2012

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Recommended Citation

Crete, Zachary Jon, "The Ecology of Parafluvial Ponds on a Salmon River" (2012). *Graduate Student Theses, Dissertations, & Professional Papers*. 984.
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THE ECOLOGY OF PARAFLUVIAL PONDS ON A SALMON RIVER

By

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A Thesis
presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Environmental Studies

The University of Montana
Missoula, MT

May 2012

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Crete, Zachary, M.S., Spring 2012 Environmental Studies

The Ecology of Parafluvial Ponds on a Salmon River

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Parafluvial ponds are discrete lentic habitats embedded in the alluvia of gravel bed rivers that are formed by flooding and persist in relation to floodplain geohydrology. On the expansive flood plains of the Kwethluk River, I observed thousands of juvenile salmon apparently trapped by surface disconnection of the ponds from the river. I was interested in whether the salmon could survive until flooding reconnected the ponds to the river. I sampled ponds along the river corridor to describe habitat quantity and juvenile salmon presence, growth, and diet. Furthermore, I looked at pond hydrology, temperature regime, and the role groundwater plays in pond ecology. Total ponds along the river corridor (145km) varied in space and time as the season progressed from spring (n=81), summer (n=166), and fall (n=175) revealing that they were persistent and ubiquitous from the headwaters to the lower river. Five fish species were found, of which three were Pacific salmon, and 51 invertebrate taxa with 15 unique to ponds. Salmon, primarily coho (*Oncorhyncus kisutch*), were most abundant in ponds. Fish populations ranged from 0 to 772 in the 12 main study ponds. The mean area of ponds was small ($44.1m^2$), but this did not inhibit growth and high survival. Coho consistently fed on small invertebrates, predominantly Chironomids and Cladocera, and growth rates were as high as 1.35mm per week. Not only were fish able to grow, but population estimates were similar throughout the season indicating low mortality, and the annual bimodal occurrence of floods allowed juvenile salmon to actively move in and out of ponds. I concluded that juvenile salmon proactively occupy the shallow environments of parafluvial ponds because they function as nursery habitat that is commonly available on natural floodplain rivers like the Kwethluk.

Key words: parafluvial pond, salmon, foodweb, groundwater, Kwethluk River, Yukon Delta, Alaska, floodplain pond

Acknowledgements

First, I would like to thank my advisor Dr. Jack Stanford for the opportunity to study in such a remote and natural place like the Yukon Delta National Wildlife Refuge. Also, I thank my committee members Dr. Bonnie Ellis and Dr. Vicki Watson for their help with editing and final preparations. Much thanks to the Yukon Delta National Wildlife Refuge fisheries biologist Dan Gillikin for all his support and patience towards new recruits, and his very unselfish willingness to come up river on his own time to rescue us from our own ignorance on many occasions. Additionally, I thank Olin Twitchell for all his help along with Jessica Lewis, Tom Chandler, and Aaron Moses. Extra special thanks to Nathan Hoeme for volunteering his time day after day which made a profound difference in the end result of this work. Back at FLBS, Dr. Bob Newell spent many days teaching me about invertebrate taxonomy making it possible for me to identify my benthic samples and I thank Diane Whited for her tolerance towards my shallow learning curve with GIS. Furthermore, Tom Bansak helped on many occasions with SaRON data and Excel insights, and Tyler Tappenbeck helped with fish and invertebrate data. This work was supported by the Gordon and Betty Moore foundation and the Yukon Delta National Wildlife Refuge.

Dedications

This work is dedicated to my family. First, my wife and children who very unselfishly put up with me living in bush Alaska for 5 years to pay for graduate school and collect my data. Also, to my parents for being the only two people for most of my life that always believed and never gave up on me.

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Introduction

Flood plains are complex, dynamic elements of riverscapes (Junk et al., 1989; Stanford et al., 2005) characterized by a wide variety of habitat types (Tomaz et al., 2007; Naiman et al., 2005), such as: main channel, secondary and tertiary channels, wetlands, oxbow lakes, springbrooks, backwaters, beaver ponds, and smaller parafluvial and orthofluvial ponds all embedded in the riparian corridor that almost always is underlain by a shallow, alluvial aquifer fed predominantly by the river. Lateral habitats of river flood plains can be divided into parafluvial and orthofluvial zones (Stanford et al., 2005). The parafluvial zone receives active scour from flooding on an annual basis and is formed through erosive processes while the orthofluvial zone only receives flood water occasionally and is formed through depositional processes. Lateral habitats like ponds and springbrooks (parafluvial zone) are shallow with low velocities making them ideal rearing areas for juvenile pacific salmon (Murphy et al., 1989; Beechie et al., 2005). Development of the floodplain occurs over long periods of time through lateral migration of the channel, predominantly from flooding, sediment transport and deposition, avulsion (Stanford et al., 2005) along with the biological linkages associated with the riparian corridor (Fetherston et al., 1995; Huggenberger et al., 1998; Gurnell and Petts, 2002). These interactions, coupled with ground-surfacewater exchange, are the drivers of habitat heterogeneity (Stanford and Ward, 1993; Ward et al., 2002; Lorang and Hauer, 2006) and maintain physical complexity and associated biodiversity.

During floods, increasing river discharge transports sediment and riparian wood to new geographical locations on the flood plain. These erosive processes cause the channel to migrate allowing bed-sediments composed of sorted materials (sand, gravel, and cobble) to accumulate on the lee side thereby forming lateral, point, and island (mid channel) bars (Hickin, 1974; Nanson, 1980; Ward et. al, 2002; Gurnell et al., 2005) that also collect drift wood eroded from the river corridor. During subsequent flood events, drift wood acts as a flow obstruction causing local hydraulic scouring below the level of the water table. The scour holes become parafluvial ponds as floodwaters recede. Initially the ponds are connected by surface flows, but as discharge decreases water flux is from groundwater moving through the gravel bar. If flow in the river decreases such that the water table drops below the scour depth, the ponds may completely dewater (Karaus et al., 2005; Chilcote, 2004.)

Thus, parafluvial ponds are potentially an important habitat component of rivers, especially those with expansive and dynamic flood plains. Indeed, Karaus (2004) found that 72% of the benthic biodiversity of the Tagliamento River, Italy resided in parafluvial ponds. Furthermore, Chilcote (2004) showed that parafluvial ponds had a diverse benthic invertebrate community and were used by several fish species on the Nyack flood plain of the Middle Fork of the Flathead River, Montana. Therefore, parafluvial ponds function as concave islands in the flood plain landscape (Karaus et al., 2005) and can be seen as windows into the aquifer.

As a part of another study, I observed large numbers of juvenile salmon in numerous parafluvial ponds on the flood plains of the Kwethluk River, Alaska, apparently a common phenomenon. But, were the ponds suitable nurseries for these fish or merely a mortality trap? Are the ponds and the fishes contained in them abundant enough to significantly influence salmon productivity? The study reported herein addresses these questions with our main objective being to describe the ecology of parafluvial ponds focusing on pond and salmon abundance and persistence along with growth and diet of coho.

Methods

Study Area

The Kwethluk River is a 5th order tributary to the Kuskokwim River on the Yukon Delta National Wildlife Refuge, Alaska, USA. It originates in the Eek and Crooked Mountains, flows northwest for 222 km through tundra and drains a watershed of 3367 km^2. The region has a subarctic climate with temperatures ranging from highs above 12 °C in summer to -12 °C as a winter average (Alt, 1977). The river is bordered by a tundra landscape underlain by permafrost (Johnson and Hartman, 1969) and interspersed with short vegetation dominated by mosses (*Sphagnum* spp. and others), willow (*Salix* spp.*)*, alder (*Alnus* spp.), and a variety of berries. The riparian corridor is comprised of various plant species, such as: willow (*Salix* spp), alder (*Alnus* spp.), cottonwood (*Populus sp.)*, and spruce (*Picea glauca*) with unfrozen alluvium that can be tens of meters deep. The climate is dry averaging approximately 50 cm/year of precipitation with most of it falling as rain in late summer. The Kwethluk becomes ice free in May and freezes again in November (Roettiger et al., 2004). The headwaters of the Kwethluk River are formed primarily by Crooked Creek which flows west out of the Crooked Mountains and joins the Kwethluk River in the upper Kilbuck Mountain foothills. Below the headwaters, it is a low gradient wandering river with an anastomosing, sometimes anabranching network of primary, secondary, and tertiary channels with many flood channels and lateral habitat types—a shifting habitat mosaic (after Stanford et al., 2005). Farther downstream the Kwethluk River becomes a single thread river characterized by gravel substrates and mud banks, and the lower 46.6 km consists of a deeper muddy bottom channel averaging 53 m in width. The gradient is much shallower and the sinuosity greatly increases. The Kwethluk River enters the Kuskokwim River about 32 km upstream from Bethel Alaska.

Distribution of Ponds

In 2007, a pilot study was conducted to examine the feasibility of a project on parafluvial ponds. I surveyed the river for ponds on the expansive flood plain of the lower Kwethluk above the meander zone and near our research camp. Although I did not quantify ponds, they were a common attribute on most gravel bars with many inhabited by juvenile salmon. I sampled 5 ponds employing single pass minnow trapping and collected 737 juvenile fishes in two genera, *Oncorhyncus* and *Cottus*, totaling 5 species: rainbow trout (*O. mykiss*), coho salmon (*O. kisutch*), Chinook (*O. tshawytscha*), sockeye (*O. nerka*), and slimy sculpin (*Cottus cognatus*). The dominant species collected was coho, accounting for 719 of the 737 fish captured.

In 2008, I studied parafluvial ponds (Figure 1a-b) on gravel bars from the headwaters at Boundary Lake to the US Fish and Wildlife Service weir (FWS) which is located where the river becomes a single thread, meandering channel. Only ponds that occurred on gravel bars within the parafluvial zone were sampled. All ponds studied were permanent, meaning they did not dry out before the fall flood; see table 1 for GPS coordinates of major study ponds and FWS weir. Fish were present in eleven of the twelve major study sites chosen when they disconnected from the main channel.

I floated the Kwethluk River three times (spring—June 18th to 28th), (summer—August 7th to 30th), and (fall—September 8th to 24th) to quantify the abundance, area, and perimeter of parafluvial ponds. All ponds on every gravel bar from Boundary Lake (where the river becomes floatable) to the FWS weir (145 river kilometers) were surveyed during each float to characterize habitat quantity. Pond area and perimeter were determined using a Geo XM handheld GPS (Trimble Inc. USA). Additionally, observations were made during the summer and fall seasons to account for presence or absence of fish in all the ponds surveyed. Twelve ponds were chosen for detailed study; all were located on the flood plain of the lower Kwethluk River (from Elbow Mountain to the FWS weir) near our research camp.

Pond Hydrology Relative to the Main Channel and Timing of Connection and Disconnection

Water surface elevations in the study ponds were determined by installing graduated staff gauges in the deepest part of each pond. Five of the twelve main study ponds on the flood plain had staff gauges tied to benchmarks using a Trimble LL 200 laser level. A main channel staff gauge was also installed and tied to a benchmark in a single channel section of the river. Water surface elevations of the pond and main channel were surveyed and comparative stage curves were calculated for each of the five ponds and the main channel.

Additionally, I created a map of groundwater bathymetry to understand how water was flowing through one gravel bar that contained six of the study ponds. First, I dug holes along a longitudinal transect from the head to the end of the bar every five meters until the water table was breached. Then, 19 perpendicular transects were made every fifteen meters and holes were dug from the main channel to the first orthofluvial shelf. Once all the holes were dug, I surveyed the water elevations in the holes and tied this to the same benchmark as the pond on this gravel bar. I used Surfer 7.0 software to create the map and overlaid it onto Quick Bird imagery using GIS.

Thermal Regime of Ponds

Temperature loggers (VEMCO minilog, Nova Scotia, Canada) were installed in twelve ponds from the time the ponds became disconnected with the main channel until they reconnected from fall flooding. They were installed in the deepest part of the pond and set to record every 20 minutes. Installation dates varied because not all ponds separated from main channel influence simultaneously. Five key metrics were extracted from the data: (i.) mean daily temperature, (ii) mean minimum daily temperature, (iii) absolute maximum temperature, (iv) time over 15 $^{\circ}$C, and (v) time over 20 $^{\circ}$C. In addition, I used continuous temperature loggers to show the variability within and between three ponds (Figure 5). I used these metrics to show the variation between ponds and weather the temperature regime exceeded the thermal requirements of salmonids. For growth, 15 $^{\circ}$C is the upper limit assuming unlimited food (Quinn, 2006) and temperatures that exceed 20 $^{\circ}$C for too long can become lethal (Richter and Kolmes, 2000).

Water Chemistry of Ponds Relative to Main Channel and Groundwater

I collected point measures of water chemistry along the shallow shore of the main channel and ponds each time they were visited. The instruments used for point measures were the Oakton DO 300 for measuring dissolved oxygen concentration and saturation, and the Oakton PC-10 for conductivity, pH, and temperature. In 2010 after realizing the importance of groundwater flux, I used piezometers to pump groundwater and compared the chemical metrics of groundwater to ponds.

Fishes in Parafluvial Ponds

I sampled juvenile fishes using minnow traps (Bloom, 1976; Layman and Smith, 2001) because electrofishing is not a viable option in shallow lentic environments with a sand silt substratum that easily clouds the water making the fish difficult to net. Only seven of the twelve main study ponds were sampled for fish. The number of traps deployed varied based on the size of the pond at the time of sampling. I placed salmon eggs into black film canisters, positioned them in the trap, and placed the traps in the pond. All traps fished for one hour, which was time enough to obtain hundreds of fish in most cases. Three sets were deployed on most ponds, and all fish were kept in buckets so population estimates could be calculated from depletion sampling using the software program Capture (White et al., 1978). The principle behind this method is that if a body of water is sampled multiple times, and the fish captured are removed, then each time sampling occurs fewer fish will be caught creating a regression (Habera et al., 1996). For example, the number of fish caught during three sets at pond D was 176, 163, and 87. Then, the software program extrapolates this regression and estimates the population. Once the hour was up, the traps were retrieved and all fish were placed in a 20 liter bucket of water and oxygenated with a portable battery powered aerator. Fish were then identified (Pollard et al. 1997), weighed to the nearest tenth gram, and measured for fork length to the nearest millimeter. All fish were returned to the pond of origin, and mortality associated with sampling was nil.

Coho Growth, Condition and Diet

In preliminary work, I found that coho dominated the populations so histograms were created for young of the year (YOY) and 1+ coho. I used the beginning and end of each histogram curve as a guide for defining where the YOY cohort ended and the 1+ cohort began. Then, I used the raw changes in length and weight to determine growth.

I calculated Fulton's condition factor for both YOY and 1+ coho (Ricker, 1975; Nash et al., 2006). The following formula was used: $K = (W * 10^5) / L^3$ where W is weight in grams, L is length in millimeters, and 10^5 is the scaling factor for Pacific salmon when using metric measurements. Because all but one pond were isolated from any main channel influence, there were no opportunities for immigration or emigration. Pond J did reconnect to the main channel after the first sample event so no comparison of condition or growth was made for this pond.

To describe the diet of juvenile coho salmon, I collected stomach samples. The first ten fish ranging from 50 to 75 mm fork length were kept in a separate bucket during each minnow trapping event. This size class was chosen because they were big enough to use a one milliliter pipette without damaging the fish. I used water from the pond to fill the pipette, inserted it into the gut of the fish, and squirted the water into the stomach three times to lavage the contents (after Foster, 1977; Gelwick and Matthews, 2006). All contents were spilled into a container with 100 µm netting over the aperture. The sample and netting were then placed in a vial and preserved with 95% ethanol. All samples were identified to the lowest practical taxonomic level using standard dichotomous keys (Merritt and Cummins, 2009).

I*nvertebrate Assemblages (Food Sources) in the Ponds*

A number of quantitative methods were combined to sample the macroinvertebrate communities present in ponds that were potential prey items for fish. First, shoreline picks were conducted two to three times at each main study pond to examine prey availability for salmonids.

Each time a pond was visited I walked around the perimeter of the pond collecting invertebrates on rocks, the bottom of the pond, and submerged wood to account for the presence and abundance of taxa (Chilcote, 2004). This effort continued until the entire perimeter of the pond was sampled and ranged from 10 to 30 minutes. All specimens were placed into a vial and preserved in 95% ethanol.

Second, I used a 100 µm sweep net. I swept through the water column, submerged and emergent vegetation along with back sweeping to collect any organisms that were displaced into the water column by walking (Chilcote, 2004). This was done one time during the season at the five ponds with staff gauges. The time ranged from 10 to 15 minutes based on the size of the pond being sampled. Samples were preserved in 95% ethanol.

Finally, I used piezometers to sample groundwater organisms. The piezometers were installed by pounding them into the substrate until the water table was breached. One piezometer was installed immediately upstream of the pond in the influent groundwater flow path. A second piezometer was installed directly below the pond and a final one towards the end of the gravel bar. Thus, the pattern and location of the wells were in the direction of flow with the pond at a mid point. Water was then pumped from each piezometer using a Guzzler® GH 0400D hand water pump until a 20 liter bucket was filled. The sample water was filtered through a 100 um net, and the contents of the net were placed into 12 ounce Nalgene bottles and filled with 95% ethanol as a preservative.

A reference collection was made for all invertebrate taxa and is archived at Flathead Lake Biological Station (FLBS). Taxa identifications were reviewed and confirmed by Dr. Robert Newell, curator of aquatic entomology at FLBS.

Statistical Analysis

All statistical analyses (means, standard deviations, confidence intervals, and single factor ANOVA) were performed in Excel. The ANOVAs for coho growth were carried out in the following way. First, histograms were made so the YOY and 1+ cohorts could be deciphered. Then, I was able to define the starting and ending length of the fish in each cohort. The fish corresponding to each cohort were retrieved from the raw data, and the differences in length and weight were compared for each sample event using ANOVA.

Results

Distribution of Ponds

Throughout the season the total number of ponds from the headwaters at Boundary Lake to the USFWS weir (145 river km) increased from spring (n=81), to summer (n=166), and fall (n=175) with the highest densities occurring in the unconfined sections of the river (Figure 2). The area of ponds diminished as the season progressed from 8044 m^2 (mean area 48.5 m^2 +/- SE 7.2 m^2) during the summer event to 6078 m^2 (mean area 39.7 m^2 +/- SE 6.8 m^2) in the fall sampling. Perimeter increased from 9118 m to 12902 m during the same time period as the main channel stage dropped towards base flow (Figure 2). The relationship between area and perimeter may not seem intuitive because area decreased while perimeter increased. Pond morphometry, one pond becoming two ponds, and additional ponds disconnecting from the main channel between sample events would account for the increase in perimeter.

While surveying ponds on float trips down the river, I made observations accounting for the presence or absence of fish in all ponds and determined if any ponds had dead fish. The number of ponds with fish dropped from 69 to 67 % (summer to fall), and dead fish were found in 1.7 and 1.3 % of ponds, respectively, indicating that mortality was not significant. I did not find any ponds where all the fish were dead, although I did find ponds that dried up, but interestingly, and as noted above, fish apparently left before the ponds disconnected.

Pond Hydrology Relative to the Main Channel and Timing of Connection and Disconnection

In the spring flood, the entire parafluvial area was inundated. When the flood abated, fish collected in the ponds which gradually disconnected from any main channel influence, although the timing of disconnection varied. The earliest separation date was July 22nd at pond D and the latest separation was at pond J on August 27th (Figure 3a-e). In the fall flood, ponds reconnected to the main channel as the parafluvial area became inundated again. The earliest reconnection date was September 5th at pond J, but the remaining ponds reconnected between September 22nd and 27th (Figures 3a-e).

During the period of disconnection, discharge in the main channel fluctuated. Rising river levels were associated with rain events, and the river decreased in volume during dry periods. The ponds responded to these events by increases and decreases in depth (Figure 3a-e). For example, on the falling limb of the spring hydrograph the depth of pond D decreased 29.8 cm while the main channel decreased 45.7 cm. Conversely, on the rising limb of the fall flood the depth of pond D increased 12.0 cm while the main channel increased 33.2 cm at which point the pond reconnected to the main channel. This same hydrologic response occurred at all ponds

(Figure 3a-e). Only one of the twelve main study ponds (J) reconnected to the main channel during a rain event (Figure 3d). A plot of the water table depth across an expansive gravel bar that contained several of the study ponds (A, C, D, E, F, and G – see Table 1 for exact locations) showed that river water flowed from the channel at the top and progressed through the bar to the backwater at the bottom (Figure 4). These data, coupled with stage changes coherent with river flow confirmed the hydrologic connectivity between the aquafer and the ponds.

Furthermore, the hydrology of the river also affected the time periods that ponds were disconnected from the main channel, along with area, depth, and fish densities (Table 2). The duration of separation from the main channel varied from nine days at pond J to sixty-eight days at pond D. The maximum area ranged from 8 to 393 m^2 and depth varied from 0 to 97.7 cm for main study ponds (Table 2). Fish densities (Table 2 and Figures 3a-e) ranged from 0.7 $fish/m^2$ at pond J to 5.7 $fish/m^2$ at pond B. Fish density per unit area increased over time because pond volume generally decreased over the study period whereas population estimates stayed fairly constant.

Thermal Regimes of Ponds

Across the main study ponds, mean daily temperatures ranged from 6.5 °C to 11.8 °C (Table 4), apparently varying in relation to length of groundwater flow path feeding them and air temperatures. The mean minimum temperature varied from 5.4 °C at pond G to 11.8 °C at pond E. The absolute maximum temperature ranged from 10.9 °C at pond G to 23.7 °C at pond L. Six of the twelve main study ponds had temperatures that exceeded 15 °C, although the time above 15 °C varied substantially between ponds. One pond in particular (L) was over 15 °C for 388 hours and 69 of those hours it exceeded 20 °C (Table 1). Pond L was the only pond sampled that exceeded 20 °C. Additionally, I compared the thermal heterogeneity of three ponds, L, K, and D, using continuous temperature data demonstrating that the temperature regime varied considerably within and among parafluvial ponds (Figure 5).

Water Chemistry of Ponds Relative to Main Channel and Groundwater

For main study ponds, the mean pH ranged from 6.92 to 7.6 (Table 3). The mean specific conductance ranged from 104.2 to 173.9 µS with pond L having the highest value. Mean dissolved oxygen ranged from 39.6 to 98.7 % saturation and 4 to 10.4 mg/L. As expected from the study of bar geohydrology, ponds most closely resembled the chemical nature of the groundwater fluxing through the bar (Table 3) not the main channel. The main channel, springbrook, and groundwater metrics are reported to show how ponds compared to other flood plain habitats (Table 3).

For ponds surveyed on floats, the mean pH ranged from 7.44 to 7.91 (Table 4), mean specific conductance from 128.8 to 163.4 µS and mean dissolved oxygen from 71 to 84 % saturation and 7.2 to 9.3 mg/L. The main channel metrics were included for the ponds examined during the float surveys to show the difference between the main channel and ponds (Table 4). In general, the full set of metrics collected from ponds on float trips did not differ much from the main study ponds on the piedmont flood plain.

Fishes in Parafluvial Ponds

Five species of fish in two genera, *Oncorhyncus* and *Cottus*, inhabited parafluvial ponds. The species in order of relative abundance were coho (*O. kisutch*), Chinook (*O. tshawytscha*), sockeye (*O. nerka*), slimy sculpin (*Cottus cognatus*), and rainbow trout (*O. mykiss*). Not all ponds had all five species of fish. For instance, pond I had coho, sockeye, rainbow, and sculpin but pond K had only coho, Chinook, and sockeye. The only species found in all ponds sampled were coho, and they were by far the most abundant, constituting 95 % of the catch. All fish collected in ponds were juvenile young of the year or parr (1+ age).

Fish populations were determined in time series in seven of the twelve ponds on the lower floodplain (Table 2). Some ponds were only sampled once or twice because they reconnected to the main channel on different dates. For example, two ponds (J and I) were sampled three times; four ponds (D, C, G, and B) twice; and one pond once (J). Ponds G and C were sampled twice, but population estimates were only calculated when depletion sampling took place (Table 2).

Total fish populations (all species included) ranged from 0 to 772 fish, but fish populations between ponds were substantially different (Table 2). Fish populations show a slight increase through time at three ponds, D, I, and B. Although, pond K had a decrease in fish population between the first and second sample event, it had an increase from the second to the third sampling (Table 2). The increase in population size was not statistically significant for any of the ponds. Pond L did have fish present when it was connected, but they all emigrated before it disconnected from the main channel. The remaining ponds, C and G, had only one population estimate for the season (Table 2).

Fish densities ranged from 0 to 5.7 fish/m^2. Fish densities in ponds fluctuated with population estimates and the change of pond area though time. For example, pond D went from 4.7 to 2.6 fish/m^2 as the areas fluctuated from 112 m^2 to 227 m^2. Pond I fish densities were 2.2, 2.9, and 1.7 fish/m^2 as the areas changed from 118 m^2, 97 m^2, to 168 m^2. And, pond K had fish densities of 1.6, 1.6, and 2.6 fish/m^2 as the areas went from 393 m^2, 295 m^2 to 218 m^2 (see Figure 3a-e) and (Table 2).

Coho Growth, Condition, and Diet

Growth rates of juvenile coho were calculated for six of the seven ponds sampled for fish by comparing cohort length and weight over time (Figure 6a-f). Pond J was excluded because it reconnected to the main channel after the first sampling event allowing for immigration and emigration to skew growth results. Growth varied between the young of the year (YOY) and 1+ cohorts. At all ponds, the YOY coho all showed significant increases in length (ANOVA $p < 0.05$) and weight (ANOVA $p < 0.05$). The change in mean length, across all ponds, for YOY coho was 1.35 mm (+/- 0.31 SE) per week, and for weight it was 0.07 g (+/- 0.01 SE) per week.

The 1+ parr showed no growth increase in weight in any ponds, but length was more variable. Only five of the six ponds where fish were sampled had 1+ coho present. Three ponds, D, K, and G, showed significant growth in length (ANOVA $p < 0.05$), but the other two ponds, C and B, had non-statistically significant growth for length (ANOVA $p > 0.05$). The 1+ had non-statistically significant growth for weight (ANOVA $p > 0.05$) at all ponds. The change in mean length, across all ponds, for 1+ coho was 0.93 mm (+/- 0.26 SE) per week, and for weight it was

0.04 g (+/- 0.04 SE) per week. Coho were the only species I used for growth because all other fish populations were too small.

The condition factor of YOY coho declined (mean 0.92 to 0.87) as the season progressed for ponds, D, I, C, G, and K, although K did show an increase between sample event two and three (Table 5). The only pond that had an increase in condition for YOY coho was pond B which increased from 0.85 to 0.86. The 1+ coho in all ponds exhibited a decline (mean 0.95 to 0.89) in condition factor except pond K which had a slight increase between the second and third sampling events (0.90 to 0.91) (Table 5).

Coho stomach contents were made up of entirely adult and immature aquatic invertebrates. Twenty-one taxa were found in stomach samples from juvenile coho (Figure 7). The most abundant taxon found was Chironomidae, comprising 41 % of coho diet. Other dominant taxa were Cladocera, Corixidae, Ostracoda, and adult Diptera. There were many rare taxa found in gut contents. There were no coho sampled that had empty stomachs suggesting that food was regularly available.

Invertebrate Assemblages in the Ponds

Thirty-nine taxa of invertebrates were collected during shoreline picks (Figure 8). Cased caddis (Trichoptera) and snails (Gastropoda) dominated the picks. The mayflies (Ephemeroptera) and stoneflies (Plecoptera) were present in very low abundance due to the sand silt substrate common to most ponds. The predaceous diving beetle (Dytiscidae) comprised 6 genera, although they occurred in low numbers. Not all taxa were found in every pond. The total is a composite of the diversity from all 12 main study ponds via this method.

In sweep net samples, 20 taxa were collected. This method produced an enormous amount of small sized individuals, indicating a copious food supply for the fish. For example, the Ostracoda averaged 6705 individuals per sample event. Other dominant taxa in this method were the Copepoda with 1465, Cladocera with 2007, and Chironomidae with 2013 individuals on average per sample (Figure 9). Taxa collected in this method reflect many of the dominant taxa consumed by juvenile coho: Chironomidae, Ostracoda, and Cladocera.

A total of 18 taxa of invertebrates were identified from the hyporheos of gravel bars on the Kwethluk River (Figure 10). Groundwater taxa were dominated by Copepods averaging 316 individuals per sample event. Other abundant taxa were the Chironomidae, Ostracoda, and Nematoda. The combined methods employed to describe the invertebrate diversity associated with parafluvial ponds totaled 51 taxa with 15 taxa unique to ponds. Rare taxa were placed in the "other" category because they represented less than two individuals per sample event. For a full description of all taxa via each method see appendix A.

Discussion

The density, area, and perimeter of ponds fluctuated with changes in the hydrograph. The maximum number of ponds existed at or near base flow and most occurred in the unconfined sections of the river. Ponds at peak numbers (n=175) had 12.9 km of shallow shoreline compared to 145 km for the main channel from the headwaters to the FWS weir. Therefore, ponds represented a relatively small proportion of available shoreline habitat for the entire river. The slight increase in the quantity of ponds between the summer and fall sample events (Figure 2) was likely due to one pond becoming two ponds as the main channel continued to drop towards base flow. This phenomenon would also account for the increase in perimeter during this period and the decrease in area. Fluctuations in pond area, depth, or perimeter while separated from the main channel were from groundwater flux, demonstrating the level of connectivity with the alluvial aquifer (Figure 3a-e). Chilcote (2004) also noted that pond volume and area changed with main channel discharge (stage) on the Nyack flood plain, Middle Fork of the Flathead River, Montana. The physical dynamics of ponds were controlled by flooding, groundwater flux, lateral migration of the channel, and the association of drift wood that creates and maintains these habitats.

The temperature regime varied within and among ponds (Figure 5), but overall stayed within the range for effective salmon growth and persistence (Eaton et al., 2001) (Table 1). The variation in the temperature was likely the result of length of daylight (aspect), proximity to riparian vegetation (Arscott et al., 2000), changes in ambient air temperature, and the ameliorating effects of ground water flux. Additionally, morphometry controls temperature patterns in different areas of the pond. The shallow areas of the pond tend to stay warmer allowing greater accumulation of degrees which increases growth potential while congregating food items for higher trophic levels. Only one of the 12 main study ponds (L) exceeded 20 $^{\circ}$C, and this pond had no fish present after separation from the main channel (Table 1). I regularly visited all main study ponds to record the dates that ponds separated from the main channel, and I did not see any dead fish in pond L after separation or predators eating the fish before separation. This suggests fish somehow sense that the habitat is not suitable, perhaps by recognizing low groundwater flux rates, and leave these ponds before they disconnect from the main channel.

I have shown that coho and other salmonids were able to grow and survive in isolated parafluvial ponds and that coho populations remained relatively constant throughout the season (Figures 3a-e). This illustrates their importance as a viable rearing habitat (Swales and Levings, 1989; Sabo and Kelso, 1991) on salmon rivers with expansive flood plains, and that parafluvial ponds are not a mortality trap. Moreover, it appears that the fish can sense whether to stay in a pond or not. There were a few ponds that dried out, but no dead fish were present. Also, I observed one pond (L) that had fish while connected to the main channel but not after separation. Ponds perhaps were attractive because they offer fish a lentic environment requiring less energy for daily activities than in main channel habitats, and they are apparently protected from predation , even birds, on the Kwethluk because they are located on relatively open gravel bars and fish population estimates remained similar throughout the season. Since coho commonly rear in the river for two years and some as long as three years in the northern latitudes (Quinn, 2005) parafluvial ponds provided an additional habitat for juvenile pacific salmon on flood plains, which has also been documented by a recent study of some lateral ponds on the Fraser River used by salmonids (Frake et al., 2009 unpublished data).

Fish were present in 68% of parafluvial ponds and they contained approximately 54,000 fish along the river corridor when pond population estimates were extrapolated. The estimated production of juvenile salmon for the entire Kwethluk River across all habitats (beaver ponds, main channel, springbrooks, and tundra tributaries) was 6.6 million and calculated by extrapolating fish densities by habitat and multiplying them by habitat quantity (Stanford, 1999-2012). Parafluvial ponds accounted for less than 1% of the total production on the Kwethluk. Fish densities in ponds were the highest on the Kwethluk (2008) averaging 2.8 fish/m^2 for the main study ponds. Other floodplain habitats averaged 0.3 fish/m^2 (shallow shores), 2.5 fish/m^2

(parafluvial springbrooks), and 1.2 fish/m^2 (orthofluvial springbrooks) (Goodman et al., in review). It is important to note that the quantity of fish in ponds ranged from a few dozen to hundreds per pond.

The SaRON (Salmonid Research Observatory Network) project conducted repeated measures of salmon juvenile densities in rivers around the Pacific Rim using electrofishing. The mean densities of fish on anastomosing rivers in Alaska and British Columbia averaged 0.86 fish per m^2 and 4.62 fish per m^2 in Kamchatka Russia. All SaRON research sites were on flood plain rivers and all of them had parafluvial ponds with coho commonly residing in them. Even though parafluvial ponds did not substantially contribute to salmon productivity on the Kwethluk River, when compared to all the other habitats on the river, they are nonetheless important habitat components of river flood plain systems.

Coho dominated all fish populations and were constantly feeding on Chironomids, Cladocerans, adult Dipterans, Corixids, and Ostracods (Figure 7). They exhibited significant growth for all YOY but not for all 1+ fish suggesting ponds are excellent habitats for newly emerged coho that are well known to prefer slow moving lateral habitats (Mundie, 1969; Bisson et al., 1988; Fausch, 1993). Food sources available to fish were diverse and robust. I collected 51 taxa of invertebrates with 15 unique to ponds. Thousands of prey items residing in ponds were small and had groundwater associations (Figures 9 and 10) which were preferentially consumed by coho. This is significant because many of the invertebrates found in ponds were too big for fish to eat, e.g. limnephilid caddis and snails which were the dominant taxa collected during shoreline picks (Figure 8).

I conclude that parafluvial ponds are common habitats on anastomosing rivers like the Kwethluk where juvenile Pacific salmon survive and grow, especially coho. I established that ponds are not a mortality trap, but may be selected for, because fish left ponds that eventually dried up or became unsuitable e.g. high temperature. They are an important component of the habitat mosaic of the Kwethluk River and are likely the same on other salmon rivers. Although ponds do not substantially contribute to the overall salmon productivity of the Kwethluk; they are nonetheless exploited by thousands of juvenile salmon.

Because of the physical and biological requirements to maintain and create these habitats, they are sensitive to anthropogenic manipulations (Homes et al., 1999) and therefore rapidly disappear making them useful as indicators of physical complexity. Additionally, the numbers of juvenile salmon in the ponds are a reflection of overall salmon abundance in the river. If productivity declines one would expect the fish numbers in ponds to likewise decline. Thus, the ponds may be useful for population monitoring, especially since they are so easy to sample as shown herein. As a final point, flood plains are the most endangered natural environments on the planet owing to dams, diversions, revetments and other cultural influences (Tockner and Stanford, 2002); and expansive flood plains are critical spawning and rearing areas for Pacific salmon.

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Appendix A

Invertebrate taxa present in all samples and grouped by collection method. The number of taxa reported via each method is calculated by counting taxa that are present, but not counting the family if there are genera present within that family. For example, the family Tipulidae is counted if there are no genera identified for that method. If there are genera within the Tipulidae family, e.g. *Tipula* sp., then only the genus would be counted as one instead of adding the family and the genus.

Taxa	Lavage	Shoreline Pick	Sweepnet	Groundwater	In common with other floodplain habitats
TRICHOPTERA					
Hydroptilidae	X				X
Limnephilidae	X		X		X
Onocosmoecus sp.		X			X
Homophylax sp.		X			
Ecclisomyia sp.		X			X
Brachycentrus americanus		X			X
Brachycentrus sp.			X		X
Psychoglypha sp		X			X
Apatania sp.		X			X
Apatania stigmatella		X			X
Glyphopsyche sp.		X			
Asynarchus sp.		X			X
PLECOPTERA					
Chloroperlidae	X		X	X	X
Isoperla sp.	X	X			X
Suwallia sp.		X	X		X
Kathroperla perdita				X	X
EPHEMEROPTERA					
Heptageniidae				X	X
Ephemerella sp.		X			X
Siphlonurus occidentalis		X			X
Siphlonurus sp.	X	X			X
Diptera					
Diptera Adult	X				X
Tipulidae	X		X		X
Tipula sp.		X			X
Hexatoma sp.	X	X			X
Dicranota sp.		X			X
Chironomidae	X	X	X	X	X

Ceratopogonidae	X		X	X	X
Culicidae	X				X
GASTROPODA					
Planorbidae		X	X		X
Lymnaeidae	X	X	X		X
Lymnaea arctica		X			
Gyraulus deflectus		X			
Gyraulus parvus		X			
Valvata sincera		X			
Physidae		X			
HEMIPTERA				X	
Callicorixa sp.	X	X	X		X
Saldula sp.	X	X			X
COLEOPTERA				X	
Dytiscidae	X				
Agabus sp.		X			X
Colymbetes sp.		X			X
Rhantus sp.		X			
Potamonectes sp.	X	X			
Hydroporus sp.		X			
Oreodytes sp.		X			X
HYMENOPTERA			X		
CRUSTACEA					
Copepoda	X	X			?
Harpacticoida			X	X	
Cyclopoida			X	X	
Cladocera	X	X	X	X	X
Ostracoda	X	X	X	X	X
MOLLUSCA					
Sphaeridae		X	X	X	
OTHER					
Tubellaria		X			X
Oligochaetae	X	X	X	X	X
Unknown		X	X	X	
Hydracarina	X	X	X	X	X
Araneae	X			X	
Collembola	X		X	X	X
Nematoda			X	X	
	21	39	20	18	36

Figures

Figure 1. (a) Photograph of parafluvial pond I and (b) photograph of pond K on the lower flood plain of the Kwethluk River, Alaska. Note the minnow trap in the photo.

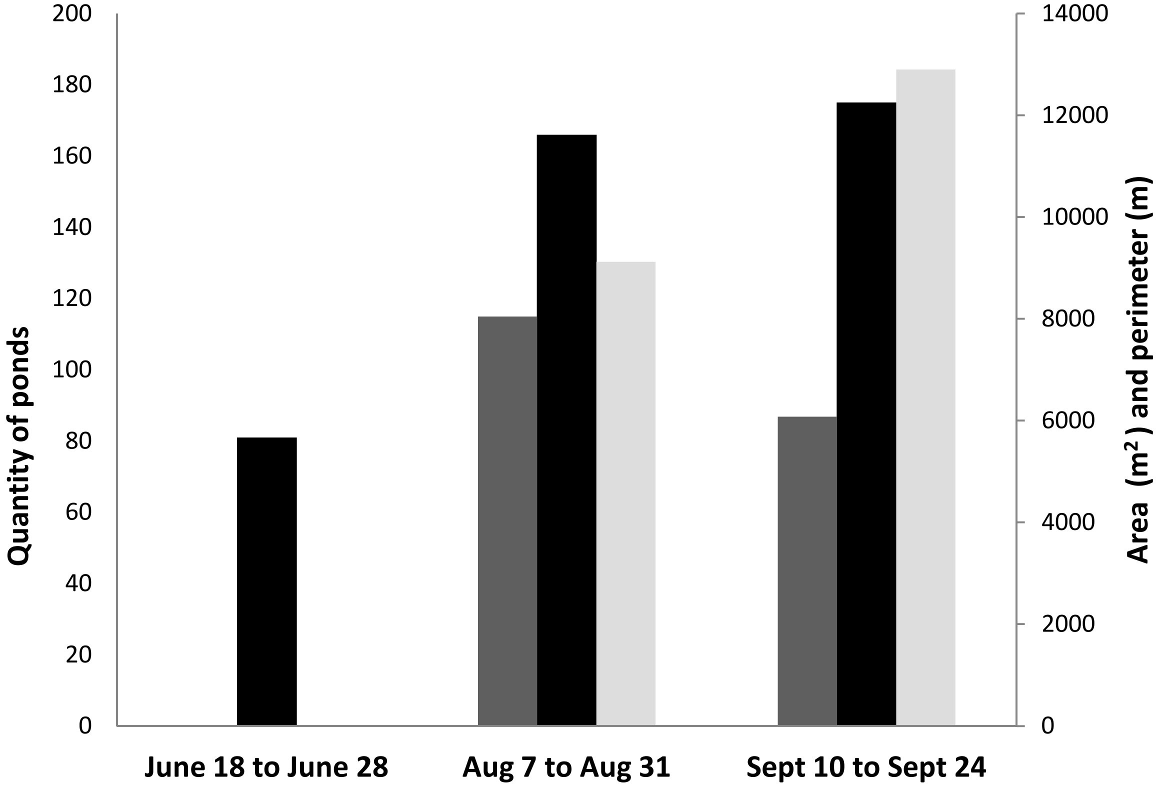
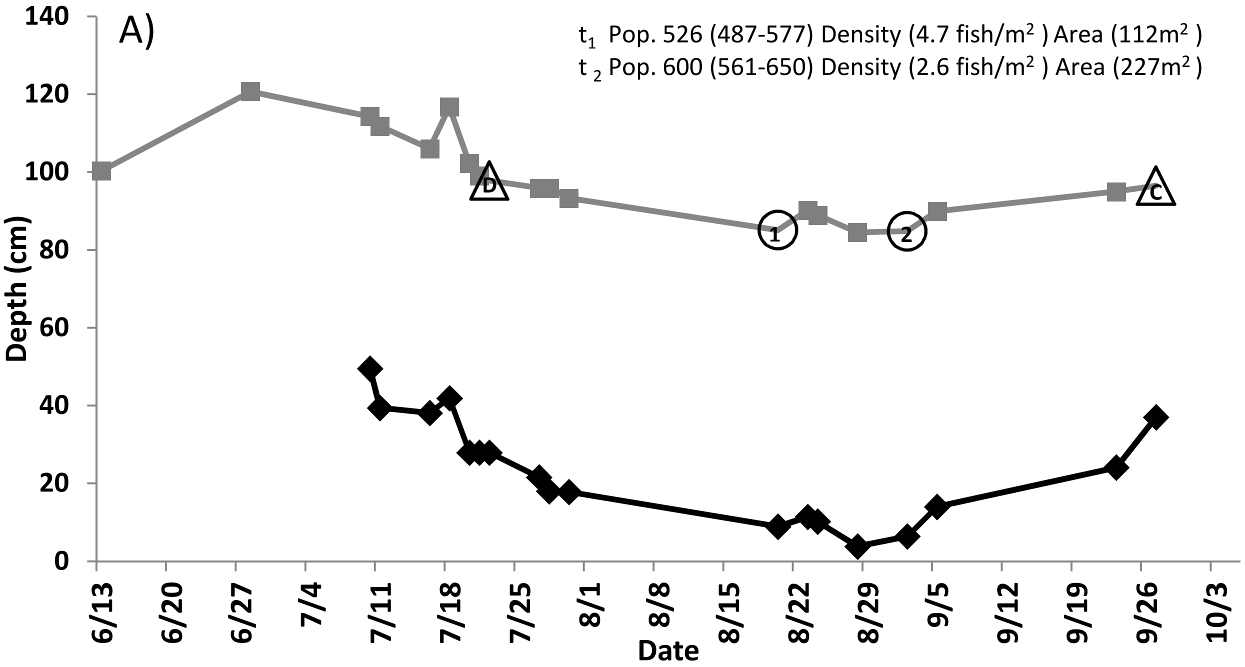
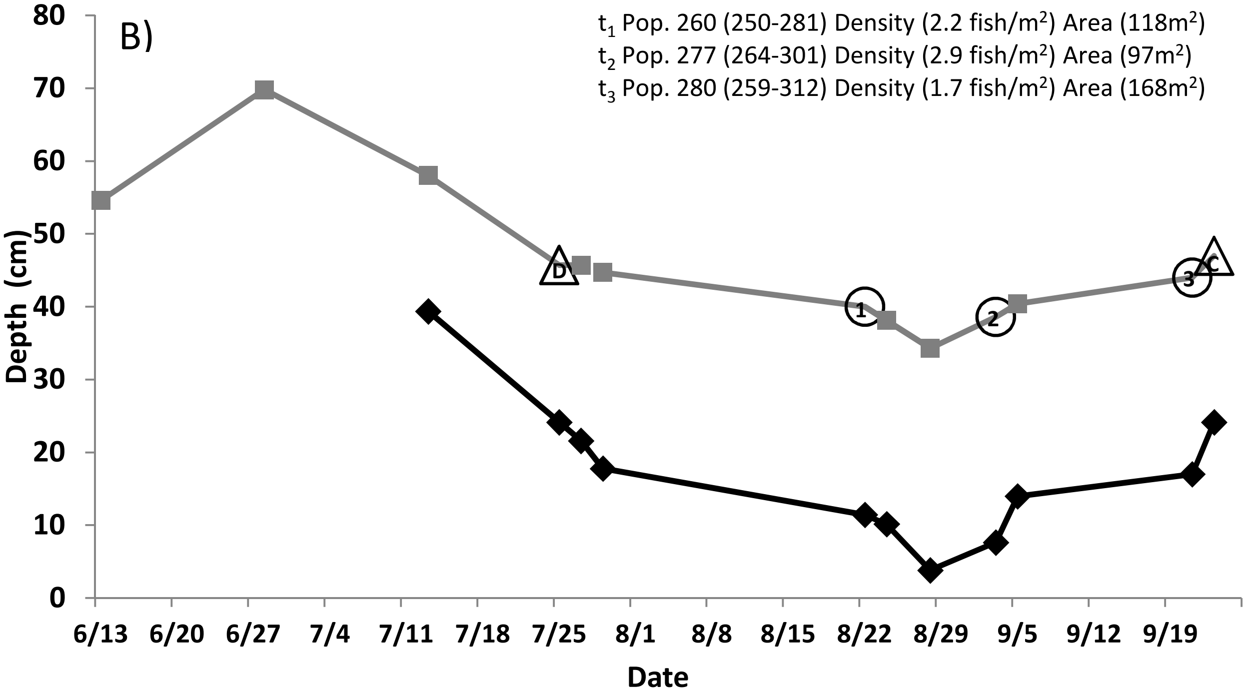
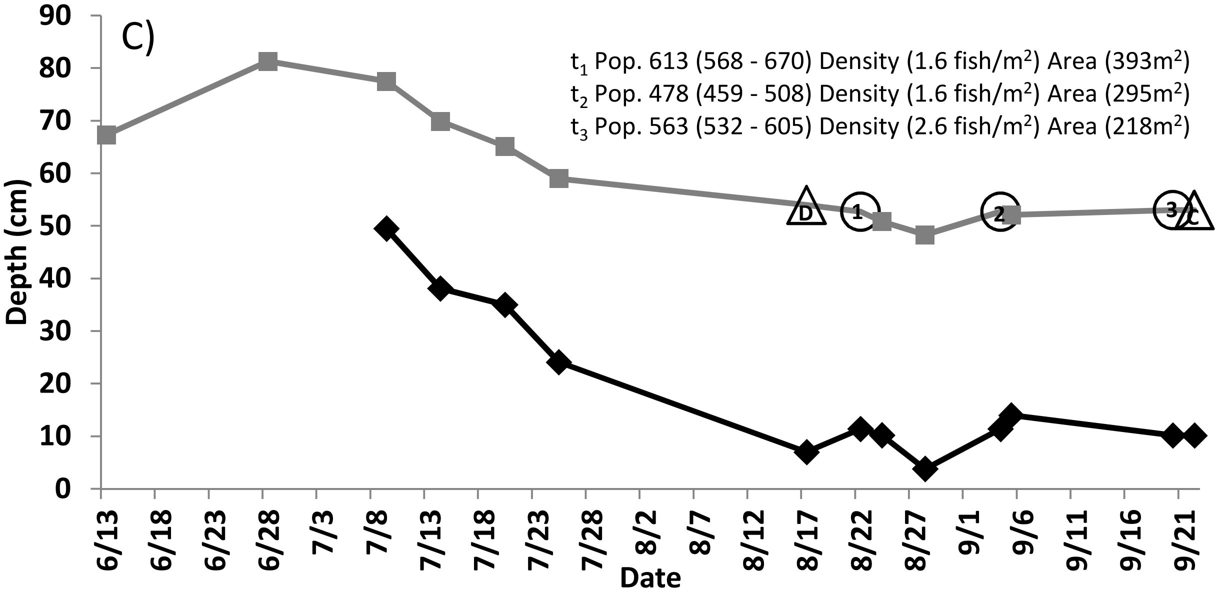


Figure 2. The quantity (black histograms), area (dark grey histogram), and perimeter (light grey histogram) of parafluvial ponds on the Kwethluk River during three study periods, 2008.


A)
t₁ Pop. 526 (487-577) Density (4.7 fish/m²) Area (112m²)
t ₂ Pop. 600 (561-650) Density (2.6 fish/m²) Area (227m²)
Depth (cm)
140
120
100
80
60
40
20
0
D
1
2
C
6/13
6/20
6/27
7/4
7/11
7/18
7/25
8/1
8/8
8/15
8/22
8/29
9/5
9/12
9/19
9/26
10/3
Date


B)
t₁ Pop. 260 (250-281) Density (2.2 fish/m²) Area (118m²)
t₂ Pop. 277 (264-301) Density (2.9 fish/m²) Area (97m²)
t₃ Pop. 280 (259-312) Density (1.7 fish/m²) Area (168m²)
Depth (cm)
80
70
60
50
40
30
20
10
0
D
1
2
3
C
6/13
6/20
6/27
7/4
7/11
7/18
7/25
8/1
8/8
8/15
8/22
8/29
9/5
9/12
9/19
Date


C)
t$_1$ Pop. 613 (568 - 670) Density (1.6 fish/m^2) Area (393m^2)
t$_2$ Pop. 478 (459 - 508) Density (1.6 fish/m^2) Area (295m^2)
t$_3$ Pop. 563 (532 - 605) Density (2.6 fish/m^2) Area (218m^2)
Depth (cm)
0
10
20
30
40
50
60
70
80
90
D
1
2
3
C
6/13
6/18
6/23
6/28
7/3
7/8
7/13
7/18
7/23
7/28
8/2
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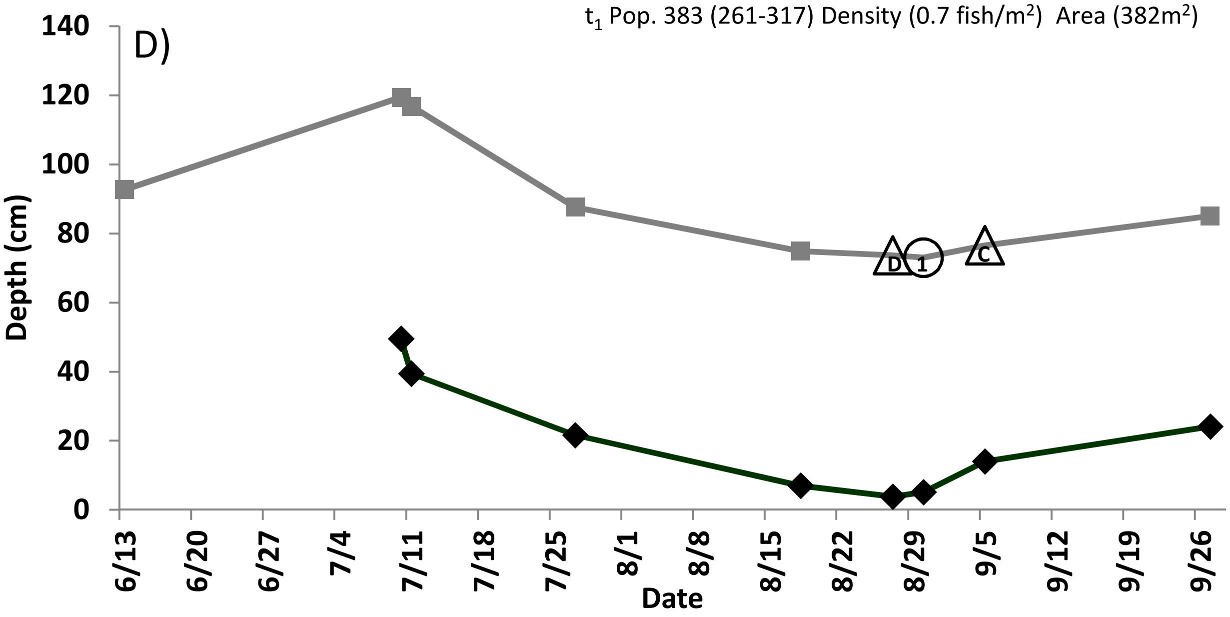
8/12
8/17
8/22
8/27
9/1
9/6
9/11
9/16
9/21
Date


t$_1$ Pop. 383 (261-317) Density (0.7 fish/m^2) Area (382m^2)
D)
Depth (cm)
0
20
40
60
80
100
120
140
D
1
C
6/13
6/20
6/27
7/4
7/11
7/18
7/25
8/1
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8/15
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8/29
9/5
9/12
9/19
9/26
Date

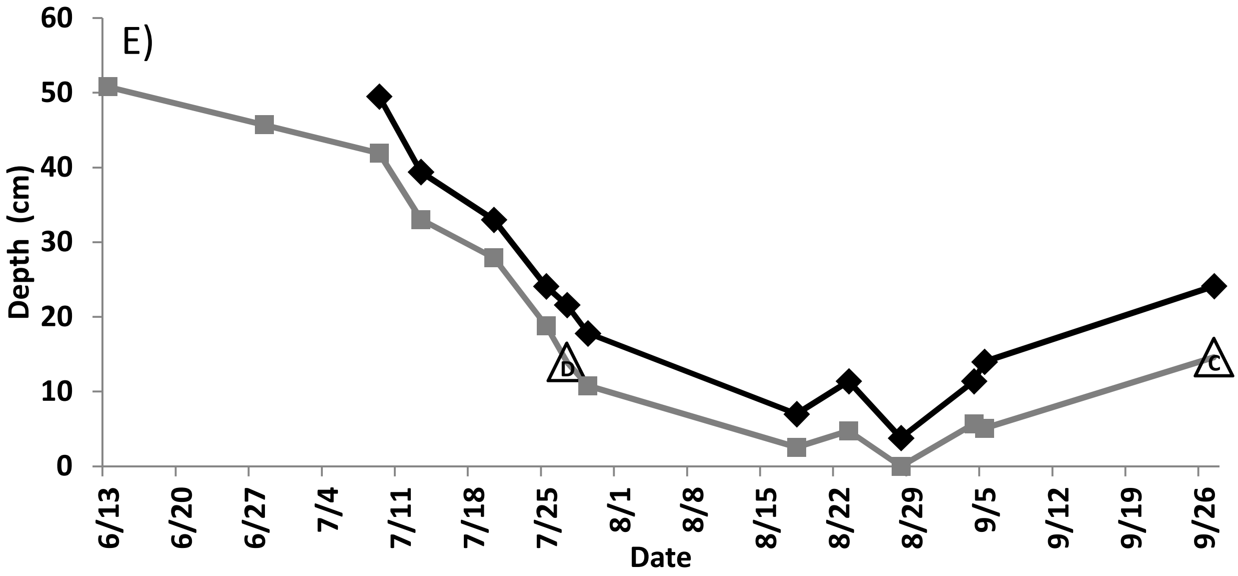

Figure 3(a-e). Depth of 5 parafluvial ponds (grey lines) relative to the main channel (black lines) of the Kwethluk River, 2008. The triangles on the grey line are the dates that the pond disconnected (D) and connected (C) to the main channel. The circles indicate sampling dates (t_1, t_2, and t_3) showing fish population estimates with 95% confidence intervals, fish density, and area of pond. Panels are ordered a-e for ponds D, I, K, J, and L. Pond L did not have any fish present after separation, so no fish data were reported for this pond.

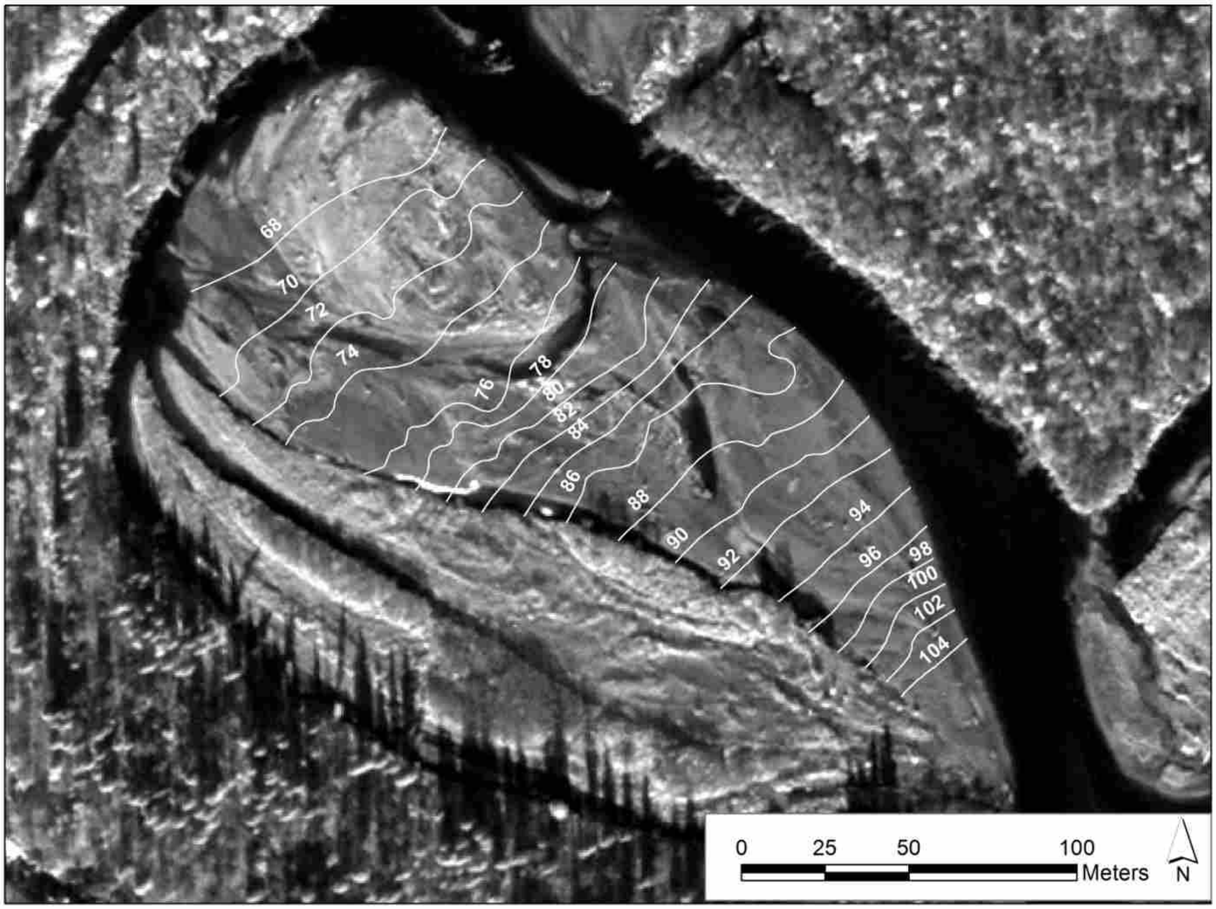

Figure 4. Satellite view (Oct. 10th, 2008) of a gravel bar containing parafluvial ponds (A, C, D, E, F, G) with superimposed isopleths of depth (cm) of ground water relative to a surveyed benchmark Kwethluk River, 2008. Thus, ground water is flowing from the channel at the top of the bar (lower right, deeper depths) towards the back water at the bottom of the bar (upper left, shallower depths).

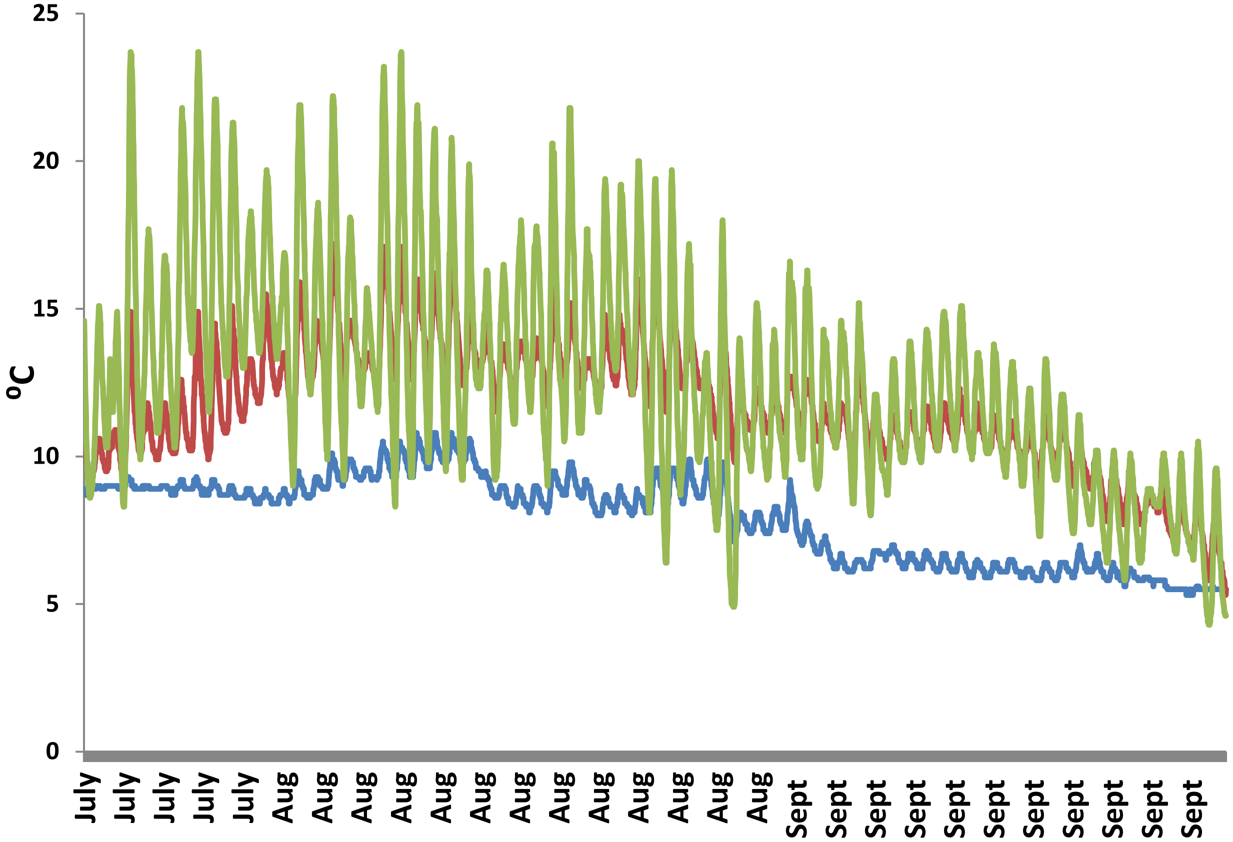

Figure 5. Continuous temperature comparison of three parafluvial ponds showing variability within and among sample sites on the Kwethluk River, 2008. The green line is pond L, the red line is pond K, and the blue line is pond D.

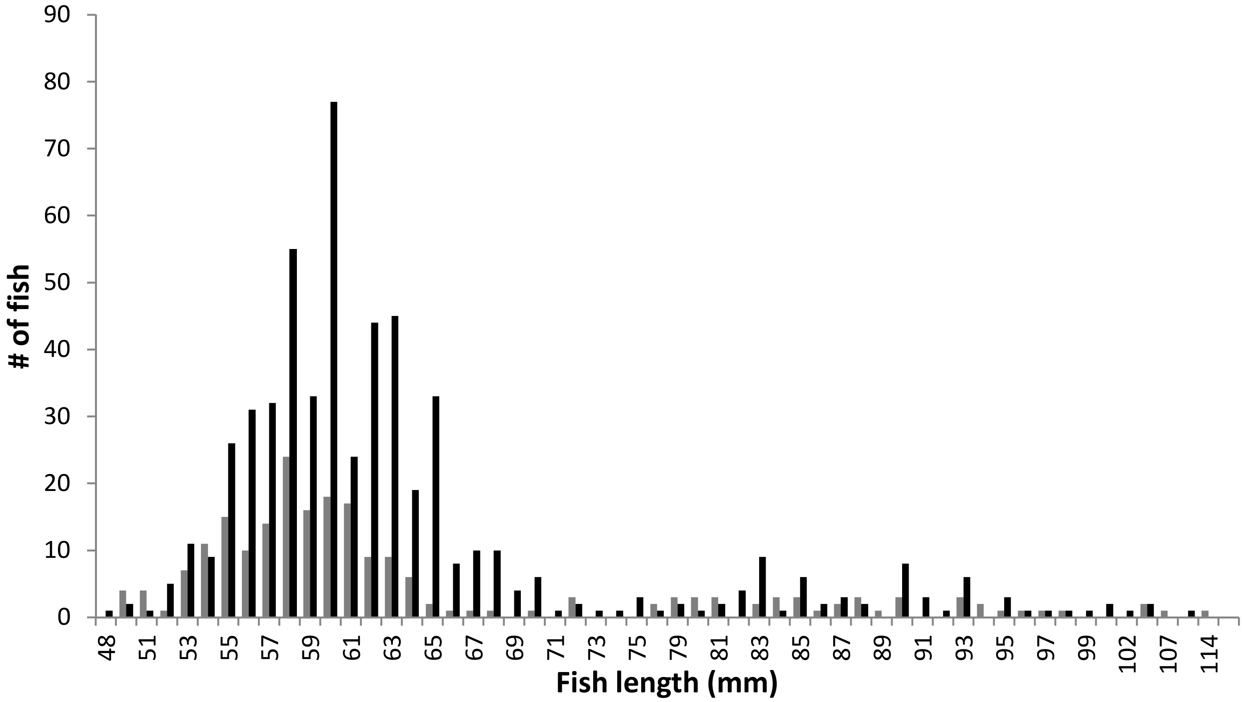

Figure 6a. Size frequency distribution of juvenile coho in the first (grey bars, 08-21-08) and second (black bars, 09-02-08) samplings at parafluvial pond C, Kwethluk River.

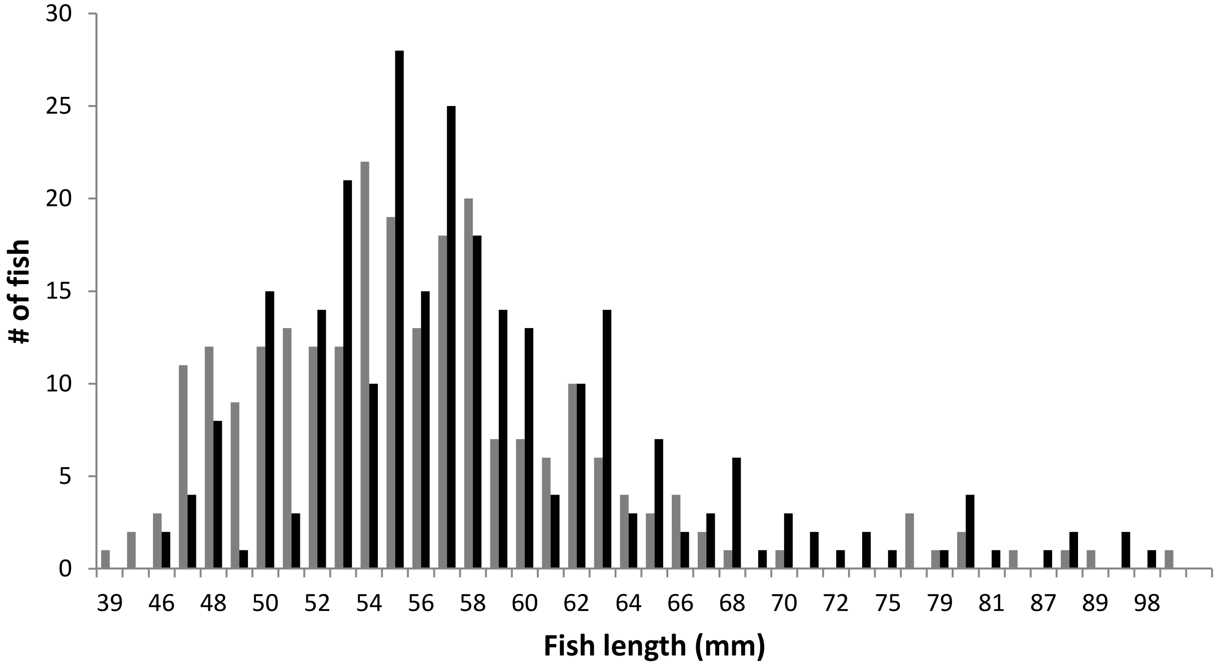

Figure 6b. Size frequency distribution of juvenile coho in the first (grey bars, 08-24-08) and second (black bars, 09-04-08) samplings at parafluvial pond B, Kwethluk River.

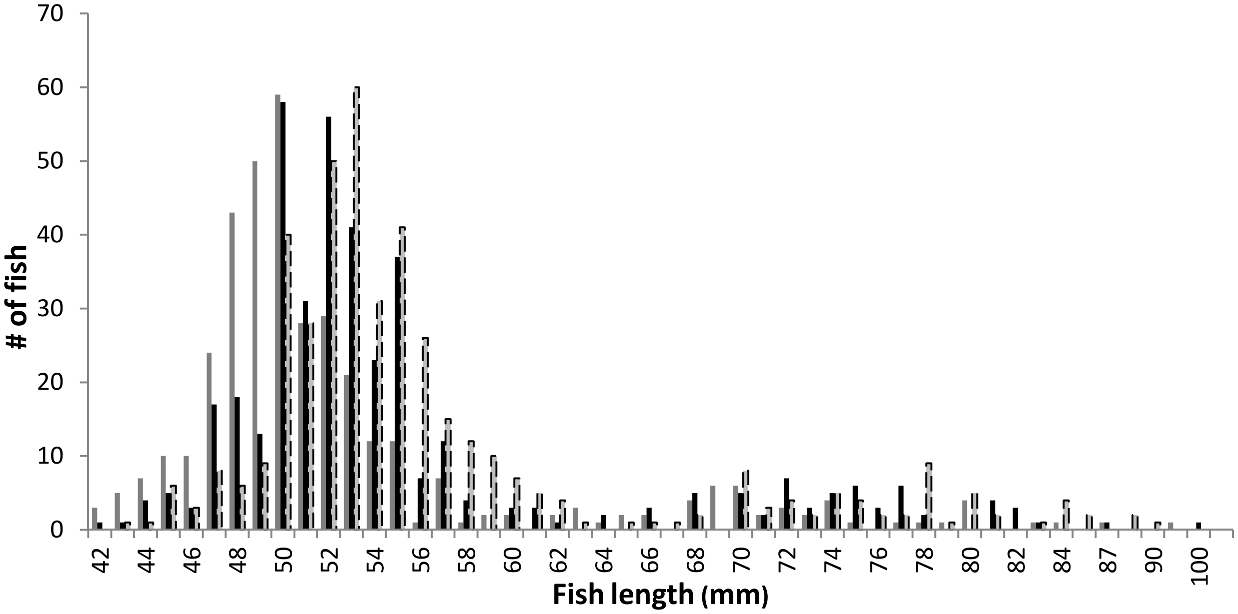

Figure 6c. Size frequency distribution of juvenile coho in the first (dark grey bars, 08-22-08), second (black bars, 09-04-08), and third (light grey bars with dashes, 09-20-08) samplings at parafluvial pond K, Kwethluk River.

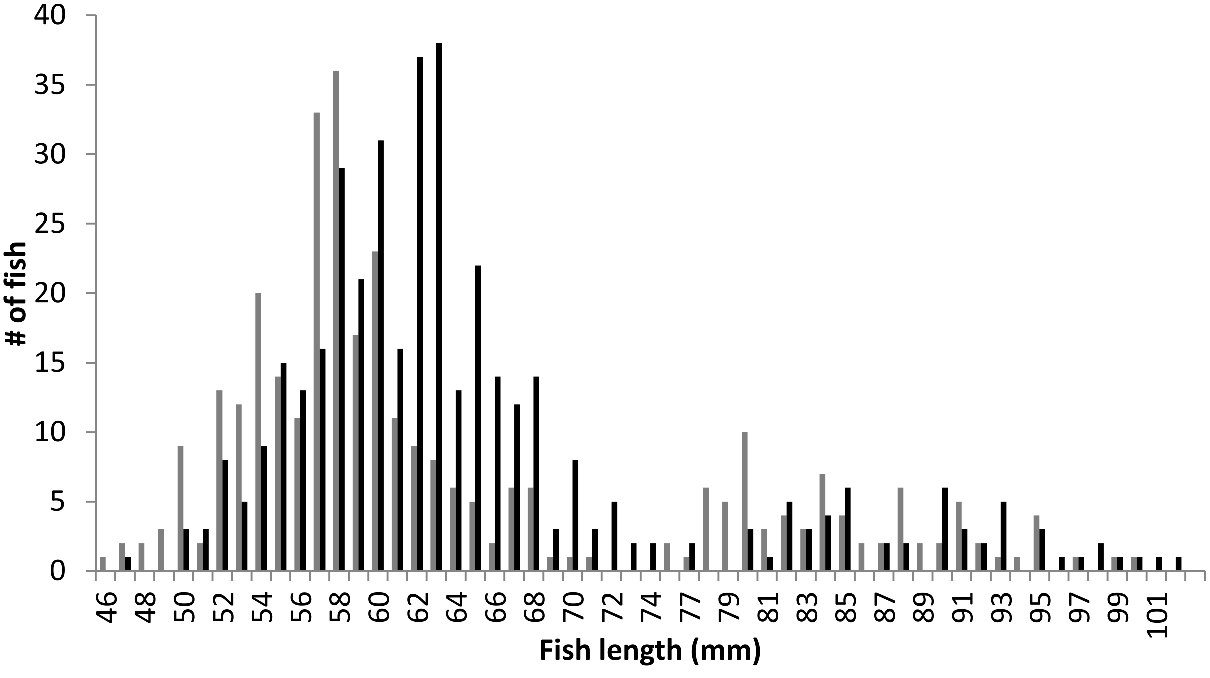

Figure 6d. Size frequency distribution of juvenile coho in the first (grey bars, 08-20-08) and second (black bars, 09-02-08) samplings at parafluvial pond D, Kwethluk River.

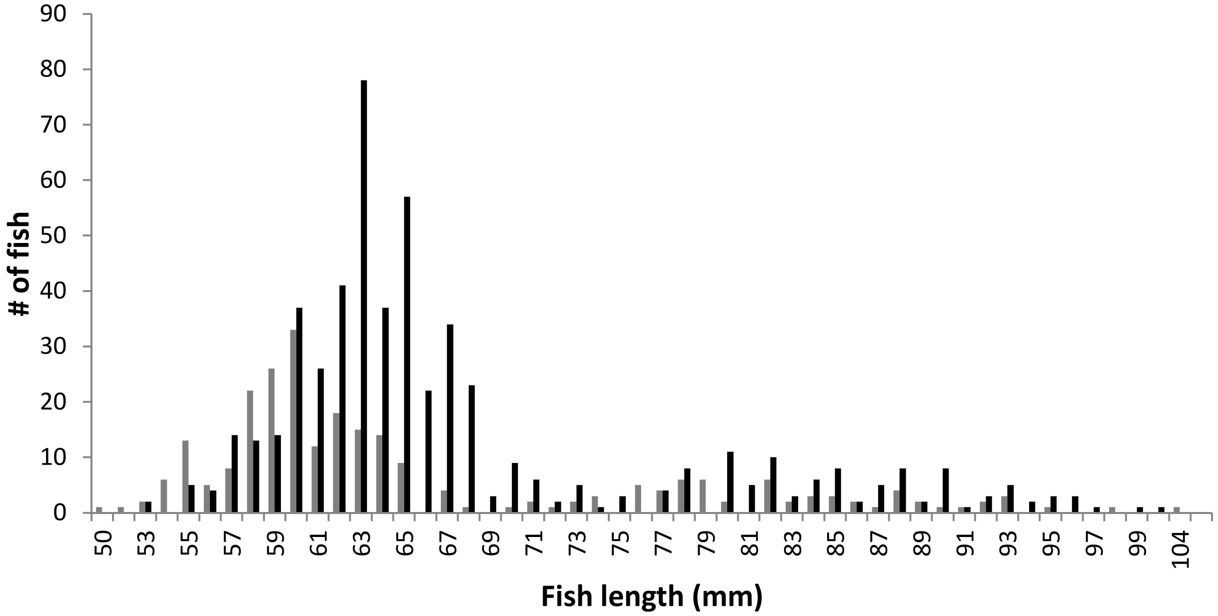

Figure 6e. Size frequency distribution of juvenile coho in the first (grey bars, 08-21-08) and second (black bars, 09-03-08) samplings at parafluvial pond G, Kwethluk River.

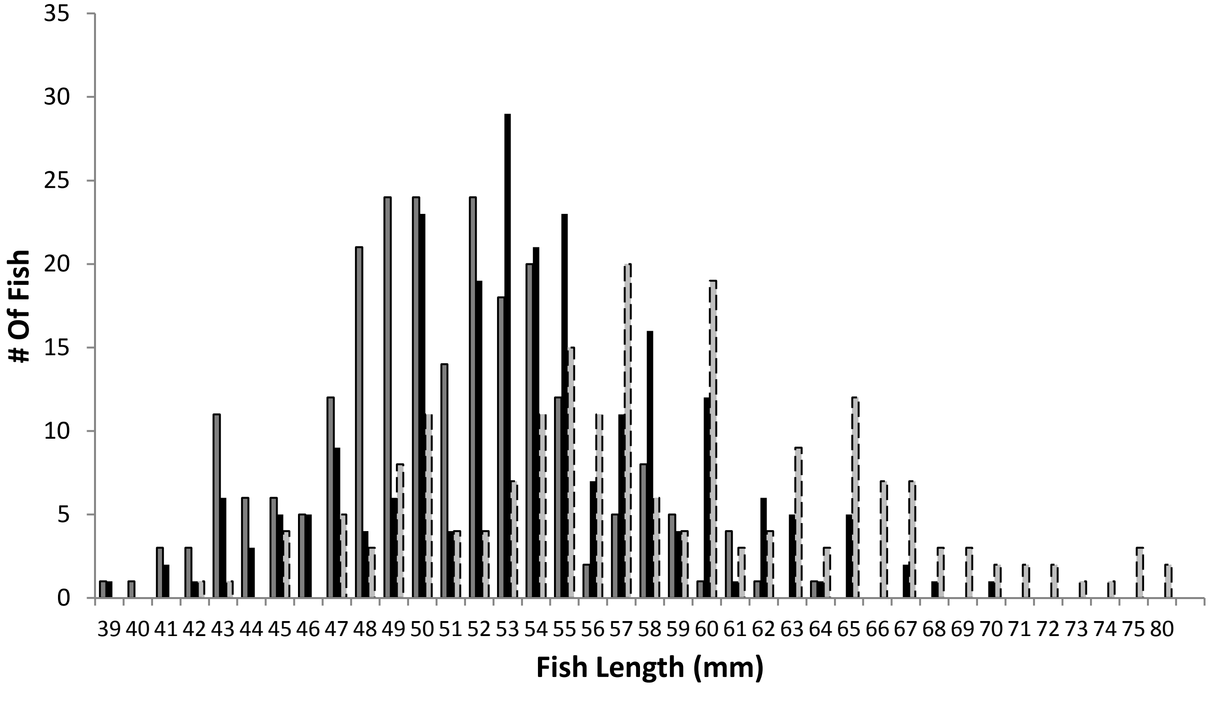

Figure 6f. Size frequency distribution of juvenile coho in the first (dark grey bars, 08-22-08), second (black bars, 09-03-08), and third (light grey bars with dashes, 09-21-08) samplings at parafluvial pond I, Kwethluk River.

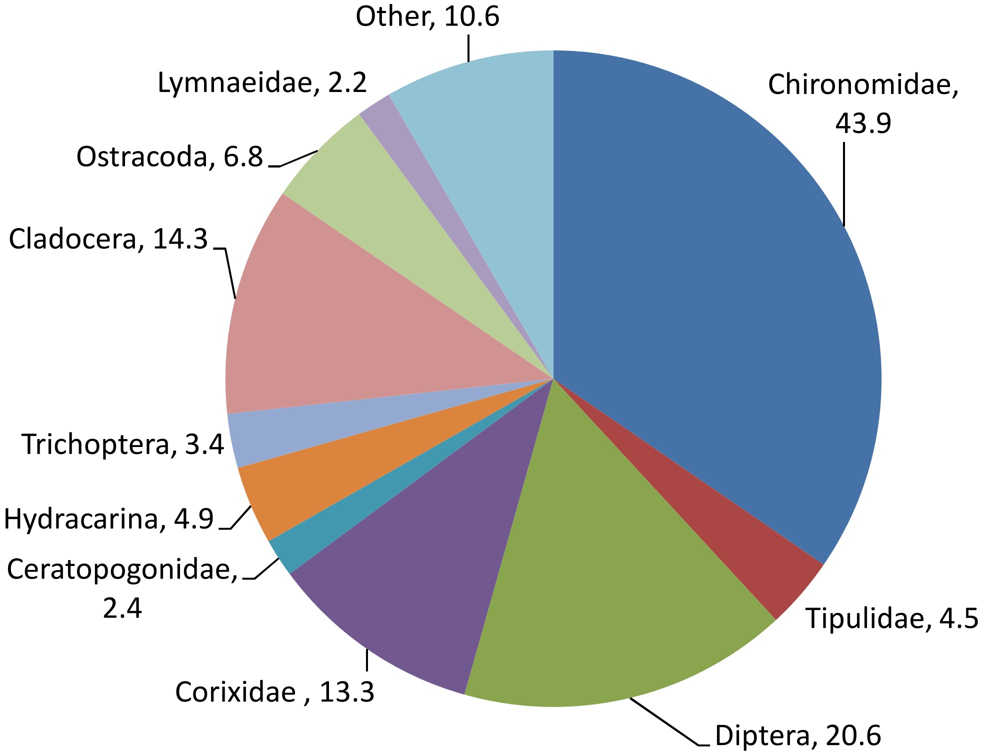

Figure 7. Mean number of prey items consumed by juvenile coho in main study parafluvial ponds on the Kwethluk River, 2008. Total sample size was 150 fish from 15 ponds. The “other” category represents rare taxa numbering less than two individuals per sample event.

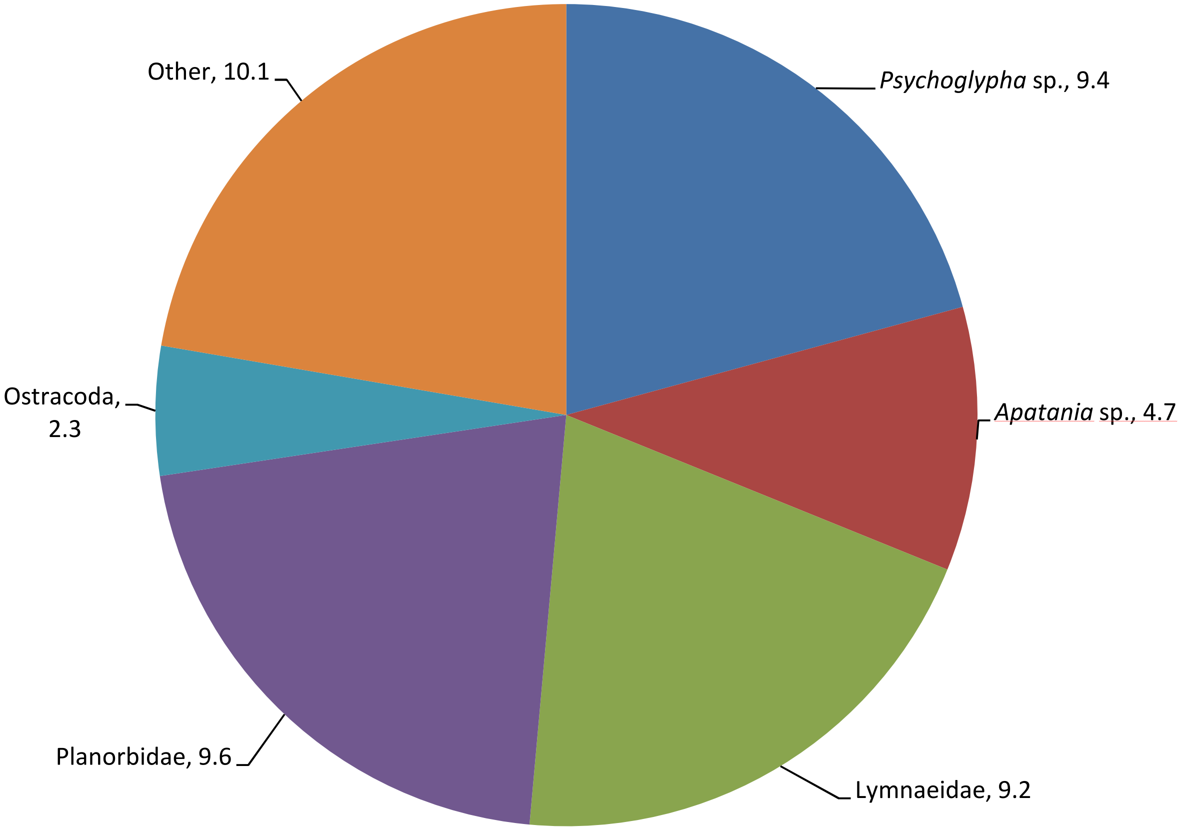

Figure 8. Mean number of invertebrates collected during shoreline picks in parafluvial ponds (n=26) on the Kwethluk River, 2008. The "other" category represents rare taxa numbering less than two individuals per sample event.

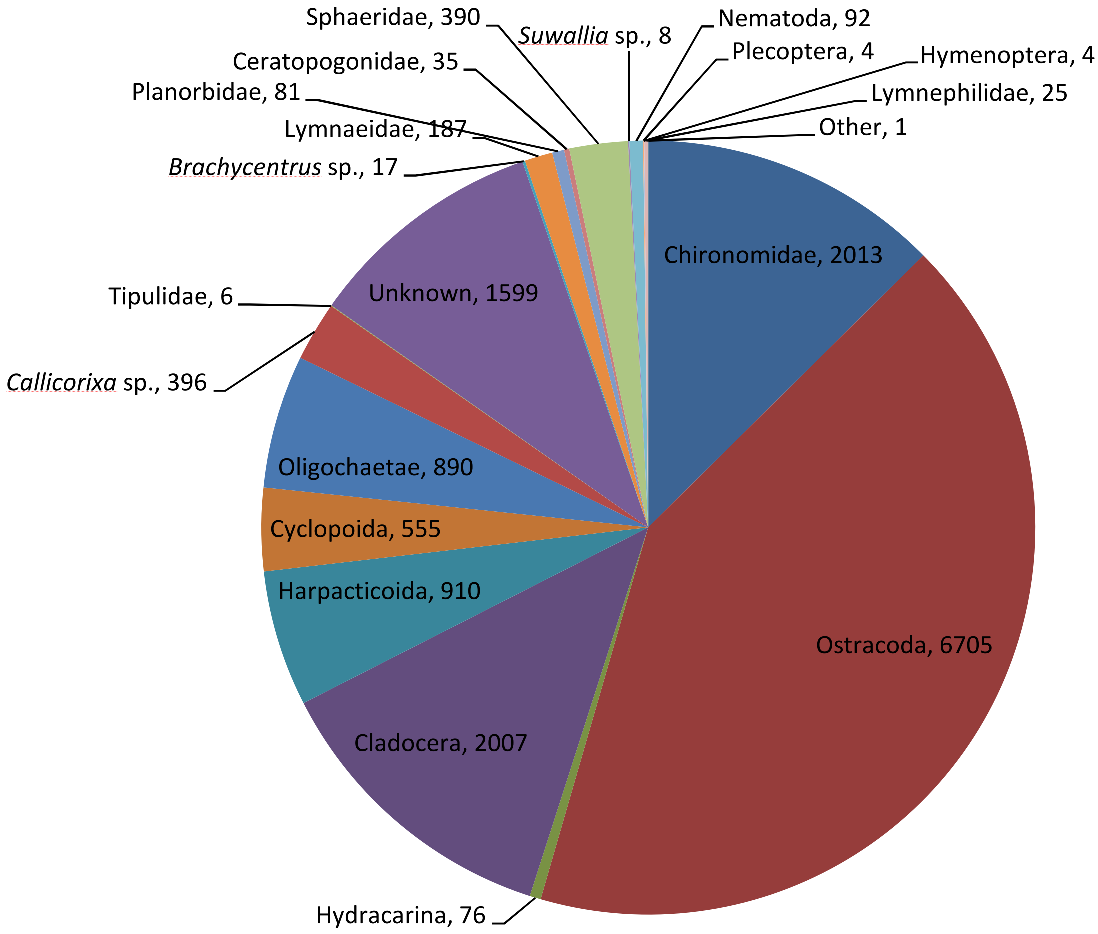

Figure 9. Mean invertebrate composition of sweep net samples (n=5) in parafluvial ponds on the Kwethluk River, 2008. The “other” category represents rare taxa numbering less than two individuals per sample event.

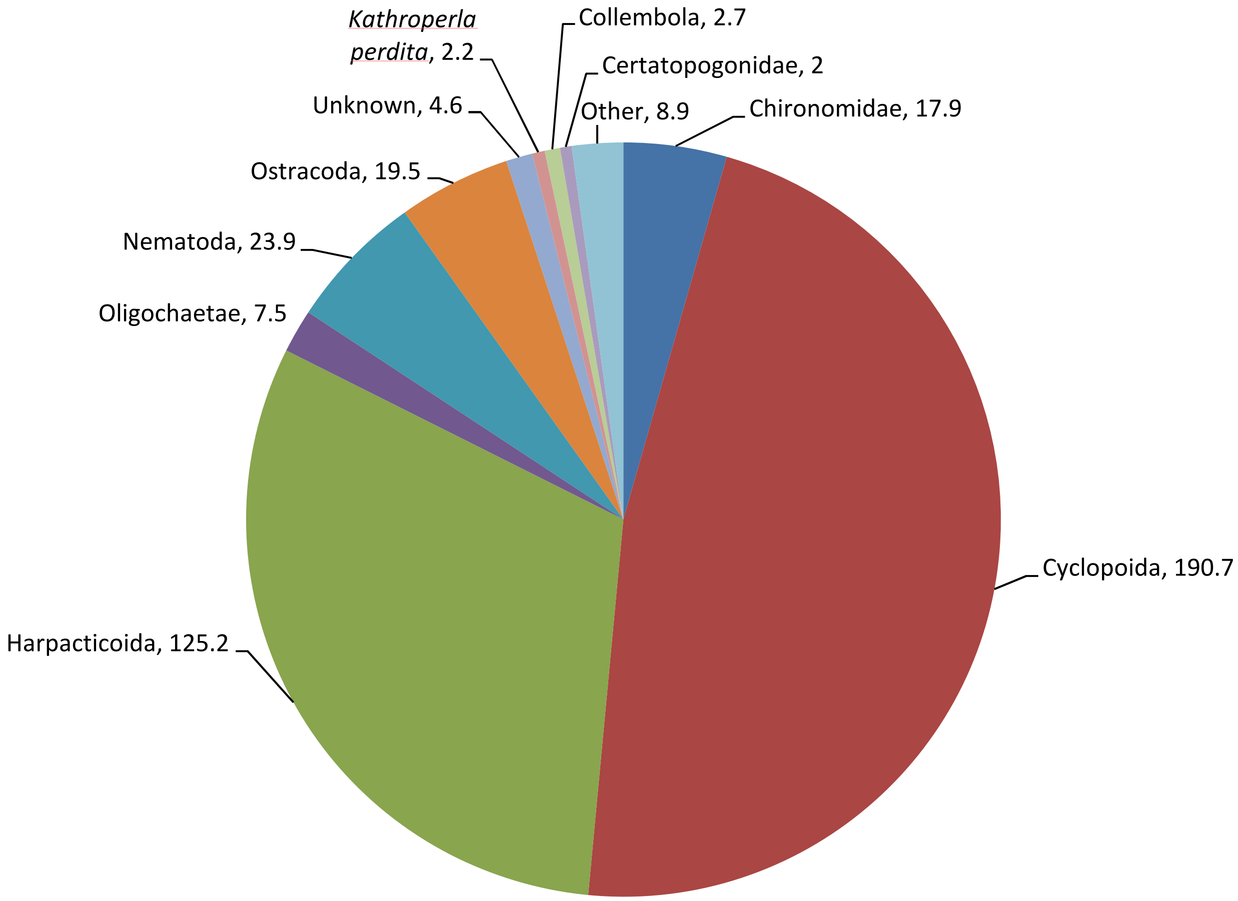

Figure 10. Mean number of groundwater invertebrates per gravel bar (n=5) where parafluvial ponds are found on the Kwethluk River, Alaska 2010. The "other" category is all taxa numbering less than 2 individuals.

Table 1. Temperature (^oC) data for all main study ponds with last two columns showing max temperature for growth assuming unlimited food and time over lethal temperature on the Kwethluk River, 2008. The absolute max column shows the highest temperature recorded for the entire study period. The SaRON (Salmonid Research Observatory Network) names correspond to the nomenclature used in our database at Flathead Lake Biological Station.

Main study pond names	SaRON names	GPS UTM zone 4	Mean daily	Mean minimum	Absolute maximum	Time over 15 ^oC (hours)	Time over 20 ^oC (hours)
A	[CJ]C	N 6701974 E 383499	9.3	7.5	17.2	17.6	0
B	[CP]A	N 6691646 E 384641	10.2	9.7	13.0	0	0
C	[CJ]B	N 6701984 E 383507	7.6	6.7	12.6	0	0
D	[CJ]M	N 6701910 E 383550	8.2	7.9	11.2	0	0
E	[CJ] D	N 6701997 E 383524	11.8	10.2	18.0	61.3	0
F	[CJ]E	N 6701962 E 383548	9.9	8.3	17.2	22.7	0
G	[CJ]G	N 6701964 E 383479	6.5	5.4	10.9	0	0
H	[CP]M	N 6691688 E 384720	10.6	8.8	19.2	35.7	0
I	[DT]	N 6691201 E 385301	10.9	9.6	19.2	0	0
J	[DW]	N 6704604 E 384026	9.9	9.4	15.7	0	0
K	[JJ]	N 6689178 E 388029	11.6	10.5	17.2	79.3	0
L	[RR]	N 6691052 E 385633	10.3	8.2	23.7	388	69
Kwethluk Weir	[WK]	N 6708471 E 384770					

Table 2. Max area, pond depth, number of days separated from main channel, fish density and population estimates with 95% confidence intervals of parafluvial ponds where fish were sampled on the Kwethluk River, 2008. For fish density and population, the first set of numbers represent the values for each sampling event with 95% confidence intervals (+/- values) below. The * represent ponds without staff gauges.

Pond name	Max area m^2	Depth range (cm)	Duration (days)	Density fish / m^2	Fish population
D	227	84.5 - 97.7	68	4.7; 2.6 CI 0.8; 0.4	526; 600 CI 90; 89
I	168	34.3 - 45.7	61	2.2; 2.9; 1.7 CI 0.3; 0.4; 0.3	260; 277; 280 CI 31; 37; 53
J	382	73.7 - 76.5	9	0.7 CI 0.2	283 CI 56
K	393	48.3 - 50.5	36	1.6; 1.6; 2.6 CI 0.3; 0.2; 0.3	613; 478; 563 CI 102; 49; 73
L	8	0 - 13.9	62	0	0
C	211	*	68	5.1 CI 0.6	734 CI 85
G	364	*	65	2.1 CI 0.3	772 CI 96
B	103	*	35	2.7; 5.7 CI 0.2; 0.7	274; 313 CI 27; 41

Table 3. Mean point measures of water chemistry +/- one standard deviation taken from main study parafluvial ponds, main channel, spring brooks, and groundwater on the Kwethluk River, 2008. The first number in each column is the mean value and the second number is the standard deviation.

Pond Name	**pH**	**Specific Conductance µS**	**° C**	**DO %**	**DO mg/L**
D	7.26 0.90	120 1.2	11 0.6	39.6 9.2	4.0 1.3
I	7.54 0.41	107.4 5.1	11.7 4.4	84.1 10.4	9.2 1.6
J	7.50 0.22	104.2 0.8	11.9 1.4	89.2 5.4	9.3 1.4
K	7.34 0.38	110.6 9.7	10.5 2.5	81.9 12.3	8.4 1.3
L	7.42 0.61	173.9 76.2	14.9 3.2	98.7 13.7	10.4 1.5
C	6.95 1.04	108.4 17.7	12.7 1.8	86.5 8.1	8.3 0.2
G	7.02 1.49	110.8 5.8	9.2 0.8	44.7 0.3	4.8 0.3
B	7.55 0.03	112.8 8.1	11.7 1.0	56.7 13.5	5.8 1.1
E	6.94 0.73	137.4 20.2	17.6 3.0	50.9 10.7	5.0 1.3
A	6.92 1.30	131.4 8.4	14.8 1.5	85.3 6.0	8.3 0.5
F	7.13 0.66	117.3 10.5	14.9 1.1	54.5 15.6	5.9 1.5
H	7.60 0.06	109.4 8.2	11.4 0.1	73.6 32.0	7.4 2.9
Mean all ponds	7.36 0.59	122.7 36.7	12.8 3.1	74.4 25.3	8.0 2.5
Main channel	7.45 0.50	105.8 4.0	10. 2 1.9	91.7 18.1	9.6 2.0
Spring brooks	7.28 0.52	119.1 18.3	8.3 2.3	58.5 17	6.6 1.9
Groundwater	7.34 0.51	105.5 20.5	12.4 1.3	62.2 14.8	6.9 1.0

Table 4. Mean point measures of water chemistry +/- one standard deviation from parafluvial ponds and main channel on three floats. First float was from June 18th to June 28th; second float August 7th to August 31st; third float September 10th to September 24th on the Kwethluk River, 2008. The first number in each column is the value and the second number is the standard deviation.

Floats	**pH**	**Specific Conductance**	**° C**	**DO %**	**DO mg/L**
Ponds float one	7.91 0.40	163.4 16.9	8.5 3.4	84 14.4	9.3 1.6
Main channel float one	7.81 0.30	145.7 27.1	6.1 1.6	86.5 7.6	10.3 1.2
Ponds float two	7.51 0.50	133.9 16.9	12.7 2.7	71 19.8	7.2 2.1
Main channel float two	7.61 0.59	123.6 19.4	9.0 1.5	81.7 8.4	9.0 1.0
Ponds float three	7.44 0.50	128.8 20.6	9.9 2.1	78.9 15.9	8.7 1.7
Main channel float three	7.55 0.48	121.0 18.0	7.5 1.2	82.9 4.1	9.6 0.6

Table 5. Fulton's condition factor for YOY and 1+ coho in main study parafluvial ponds for each sampling event. On the Kwethluk River, 2008.

Pond	**K Factor YOY Sample Event 1**	**K Factor YOY Sample Event 2**	**K Factor YOY Sample Event 3**	**K Factor 1+ Sample Event 1**	**K Factor 1+ Sample Event 2**	**K factor 1+ Sample Event 3**
D	0.93	0.85	n/a	0.96	0.89	n/a
I	0.94	0.93	0.92	n/a	n/a	n/a
K	0.95	0.85	0.88	0.98	0.9	0.91
C	0.92	0.88	n/a	0.94	0.9	n/a
G	0.9	0.84	n/a	0.92	0.86	n/a
B	0.85	0.86	n/a	0.95	0.88	n/a
Mean	0.92	0.87	0.9	0.95	0.89	n/a