ABSTRACT

THE INFLUENCE OF HABITAT CHARACTERISTICS ON ABUNDANCE AND GROWTH OF JUVENILE COHO SALMON *ONCORHYNCHUS KISUTCH* IN CONSTRUCTED HABITATS IN THE MIDDLE KLAMATH RIVER BASIN

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Substantial investment has been directed toward construction of off-channel ponds in the middle Klamath River basin to benefit Coho Salmon populations. Previous research showed that abundance, retention, and growth of juvenile Coho Salmon varied across sites but were not consistently different between constructed ponds and natural habitats; instead, variation was attributed to individual site characteristics. However, the characteristics responsible for these differences are not clear. In this exploratory study, I investigated the effect of accessibility on juvenile Coho Salmon abundance within nine constructed ponds. I also assessed whether habitat conditions, Coho Salmon density, and food availability within the ponds could predict abundance, retention, and growth of Coho Salmon. Few strong relationships were found between characteristics of ponds and the response variables. Despite potentially stressful conditions at some sites, Coho Salmon occupied most ponds through the summer, suggesting that they provide suitable rearing habitats. Lack of accessibility throughout the year had potentially important effects on the survival and life history of individuals trapped in constructed ponds. Retention rates were strongly correlated with zooplankton availability, while Coho
Salmon density and available benthic prey displayed little correlation with retention. While growth rate differed among ponds; while measures of prey availability did not explain variation in growth rate, growth rate was negatively correlated with Coho Salmon density in the ponds. Constructed off-channel ponds serve as important rearing habitat for Coho Salmon and an increased understanding of their role in Coho Salmon rearing and production is necessary.
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INTRODUCTION

Coho Salmon *Oncorhynchus kisutch* are distributed across western North America from Alaska to central California. Since the late nineteenth century, populations of Coho Salmon and other salmonids have declined throughout their native range (e.g. Moyle and Williams 1990; Bisson et al. 1992; Quinn 2005). Activities including hydropower generation, mining, logging, and agriculture have severely degraded salmon habitat and led to a substantial decline in Coho Salmon abundance and distribution relative to historic levels (Moyle and Williams 1990; Nehlsen et al. 1991; Quinn 2005; NOAA 2011). Habitat enhancement efforts aimed at conserving and restoring these populations are a large, ongoing investment. To provide information about the characteristics of restored habitats that provide benefit to juvenile Coho Salmon, I evaluated the performance of juvenile Coho Salmon in constructed off-channel habitats in the middle Klamath River basin.

Coho Salmon are grouped into six evolutionary significant units (ESU) in Washington, Oregon, and California for the purpose of state and federal Endangered Species Act (ESA) species listing. Coho Salmon populations of particular concern due to declining abundance are located in the southern end of their range, which includes the Southern Oregon/Northern California Coast (SONCC) ESU within the Klamath River basin. Coho Salmon within the SONCC ESU were ESA listed as threatened in 1997 (NMFS 2014).
Most Coho Salmon in the SONCC ESU have a three-year life cycle that begins in a natal stream when spawning occurs in late fall or early winter. Surviving fry emerge from the gravel in early spring and typically spend one year rearing in fresh water. The following spring, juvenile Coho Salmon undergo smoltification to enter the marine environment and undergo a period of rapid ocean growth before returning to spawn as adults. Even before leaving for the ocean, juvenile Coho Salmon may leave their natal streams and travel considerable distances (> 10 km) to new rearing locations. This redistribution is often associated with seasonal shortages of suitable habitat in the natal site, such as slow-water-velocity habitat in winter (Peterson 1982; Bisson et al. 1988b; Nickelson et al. 1992b; NOAA 2011) or cool water temperatures during the summer (Bilby and Bisson 1987; Belchik 1997; Kahler et al. 2001; Quinn 2005; Sutton et al. 2007; Hillemeier et al. 2009).

Juvenile Coho Salmon generally prefer low-velocity pools and ponds to high-velocity riffles and runs (Bisson et al. 1988b; Nickelson et al. 1992b; Healy and Lonzarich 2000). Previous research indicates that limited availability of slow-water habitats—including off-channel ponds, side-channels, backwaters, and alcoves—during high-flow periods can limit survival and production of juvenile Coho Salmon (Peterson 1982; Nehlsen et al. 1991; Nickelson et al. 1992b; Beechie et al. 1994; Solazzi et al. 2000; Morley et al. 2005; Rosenfeld et al. 2008). Thus, considerable effort has been devoted to habitat construction and improvement to increase the quality and quantity of slow-water winter rearing habitat in watersheds with Coho Salmon recovery efforts. Efforts to provide slow water habitat have long relied on the addition of log jams and
other structures directly in the stream channel. However, the construction and enhancement of off-channel habitats has recently become a common management action to help provide increased slow-water winter rearing habitat for juvenile Coho Salmon (Nickelson et al. 1992b; Morley et al. 2005; Cooperman et al. 2006; Beesley and Fiori 2012).

Though off-channel habitat restoration efforts are generally intended to provide winter rearing habitat for juvenile Coho Salmon, juvenile salmon also use off-channel habitats during the summer (Witmore 2014). In some cases, summer movement of juvenile Coho Salmon into off-channel habitats may represent an escape from spring runoff and high flows in the main stem river (Hillemeier et al. 2009); in other cases, the movement may be a response to temperature. As flows decrease and ambient water temperatures increase during summer, juvenile Coho Salmon may either stay in place and experience elevated metabolic demands, potentially leading to reduced performance, growth suppression, increased disease susceptibility, and mortality, or they may move away from their natal stream in search of thermal refugia (Brett 1979; Nielsen et al. 1994; Quinn 2005; Sutton and Soto 2012). Juvenile salmonids may survive periods of unsuitable main stem water temperatures through the use of thermal refugia created naturally by tributaries, groundwater seeps, and thermal stratification within a stream channel or off-channel habitat (Swales and Levings 1989; Nickelson et al. 1992a; Nielsen et al. 1994; Matthews and Berg 1997; Belchik 1997; Ebersole et al. 2001; Sutton et al. 2007). Off-channel habitats may provide such a refuge, as ponds that are supplied with
groundwater often provide more stable and suitable temperatures compared to main stem habitats (Swales and Levings 1989; Sommer et al. 2001; Limm and Marchetti 2009).

The thermal habitat provided by ponds in summer may be particularly important for Klamath River Coho Salmon. Juvenile Coho Salmon are particularly sensitive to high temperature (Elliott 1981; Thomas et al. 1986). Preferred temperatures for juvenile Coho Salmon may range from 10 to 16 °C (Stenhouse et al. 2012), dependent on food availability, with Coho Salmon potentially avoiding sites with maximum weekly maximum temperatures (MWMT) greater than 18 °C (Welsh et al. 2001). Sutton and Soto (2012) found high abundances of Coho Salmon seeking thermal refuge as water temperatures in the main stem Klamath River increased to 23 °C.

Fish movement into ponds in the summer may also be a response to interrelated factors such as seasonally changing flow (Gowan and Fausch 2002), food availability (Wilzbach 1985; Nielsen 1992; Grand and Dill 1997; Giannico 2000), and competitive interactions (Coutant 1987; Nielsen 1992; Rhodes and Quinn 1998; Kahler et al. 2001). These factors may drive fish from stream habitats and into off-channel habitats. In some cases, off-channel habitats provide more prey organisms than stream habitats, leading to increased growth in juvenile salmonids that move into ponds (Sommer et al. 2001; Jeffres et al. 2008; Limm and Marchetti 2009). Regardless of the causes of movement, seasonal connections between nearby creeks and off-channel habitats are important to allow movement in and out of the habitats when they are most needed (Brown and Hartman 1988; Ebersole et al. 2006), such as to allow for escape into ponds when stream habitats
are stressful and escape from ponds when conditions deteriorate or to outmigrate to the ocean (Henning et al. 2006).

Numerous off-channel habitats have been constructed along tributaries of the middle and lower Klamath River basin since 2009 to provide winter rearing habitat for juvenile salmonids. That fish use these constructed habitats throughout the summer season has already been reported (Beesley and Fiori 2012; YTFP 2013; Witmore 2014). Witmore (2014) found that average growth rate, retention, and abundance of juvenile Coho Salmon did not differ between constructed habitats and natural refuge habitats within the middle Klamath River basin. However, summer growth and abundance varied more than tenfold across individual sites. Depth, water temperature, volume of habitat, and percent riparian cover did not explain these differences across sites (Witmore 2014). It is not clear what mechanisms are responsible for the differences in abundance and growth rates among the constructed off-channel habitats and what features are associated with summer rearing by juvenile Coho Salmon. Previous research in these habitats has not addressed food availability within the constructed off-channel sites or accessibility of the sites to fish to determine if these contribute to variation in summer residence and growth of juvenile Coho Salmon.

Given the investment in off-channel pond construction and the imperiled status of Coho Salmon in the region, it is important to assess whether constructed ponds are meeting seasonal habitat requirements of juvenile Coho Salmon and if they can support sufficient Coho Salmon abundance and growth to contribute to recovery. I sampled off-channel ponds to identify characteristics of ponds that support higher summer abundance,
growth, and retention of juvenile Coho Salmon. I explored three specific questions: 1) Is the summer abundance of juvenile Coho Salmon in constructed habitats better predicted by measures of accessibility of the habitat to fish redistributing from natal sites than by the habitat conditions within the site itself? 2) Does summer retention of juvenile Coho Salmon in the constructed habitats increase with food availability and low fish density? 3) Is juvenile Coho Salmon growth in constructed habitats affected by invertebrate food abundance or densities of Coho Salmon?
METHODS

Study Location

The Klamath River is located in southern Oregon and northwestern California and is the second largest river basin in California, draining almost 41,000 km² (National Research Council 2008; Figure 1). The river flows approximately 423 km, beginning as an expansive alluvial river in the upper basin and transitioning into a confined, erosive mountainous river in the middle and lower basin. Due to this geography being different from many river systems that typically decrease in gradient and increase in floodplain width from headwaters to mouth, the basin is often referred to as an upside down river (Rymer 2008). Agriculture is the dominant land use in the semi-arid upper basin while land in the lower basin is primarily managed by the US Forest Service and Native American tribes.
Five major hydroelectric dams, built in the early- and mid-1900’s between river kilometer 306 and 375, block the Klamath River as it transitions from the upper to the
middle portion of the basin. The dams alter the hydrologic regime and sediment transport of the river, reducing the interaction of the river with its floodplain. Further, the dams reduce summer water quality and flows and increase water temperature downstream (Bartholow et al. 2004). Nutrient-rich water from the upper basin is trapped behind the dams and warms during the summer months, promoting blooms of hepatotoxic cyanobacteria *Microcystis aeruginosa* (Kann 2006). These altered conditions lead to increased stress to juvenile and adult salmonids occupying the main stem and increased outbreaks of fish disease (Bartholomew et al. 2007; Ray et al. 2012).

In addition to changes associated with the hydroelectric dams, mining, logging, diking, and extensive road building have reduced habitat quality and quantity for Coho Salmon in the main stem and tributaries throughout the Klamath River basin (NMFS 2014). Historic mining practices, including stream-bed dredging, channelization, and deposition of gravel tailing piles along the stream margins, continue to affect stream channels today. Extensive timber harvest was prevalent from the 1940’s to 1990’s, with practices today involving fuels reductions, salvage logging, and maintenance of healthy stand structures. Roads used for logging are dense throughout the basin and continue to supply sediment to tributary and main stem channels.

The combination of an altered hydrologic regime from the dams and physical habitat alteration from other land use practices have left little off-channel habitat available for summer or winter rearing of juvenile salmon along the main stem and tributaries and has reduced access to the habitat that remains (NMFS 2014). Limits to the
amount of accessible off-channel refuge habitat may lead to reduced growth and survival of juvenile Coho Salmon, and reduced population abundance.

The study area for this project was in the middle Klamath basin between Iron Gate Dam (river kilometer 305.9) and the Trinity River confluence (river kilometer 69.8) in Siskiyou and Humboldt counties of California. I focused on nine constructed off-channel ponds built by the Mid Klamath Watershed Council to increase the habitat complexity and floodplain connectivity for summer and winter rearing as well as to increase the amount of non-main stem type habitat (Figure 2). The off-channel ponds were built to aid in the recovery of Coho Salmon populations in the basin and are used by juvenile salmonids throughout the year (Witmore 2014).
Figure 2. Detail of the study area of the middle Klamath River basin with major tributaries and off-channel habitat study locations labeled with grey circles. Creeks and rivers are in bold while town locations are italicized.
Since 2010, thirteen off-channel ponds have been constructed in the middle Klamath River basin, with the latest construction of habitats in fall 2015. Only nine of these constructed habitats were studied in the summer of 2014 due to limited accessibility and the timing of habitat construction. Study sites, listed from upriver to downriver along the Klamath River, were located at Tom Martin Creek, O’Neil Creek, Seiad Creek (Stender, Alexander, May, and Lower Seiad ponds), West Grider Creek, Stanshaw Creek, and Camp Creek. Each pond, with the exception of the Stanshaw Pond, was constructed in the floodplain of the associated tributary and was connected to a groundwater source at the time of construction. Stanshaw Pond formed naturally at the mouth of the creek, in the Klamath River floodplain, and was excavated to increase the pool volume, which has been lost due to sediment input. Off-channel sites were constructed in different years: Stender and Alexander ponds were constructed in fall 2010, Lower Seiad and West Grider ponds in fall 2011, May Pond in fall 2012, and Tom Martin, O’Neil, Camp, and Stanshaw ponds in fall 2013.

Previous work by the Karuk Tribe Department of Natural Resources Fisheries Program characterized the origin of juvenile Coho Salmon using some of the study ponds through observations of the distribution of spawning adults and the recapture of marked juveniles (Witmore 2014; T. Soto, Karuk Tribe, personal communication). Tom Martin and O’Neil creeks are located just downstream of the Scott River confluence with the Klamath River. Neither creek supports Coho Salmon spawning, but are used by juvenile non-natal salmonids presumed to be migrating downstream from the upper Klamath, Scott, and Shasta rivers. Seiad Creek, with four study sites, is a low-gradient tributary
with Coho Salmon spawning. The Seiad Creek sites are used by natal juveniles from within the watershed, as well as by non-natal juvenile Coho Salmon. Seiad Creek has been impacted by extensive diking and channelization for flood control and road building. West Grider and Camp creeks support low numbers of adult Coho Salmon spawners and are known to also support non-natal juvenile Coho Salmon. Stanshaw Creek does not have spawning, but non-natal juvenile Coho Salmon have been observed there.

Capture and Tagging

All research for this study was conducted under the approved Humboldt State University Institutional Animal Care and Use protocol 13/14.F.62-A. I used a mark-recapture method using Passive Integrated Transponder (PIT) tags to determine Coho Salmon abundance, retention, and growth at each of the nine off-channel study locations. Beginning in mid-May 2014, juvenile Coho Salmon were captured using seine nets in each pond. Sampling was repeated once per month until the end of September 2014. Capture events in June and the last event of the season in late September included two paired sampling efforts at each pond, conducted on consecutive days, to estimate juvenile Coho Salmon abundance.

Captured juvenile Coho Salmon were first anesthetized with MS-222 (tricaine methanesulfonate). All juvenile Coho Salmon were then measured (fork length, nearest mm), weighed (nearest 0.1g), and scanned for a PIT tag. Untagged juvenile Coho Salmon larger than 65 mm fork length were tagged using a Biomark FDX 12.5 mm PIT tag
inserted posterior to the pelvic fin. Recaptured tagged Coho Salmon were only identified by their PIT tags, measured, and weighed. All fish were subsequently released into the habitat of initial capture.

Population Abundance

The abundance of juvenile Coho Salmon occupying each constructed off-channel habitat was estimated using a mark-recapture method. Population estimates were conducted twice: in June after the redistribution of juvenile Coho Salmon into the off-channel habitats when water temperatures in the main stem Klamath River increased to stressful levels and in September prior to a seasonal decrease in water temperatures and increased flows from rain events.

The Lincoln-Peterson Method was used to estimate population size, which requires two sampling events for each estimate and assumes a closed system, with no movement in or out of the site and no mortality between the two sampling events. The two sampling events occurred on consecutive days to minimize violation of the no-mortality assumption and the inlet to the off-channel habitat was closed with a block net on the two days to eliminate movement of fish in and out of the habitat. Population estimates, $N$, and the standard error, $SE$, of the estimates were calculated as,

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

and

$$SE \approx \sqrt{\frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}}$$
where $M$ is the total number of fish captured and marked on the first visit, $C$ is the total number of fish captured on the second visit, and $R$ is the number of fish captured on the first visit and recaptured on the second visit.

A two-way analysis of variance (ANOVA) was used to determine if the June and September abundances within each off-channel pond differed among ponds and months. If results showed no significant differences in abundances between June and September, we averaged abundance for each pond to get one population estimate per pond for the summer.

Site Accessibility

I assessed a suite of characters to describe site accessibility. There are no standard methods for assessing accessibility as a quantitative habitat characteristic. The measures I collected in this study were used in an exploratory analysis to generate hypotheses for future research. The lotic habitat (i.e. pool, riffle) adjacent to the inlet of the off-channel habitat was assigned in the field. Habitats constructed with slow water adjacent to their inlet channel may allow for fish to find the inlet better than in fast moving water. The distance from the main stem Klamath River to the pond entrance and the gradient of that distance were measured using the measuring tool in ArcMap to assess the impact of distance traveled by likely non-natal fish. I also classified a tributary as natal (adult spawning) or non-natal (no adult spawning) in an attempt to account for differences in juvenile Coho Salmon recruitment to off-channel ponds. Finally, I measured the average depth of the inlet channel of each pond once a month from May to September and
averaged those measurements and also assigned whether an off-channel pond ever became disconnected from the adjacent channel at any point during the summer.

Continuous temperature loggers were suspended in the water column in the Klamath River near O'Neil and Stanshaw creeks, in Seiad Creek near May and Alexander ponds, and in Camp and West Grider creeks near the off-channel ponds. Temperature readings were taken every hour and the data were used to calculate maximum weekly maximum temperature (MWMT) in the channel adjacent to the off-channel ponds. I calculated MWMT by averaging the daily maximum temperature for each 7-day period and then selecting the highest average for the entire summer. Klamath River MWMT near O'Neil Creek was used as the adjacent MWMT for O'Neil and Tom Martin ponds. The adjacent channel MWMT was assigned to ponds on Seiad Creek based on proximity to the temperature loggers such that Lower Seiad and May ponds used the temperature logger placed near May Pond and Stender and Alexander ponds used the temperature logger placed near Alexander Pond.

Habitat Conditions

At each of the nine constructed off-channel habitat sites, I measured physical habitat conditions of the site that may influence juvenile Coho Salmon growth and abundance. Continuous temperature loggers were suspended in the water column in each off-channel pond and took readings every hour. Temperature data were used to calculate MWMT and mean diel temperature variation in the off-channel ponds. Mean diel temperature variation was calculated by subtracting the minimum temperature from the
maximum temperature measured within the study site for each day and then averaging those values across the summer.

In addition to continuous temperature monitoring, spatially detailed temperature and dissolved oxygen measurements were collected within each habitat each month with an optical YSI Professional handheld multi-parameter meter. Measurements were collected in the mornings in a 3-dimensional grid formation along two parallel transects stretching the longest dimension of the pond. Horizontal measurements were taken every four meters along transects and vertical measurements through the water column were taken at the surface, mid-water column, and bottom when depths allowed (Figure 3). These data were used to calculate average dissolved oxygen throughout the habitat each month, average depth of the habitat, pond volume, and to map thermal variation within each habitat not captured by a single monitoring logger.

Figure 3. Diagram of the two parallel transects running the length of the off-channel habitat from an aerial view (A) and the measurements taken along each transect seen from the side down the water column vertically (B). The grey circles represent the measurements taken down the water column.

Ten random samples were taken along the water surface of each study site to measure turbidity in Nephelometric Turbidity Units (NTU) and chlorophyll $a$ each month.
with an AquaFluor handheld fluorometer/turbidimeter. Because the fluorometer was calibrated to a fluorescence standard instead of a known chlorophyll \( a \) concentration, the chlorophyll \( a \) readings are a relative measure that can be compared from one month to another and from one study site to another. To determine if this measurement approach captured significant variation across ponds, I ran two-way ANOVAs with average monthly chlorophyll or turbidity measurements for each pond as response variables and pond and month as predictors.

**Prey Availability**

I sampled benthic and pelagic prey resources at each study site to evaluate the contribution of prey availability and composition within the ponds to differences in summer retention and growth rates of Coho Salmon among constructed ponds.

**Hester-Dendy Sampling**

Benthic macroinvertebrate sampling was conducted at all nine off-channel locations using six-layered, 8 cm x 8 cm Hester-Dendy samplers. Five samplers were placed at each site in July and August. The samplers were evenly distributed through the site at approximately 0.5 meters depth and left for three weeks to allow for colonization. When collected, the samplers were lifted and placed into a Ziploc bag with 70% ethanol until the sampler could be cleaned to collect macroinvertebrates. The organisms were identified to the lowest practical taxonomic level, typically family, using Merritt and Cummins (1996), and also categorized into life stages of nymph or larvae, pupae, and adult.
Dry weight estimates were calculated from total length or head width of the organisms using regression equations for larvae, pupae, and adult invertebrates from Benke et al. (1999), Rogers et al. (1977), Sabo et al. (2002), and Smock (1980). Dry weight (mg), $DW$, calculations were made using,

$$DW = aL^b$$

where $L$ is length (mm) of the total organisms or width of the head and $a$ and $b$ are invertebrate-specific coefficients.

I visualized patterns in the relative abundances of available prey at each site using nonmetric multidimensional scaling (NMDS). NMDS was used as a qualitative assessment to characterize multivariate differences in prey communities among ponds. This analysis allows me to look for differences among individual Hester-Dendy samples and for differences among study sites. The NMDS used individual Hester-Dendy samples from both July and August as the unit of observation. Taxa found at only one site were excluded from the data set (Malison et al. 2015). The plots provide a visual representation of the patterns in prey communities based on the positioning of ponds and prey taxa. Taxa that are closer to an off-channel pond in an NMDS plot make up a larger portion of the available prey for that pond than taxa that are further away.

Zooplankton Sampling

Zooplankton were collected in May and August using 13-cm-diameter plankton nets with 125 micron mesh. Each tow was three meters in length, gauged from the rope length. Eighteen horizontal plankton tows were collected at various locations throughout an off-channel ponds. These tows were combined into one sample and stored in 70%
ethanol. This process was repeated twice more at each pond on the same day for a total of three samples each month. At sites with abundant zooplankton, fewer tows were collected throughout the pond per sample.

The samples were rinsed in a sieve and the zooplankton was collected and identified. If the sample included large numbers of zooplankton, then a portion of the collection was sub-sampled. Sub-sampling was conducted by diluting the zooplankton in 250 mL of water and agitating to an even distribution. A 12 mL subsample was taken out of the solution with a pipette and identified. Sub-sampling continued until 50 organisms were counted, with the last sub-sample fully identified. The zooplankton numbers were then used to extrapolate the zooplankton count to the entire sample. Zooplankton counts in each sample were then converted to the number of zooplankton per cubic meter of water in the off-channel habitats.

To determine if this measurement approach captured significant variation across ponds, I ran a two-way ANOVA with monthly zooplankton abundance as a response and pond and month as predictors.

Diet Composition

I collected diet contents of juvenile Coho Salmon in July and August at each site to determine if diets were related to prey availability and influenced fish growth within the ponds. At Lower Seiad and May ponds, I collected additional samples monthly from June and September. At all sites, the first 20 Coho Salmon captured that exceeded 65 mm in length were sampled. If 20 juvenile Coho Salmon over 65 mm were not collected from
the site, then the actual number collected was the sample size. Non-lethal stomach content samples were collected using gastric lavage. Fish were held head-down over a 250 micron sieve and stomach contents rinsed out with a stream of water from the nozzle of a rinse bottle (< 1 cm diameter) inserted in the mouth. Once the stomach contents were removed, they were individually preserved in 70% ethanol until they could be identified to the lowest practical taxonomic level, typically family. Taxa were also categorized into life stages of larvae or nymph, pupae, and adult. Dry weight estimates were calculated from total length or head width of the organisms using regression equations.

I used NMDS to visualize differences in fish diet composition between individual diet samples and among study sites. The NMDS used relative abundances of organisms in the diets, with individual diets as the unit of observation. Rare taxa found at only one site were excluded from the data set (Malison et al. 2015). The NMDS was used as a qualitative assessment to characterize multivariate differences in prey items among sites and as a visual representation of the patterns in diet composition. Taxa aligned closer to an off-channel pond in the NMDS plot make up a larger portion of the diet for that pond than taxa that are further away.

Summer Retention

Summer retention of juvenile Coho Salmon at each site was estimated using a robust design in Program MARK (White and Burnham 1999). The robust design integrates open (primary) and closed (secondary) models to estimate several parameters. Each month of sampling represented a primary event during which the population is
assumed to be open; the repeat sampling events conducted for population estimates were secondary events during which the population is assumed to be closed. Five primary sampling events (May, June, July, August, and September) and two secondary events in June and September were conducted at all sites except West Grider Pond. Only four primary sampling events (May, June, July, and August) and one secondary event in June were conducted in West Grider Pond.

Retention was modeled separately for each pond in program MARK and all parameters were modeled as either constant or as a function of time. Parameters estimated from a robust design model include apparent survival rate ($\phi$), capture ($p$) and recapture ($c$) probability, and probability of movement ($\gamma$). Apparent survival ($\phi$) is the probability a fish survives between primary sampling occasions and, conditional on surviving, remains within the population being sampled (fish did not disperse). I treated apparent survival as an estimate of retention, the proportion of fish present at the beginning of the sampling season that are still alive and present in the pond at the end of the sampling season. Capture probability ($p$) is the probability of capture during each primary sampling event, while recapture probability is the probability of being recaptured once tagged and given the fish was alive. For each primary occasion, apparent capture probability ($p$) and recapture probability ($c$) could vary with time. In the model for West Grider Pond, $p$ and $c$ equaled 1 for the last primary occasion (August) because all the fish were seined and removed from the site. Temporary movement, the probability of emigration from the pond ($\gamma^*$) and the probability of staying away from the pond given the fish left the pond ($\gamma'$), was also estimated between each primary event. Movement at
all sites was modeled as random and could vary with time. West Grider Pond was modeled with no movement since it was disconnected for the entire sampling season. I also ran models with no fish movement to compare to those with movement.

The top model for each pond was selected based on lowest Akaike Information Criterion (AIC). The same top model to estimate retention was found for each pond: apparent survival ($\phi$) varied with time, probability of capture ($p$) and probability of recapture ($c$) varied with time, and there was random movement that was constant over time. I combined the monthly $\phi$ estimates for each site into a single estimate for overall summer retention by multiplying the monthly estimates. I estimated the standard error of the overall retention estimate using 5000 bootstrapped iterations. To avoid unrealistic estimates (i.e. bootstrapped retention values > 1), bootstrapping was performed on the logit-transformed $\phi$ estimates and then back-transformed. I assumed that high retention rates indicated positive habitat selection and low mortality. However, mortality of tagged fish could reduce retention and retention estimates may also be affected by accessibility (e.g. fish may remain at a site because they cannot leave, not because they choose to stay).

Summer Growth

Specific growth (percent body weight gain / day) was calculated for PIT tagged Coho Salmon that were recaptured during the sampling period. Summer growth, $G$, was calculated as,
\[ G = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \times 100 \]

where \( W_1 \) is initial the weight at tagging, \( W_2 \) is the final weight at last recapture, \( t_1 \) is the date of initial capture and tagging, and \( t_2 \) is the date of last recapture. I used a one-way ANOVA to determine if growth rate differed among ponds, using individual fish as the unit of observation. I then used individual growth rates to calculate an average growth rate per off-channel pond.

Data Analysis

Due to the limited number of constructed off-channel habitats available to study in the middle Klamath River basin, model development with nearly as many predictors as observations has led to an exploratory analysis to identify relationships and develop hypotheses rather than a confirmatory approach. I assessed the correlation between abundance, retention, and growth and the collected predictor variables. Null-hypothesis significance testing is not appropriate and p-values are not reported for the analyses of relationships between fish performance and predictor variables.

Abundance

To answer the question regarding the relationship between Coho Salmon abundances and habitat conditions within and accessibility to the ponds, I used correlation to test for a relationship between the natural-log-transformed average summer Coho Salmon abundance per pond and individual predictors. Due to the correlation test using a single predictor variable to assess the relationship with abundance, several
predictor variables that would be better assessed together (natal stream, distance and
gradient from the Klamath River), rather than separately, were left out of the analysis but
are still reported in the results. Other accessibility and habitat variables included in the
test were then selected based on whether they varied across ponds and if that difference
was likely to be biologically meaningful for fish (see Results). The final correlation
analysis included the following potential predictors: whether the pond was ever
disconnected from the adjacent channel, the MWMT in the adjacent channel, MWMT of
the off-channel pond, average pond volume, and average chlorophyll $a$. West Grider
Pond was not included in this analysis due to the lack of connectivity in the spring 2014
to allow for fish to migrate out of the habitat.

Summer Retention

To answer the question regarding the relationship between Coho Salmon retention
in constructed habitats and density of Coho Salmon and food availability within the off-
channel habitats, I used correlation to test for a relationship. Predictor variables used in
the test included: the average summer density of Coho Salmon, as natural-log-
transformed plus 0.01, average zooplankton per cubic meter, and total estimated dry
weight of several available prey organisms (Chironomidae larvae and pupae,
Ceratopogonidae pupae, and Ephemeroptera nymphs) from the Hester-Dendy samplers.
The selected organisms were the most frequent prey items in the average diet of three or
more ponds. Zooplankton and available prey organisms were were natural-log-
transformed. West Grider Pond was not used in this analysis due to the lack of
connectivity in the spring 2014 to allow for fish to migrate out of the habitat. Camp Pond
was also not included in the analysis because there was no summer retention rate
calculated due to the lack of PIT tagged Coho Salmon.

**Growth**

To investigate whether available food within the habitats affected growth rates
among ponds, I used correlation to test for a relationship between average growth per
pond and several predictor variables. The predictor variables included: the average
summer density of Coho Salmon, as natural-log-transformed plus 0.01, average
zooplankton per cubic meter, and total estimated dry weight of several available prey
organisms (Chironomidae larvae and pupae, Ceratopogonidae pupae, and Ephemeroptera
nymphs) from the Hester-Dendy samplers. The prey organisms selected as predictors
were the most frequent prey items in the average diet of three or more ponds.
Zooplankton abundance and available prey organisms were were natural-log-
transformed. Stanshaw was not included in the analysis due to a small sample size of age-
1 Coho Salmon. The unit of observation in this analysis is the off-channel pond.
RESULTS

Capture and Tagging

Juvenile Coho Salmon were found in all nine study locations, though the numbers and sizes of the Coho Salmon captured were dramatically different across sites. Across all sites throughout the summer sampling period, a total of 1223 juvenile Coho Salmon were tagged. The recapture rate of these tagged Coho Salmon in all the study locations combined was 42% (Table 1). Overall, 23% of the fish exceeded 65 mm in May (Figure 4). As the sampling season progressed, more fish were available to PIT tag. Eighty-eight percent of fish exceeded 65 mm in September (Figure 4).

Table 1. Juvenile Coho Salmon tagging summary for May to September 2014 at nine study sites, including the total number of sampling efforts, total number of juvenile Coho Salmon tagged, and the total number subsequently recaptured. Some juvenile Coho Salmon were tagged by other organizations prior to the sampling period. These fish were only counted as recaptures if they were captured two or more times.

<table>
<thead>
<tr>
<th>Off-Channel Pond</th>
<th>No. Sampling Efforts</th>
<th>Total No. Tagged</th>
<th>Total No. Recaptured (1 or more times)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>5</td>
<td>372</td>
<td>123</td>
</tr>
<tr>
<td>Camp(^1)</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lower Seiad</td>
<td>5</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>May</td>
<td>5</td>
<td>247</td>
<td>134</td>
</tr>
<tr>
<td>O'Neil</td>
<td>5</td>
<td>28</td>
<td>8</td>
</tr>
<tr>
<td>Stanshaw(^2)</td>
<td>5</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Stender</td>
<td>5</td>
<td>71</td>
<td>46</td>
</tr>
<tr>
<td>Tom Martin</td>
<td>5</td>
<td>268</td>
<td>52</td>
</tr>
<tr>
<td>West Grider</td>
<td>4</td>
<td>231</td>
<td>143</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>44</strong></td>
<td><strong>1223</strong></td>
<td><strong>509</strong></td>
</tr>
</tbody>
</table>

Recapture rate 0.42

1. No Coho Salmon tagged because none exceeded 65 mm FL.
2. More Coho Salmon were recaptured than tagged because fish were tagged by the Karuk Tribe prior to sampling for this study.
Population Abundance

Population abundances of juvenile Coho Salmon in the summer varied significantly from one site to another (two-way ANOVA: $F_{8,8} = 68.75$, $p < 0.0001$; Table 2), but did not vary from June to September (two-way ANOVA: $F_{1,8} = 0.066$, $p = 0.80$; Table 2). The late summer West Grider Pond population estimate was conducted in August rather than September due to poor habitat conditions within the site. All fish were moved out of West Grider Pond at the beginning of August due to increasing water temperatures and decreasing water level. Some of these Coho Salmon were later detected on the antennas in Seiad Creek (Appendix A). Since ponds showed little variation in
abundance throughout the summer but differences from one site to another, I averaged June and September estimates within a site for use as a response variable in subsequent analyses.

Table 2. Juvenile Coho Salmon population estimates and standard error from June and September 2014 in each study pond. The second population estimate for West Grider Pond was measured in August rather than September.

<table>
<thead>
<tr>
<th>Off-Channel Pond</th>
<th>June</th>
<th>September</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>893 ± 40</td>
<td>879 ± 33</td>
<td></td>
</tr>
<tr>
<td>Camp</td>
<td>1 ± 0</td>
<td>0 ± 0</td>
<td></td>
</tr>
<tr>
<td>Lower Seiad</td>
<td>8 ± 2</td>
<td>0 ± 0</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>1020 ± 50</td>
<td>943 ± 61</td>
<td></td>
</tr>
<tr>
<td>O'Neil</td>
<td>179 ± 30</td>
<td>177 ± 25</td>
<td></td>
</tr>
<tr>
<td>Stanshaw</td>
<td>2 ± 0</td>
<td>2 ± 0</td>
<td></td>
</tr>
<tr>
<td>Stender</td>
<td>119 ± 11</td>
<td>80 ± 8</td>
<td></td>
</tr>
<tr>
<td>Tom Martin</td>
<td>119 ± 13</td>
<td>360 ± 25</td>
<td></td>
</tr>
<tr>
<td>West Grider</td>
<td>245 ± 11</td>
<td>215 ± 0</td>
<td></td>
</tr>
</tbody>
</table>

Unlike other sites in this study, Coho Salmon in West Grider Pond were likely age-1. This assumption is based on observations made by the Karuk Tribe and Mid Klamath Watershed Council in the winter of 2012-2013. High flows led to Grider Creek, the tributary just upriver of West Grider Creek on the Klamath River, flooding into West Grider Creek. Adult Coho Salmon then returned to spawn up West Grider Creek, which does not normally support spawning. The juveniles produced by these spawning adults then entered West Grider Pond for the summer and winter rearing periods of 2013-2014. Since the pond was disconnected in the spring of 2014, it is believed that the juvenile salmon encountered in this habitat were trapped age-1 fish, unable to migrate to the ocean.

Similar to abundance, densities of juvenile Coho Salmon varied significantly from one site to another (two-way ANOVA: F_{8,8} = 4.59, p = 0.02; Figure 5), but did not vary
significantly from June to September (two way ANOVA: $F_{1,8} = 2.88, p = 0.13$; Figure 5). However, there was a general trend of increasing density from June to September (Figure 5). A decrease in water volume, not an increase in fish abundance, was responsible for the density increase at most sites. The West Grider Pond volume decreased from 278 m$^3$ in June to just 47 m$^3$ at the beginning of August while the number of Coho Salmon stayed about the same. However, the large increase in population density in Tom Martin Pond was likely due to an increase in the number of Coho Salmon in the site, rather than decreasing volume.

![Figure 5. Densities (fish/m$^3$) and standard error bars of juvenile Coho Salmon from June (dark grey) and September (light grey) 2014 in each of the study sites. The second density estimate for West Grider Pond was estimated in August rather than September.](image)
A variety of other vertebrates were found in each study site. Other salmonids included Chinook Salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss*. Brown bullhead catfishes *Ameiurus nebulosus*, speckled dace *Rhinichthys osculus*, fathead minnow *Pimephales promelas*, three-spined stickleback *Gasterosteus aculeatus*, and sunfish *Lepomis* spp. were present (Figure 6). Few species besides Coho Salmon were found in Alexander, May, Stender, and West Grider ponds.

![Graph showing number of different fish species found in each study site](image)

**Figure 6.** Number of bullhead catfish (orange), Chinook Salmon (darker blue), fathead minnow (pink), steelhead (green), three-spined stickleback (purple), sunfish species (light blue), and tadpoles (yellow) found in the study sites during monthly seining events.
Site Accessibility

Site accessibility and other physical habitat characteristics measured throughout the summer varied among sites (Table 3). Only two accessibility variables (adjacent MWMT, disconnected or not) were ultimately assessed during the correlation analysis. The MWMT of the adjacent channel variable among pond was above 20°C for all ponds, potentially causing juvenile salmonids to avoid the main channel and seek thermal refuge elsewhere (Welsh et al 2001; Sutton and Soto 2012; Brewitt and Danner 2014). Though the depth of the inlet channels varied among sites, they did not vary considerably. Fish were likely to move through the inlet channel no matter the depth, as long as the inlet was connected. Therefore, this variable was not used in the correlation analysis. Instead, I considered whether the constructed pond was ever disconnected from the adjacent channel during summer 2014. Finally, though the type of habitat at the inlet (pool or riffle) was collected, it was determined that this variable may not be an important variable in determining fish abundance in the constructed ponds during low summer flows and thus removed from the analysis.
Table 3. Physical habitat characteristics and site accessibility variables representing summer 2014 conditions for each study sites. Standard errors are included for values that are an average of multiple observations.

<table>
<thead>
<tr>
<th>Predictor Variable</th>
<th>Alexander Pond</th>
<th>Camp Pond</th>
<th>Lower Seiad Pond</th>
<th>May Pond</th>
<th>O’Neil Pond</th>
<th>Stanshaw Pond</th>
<th>Stender Pond</th>
<th>Tom Martin Pond</th>
<th>West Grider Pond</th>
</tr>
</thead>
<tbody>
<tr>
<td>Access</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natal</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Habitat at Inlet</td>
<td>pool</td>
<td>riffle</td>
<td>pool</td>
<td>riffle</td>
<td>riffle</td>
<td>pool</td>
<td>pool</td>
<td>pool</td>
<td>riffle</td>
</tr>
<tr>
<td>Distance from Klamath (m)</td>
<td>4509</td>
<td>1276</td>
<td>430</td>
<td>498</td>
<td>45</td>
<td>22</td>
<td>4079</td>
<td>14</td>
<td>385</td>
</tr>
<tr>
<td>Gradient from Klamath (%)</td>
<td>1.4</td>
<td>1.8</td>
<td>0.4</td>
<td>0.7</td>
<td>5.4</td>
<td>1.4</td>
<td>1.3</td>
<td>6.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Avg. Inlet Depth (m)</td>
<td>0.12 (0.03)</td>
<td>0.34 (0.07)</td>
<td>0.06 (0.04)</td>
<td>0.14 (0.04)</td>
<td>0.11 (0.01)</td>
<td>0.03 (0.02)</td>
<td>0.09 (0.01)</td>
<td>0.49 (0.04)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Adjacent MWMT (°C)</td>
<td>23.2 (0.6)</td>
<td>20.4 (0.4)</td>
<td>23.2 (0.5)</td>
<td>22.9 (0.5)</td>
<td>26.5 (0.5)</td>
<td>22.3 (0.3)</td>
<td>23.2 (0.6)</td>
<td>26.5 (0.5)</td>
<td>21.8 (1.1)</td>
</tr>
<tr>
<td>Ever Disconnected during summer</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Volume (m³)</td>
<td>947 (104)</td>
<td>549 (94)</td>
<td>245 (29)</td>
<td>934 (200)</td>
<td>465 (66)</td>
<td>730 (217)</td>
<td>396 (31)</td>
<td>398 (84)</td>
<td>163 (116)</td>
</tr>
<tr>
<td>Avg. Depth (m)</td>
<td>1.3 (0.06)</td>
<td>1.3 (0.01)</td>
<td>0.9 (0.04)</td>
<td>1.2 (0.15)</td>
<td>0.5 (0.01)</td>
<td>1.3 (0.37)</td>
<td>0.9 (0.05)</td>
<td>1.0 (0.03)</td>
<td>0.6 (0.24)</td>
</tr>
<tr>
<td>Avg. Chlorophyll a</td>
<td>7 (3)</td>
<td>18 (9)</td>
<td>20 (5)</td>
<td>6 (2)</td>
<td>7 (2)</td>
<td>12 (6)</td>
<td>15 (4)</td>
<td>11 (3)</td>
<td>9 (3)</td>
</tr>
<tr>
<td>Avg. Turbidity (NTU)</td>
<td>1.5 (0.3)</td>
<td>0.4 (0.2)</td>
<td>1.1 (0.1)</td>
<td>1.5 (0.2)</td>
<td>1.2 (0.3)</td>
<td>0.8 (0.2)</td>
<td>1.7 (0.5)</td>
<td>0.3 (0.1)</td>
<td>1.4 (0.5)</td>
</tr>
<tr>
<td>MWMT (°C)</td>
<td>19.0</td>
<td>21.8</td>
<td>27.0</td>
<td>15.1</td>
<td>24.6</td>
<td>18.6</td>
<td>21.5</td>
<td>20.2</td>
<td>18.9</td>
</tr>
<tr>
<td>Avg. Dissolved Oxygen (mg/L)</td>
<td>7.0 (0.6)</td>
<td>8.8 (0.5)</td>
<td>9.8 (1.5)</td>
<td>5.0 (0.5)</td>
<td>7.5 (0.6)</td>
<td>10.2 (0.5)</td>
<td>7.2 (1.4)</td>
<td>9.4 (0.9)</td>
<td>7.9 (0.9)</td>
</tr>
<tr>
<td>Diel Temperature Variation (°C)</td>
<td>0.7 (0.0)</td>
<td>1.2 (0.1)</td>
<td>3.5 (0.1)</td>
<td>1.1 (0.1)</td>
<td>3.8 (0.3)</td>
<td>1.3 (0.1)</td>
<td>0.6 (0.1)</td>
<td>1.7 (0.1)</td>
<td>1.0 (0.3)</td>
</tr>
</tbody>
</table>
Habitat Conditions

Measured physical habitat variables varied across study sites (Table 3). Though several habitat variables varied among sites, only MWMT of the pond, pond volume, and average summer chlorophyll a were used in the correlation test. Water temperatures were not consistent among sites (Figure 7) with Lower Seiad Pond MWMT exceeding potentially lethal temperatures (Beschta et al. 1987) and several other pond MWMT reaching stressful limits. Most MWMT in ponds were cooler than the adjacent stream habitats; however MWMT in Camp and Lower Seiad ponds was higher than that in the adjacent channels (Table 4). Though several sites had high temperatures, there were locations within sites with tolerable temperatures for Coho Salmon. Temperatures within sites varied along the entire length or throughout the water column. The ponds were stratified, with temperatures that were warmer at the surface than the bottom, with as much of a difference in temperature at 6°C at some ponds (Figure 8). Diel temperature variation within the sites did not vary considerably among ponds. Though there was some variation, diel temperature variation is correlated with MWMT and depth and was therefore left out of the analysis. Average pond depth and volume varied across ponds, though only volume was used in the analysis due to the correlation between the two variables.
Figure 7. Mean weekly maximum temperatures (MWMT) of all the study sites from May to October 2014. The different blue sites (Alexander, Lower Seiad, May, and Stender ponds) are all located on Seiad Creek. The red sites are upriver of Seiad Creek and the green sites are located downriver of Seiad Creek, near the town of Orleans. The moving dashed lines are the Klamath River water temperature and the two horizontal dashed lines represent the cessation of growth (Brett 1952) and lethal temperatures (Beschta et al. 1987) for Coho Salmon. The gap in water temperature data for West Grider Pond is due to a decrease in water level that exposed the temperature logger to the air.
Table 4. Temperature difference in MWMT in the off-channel habitat compared to MWMT in the adjacent channel. A negative number indicates that the off-channel habitat had a lower MWMT than the adjacent channel.

<table>
<thead>
<tr>
<th>Off-Channel Pond</th>
<th>Adjacent Channel</th>
<th>MWMT (°C) of the Pond</th>
<th>MWMT (°C) of Adjacent Channel</th>
<th>Temperature Difference (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>Seiad Creek</td>
<td>19.0</td>
<td>23.2</td>
<td>-4.2</td>
</tr>
<tr>
<td>Camp</td>
<td>Camp Creek</td>
<td>21.8</td>
<td>20.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Lower Seiad</td>
<td>Seiad Creek</td>
<td>27.0</td>
<td>23.2</td>
<td>3.8</td>
</tr>
<tr>
<td>May Pond</td>
<td>Seiad Creek</td>
<td>15.1</td>
<td>22.9</td>
<td>-7.8</td>
</tr>
<tr>
<td>O'Neil</td>
<td>Klamath River</td>
<td>24.6</td>
<td>26.5</td>
<td>-1.9</td>
</tr>
<tr>
<td>Stanshaw</td>
<td>Klamath River</td>
<td>18.6</td>
<td>22.3</td>
<td>-3.7</td>
</tr>
<tr>
<td>Stender</td>
<td>Seiad Creek</td>
<td>21.5</td>
<td>23.2</td>
<td>-1.7</td>
</tr>
<tr>
<td>Tom Martin</td>
<td>Klamath River</td>
<td>20.2</td>
<td>26.5</td>
<td>-6.3</td>
</tr>
<tr>
<td>West Grider</td>
<td>West Grider Creek</td>
<td>18.9</td>
<td>21.8</td>
<td>-2.9</td>
</tr>
</tbody>
</table>
Figure 8. Temperature stratification from one transect in July in the off-channel habitats. Note that the x-axis is the length of the ponds starting at the back and moving to the inlet or front area. Ponds vary in length and depth. Though measurements were taken each month, July is provided to demonstrate the stratification experienced during the hottest month of summer 2014.
Chlorophyll \( a \) was significantly different among sites (two-way ANOVA: \( F_{8,30} = 2.17, p = 0.05 \); Table 3) and also varied from month to month (two-way ANOVA: \( F_{4,30} = 12.06, p < 0.0001 \)). Lower Seiad, Stender, and West Grider ponds had high chlorophyll \( a \) readings throughout the summer while Camp and Stanshaw ponds had low levels at the beginning of sampling and increased through the summer. Chlorophyll \( a \) was selected for analysis due to varying significantly among ponds and the possibility of representing differences in primary production within the ponds.

Average dissolved oxygen had relatively consistent values among ponds and were above tolerable levels for juvenile salmonids throughout a majority of the habitats (Table 3). Matthews and Berg (1997) also found juvenile trout, when faced with the choice between high temperature and low dissolved oxygen, distributed based on lowest water temperature despite the potential association with low dissolved oxygen due to groundwater influence. Due to these reasons, dissolved oxygen was left out of the analysis.

Though turbidity differed among sites (two-way ANOVA: \( F_{8,30} = 5.52, p = 0.0003 \)), and month (two-way ANOVA: \( F_{4,30} = 1.05, p = 0.04 \)), the summer average only ranged from 0.3 to 1.7 NTU (Table 3), excluding measurements from West Grider Pond in August, which had high turbidity readings (32.6 NTU) due to disturbance associated with fish removal and lack of flow. Due to this small range across ponds, which likely had no biological impact on juvenile Coho Salmon, turbidity was left out of the correlation analysis.
Of the predictors considered, average chlorophyll $a$ had the strongest correlation with abundance of juvenile Coho Salmon in the ponds (Table 5; Figure 9, Figure 10). Ponds with high chlorophyll $a$ had fewer Coho Salmon. None of the other predictors had strong associations with abundance. For the selected accessibility variables, MWMT of the adjacent channel was positively correlated with Coho Salmon abundance and whether a pond had been disconnected at some point during the sampling season was negatively correlated with abundance (Table 5; Figure 9). For the remaining selected habitat variables, MWMT of the pond was weakly, negatively correlated with abundance, while pond volume was positively correlated with abundance (Table 5; Figure 10).

Table 5. Correlation values for tested access and habitat predictors of juvenile Coho Salmon abundance in constructed habitats.

<table>
<thead>
<tr>
<th>Predictor Variables</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Access</strong></td>
<td></td>
</tr>
<tr>
<td>Adjacent Maximum Weekly Maximum Temperature (°C)</td>
<td>0.51</td>
</tr>
<tr>
<td>Ever Disconnected</td>
<td>-0.44</td>
</tr>
<tr>
<td><strong>Habitat</strong></td>
<td></td>
</tr>
<tr>
<td>Average Chlorophyll $a$</td>
<td>-0.78</td>
</tr>
<tr>
<td>MWMT (°C)</td>
<td>-0.41</td>
</tr>
<tr>
<td>Volume (m$^3$)</td>
<td>0.39</td>
</tr>
</tbody>
</table>
Figure 9. Raw data plots of average summer juvenile Coho Salmon abundance in off-channel habitats related to the MWMT of the adjacent channel (A) and whether the habitat ever became disconnected (0 = never disconnected, 1 = disconnected at some point) from the adjacent channel during summer 2014 (B). Symbols distinguish pond: Alexander (open square), Camp (open circle), Lower Seiad (open triangle), May Pond (open diamond), O’Neil (open inverted triangle), Stanshaw (closed square), Stender (closed triangle), and Tom Martin (closed diamond) ponds.
Figure 10. Raw data plots of average summer juvenile Coho Salmon abundance in off-channel habitats related to the average summer chlorophyll $a$ level (A), the MWMT of the pond (B), and whether the pond volume (C). Symbols distinguish pond: Alexander (open square), Camp (open circle), Lower Seiad (open triangle), May Pond (open diamond), O'Neil (open inverted triangle), Stanshaw (closed square), Stender (closed triangle), and Tom Martin (closed diamond) ponds.
Prey Availability

**Hester-Dendy Sampling**

The most abundant organism by total number differed among sites and between months (Figure 11). Gastropoda had the greatest biomass in all sites except Alexander and May ponds, where Oligochaeta and Chironomidae pupae had the greatest biomasses, respectively (Table 6).

![Figure 11. Proportion of total number of organisms per Hester-Dendy sampler by site in the months of July and August 2014. Alex=Alexander, Stan=Stanshaw, and Sten=Stender.](image)
Table 6. Dry estimated weight (mg) and standard errors of available prey items from Hester-Dendy sampler by site, averaged across samples from July and August 2014 within each pond.

<table>
<thead>
<tr>
<th>Available Prey Organism</th>
<th>Alexander Pond</th>
<th>Camp Pond</th>
<th>Lower Seiad Pond</th>
<th>May Pond</th>
<th>O'Neil Pond</th>
<th>Stanshaw Pond</th>
<th>Stender Pond</th>
<th>Tom Martin Pond</th>
<th>West Grider Pond</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphipoda</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.7 (0.6)</td>
<td>0.1 (0.1)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Anisoptera (L)</td>
<td>0.0 (0.0)</td>
<td>0.1 (0.1)</td>
<td>3.8 (1.6)</td>
<td>0.0 (0.0)</td>
<td>21.3 (2.0)</td>
<td>0.0 (0.0)</td>
<td>6.1 (0.1)</td>
<td>8.7 (8.7)</td>
<td>3.8 (1.9)</td>
</tr>
<tr>
<td>Bivalvia</td>
<td>0.1 (0.1)</td>
<td>0.0 (0.0)</td>
<td>1.2 (1.2)</td>
<td>0.0 (0.0)</td>
<td>2.6 (2.0)</td>
<td>0.1 (0.1)</td>
<td>0.6 (0.5)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Ceratopogonidae (L)</td>
<td>1.2 (0.1)</td>
<td>0.1 (0.1)</td>
<td>1.2 (0.5)</td>
<td>6.4 (5.2)</td>
<td>0.8 (0.2)</td>
<td>0.0 (0.0)</td>
<td>2.0 (0.3)</td>
<td>1.7 (0.3)</td>
<td>3.2 (2.0)</td>
</tr>
<tr>
<td>Ceratopogonidae (P)</td>
<td>1.2 (1.2)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.3 (0.3)</td>
<td>0.0 (0.0)</td>
<td>2.7 (1.3)</td>
</tr>
<tr>
<td>Chironomidae (L)</td>
<td>1.5 (0.4)</td>
<td>1.4 (0.4)</td>
<td>3.1 (0.4)</td>
<td>4.0 (0.6)</td>
<td>4.1 (2.9)</td>
<td>0.4 (0.1)</td>
<td>1.8 (1.0)</td>
<td>5.0 (2.5)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Chironomidae (P)</td>
<td>1.8 (1.7)</td>
<td>2.2 (1.5)</td>
<td>0.6 (0.5)</td>
<td>36.9 (0.2)</td>
<td>3.0 (1.9)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>9.6 (0.6)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Coleoptera (L/A)</td>
<td>0.1 (0.1)</td>
<td>0.1 (0.1)</td>
<td>0.9 (0.0)</td>
<td>0.4 (0.3)</td>
<td>0.3 (0.3)</td>
<td>0.1 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.2 (0.0)</td>
<td>0.2 (0.0)</td>
</tr>
<tr>
<td>Diptera Other (P)</td>
<td>0.1 (0.1)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.3 (0.3)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Ephemeroptera (N)</td>
<td>0.1 (0.1)</td>
<td>3.3 (3.3)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>1.0 (0.3)</td>
<td>0.0 (0.0)</td>
<td>3.9 (1.2)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>7.1 (3.5)</td>
<td>402 (254)</td>
<td>152 (273)</td>
<td>115 (131)</td>
<td>86.7 (13)</td>
<td>23.9 (2.7)</td>
<td>34.8 (9.0)</td>
<td>49.7 (50)</td>
<td>251 (26)</td>
</tr>
<tr>
<td>Hydrozoa</td>
<td>0.5 (0.4)</td>
<td>0.3 (0.3)</td>
<td>0.1 (0.1)</td>
<td>0.1 (0.1)</td>
<td>0.1 (0.1)</td>
<td>0.1 (0.0)</td>
<td>0.1 (0.0)</td>
<td>1.3 (1.3)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Isopoda</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Megaloptera (L)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>33.9 (5.5)</td>
<td>1.1 (0.3)</td>
<td>16.6 (1.9)</td>
<td>7.6 (7.6)</td>
<td>7.6 (5.5)</td>
<td>1.4 (1.3)</td>
<td>7.7 (2.8)</td>
<td>12.5 (1.9)</td>
<td>4.1 (1.0)</td>
</tr>
<tr>
<td>Trichoptera (L/P)</td>
<td>0.0 (0.0)</td>
<td>12.0 (3.9)</td>
<td>0.0 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.1 (0.0)</td>
<td>1.2 (0.9)</td>
<td>0.0 (0.0)</td>
<td>10.4 (10.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Worm-like</td>
<td>0.6 (3.0)</td>
<td>0.0 (0.0)</td>
<td>0.5 (0.2)</td>
<td>0.2 (0.1)</td>
<td>0.2 (0.2)</td>
<td>0.1 (0.1)</td>
<td>0.5 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.2 (0.2)</td>
</tr>
<tr>
<td>Zygoptera (L)</td>
<td>2.3 (1.1)</td>
<td>5.0 (4.8)</td>
<td>0.0 (0.0)</td>
<td>0.3 (0.0)</td>
<td>0.3 (0.1)</td>
<td>0.0 (0.0)</td>
<td>2.1 (1.8)</td>
<td>0.8 (0.7)</td>
<td>4.2 (2.1)</td>
</tr>
<tr>
<td>Zooplankton</td>
<td>0.1 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.1 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
</tbody>
</table>
NMDS ordination of relative abundance of organisms on the Hester-Dendy samplers had a solution that represented 64.8% of the total variation samples two axes (Figure 12). Those sites that orient closer together are more similar than those sites that ordinate further away. Results show that individual samples from the same site tend to orient near one another, with the averaged center point of each pond oriented in several locations along both axes. These results suggest there was variation in available benthic prey items among ponds.
Figure 12. Ordination plot obtained by nonmetric multidimensional scaling (NMDS) of the relative abundances of organisms collected on the Hester-Dendy samplers in all study sites. Alexander (Alex; open square), Camp (open circle), Lower Seiad (LS; open triangle), May (open diamond), O’Neil (ON; open inverted triangle), Stanshaw (Stan; closed square), Stender (Sten; closed triangle), Tom Martin (TM; closed diamond), and West Grider (WG; closed circle) ponds. Panel A has individual samples represented as symbols and site names are centroid locations. Panel B had the invertebrate vector locations obtained through NMDS. Stages include: L=larvae, P=pupae, A=adult. Taxa include: Am=Amphipoda, Bv=Bivalvia, Ga=Gastropoda, Hy=Hydrozoa, An=Anisoptera, Col=Coleoptera, Cer=Ceratopogonidae, Cer/O=Ceratopogonidae/Other Diptera, Chi=Chironomidae, DO=Diptera Other, Ep=Ephemeroptera, Hem=Hemiptera, Me=Megaloptera, Ost=Ostracoda, Tr=Trichoptera, Zp=Zooplankton, Zyg=Zygoptera.
Zooplankton Sampling

Zooplankton per cubic meter varied among study sites (two-way ANOVA: $F_{8,8} = 3.73, p = 0.04$) but not between June and August (two-way ANOVA: $F_{1,8} = 2.50, p = 0.15$). Cladocera were most abundant in both sampling events compared to other zooplankton. Zooplankton abundances in West Grider Pond in August were collected a week after Coho Salmon removal due to declining habitat conditions, potentially creating a large increase (Figure 13). Non-zooplankton organisms found in the zooplankton tows included: Simuliidae in Stanshaw Pond; Chironomidae, Ephemeroptera, and Oligochaeta in Stender Pond; and Oligochaeta and Ephemeroptera in West Grider Pond. Non-zooplankton organisms were not included as a part of the zooplankton counts.
Figure 13. Number of zooplankton per cubic meter of water in the months of May (dark grey) and August (light grey) at each of the off-channel habitats based on zooplankton tows from each study site. The measurement from West Grider Pond in August was taken a week after all juvenile Coho Salmon were removed from the site.

Diet Composition

Zooplankton numerically dominated the diets of juvenile Coho Salmon, making up about 51% of all diets items. Diptera was the second most abundant prey item, making up 25% percent of all the diet items of the juvenile Coho Salmon. In terms of prey biomass, Coho Salmon diets were dominated by Diptera (larva, pupa, and adult combined), which made up about 57% of the total diet biomass (Figure 14). Sample size varied among ponds based on availability of Coho Salmon and average length of fish utilized for diet content analysis typically ranged from 67 to 77 mm (Table 7). Stanshaw
Pond had several larger Coho Salmon present within the pond that were captured and sampled.

Figure 14. Relative biomass of organisms in the diets of juvenile Coho Salmon at the study sites. There were no juvenile Coho Salmon captured in Camp Pond greater than 65 mm for diet collection. Values across the top of the bars are the number of juvenile Coho Salmon sampled and averaged to estimate the proportion of organisms in the diets.
Table 7. Average Coho Salmon length (mm) and weight (g) and their standard error for each study site. All sites were averaged from the months stomach contents were collected. Alexander, O’Neil, Stender, and Tom Martin ponds had stomach contents collected in July and August, Lower Seiad Pond was in June and August, Stanshaw Pond was in August, and May Pond was in June, July, August, and September.

<table>
<thead>
<tr>
<th>Off-Channel Pond</th>
<th>Sample Size</th>
<th>Average Length of Lavaged Fish (mm)</th>
<th>Average Weight of Lavaged Fish (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>40</td>
<td>74 ± 2</td>
<td>5.6 ± 0.4</td>
</tr>
<tr>
<td>Lower Seiad</td>
<td>4</td>
<td>76 ± 1</td>
<td>5.0 ± 0.2</td>
</tr>
<tr>
<td>May</td>
<td>80</td>
<td>76 ± 1</td>
<td>5.4 ± 0.2</td>
</tr>
<tr>
<td>O’Neil</td>
<td>23</td>
<td>67 ± 2</td>
<td>3.5 ± 0.1</td>
</tr>
<tr>
<td>Stanshaw</td>
<td>4</td>
<td>110 ± 10</td>
<td>16.7 ± 1.8</td>
</tr>
<tr>
<td>Stender</td>
<td>40</td>
<td>74 ± 12</td>
<td>5.9 ± 0.6</td>
</tr>
<tr>
<td>Tom Martin</td>
<td>40</td>
<td>69 ± 1</td>
<td>4.1 ± 0.2</td>
</tr>
<tr>
<td>West Grider</td>
<td>20</td>
<td>77 ± 1</td>
<td>5.6 ± 0.2</td>
</tr>
</tbody>
</table>

The NMDS ordination of relative abundance of organisms in juvenile Coho Salmon diets had a solution that represented 89.8% of the total variation among sites on two axes (Figure 15). Those sites that ordinate closer together are more similar than those sites that ordinate further away. Prey taxa that are oriented along the same axes as an off-channel pond and closer to the pond in the NMDS plot make up a larger portion of the diet for that pond than other taxa. A majority of the individual diet samples orient near one another (dense cluster of points near the origin in Figure 15A), indicating that fish in all of the ponds generally had similar diets. The results suggest that fish were selecting similar prey items even though there were visual differences in the available prey items among ponds (Figure 12A). However, there were individual fish with distinct diets from several ponds, reflecting substantial idiosyncrasy in foraging (Figure 15A). Tom Martin and O’Neil ponds have a high proportion of diet samples oriented away from the main cluster of samples due to great prevalence of adult Diptera, Hemiptera, and adult...
Trichoptera/Ephemeroptera/Megaloptera (Figure 15B) in the diet compared to the other ponds, thus the centroid values for the two ponds orient away from the others.
Figure 15. Ordination plot obtained by nonmetric multidimensional scaling (NMDS) of the relative abundances of organisms in the diets of juvenile Coho Salmon rearing in constructed off-channel habitats. Symbols distinguish ponds: Alexander (Alex; open square), Lower Seiad (LS; open triangle), May (open diamond), O’Neil (ON; open inverted triangle), Stanshaw (Stan; filled square), Stender (Sten; filled triangle), Tom Martin (TM; filled diamond), and West Grider (WG; filled circle) ponds. Panel A has individual diets represented as symbols and site names are the centroid locations. Panel B has the invertebrate vector locations obtained through the NMDS. Stages include: L=larvae, P=pupae, A=adult. Taxa include: Am=Amphipoda, Bv=Bivalvia, Ga=Gastropoda, Hy=Hydrozoa, An=Anisoptera, Col=Coleoptera, Cer=Ceratopogonidae, Cer/O=Ceratopogonidae/Other Diptera, Chi=Chironomidae, DO=Diptera Other, Ep=Ephemeroptera, Hem=Hemiptera, Me=Megaloptera, Ost=Ostracoda, Tr=Trichoptera, Zp=Zooplankton, Zyg=Zygoptera.
Summer Retention

Summer retention rate of juvenile Coho Salmon was the highest in West Grider Pond and lowest in Lower Seiad Pond (Figure 16); however, West Grider Pond was not used in the analysis because it was not connected, so the retention estimate is not comparable to the other ponds. Retention could not be estimated in Camp Pond because there were no PIT-tagged Coho Salmon in the pond.

Figure 16. Summer retention rate (Overall $\phi$) and standard error of juvenile Coho Salmon at each of the study sites over the summer of 2014.
When testing the correlation of Coho Salmon retention and the predictor variables, I found a weak positive correlation with average Coho Salmon density and a strong positive correlation with zooplankton abundance (Table 8; Figure 17A, B). Though there is a strong relationship between retention and zooplankton, Alexander Pond is an outlier in this analysis and results may not be biologically meaningful with only one pond greatly driving this relationship. There was no strong association between retention and population density or the total estimated dry weight of several available prey organisms (Chironomidae larvae and pupae, Ceratopogonidae pupae, and Ephemeroptera nymphs) from the Hester-Dendy samplers that were the most frequent prey items in the average diets of several ponds (Table 8; Figure 17C).

Table 8. Correlation values for the tested predictors of juvenile Coho Salmon retention in constructed habitats. All variables were natural-log-transformed.

<table>
<thead>
<tr>
<th>Predictor Variables</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Coho Salmon Density (fish/m$^3$)</td>
<td>0.30</td>
</tr>
<tr>
<td>Zooplankton per cubic meter</td>
<td>0.69</td>
</tr>
<tr>
<td>Weight (mg) of available prey organisms that were frequent in diet composition</td>
<td>-0.09</td>
</tr>
</tbody>
</table>
Figure 17. Raw data plots of juvenile Coho Salmon retention in off-channel habitats related to average Coho Salmon density (A), zooplankton per cubic meter (B), and the total dry weight of several available prey organisms that were frequent in the diets of Coho Salmon (C). Symbols distinguish pond: Alexander (open square), Lower Seiad (open triangle), May Pond (open diamond), O'Neil (open inverted triangle), Stanshaw (closed square), Stender (closed triangle), and Tom Martin (closed diamond) ponds.
Summer Growth

Average summer growth rates of juvenile Coho Salmon were significantly different among study sites (one-way ANOVA: $F_{6,461} = 18.74$, $p < 0.0001$). Fish from West Grider Pond had the lowest specific summer growth rate at 0.03 % body weight per day, fish from Tom Martin Pond had the highest at 0.60 % per day (Figure 18). Despite higher growth rates in Tom Martin and O'Neil ponds, retention was lower in these ponds than sites with lower growth rates.

Figure 18. Box and whisker plot of summer growth rates of juvenile Coho Salmon at the study sites and the total number of recaptured Coho Salmon used for the estimate. Growth could not be estimated at two study sites where no Coho Salmon were recaptured.
Average Coho Salmon growth per pond was negatively correlated with average Coho Salmon density (Table 9; Figure 19A, B), but this relationship was driven primarily by low growth and high population density in West Grider Pond. There was no strong association between growth and zooplankton abundance or the total estimated dry weight of several available prey organisms (Chironomidae larvae and pupae, Ceratopogonidae pupae, and Ephemeroptera nymphs) from the Hester-Dendy samplers that were the most frequent prey items in the average diets of several ponds (Table 9; Figure 19C).

Table 9. Correlation values for the tested predictors of average juvenile Coho Salmon growth in constructed habitats. All variables were natural-log-transformed.

<table>
<thead>
<tr>
<th>Predictor Variables</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Coho Salmon Density (fish/m³)</td>
<td>-0.77</td>
</tr>
<tr>
<td>Zooplankton per cubic meter</td>
<td>-0.29</td>
</tr>
<tr>
<td>Weight (mg) of available prey organisms that were frequent in diet composition</td>
<td>0.35</td>
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</table>
Figure 19. Raw data plots of average growth of Coho Salmon utilizing off-channel habitats related to average Coho Salmon density (A), zooplankton per cubic meter (B), and the total dry weight of several available prey organisms that were frequent in the diets of Coho Salmon (C). Symbols distinguish pond: Alexander (open square), May Pond (open diamond), O’Neil (open inverted triangle), Stender (closed triangle), Tom Martin (closed diamond), and West Grider (closed circle) ponds.
DISCUSSION

This study was conducted with an exploratory approach to better understand the different factors that may affect juvenile Coho Salmon abundance, retention, and growth in constructed off-channel ponds. Though these habitats are initially constructed for winter rearing, juvenile Coho Salmon winter survival is also partially mediated by summer conditions that may affect growth and condition into the winter. Juvenile Coho Salmon summer abundance, retention, and growth in constructed off-channel habitats varied widely among ponds suggesting that constructed habitats may not all have the same potential to support Coho Salmon during summer rearing. However, the potential predictor variables that I measured did not explain this variation, suggesting that these habitat characteristics in the constructed ponds are within a suitable range for juvenile Coho Salmon.

Abundance

The constructed off-channel habitats I sampled in this study supported varying abundances of juvenile Coho Salmon, ranging from as few as one in Camp Pond to as many as 1000 in May Pond. Coho Salmon use of the off-channel habitats I sampled is similar to other studies conducted in pool habitats (Swales and Levings 1989; Nickelson et al. 1992a; Solazzi et al. 2000; Morley et al. 2005; Witmore 2014). Coho Salmon summer densities in individual constructed ponds ranged from 0 fish/m² to 1.33 fish/m², similar to other studies on Coho Salmon (Nielsen 1992; Lang et al. 2006; Rosenfeld and
Raeburn 2009; Kiffney 2014; Malison et al. 2015). Note that this density is in units of fish per area in order to compare to other studies. However, fish per cubic meter was a better representation of densities for this study due to the varying depths of the constructed ponds.

Summer 2014 was a continuation of drought conditions resulting in very low flows and high water temperatures. The off-channel ponds experienced extremely variable habitat conditions between the sites during the sampling period. Several sites had suitable temperatures (less than 22 °C) and dissolved oxygen (greater than 4 mg/L) in a majority of the habitat; However, there were also some sites (Lower Seiad and Camp ponds) that had unsuitable conditions throughout the off-channel habitat during peak air and there were few Coho Salmon captured in these ponds. As in previous work in the main stem and tributaries of the Klamath River (Sutton et al. 2007; Hillemeier et al. 2009; Sutton and Soto 2012; Brewitt and Danner 2014; Witmore 2014), temperature seemed to be a driver of fish distribution and abundance into thermal refugia and off-channel habitats. High ambient stream temperatures in the creek channel may drive fish into off-channel habitats if they provide suitable temperatures for growth and survival (Nielsen et al. 1994; Sutton and Soto 2012; Brewitt and Danner 2014).

Though abundance was strongly correlated with an index of habitat productivity (chlorophyll a), the strong negative association of suspended chlorophyll a (phytoplankton) to fish abundance seen in this study was not expected. Zooplankton abundance typically increases with the presence of phytoplankton (Conde-Porcuna et al. 2002; Goldyn and Kowalczewska-Madura 2008), thus providing a food source of
zooplankton for fishes. However, I found a weak correlation between chlorophyll $a$ and the number of zooplankton in the water column, though chlorophyll $a$ was positively correlated with pond MWMT. There may have been a confounding effect of temperature on the results of this correlation test because increased temperature is typically associated with increased primary productivity (Barko and Smart 1981; Butterwick et al. 2004; Ziauddin et al. 2013).

Accessibility of these habitats throughout the year is important to allow juvenile salmonids to move in different seasons and utilize different habitats necessary for growth and survival. Constructed off-channel habitats need to be connected not only for fish to move into the habitats for refuge, but also to escape poor water quality conditions or to move out of the habitats for ocean migration (Bilby and Bisson 1987; Brown and Hartman 1988; Henning et al. 2006). Without the ability to emigrate from the habitat, there is a decrease in the benefits and contribution to the population associated with the constructed ponds, even if they provide ideal rearing conditions. Coho Salmon in West Grider Pond were unable to migrate to the ocean during spring 2014 after a year of rearing because the habitat was not connected. Although considerable effort is directed toward selecting pond locations and designing ponds so that they will provide suitable habitat and be accessible to fish, there are several constraints imposed by land ownership, permitting, site geology, available funds, and our understanding of Coho Salmon requirements as well as seasonal variation that might limit their production.
Alternative Explanations of Abundance

Because there was a difference in abundance among constructed ponds that was not well explained by the predictors I measured, other factors may play a role in the determining the Coho Salmon utilizing these ponds. Differences in the numbers of spawning adult Coho Salmon and the proximity of spawning to these off-channel habitats may impact the abundances of juvenile Coho Salmon available to move into the habitats, as suggested by Swales and Levings (1989) and Cooperman et al. (2006). The ponds researched in this study were constructed in locations where juvenile Coho Salmon were known to occur; however, total numbers of juveniles in search of seasonal off-channel habitats likely differs from one drainage to another.

Juvenile fish abundance may also be attributed in part to seasonal variation in off-channel pond connections to the main channel in relation to the timing of juvenile Coho Salmon migration (Swales and Levings 1989). Spring flow regime may play an important role in Coho Salmon abundances in off-channel ponds, more so than summer accessibility. If flows are high in the spring, recently hatched juvenile Coho Salmon may have better access to good sites, such as Stanshaw Pond, which relies on higher creek flows to maintain its connection to the Klamath River (M. Wickman, Mid Klamath Watershed Council, personal communication). Stanshaw Pond had good habitat conditions for Coho Salmon, however without connection to the Klamath River, the fish could not benefit from use of the habitat during the summer when there are stressful temperatures in the main channel. Accessibility to West Grider Pond was also initially
lost due to West Grider Creek drying up near the confluence with the Klamath River, prior to the disconnection of the pond inlet to the creek.

Summer Retention

Estimates of juvenile Coho Salmon retention in off-channel ponds in this study ranged from zero in Lower Seiad Pond to 0.55 in Alexander Pond. Though retention was generally low in all the study sites, juvenile Coho Salmon abundance in the ponds was consistent through the summer study period. This suggests that there was either a high turnover of Coho Salmon in the off-channel ponds or high mortality in the ponds with dead fish being replaced through the summer. The off-channel ponds are frequently monitored and observations of heavy predation or dead Coho Salmon are rare, suggesting there was high turnover of Coho Salmon at ponds.

High turnover may be an indication that there are habitat deficiencies in the ponds; Belanger and Rodriguez (2002) found the least-preferred habitats had the highest turnover rates while Kahler et al. (2001) also found high rates of Coho Salmon turnover among sites in three western Washington streams during the summer. Coho Salmon densities in my study were comparable to Kahler et al. (2001), who found that habitats from which fish moved had lower densities than those where they stayed. Though the trend in the relationship between retention and density that I observed in this study was consistent with that pattern (Figure 17A), there was a relatively low correlation, suggesting density may not have played an important role in determining summer
retention. Fish movement in Kahler et al. (2001) was associated primarily with habitat size and depth, variables that I did not test in my analysis, rather than density.

The differences observed in retention rates may be due to availability of food within the off-channel ponds. Available benthic prey was weakly correlated with retention, suggesting that the range of benthic prey availability across the ponds is similarly suitable for Coho Salmon retention. However, zooplankton had a relatively strong positive correlation with retention. This relationship was driven by Alexander Pond, which had the highest summer retention and over three times the available zooplankton as the next closest ponds. Voigts (1976) found Cladocera (the most abundant zooplankton in the study ponds) to be abundant in quiet, open habitats with little vegetation. Alexander Pond was constructed with a shallow ledge that drops off into a much deeper, open pond. The pond has areas with submerged vegetation and large wood for fish cover and still provides the open habitat necessary for zooplankton growth as well as fish foraging (Giannico 2000). If high summer retention is identified as an important outcome, further research into the effect of zooplankton on retention and strategies to enhance zooplankton production would be beneficial.

Growth Rate

Average summer growth rates ranged from 0.09 to 0.57 percent body weight per day at the different study sites. I found a negative correlations between average growth rate and Coho Salmon density, suggesting that growth may be density dependent, but this trend should be interpreted with caution as the very low growth rates in West Grider
Pond drives the results. West Grider Pond had habitat conditions decline dramatically as the summer progressed, leading to a stressful environment with a dramatic increase in water temperature and loss of habitat volume, thus increasing Coho Salmon density. Though there was food available for fish to eat, it may not have been enough to offset the increasing metabolic demand associated with temperature increases (Elliott 1979). There was no strong association between measures of food availability and growth rate.

Based on stomach contents, Coho Salmon were eating benthic prey but were also surface feeding on aerial input and invertebrates living at or near the water surface in all of the sites. A lack of drift in these off-channel ponds may cause an increase in benthic foraging of Coho Salmon (Rosenfeld et al. 2005). A large portion of the biomass of juvenile Coho Salmon diets was dominated by Diptera from both aquatic (larvae and pupa) and aerial sources, as seen in several other studies (Glova 1984; Nielsen 1992; Rosenfeld et al. 2008; Malison et al. 2015). Though I did not measure aerial prey input into off-channel ponds, I did find substantial predation on aerial prey from gut contents samples, particularly at O'Neil, Tom Martin, and Lower Seiad ponds, demonstrating the importance of aerial drop as a food source in these small lentic water bodies (Wipfli 1997; Allan et al. 2003; Rosenfeld and Raeburn 2009). However, Lower Seiad Pond diets are based off a sample size of three and growth was not estimated because no Coho Salmon were recaptured.

Though the NMDS analyses showed available food to be different among ponds, a majority of the Coho Salmon diets orient near one another with considerable overlap, suggesting diets both within and among ponds are similar to one another. Tom Martin
and O'Neil ponds had the highest average growth rates of all the study sites and fish diets from these two ponds are quite different from the other ponds (Figure 15A). The positive association of the samples from Tom Martin and O'Neil pond with adult Diptera, Trichoptera, and Ephemeroptera suggest that these aerial prey items are particularly important for growth of juvenile Coho Salmon in pond habitats. This conclusion is supported by similar observations from Allan et al. (2003) and Malison et al. (2015) who found high proportion of aerial prey items in Coho Salmon diets. This pattern in Tom Martin and O'Neil also suggests a potential subsidy effect; these ponds are within 45 meters of the Klamath River. The proximity of the ponds to the Klamath River may increase the numbers of emerging invertebrates that fall into the off-channel habitats for fish to consume, an input that ponds further away from the Klamath River would not experience. Coho Salmon may also move into the Klamath River (Witmore 2014) during cooler evening water temperatures, which provides a feeding opportunity that is not available at sites located on tributary streams and far from the main stem channel.

Though the range of Coho Salmon densities in this study encompasses the range in previous studies that report both density and growth (Bisson et al. 1988a; Nielsen 1992; Gonzales 2006; Lang et al. 2006; Rosenfeld and Raeburn 2009; Kiffney 2014; Malison et al. 2015), the average growth that I observed is much lower (Figure 20). The juvenile Coho Salmon occurring at high population density in this study have similar growth rates to studies with comparable densities (Nielsen 1992; Gonzales 2006; Rosenfeld and Raeburn 2009), while the growth rate in the off-channel ponds with the lowest densities are among the slowest growth rates from studies with similarly low
densities (Bisson et al. 1988a; Kiffney 2014; and Malison et al. 2015). The increased growth rate at lower densities in these other studies was attributed to high food availability. This suggests that off-channel ponds in my study did not have sufficient available food to support fast growth rates even with low densities of Coho Salmon, preventing a substantial effect of reduced density on growth.

Figure 20. Average summer Coho Salmon density (fish/m²) related to average Coho Salmon growth (% weight/day) in several studies conducted in different stream environments. Note that density is in fish per area, rather than fish per volume as in Figure 19. This study (filled circle, black), Bisson et al. (1988a) (filled triangle), Nielsen (1992) (open inverted triangle), Gonzales (2006) (open square), Lang et al. (2006) (filled square), Rosenfeld and Raeburn (2009) (open triangle), Kiffney (2014) (open diamond), and Malison et al. (2015) (open circle).
Site Comparison from 2012 and 2014

Four sites from this study were also studied by Witmore (2014) in the summer of 2012. Coho Salmon abundance, retention, and growth in constructed habitats in 2014 were very different from those measured by Witmore (2014) in 2012 (Table 10). Abundances within the sites were much higher at two sites in 2014 than 2012, but much lower at the other two sites. Low abundance in ponds 2014 may have been due to drought conditions that eliminated the need for recently-emerged Coho Salmon to seek refuge from high flows during spring runoff (Figure 21) (Swales and Levings 1989; Witmore 2014; M. Wickman, Mid Klamath Watershed Council, personal communication), disconnection from the channel when stream temperatures warmed preventing fish entering the pond, or a unsuitable conditions in the pond leading fish to avoid using it. Alternatively, high abundance in the ponds in 2014 may have been associated with hot main stem and tributary temperatures as well as dry channel conditions potentially driving fish into cooler off-channel habitats, such as Alexander Pond, or due to ponds becoming disconnected after fish entered during the previous year as in West Grider. Both retention and growth were uniformly lower in 2014 than 2012, likely associated with water temperatures both within the ponds and in the adjacent channels being higher in summer 2014 than 2012.
Table 10. Summer growth and retention rates of juvenile Coho Salmon in study habitats in 2012 and 2014. 2014 was an extreme drought summer with hotter temperatures and lower flows relative to 2012.

<table>
<thead>
<tr>
<th>Site</th>
<th>2012 Abundance</th>
<th>2014 Abundance</th>
<th>2012 Retention</th>
<th>2014 Retention</th>
<th>2012 Growth (%/day)</th>
<th>2014 Growth (%/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>154</td>
<td>886</td>
<td>0.89</td>
<td>0.55</td>
<td>0.58</td>
<td>0.41</td>
</tr>
<tr>
<td>Lower Seiad</td>
<td>387</td>
<td>4</td>
<td>0.23</td>
<td>0.04</td>
<td>0.56</td>
<td>NA</td>
</tr>
<tr>
<td>Stanshaw</td>
<td>140</td>
<td>2</td>
<td>0.81</td>
<td>0.30</td>
<td>0.45</td>
<td>0.20</td>
</tr>
<tr>
<td>West Grider</td>
<td>98</td>
<td>230</td>
<td>0.79</td>
<td>0.71</td>
<td>0.54</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Figure 21. Daily mean discharge (cubic feet per second) in the Klamath River near Seiad Creek for the 2012 (solid line) and 2014 (dotted line) water year.

Construction of off-channel habitats in the middle Klamath River basin is an increasingly popular form of stream habitat restoration as a means to increase Coho Salmon population numbers by increasing available rearing habitat through the year. The differences between the 2012 and 2014 summer sample periods demonstrate the high yearly variability of these constructed habitats in response to annual climatic conditions.
However, even in years when a particular constructed habitat does not provide suitable summer rearing conditions, it may be utilized by fish and provide suitable habitat in other seasons. All of the study ponds are generally occupied by fish seeking velocity refuge during high winter flows. Therefore, even if ponds do not provide suitable summer habitat, they may still provide a net population benefit as long as fish are not trapped in unsuitable ponds when conditions change in summer. This annual and seasonal variability needs to be taken into account when planning off-channel pond projects, potentially by designing different ponds to target particular rearing seasons while ensuring consistent connection to allow emigration as seasonal conditions change. This could involve constructing ephemeral ponds for winter use only or constructing ponds with persistent connections to the Klamath River or one of its tributaries, which may require seasonal maintenance to ensure that fish can leave if habitat becomes unsuitable.

Future Research

There is a lack of studies on the summer use and benefits of constructed off-channel habitats for juvenile Coho Salmon which must continue to be researched in order to assess whether they positively affect Coho Salmon recovery and production. This study offers some support for the potential importance of constructed off-channel ponds as a restoration tool in the middle Klamath River basin. Many ponds were occupied and supported juvenile Coho Salmon during periods when main stem conditions were likely unsuitable for survival. Despite differences in habitat characteristics among ponds, few strong correlations were identified with the characteristics I selected. This suggests that,
even though ponds vary, the current design process is producing ponds that are within a suitable range for juvenile Coho Salmon for these habitat characteristics. Additional research could further our understanding of the Coho Salmon use of these ponds and factors that affect Coho Salmon rearing in these habitats.

There are several limitations to my study that may have affected my ability to detect strong relationships among measured variables and abundance, retention, and growth of Coho Salmon. Due to the limited number of constructed habitats in the middle Klamath River basin and the wide array of habitat characteristics within each pond, my analysis was exploratory rather than definitive. An increase in the number of ponds sampled and wider geographic location of those ponds within the basin would provide a better basis for further analysis. An increased number of study sites may allow for the use of covariates in understanding how variables may interact to determine abundance, retention, or growth of Coho Salmon. Though there has been an effort to describe different habitat characteristics that may impact Coho Salmon in these constructed ponds, research has not combined water quality parameters, habitat features, and prey availability. Future research should focus on how characteristics that have had a positive association with abundance, retention, and growth of Coho Salmon in previous research (temperature, depth, zooplankton, external prey sources) work together to impact the success of these constructed ponds.

Future work evaluating Coho Salmon performance in off-channel ponds should explore aerial input of prey items into the habitats due to the number of adult prey items in Coho Salmon diets of this study and based on the results of the NMDS analysis. Aerial
prey input may vary based on the amount of canopy cover and the type of surrounding vegetation (Bilby and Bisson 1992; Hetrick et al. 1998; Kawaguchi and Nakano 2001) or in relation to pond distance from the Klamath River. Rather than only analyzing benthic prey items, assessing the importance of overall available biomass (benthic and aerial) within a pond of prey items that are generally consumed may better explain retention and growth of Coho Salmon.

Additional research addressing accessibility of the ponds throughout the year, rather than just during the summer, may be beneficial to understanding the environmental cues that lead to fish movement into these sites. Access duration and timing may drive use of habitat in other seasons besides summer. There were several disconnected ponds in my study that fish either could not utilize during the summer, even though they had good rearing conditions, or could not leave, even when rearing conditions deteriorated. Pond connections that depend on spring discharge, such as Stanshaw and West Grider ponds, may continue to face problems with disconnecting late in the spring and limiting movement of fish in and out of these habitats. Spring runoff may drive summer Coho Salmon abundances in these habitats (M. Wickman, Mid Klamath Watershed Council, personal communication), suggesting the importance of starting research earlier than May to assess accessibility to the constructed ponds with increased spring runoff flows.

Future research should more rigorously track the movement of juvenile Coho Salmon between the off-channel habitat and the adjacent stream channel. This will improve our understanding of habitat utilization and develop our retention estimate. A more rigorous estimate of retention from month to month may also provide evidence of
pond performance as summer progresses to better understand what changes in habitat characteristics may be limiting for fish rearing in the ponds. Tracking the diets of the fish with the movements may also allow for an improved understanding of the importance of accessibility and connection to the habitat, especially in the summer season. Witmore (2014) tracked diel fish movement out of Lower Seiad Pond and into Seiad Creek as well as from Tom Martin Creek to the Klamath River. Fish may be moving to utilize a prey source outside their typical rearing habitat, suggesting the importance of a connection between the constructed habitat and the adjacent channel.

Finally, looking at trends in adult returns following the construction of these off-channel ponds will provide insight as to whether or not this restoration technique benefits the population as a whole.


contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.


Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992a. Seasonal changes in habitat use by juvenile Coho Salmon (*Oncorhynchus kisutch*) in

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


Appendix A: Juvenile Coho Salmon detection date on Seiad Creek antennas after being moved from West Grider Pond to Grider Creek on August 5, 2014 due to declining habitat conditions within the site and no connection to the main channel. This information demonstrates that Coho Salmon evacuated from poor pond conditions were still able to recover and survive following removal.

<table>
<thead>
<tr>
<th>Pit Tag Code</th>
<th>Date of First Detection on Seiad Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>985 121028922026</td>
<td>11/15/2014</td>
</tr>
<tr>
<td>985 121028944109</td>
<td>8/25/2014</td>
</tr>
<tr>
<td>985 121030727436</td>
<td>8/20/2014</td>
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<td>985 121030729587</td>
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<tr>
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<td>985 121030732619</td>
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