek). Fish arrived later and in few numbers at non-natal sites that had poor connection (e.g., confluence at a high velocity reach) or were further away in proximity to the main stem Klamath (i.e., Cade Creek, West Grider Pond, China Creek). Future studies may look at off-channel sites and relate their distance from the main stem Klamath River as well as characteristics of the outlet channel such as depth, length, and location (i.e. does it enter into a riffle or pool?) to the retention rate of juvenile coho salmon and the density of fish rearing there. We may find that these are the elements that make the best off-channel habitat in terms of allowing the maximum number of fish to benefit from the restoration site.

Additional research would be helpful in understanding the risk of introducing exotic species to watersheds with the construction of off-channel habitats. I observed varying densities and species composition of exotic species including bull frogs, bullheads, and green sunfish in Alexander Pond, Caltrans Pond, Sandy Bar, and Stanshaw study sites. No bull frogs, however, were observed in the natural habitats (Sandy Bar and Stanshaw) whereas, extremely high densities of bullfrog adults and tadpoles were observed in Caltrans Pond. These constructed habitats may serve as a stronghold for invasive species that would otherwise be displaced seasonally with high flows. Bullfrogs likely do not inhabit Sandy Bar and Stanshaw ponds because they receive flushing winter flows.

Finally, the use of beaver-influenced habitats by juvenile coho salmon in the mid-Klamath basin can be further explored. Very few sites with channel spanning dams and off-channel beaver complexes exist in the mid-Klamath watershed. The constructed off-channel ponds attempt to increase floodplain connection and replicate complex habitats similar to those natural habitats created by beaver. However, the constructed off-channel ponds may not function in the same dynamic sense as a natural system. The interaction of the main stem with the two beaver-influenced sites, Sandy Bar and Stanshaw, may be a key to the extremely high winter growth rates there. The seasonal beaver dam in Seiad Creek provided summer rearing habitat, yet washes out during the winter preventing exotic species from taking hold. Protecting and even reintroducing beaver to build salmonid habitat is a topic of discussion among restoration groups and regulatory agencies. Further documentation of the relationship between coho salmon and beaver would be a valuable contribution.

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APPENDIX A

The Presence of 1+ Juvenile Coho across Sites

Throughout the sampling seasons, 1+ juvenile coho were recorded at each site. These fish were noted as 1+ by visual observation only and when they were obviously outside of the range of possible sizes of the 2012 cohort. No scale samples were collected to verify observations.

Site	**# tagged**	**# 1+**	**Proportion 1+**
Tom Martin	443	0	0.00%
W. Grider Pond	131	0	0.00%
Seiad Creek Beaver Pond	283	0	0.00%
Alexander Pond	322	15	4.66%
Caltrans Pond	613	1	0.16%
China Creek	92	0	0.00%
Cade Creek	70	0	0.00%
Titus Creek	195	0	0.00%
Sandy Bar Creek	262	0	0.00%
Stanshaw Creek	132	1	0.76%