# Linkages between temperature, macroinvertebrates, and young-of-year Coho Salmon growth in surface-water and groundwater streams

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**Abstract:** Ecological resources for fishes in stream food webs shift over space and time, providing a complex template of available resources that can be used for growth. We tracked water temperature in conjunction with young-of-year Coho Salmon size, growth, and diet in 2 streams with contrasting thermal regimes: a groundwater stream with colder temperatures and lower thermal variability all year and a surface-water stream with greater thermal variability and warmer summer temperatures more conducive to young-of-year salmon growth. We hypothesized that fry emergence would occur when rearing conditions are optimal for growth and that, all else being equal, summer fish growth will be greater in the surface-water stream. Previous work on Coho Salmon phenology in these streams showed that peak fry emergence occurred at the same time in early summer in both streams. We measured salmon fry emergence in relation to thermal variability and macroinvertebrate prey availability with subsequent tracking of somatic growth, diet, and body size during the 1st year of life in both streams. Macroinvertebrate prey availability was highest overall in the colder and thermally-stable groundwater stream than the surface-water stream. Prey availability was particularly high in the thalweg drift during peak fry emergence in the groundwater stream. There was no difference in Coho Salmon diet composition between streams, which included invertebrates from benthic, drift, and riparian habitats. We found no differences in young-of-year Coho Salmon body size, growth, or consumption between streams. Overall, our results suggest that large differences in thermal regimes do not necessarily translate to large differences in young-of-year Coho Salmon size, growth, or diet. Many variables can influence fish growth, and there is not always a direct connection between spatial and temporal dimensions of environmental variability and their cascading effects on young-of-year Coho Salmon growth during the 1st summer of life.
**Key words:** salmon, temperature, macroinvertebrates, growth, phenology, groundwater, surface-water, Alaska

Many species in lotic ecosystems have traits that appear to be adaptive responses to exploit variation in temperature (Poff et al. 2006, Steel et al. 2017, Walters et al. 2018) and stream flows (Lytle and Poff 2004, Mims and Olden 2012, Mauger et al. 2017). Traits can vary considerably within species, which might also reflect adaptations to environmental conditions that vary across their geographic ranges (Sweeney et al. 1992, Conover and Schultz 1995, Blanck and Lamaroux 2007). The interaction between physical dimensions of variability and biological variation is particularly important for species with complex life cycles (Stenseth and Mysterud 2002, Visser and Both 2005). For example, if environmental conditions become unsuitable for just one critical stage in the life cycle (e.g., reproduction, young-of-year, or adult survival), a species might not be able to persist (Schlosser 1995). Interactions among life stages can also be very important, so understanding just one life stage is likely insufficient for understanding how a species responds to environmental variability in space and time (Schluter et al. 1991).

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Lotic ecosystems have been framed in terms of 4 dimensions (Ward 1989). These include 3 spatial dimensions: 1) longitudinal (up-downstream; Vannote and Sweeney 1980, Montgomery 1999), 2) lateral (stream-riparian/floodplain; Nakano and Murakami 2001, Baxter et al. 2005), and 3) vertical (surface/subsurface fluxes; Boulton et al. 1998). The 4$^{th}$ dimension, described by Ward (1989), is time. The temporal dimension of lotic ecosystems includes multiple scales (Fausch et al. 2002, Peterson and Dunham 2010) and temporal components, including magnitude, duration, timing, frequency, and predictability of events such as stream flow (Poff et al. 1997), temperature (Arismendi et al. 2014, Steel et al. 2017), and urbanization (Spanjer et al. 2018). Variability in physical conditions across these dimensions is also evident as variability in species traits (Poff et al. 1997).

Our overall study goal was to understand the connection between environmental variability and the growth dynamics of early life-history stages of Coho Salmon (*Oncorhynchus kisutch*) that inhabit streams with strong gradients in longitudinal, lateral, vertical, and temporal dimensions. We observed thermal variability, prey availability, and salmon growth dynamics in a groundwater stream with low thermal variability and a surface-water stream with high thermal variability. Previous work revealed that the phenology of hatching and emergence of young-of-year Coho Salmon is highly synchronous, even though these streams have very different physical characteristics (Campbell et al. 2019). In this study, we tracked the life cycle of young-of-year Coho Salmon from emergence through the 1$^{st}$ summer of life, following them to the transition into winter. Survival of salmonids is often lowest during the 1$^{st}$ year of life, a perilous time typified by a high-magnitude pulse of post-emergence mortality (Armstrong and Nislow 2006). This pulse, sometimes called the critical period (Elliott 1994), occurs when young-of-year individuals transition from relying on maternal yolk reserves to independent foraging. During this transition, the availability of macroinvertebrate prey and appropriate temperatures for growth may be of paramount importance.

We quantified variability in water temperature and standing stocks of macroinvertebrate prey from multiple habitats over the course of the summer growing season in the surface-water and groundwater streams. We tracked these factors because Coho Salmon, like all Pacific salmon, are sensitive to temperature (Brett 1952, Sandercock 1991, Quinn 2005), and macroinvertebrates make up the bulk of their diet (Nielsen 1992, Robillard 2006, Rosenfeld and Raeburn 2009). We also quantified diets and growth of individuals with coded wire tags over the course of the season. We applied a bioenergetics model (Hansen et al. 1997) to these data to better understand the processes that influence young-of-year Coho Salmon growth, consumption, and net energy gain in summer. We expected the surface-water and groundwater streams to exhibit strong differences in thermal regimes and prey availability, which would then impact the growth, size, diet, and condition of young-of-year Coho Salmon.

We posed a series of predictions and used them to evaluate the field data we collected over the course of the 1$^{st}$ summer of life for Coho Salmon in surface-water and groundwater streams. First, we predicted that emergence would be timed to coincide with availability of accessible prey resources or thermal conditions most conducive to maximizing growth. To test this prediction, we compared seasonal availability of potential macroinvertebrate prey and water temperatures observed before, during, and after Coho Salmon emergence (Campbell et al. 2019). Second, we predicted that, all else being equal (e.g., body size, bioenergetic processes), fish would grow more slowly in colder streams because of their well-documented thermal constraints (Brett 1952, Konecki et al. 1995, Quinn 2005, Armstrong et al. 2013, Mauger et al. 2017). We also evaluated lateral (main-channel vs off-channel) variability in temperature and macroinvertebrate prey to determine potential impacts on fish growth, assuming that increased lateral variation offers greater opportunity for behavioral thermoregulation (Armstrong and Schindler 2013, Armstrong et al. 2013). Standing stocks of benthic macroinvertebrate biomass were measured in main and off-channel habitats, inputs from the riparian zone, and drift in the thalweg to determine the relationship between prey availability and fish growth response. We evaluated fish condition at the end of the growing season by quantifying fish C:N, which is highly correlated with % lipid content (Simpkins et al. 2003, Post et al. 2007). Lipid content can affect survival as salmon in systems with cold winters are more likely to survive to reproduction if they have greater lipid stores (Biro et al. 2004, Berg et al. 2009, Cunjak 2011).

Finally, we used our field measurements of water temperature, fish diet, growth, and size to quantify bioenergetic processes (Hansen et al. 1997, Hartman and Hayward 2007, Beauchamp 2009). Overall, we provide a detailed picture of the connection between spatial and temporal dimensions of environmental variability and the growth dynamics of young-of-year Coho Salmon across life stages in a diverse landscape.

## METHODS

We conducted this study in 2 streams with different thermal regimes on the outwash plain of the west Copper River Delta, southcentral Alaska, USA (Fig. 1). The Copper River Delta is a diverse climatic, geologic, and geomorphic region in which thermal and flow regimes of streams that drain the system are highly variable (Boggs 2000, Adelfio 2016). The study streams included a surface-water dominated stream (18 Mile Creek: lat N60.45882°, long W145.29285°) and a groundwater dominated stream (25 Mile Creek: lat N60.44176°, long W145.11794°). Both streams have open

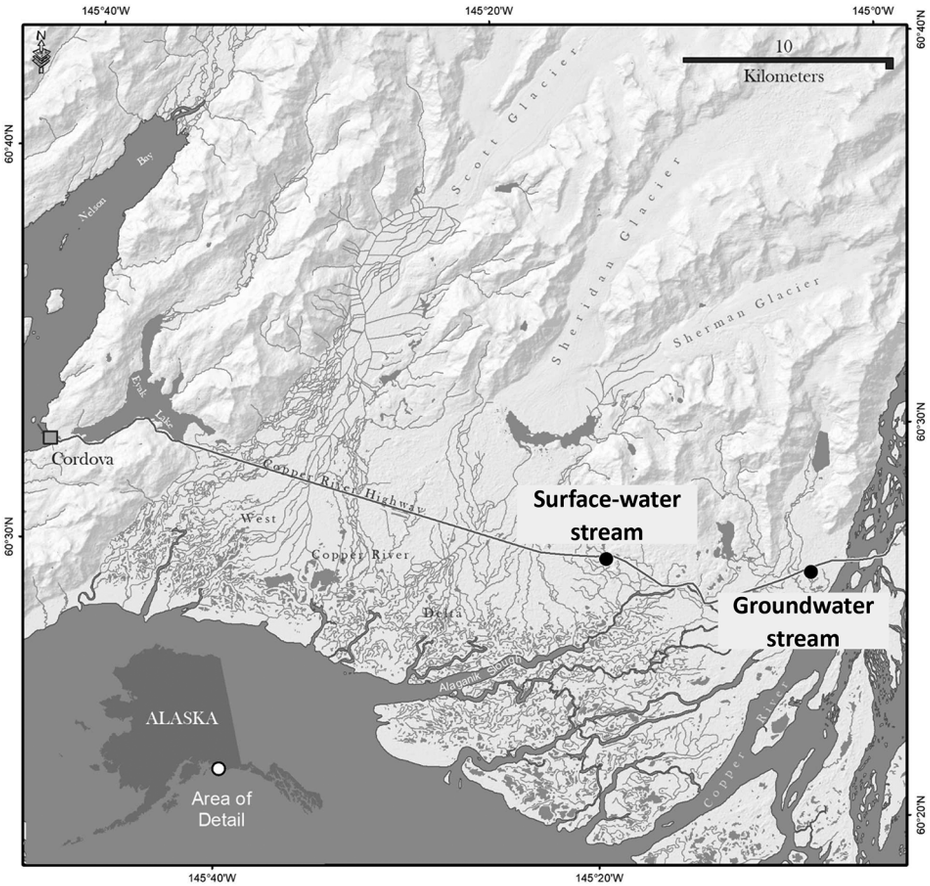


Figure 1. Location of study streams on the Copper River Delta, Alaska, USA. The surface-water stream is 18 Mile Creek and the groundwater stream is 25 Mile Creek.

canopies with riparian vegetation consisting primarily of Sitka alder (*Alnusviridis sinuata*), Sitka spruce (*Picea sitchensis*), and several species of willow (*Salix* spp.), grasses, and sedges. Off-channel habitats in both streams consist of shallow pools with fine organic material, silt, and mud substrates, and these habitats maintain a year-round connection to the mainstem of each stream. Within each stream, we selected a 200-m study reach based on the presence of Coho Salmon and similarities between the reaches including accessibility to the site, riparian vegetation, stream size, slope, and discharge.

To understand differences in thermal regimes among surface-water and groundwater streams, we measured stream temperatures continuously from 15 April 2013 to 1 June 2014 with water temperature data loggers (HOBO® Pro, model U-22; Onset®, Bourne, Massachusetts). All water temperature data loggers were encased in steel pipes for protection and attached by steel cables to duckbill anchors that were driven into the stream bed to withstand frequent storms and high flows. Eight data loggers were deployed in the main-channel and off-channel habitats of each stream. Water temperature was recorded at hourly intervals.

To understand how water temperature affects Coho Salmon diet throughout the year, we sampled young-of-year Coho Salmon diets twice/mo from April to October 2013 in each stream. On each sampling date, fish were collected with minnow traps (40 cm long × 23 cm wide) baited with salmon eggs enclosed in a perforated 7 × 17 cm plastic bag to prevent fish from consuming the bait. We placed a total of 32 traps in the main-channel and off-channel habitats throughout each study reach on each sampling date. We left the traps for ~90 min and, upon collection, placed fish in a 20-L bucket of fresh stream water with an aerator. We took a haphazard sample of 16 young-of-year Coho Salmon from each bucket, euthanized them with tricaine methanesulfonate, and kept them frozen for laboratory analysis of gut contents. All remaining captured fish were measured (fork length, mm) and released. In the laboratory, we thawed the frozen fish and made a ventral incision under a SMZ445 Nikon stereo microscope (Nikon Instruments Incorporated, Melville, New York). We then used forceps to remove stomach contents from the esophagus to the anus to ensure all prey items were collected. All macroinvertebrates in the fish guts were identified to the lowest practical taxonomic

level (Merritt et al. 2008), counted, and measured (lengths, tip of head to end of abdomen) to the nearest 0.5 mm. We then calculated the biomass (mg wet mass) of all specimens based on published length–weight regressions (Cummins and Wuycheck 1971, Meyer 1989, Sample et al. 1993, Hódar 1996, Burgherr and Meyer 1997, Kawabata and Urabe 1998, Benke et al. 1999, Sabo et al. 2002, Grunner 2003, Miyasaka et al. 2008). For partially-digested prey, actual body measurements were not always possible, so we estimated their body lengths based on intact individuals of the same taxon (Wipfli 1997). We calculated the proportion of each prey species in the diet of each fish by dividing the individual mass of the diet item by the mass of the entire gut contents.

To assess changes in Coho Salmon size over the season, we collected young-of-year Coho Salmon twice/mo, from May to October in 2013, with baited minnow traps and dip nets. All collected Coho Salmon were measured (fork length, mm) and released, except for Coho Salmon with body lengths ≥36 mm. Coho Salmon ≥36 mm were placed in aerated buckets with fresh stream water and diluted tricaine methanesulfonate until their movement slowed. These fish were then tagged (description below) to track their growth during the 1$^{st}$ year of life. The tagged fish were then revived with fresh stream water and released into the habitat in which they were found. All fish lengths (fork length, mm) were converted to mass (g) with stream-specific length–mass regressions (Campbell 2017). Mass was difficult to obtain in the field because of weather conditions, so we measured mass of a subset of the population and used the length–mass regressions to estimate the mass of all measured fish.

We tagged each Coho Salmon ≥36 mm in the right dorsal muscle with a 1.1-mm long, pre-cut, sequentially-numbered coded wire tag with a single shot coded wire tag injector (Northwest Marine Technologies, Shaw Island, Washington). We clipped the adipose fin of each tagged fish to aid in future identification, then released the fish into the habitat in which they were found. Tagged fish were later detected with a T-Wand coded wire tag detector (Northwest Marine Technologies). We euthanized recaptured fish with tricaine methanesulfonate and kept them frozen for retrieval of the coded wire tags. In the laboratory, we thawed the frozen fish, removed the coded wire tags from their dorsal muscle tissue under the Nikon stereo microscope and then read the tags with a pencil and jig (Northwest Marine Technologies) under a Nikon stereo dissecting microscope (model SMZ745). The growth period for young-of-year Coho Salmon was between 1 July 2013, when emerging individuals were first detected and tagged, and 15 October 2013, when the last fish was recaptured. After the tags were retrieved, we cut out a 1-g portion of dorsal muscle and sent it to the Colorado Plateau Laboratory (Flagstaff, Arizona, USA) for carbon and nitrogen stable isotope analysis. These stable isotope values were then converted to % lipid content with the methods described in Post et al. (2007).

We quantified benthic macroinvertebrate densities in main-channel and off-channel habitats within each study stream once/mo in July and September in 2013 and 2014 to track macroinvertebrate prey availability over the season in streams with variable thermal regimes. In the main channels, we used a Hess sampler (diameter 36 cm, 250 μm) and pushed the sampler into the benthic sediments (~10 cm) to minimize water exchange. We collected samples by disturbing the substratum (~2–3 cm deep) within the sampler for 1 min as the water flow pushed benthic macroinvertebrates into the terminal collecting net. The sample was then placed in a tray with fresh stream water, passed through a 250-μm sieve, and placed in a plastic vial with 70% ethanol for later taxonomic identification. In the off-channels, we sampled macroinvertebrates with a D-frame kicknet (250 μm) in a 1-m$^2$ area defined by a PVC quadrat to standardize macroinvertebrate densities and biomass by area. We collected these samples by disturbing the substratum (~2–3 cm deep) for 1 min while we moved the net up and down the water column within the quadrat until benthic macroinvertebrates were in the collecting net. The collected sample was then placed in a tray with stream water, passed through a 250-μm sieve, and placed in a plastic vial with 70% ethanol for later taxonomic identification. Taxonomic identification of main-channel and off-channel macroinvertebrates was done under the Nikon stereo microscope. After we identified (Merritt et al. 2008), counted, and measured (mm) the macroinvertebrates, we estimated their biomass (mg wet mass) with published length-mass regressions (Cummins and Wuycheck 1971, Meyer 1989, Sample et al. 1993, Hódar 1996, Burgherr and Meyer 1997, Kawabata and Urabe 1998, Benke et al. 1999, Sabo et al. 2002, Grunner 2003, Miyasaka et al. 2008).

We collected riparian macroinvertebrates once/mo in July and September of 2013 and 2014 following Wipfli (1997) to understand availability of macroinvertebrate prey for juvenile Coho Salmon coming from the terrestrial and riparian zone. We collected riparian invertebrates by placing 8 floating pan traps (800-cm$^2$ surface area with sides 10 cm tall) that each contained ~7 ml of dish soap (surfactant) and 3 L of stream water on streamwater surfaces within each study reach. Traps were placed haphazardly but evenly along the study reach on the surface with 4 traps in the main-channel and 4 traps in the off-channel habitats. The traps were tied with rope to stable riparian vegetation such as overhanging trees or exposed tree roots. Floating pan traps were left for 5 d and the sample was passed through a 250-μm sieve upon collection to filter out all macroinvertebrates. The macroinvertebrates were then rinsed with stream water to remove excess soap and placed in a vial with 70% ethanol until subsequent taxonomic identification. We identified, counted, measured (mm), and estimated biomass of these macroinvertebrates in the same manner as the benthic macroinvertebrates.

Drifting macroinvertebrates were collected from the study streams once/mo from May to August in 2014 and used to calculate the mean number of drifting macroinvertebrates collected in a 24-h period. We placed 3 evenly-spaced drift nets (0.32 × 0.7 m, 250-μm mesh) in the thalweg and elevated them slightly off the bottom (~5 cm) to ensure that they only captured drifting macroinvertebrates. Drifting macroinvertebrates were collected every 2 h for a 24-h period. Discharge through the net ($m^3/s$) was recorded at the upstream end of each net. Upon collection, drift nets were rinsed to flush all macroinvertebrates to the end of the net, and then the sample was placed in a tray with stream water. Any large debris, sticks, or pebbles were rinsed and removed. The sample was filtered through a 250-μm sieve and placed in a polyethylene bag with 70% ethanol for later laboratory processing to identify, count, measure (mm), and estimate biomass (mg wet mass) of all specimens in the same matter as benthic macroinvertebrates. We summarized the bi-hourly drift counts over the entire day and used them to calculate a mean.

We calculated drift density (# macroinvertebrates drifting/100 $m^3$ water) as:

$$\text{Drift Density} = \frac{[(N)(100)]}{[(t)(W)(H)(V)(3600)]} \qquad \text{(Eq. 1)},$$

where $N$ is the number of macroinvertebrates collected, $t$ is the time (h) the drift nets were set, $W$ is the width of the drift net, $H$ is the height of the drift net, and $V$ is the water velocity at the time the sample was taken (Smock 2007). We then converted drift density to drift biomass (mg macroinvertebrates drifting/100 $m^3$ water).

We organized analyses of field data to test predictions from hypotheses relating to diet, growth, and condition of young-of-year Coho Salmon from emergence through the 1st summer of their life. We hypothesized that emergence would be timed to coincide with thermal conditions conducive to maximizing growth, availability of macroinvertebrate prey, or both. We compared biomass of macroinvertebrate prey before, during, and after peak Coho Salmon emergence to test the prediction that timing of emergence is linked to increased prey availability. Differences in macroinvertebrate biomass between streams in each month were determined with Mann–Whitney rank sum $U$-tests in SigmaPlot (version 13.0; Systat Software Incorporated, San Jose, California). As with warming temperatures, we expected to observe a significant increase in prey availability during emergence.

Due to the observational nature of our study and the lack of replication at the stream level, we focused our results on seasonal patterns and effect sizes instead of $p$-values. We used non-metric multi-dimensional scaling (nMDS) ordinations with Bray–Curtis distance metrics and multiple response permutation procedures (MRPP) to examine if Coho Salmon prey composition varied between streams, seasons, and habitats.

We quantified individual growth differences by calculating the differences between measured body weights from the time of tagging to the time of recapture to test the hypothesis that young-of-year Coho Salmon grow slower in the colder stream in the summer. We retrieved 26 Coho Salmon coded wire tags from the surface-water stream and 54 coded wire tags from the groundwater stream. These data were compiled to calculate a mean observed growth rate (g/d) for each stream. Observed growth rates were plotted as box plots and differences were tested with a Mann–Whitney rank sum $U$-test. We calculated and plotted median fork length (mm) each month (June–October 2013) to assess differences in fish size between streams. Differences between lengths of young-of-year Coho Salmon in both streams in each month were determined with Mann–Whitney rank sum $U$-tests in SigmaPlot.

We described distributions of fish sizes over time in terms of medians and variances of measured fork lengths for all fish captured in each sampling event in 2013. We evaluated pairwise differences in both the median and variance of fish sizes for each sampling event in 2013 (June–October). All analyses involving pairwise comparisons used a non-parametric Mann–Whitney rank sum $U$-test. Changes in variance over time for each stream were evaluated with a non-parametric Spearman rank correlation. We conducted an analysis of covariance (ANCOVA) with size (fork length, mm) as a covariate and then compared differences among streams SigmaPlot to assess differences in % lipid composition among fish in the 2 stream types. Additionally, we used SigmaPlot to conduct an ANCOVA with size (fork length, mm) as a covariate to adjust for the effect of fish size on growth.

As a supplement to the empirical data, we also evaluated bioenergetic processes influencing growth by applying field-collected information on temperature, size, growth, and diets of young-of-year Coho Salmon using the Fish Bioenergetics 3.0 model (Hansen et al. 1997). This model assumes that inputs, gains, and losses of energy can be balanced in an energy equation, where consumption is the energy input, growth is the net energy gain, and all other uses are losses. The balanced energy equation can be represented in simplified form by the formula $C = B + R + A + S + F + U$ (Warren and Davis 1967), where $C$ is the rate of energy consumption, $B$ is somatic tissue growth, $R$ is the standard metabolic rate, $A$ is active metabolism, $S$ is the metabolic rate from specific dynamic action (heat increment), $F$ is waste loss from egestion (feces), and $U$ is waste loss from excretion (urine).

Coho Salmon diets, growth rates, and patterns of thermal variability were quantified for all recaptured fish. We then used these data as input parameters in the Fish Bioenergetics 3.0 model in R (version 3.4.0; R Project for Statistical

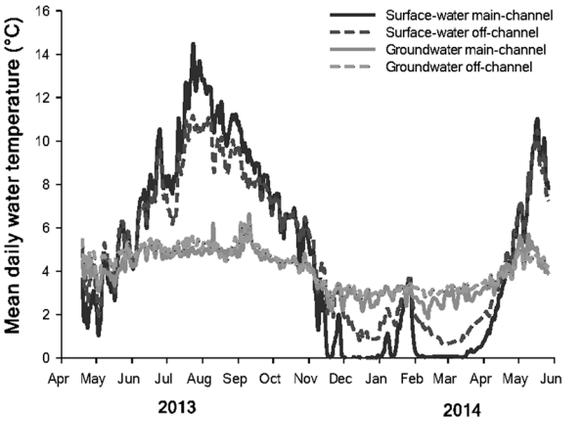


Figure 2. Mean daily water temperatures (°C) in main-channel and off-channel habitats of 2 salmon spawning tributaries of Alaska's Copper River Delta, recorded from 15 May 2013 to 15 June 2014. The surface-water stream is 18 Mile Creek and the groundwater stream is 25 Mile Creek.

Computing, Vienna, Austria) and ran bioenergetic simulations to evaluate estimated consumption, represented as specific consumption ($g^2$/d). In addition, the bioenergetic simulations of specific consumption ($g^2$/d) and the proportion of maximum consumption ($pC_{max}$) were evaluated to understand potential differences in fish consumption between streams. See Table S1 for descriptions and definitions of all parameter inputs that were not directly measured in the field but were used in the model. We plotted bioenergetic estimates of consumption in each stream with box plots and tested differences with a Mann–Whitney rank sum *U*-test.

## RESULTS

The thermal regimes of the 2 study streams differed during the growth season (emergence to the end of the 1st year of life; *U*-statistic [$U_{stat}$] = 9636, degrees of freedom [df] = 166; Fig. 2). Temperatures in surface-water-dominated 18 Mile Creek had higher annual variation (mean = 6.3°C, variance = 21.4) during the growing season, whereas the thermal regime in groundwater-dominated 25 Mile Creek was relatively stable (mean = 4.0°C, variance = 1.2). The surface-water stream reached optimal growth temperatures for Coho Salmon (10–12°C; Brett 1952, Konecki et al. 1995) for a total of 102 d from mid-July to the end of October 2013. In contrast, the groundwater stream never warmed to the optimal growth temperature range (Fig. 2). Furthermore, the surface-water stream accumulated nearly 60% more degree days (dd; 1049) than the groundwater stream (667 dd) during the 1st growth season.

Differences in thermal regimes translated to within-channel variability as well, where the surface-water stream showed high lateral thermal variation between the main-channel (thalweg) and off-channel habitats, and the groundwater stream showed stable and homogenous temperatures regardless of the spatial or temporal axes analyzed. The surface-water stream showed a much wider range of temperatures (max = 14.9°C, min = 0.03°C) than the groundwater stream (max = 6.5°C, min = 1.8°C). There were also clear differences in lateral thermal variability between study streams during the 1st young-of-year Coho Salmon growing season in 2013 ($U_{stat}$ = 3923, df = 166; Fig. 2). Temperature plots of main-channel and off-channel habitats (Fig. 2) showed greater variation in the surface-water stream and less within-channel temperature variation in the groundwater stream.

Despite the temperature differences between streams, we observed no difference in the summer growth rates (coded wire tag growth data) of juvenile Coho Salmon between streams (Fig. 3). Variation in fish growth rates was highest within the groundwater stream, which had a lower variation in temperature than the surface-water stream. Changes in median body lengths of young-of-year Coho Salmon populations over the season were nearly identical between streams, and by the end of the 1st growing season, there were no differences in the body lengths of young-of-year Coho Salmon between the 2 streams (Fig. 4). Length–mass regressions were mass = 1.37 – (0.09 × L) + (0.002 × $L^2$), $r^2$ = 0.94, $p < 0.001$ for the surface water stream and mass = 0.42 – (0.04 × L) + (0.001 × $L^2$), $r^2$ = 0.95, $p <$ 0.001 for the groundwater stream, where mass = g and L = body length (mm).

On average, we found a higher availability of benthic macroinvertebrate prey in the main-channels, off-channels, riparian/terrestrial, and thalweg drift habitats in the groundwater stream than the surface-water stream, with some variation by season and year (Figs. 5, 6). In main-channel habitats, invertebrate prey availability was 5 to 10× greater

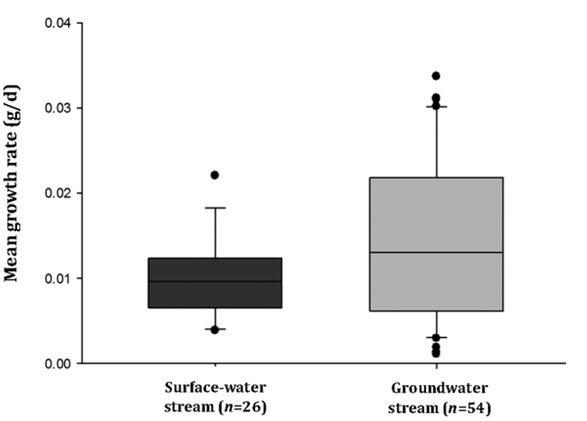


Figure 3. Observed mean growth rates (g/d) of juvenile Coho Salmon during the summer growing season (July to September) in the surface-water stream and the groundwater stream. The horizontal line represents the median. The upper and lower whiskers represent the maximum and minimum data points, respectively. Outliers are shown as dots. The top and bottom of the box plot represent the 1st and 3rd quartiles, respectively.

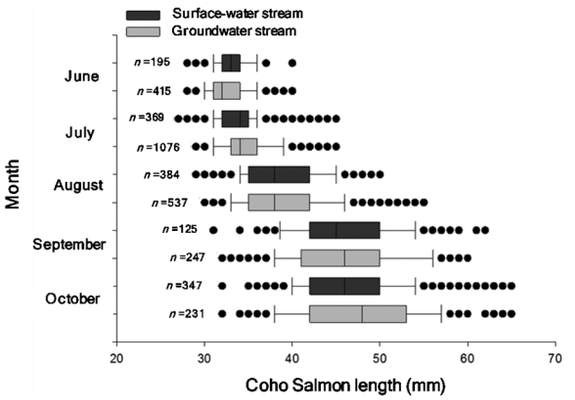


Figure 4. Box plots of juvenile Coho Salmon body lengths (fork length, mm) from June to October 2013 in the surface-water stream (dark gray bars) and the groundwater stream (light gray bars). The horizontal line represents the median. The upper and lower whiskers represent the maximum and minimum data points, respectively. Outliers are shown as dots. The top and bottom of the box plot represent the 1st and 3rd quartiles, respectively.

in the groundwater stream than in the surface-water stream based on the Mann–Whitney rank sum tests ($U_{stat}$ = 62, df = 4; Fig. 5A). In the off-channel habitats, invertebrate prey availability was 10 to 15× greater in the groundwater stream than the surface-water stream, except in September 2014 when prey biomass was higher in the surface-water stream ($U_{stat}$ = 85, df = 4; Fig. 5B). In the terrestrial/riparian pan traps, invertebrate prey availability was 10 to 20× greater in the groundwater stream than in the surface-water stream. Availability remained relatively constant among seasons and streams but was greater overall in the groundwater stream ($U_{stat}$ = 66, df = 4; Fig. 5C). Thalweg macroinvertebrate biomass drift rates (mg of macroinvertebrates/100 $m^3$/h) varied across the time of fry emergence and throughout the growing season in both study streams (Fig. 6). In May and June (prior to peak Coho emergence), drift biomass did not differ between streams. However, during peak Coho emergence in July, drifting macroinvertebrate biomass was 183× greater ($U_{stat}$ = 28, df = 24). After peak Coho emergence in August, prey biomass availability in the drift habitat was 16× greater in the groundwater stream ($U_{stat}$ = 68, df = 24; Fig. 6). Note the log scale in Fig. 6.

The nMDS ordinations and MRPP revealed no differences in Coho diet composition between streams (Fig. 7A, B). Seventy-nine % of the variation in Coho diet composition between streams was explained by a 3-axes solution with a mean stress of 15.9. The nMDS and MRPP analyses showed no clustering of Coho Salmon gut contents with any particular prey assemblages in the various habitats measured. For the surface-water stream, 71% of the variation in macroinvertebrate diet composition across habitats was explained by a 3-axes solution with a mean stress of 16.2. For the groundwater stream, 78% of the variation in macroinvertebrate diet composition across habitats was explained by a 3-axes solution with a mean stress of 15.1. All macroinvertebrate taxa collected in main-channel, off-channel, riparian, drift, and within Coho Salmon guts are listed in Table S2.

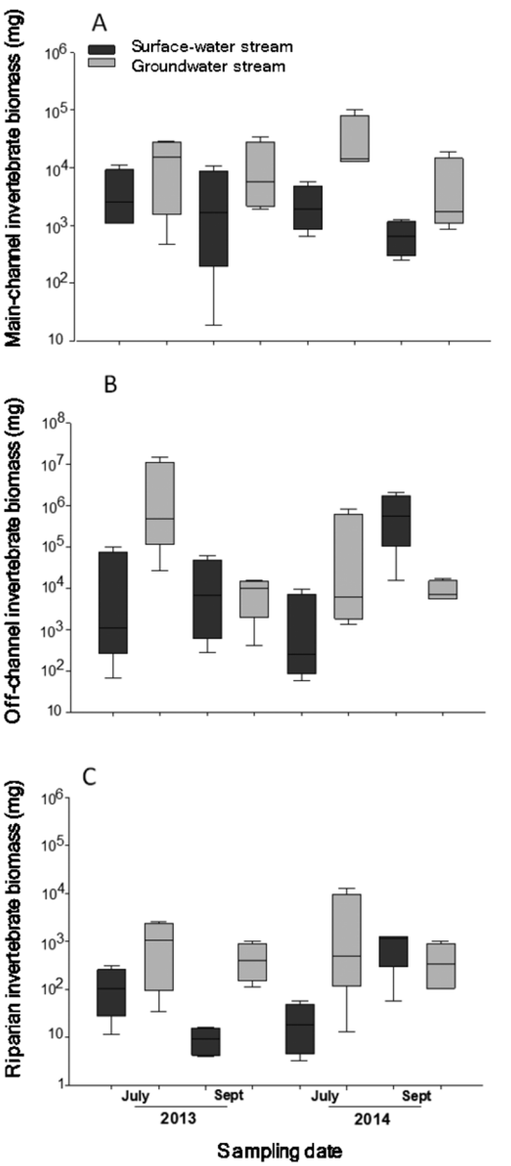


Figure 5. Macroinvertebrate prey biomass (±SE) in main-channel benthos (A), off-channel benthos (B), and riparian (terrestrial) habitats in the surface-water stream and the groundwater stream (C) in July and September 2013 and 2014. Note that the y-axis is on a $\log_{10}$ scale. The horizontal line represents the median. The upper and lower whiskers represent the maximum and minimum data points, respectively. Outliers are shown as dots. The top and bottom of the box plot represent the 1st and 3rd quartiles, respectively.

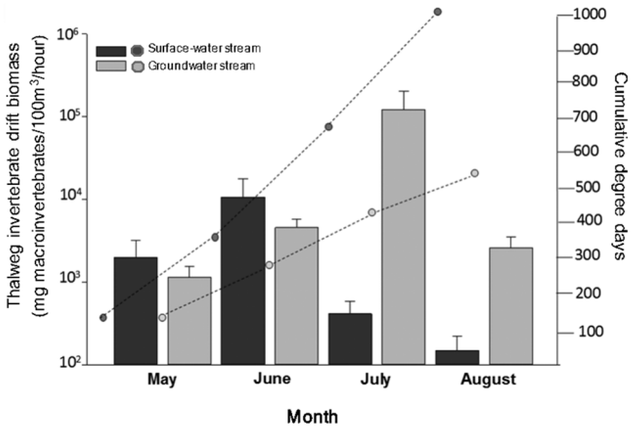


Figure 6. Macroinvertebrate prey biomass in thalweg drift (mg macroinvertebrates/100m$^3$ water/h) in the study streams from May to August 2014. Note that the y-axis is on a $\log_{10}$ scale. Line and scatter plots show cumulative degree days (baseline temperature 5°C ±SE; right y-axis) from May to August 2014 in each stream.

In each stream, the dominant prey item in Coho Salmon guts included the larvae, pupae, and adults of non-biting midges (Diptera:Chironomidae). Other dominant macroinvertebrate prey taxa in young-of-year Coho Salmon guts in both streams included water boatmen (Hemiptera:Corixidae), spiders (Arachnida), springtails (Entognatha), biting midges (Diptera:Ceratopogonidae), and seed shrimp (Ostracoda) (Table S2). We found the same macroinvertebrate taxa prey in young-of-year Coho Salmon guts in the main-channels, off-channels, riparian/terrestrial, and drift stream habitats.

The ANCOVA showed that the relationship (slopes) between % lipid and length differed between the surface-water stream ($\log_{10}$[%lipids] = 1.01 – [0.004 × length]) and the groundwater stream ($\log_{10}$[% lipids] = 0.21 – [0.01 × size]). In the groundwater dominated stream, % lipid content was positively related to body length ($y = -2.59 + 0.19x$; $r^2 = 0.36$). In the surface-water stream, % lipid content was not correlated with body length ($y = 6.32 - 0.08x$; $r^2 = 0.003$) (Fig. 8).

The bioenergetic simulations of specific consumption (g$^2$/d) and the $pC_{max}$ showed no difference in consumption between the study streams (Fig. S1). The surface-water stream had a lower $pC_{max}$ (0.28) than the groundwater stream (0.42).

## DISCUSSION

We considered the spatial and temporal dimensions of environmental variability that may influence the growth, body size, diet, and condition of young-of-year Coho Salmon in strongly-seasonal, high-latitude streams. Prior work in the study streams found that hatching and emergence of Coho Salmon occurs in the early summer and is relatively synchronous, even though the streams have different winter thermal regimes (Campbell et al. 2019). We focused on important resources that influence growth and condition, water temperature and macroinvertebrate prey availability, to understand the potential environmental drivers behind synchrony of these life-cycle events. In the surface-water stream

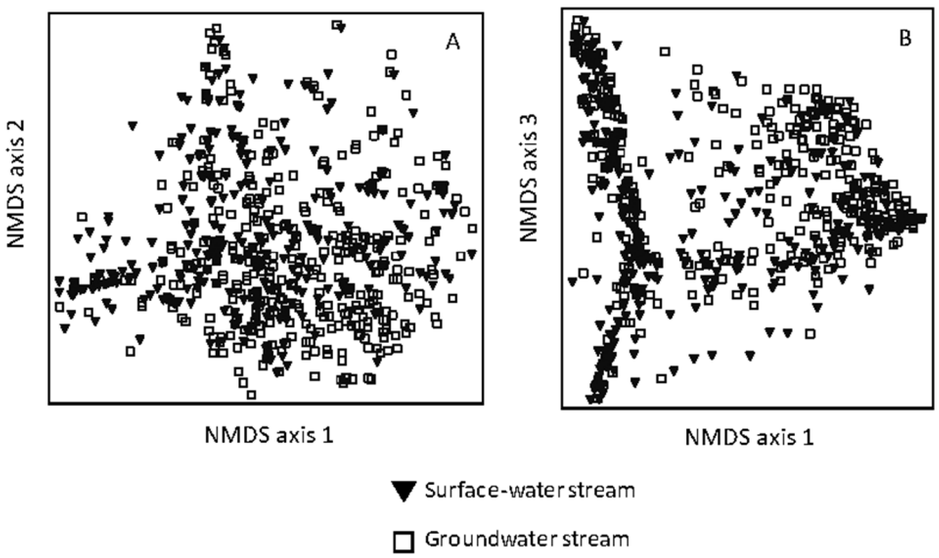


Figure 7. Non-metric multi-dimensional scaling ordination (mean stress = 15.9) showing variation in young-of-year Coho Salmon gut contents (macroinvertebrate prey assemblages) in the groundwater stream and the surface-water stream. Each point represents an individual fish. Variation along axis 1 and axis 2 (A), and variation along axis 1 and axis 3 (B).

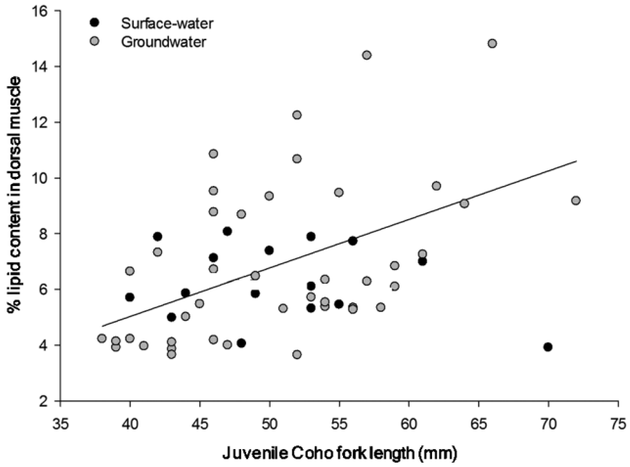


Figure 8. Estimated % lipid content based on C:N of juvenile Coho Salmon dorsal muscle as a function of fork length (mm) in the groundwater stream and the surface-water stream.

(18 Mile Creek), fry emergence coincided with the onset of temperatures that are conducive to maximizing growth (Brett 1952, Konecki et al. 1995), regardless of macroinvertebrate prey availability. In the groundwater stream (25 Mile Creek), the thermal environment stayed relatively stable all year, and Coho Salmon fry emergence coincided with peaks in macroinvertebrate prey availability, particularly in the thalweg drift.

Previous studies in Alaskan streams have shown that summer growth of juvenile Coho Salmon is strongly limited by temperature (Armstrong et al. 2010, 2013). In these studies, the surface-water stream reached temperatures that presumably maximize growth (10–12°C; Brett 1952, Konecki et al. 1995) in summer (July–September), whereas the groundwater stream never reached temperatures above 6°C. In contrast to what we expected, we found that fish growth did not differ between streams despite the groundwater stream being far below temperatures considered conducive to growth. Additionally, the groundwater stream thermal regime was stable with respect to spatial and temporal dimensions, whereas the surface-water stream exhibited high variability in temperatures over space and time, providing individuals with the potential to behaviorally thermoregulate (Armstrong et al. 2010, Armstrong and Schindler 2013, Baldock et al. 2016). However, the growth and body sizes of fish in both streams were similar, so we could not attribute opportunities for behavioral thermoregulation to increased growth or size.

A major concern regarding the impacts of climate change on fish phenology and growth is that a phenological mismatch may occur between fish and their prey (Miller-Rushing et al. 2010), so it is crucial to examine the consequences of changing environmental conditions on a species' phenology, growth, and condition. Salmon may be particularly susceptible to mismatching because multiple events in the life cycle can be strongly tied to predictable environmental conditions (Lytle and Poff 2004, Crozier et al. 2008). Our results support this expectation because Coho Salmon emergence coincided with a predictable onset of favorable thermal conditions in the surface-water stream and favorable feeding conditions (macroinvertebrate prey availability) in the groundwater stream. Fry emergence timing was the same in these streams (Campbell et al. 2019), and if future phenological changes (i.e., earlier or later hatching or emergence) occur and the timing of food availability or temperature were to change in these systems, mismatches could occur (Miller-Rushing et al. 2010). Furthermore, because the timing of Coho Salmon hatching and emergence are at least partly related to the timing of spawning, changes in the timing of spawning may carry over into effects on the growth of young-of-year offspring during the subsequent year.

Young-of-year Coho Salmon growth is critically dependent on the quality and quantity of macroinvertebrate prey available (Lang et al. 2006, Rinella et al. 2012). Salmonids consume aquatic and terrestrially-derived macroinvertebrate prey that are often most abundant in the summer and autumn months (Wipfli 1997, Nakano et al. 1999, Nakano and Murakami 2001, Baxter et al. 2005). Young-of-year Coho Salmon feed mostly on the larval and adult stages of both terrestrial and aquatic macroinvertebrates (Nielsen 1992, Quinn 2005, Robillard 2006, Rosenfeld and Raeburn 2009, White 2009). Our study corroborates those results and reinforces the importance of examining the relative availability of these prey resources in multiple young-of-year Coho Salmon rearing habitats to understand their potential for growth.

Temperature differences between streams can also drive growth rates and development times of aquatic and semi-aquatic macroinvertebrates (Scherr et al. 2010, Dallas and Rivers-Moore 2012, Marziali and Rossaro 2013) that serve as prey for young-of-year Coho Salmon. This relationship varies by taxa, however, and certain groups such as Chironomidae (non-biting midges), which were the dominant food source for young-of-year Coho Salmon in this study, often have greater production in colder waters because these insects are well adapted to glacial streams (Ferrington 2008, Ferrington et al. 2008). A separate study of macroinvertebrate secondary production in our same study streams showed significantly-higher secondary production of Chironomidae in the groundwater stream (Hertel 2016). Taxonomic variability in macroinvertebrate abundance and growth is likely high and will depend on the assemblages present and the ecological demands that each taxon faces (Lytle and Poff 2004, Yang et al. 2008, Wipfli and Baxter 2010). We did not quantify energy density or lipid content of the macroinvertebrate prey in this study, but other studies suggest that measures of prey energy content may be greater in colder

environments such as the groundwater stream (Cavaletto and Gardner 1999). This observation suggests that not only are prey more available for young-of-year Coho Salmon consumers in the groundwater stream, but the prey may also be of higher nutritional and energetic quality.

Several mechanisms may explain similarities in Coho Salmon growth between the streams, despite strong differences in thermal regimes and prey availability. One likely mechanism is that fish growth in the surface-water stream was decreased by the low availability of prey, and fish growth in the groundwater stream was decreased by low temperatures. If this is the case, then growth was probably food-limited in the surface-water stream and temperature-limited in the groundwater stream, and the combination of these limiting factors resulted in a similar fish growth rate between the thermally-contrasting streams. It is important to note the observational nature of our study and that increased replication at the stream-level would improve our inferences. There are many other factors that could also have affected growth, such as fish density (Bohlin et al. 2002), individual variability in bioenergetic rates (Tyler and Bolduc 2008, Sloat and Reeves 2014), fish condition (Bajer et al. 2004), or variability in activity (Boisclair and Sirois 1993). The energy density of consumed macroinvertebrate prey may have been greater in the groundwater stream as highlighted above, which may affect fish growth. Photoperiod is a likely phenology cue that also may explain similarities in emergence timing and fish growth. Finally, local adaptation has been documented in some cases for salmonids at close spatial scales, like those in our study (Fraser et al. 2011).

Bioenergetics modeling showed that overall consumption by young-of-year Coho Salmon did not differ in the groundwater and surface-water streams. Consumption in the surface-water stream may not be high enough to offset increased physiological costs of warmer and more variable temperatures, which may result in no increase in growth or larger size relative to fish in the groundwater stream. The surface-water stream had a lower $pC_{max}$ than the groundwater stream, indicating that growth was more limited by food in the surface-water stream. The Wisconsin Fish Bioenergetics model has been widely used in fisheries science for decades, but as with all models, its conclusions depend on the validity of its assumptions and should be interpreted with caution (Chipps and Wahl 2008).

Growth and survival are tightly coupled in the early life stages of salmonids (Elliott 1994, Armstrong and Nislow 2006). In seasonally-cold environments such as Alaska, young-of-year salmon transitioning into the winter months can benefit from greater lipid reserves and larger body sizes that may confer higher probability of survival (Biro et al. 2004, Berg et al. 2009, Cunjak 2011). We observed greater % lipid content in larger fish relative to smaller fish in the groundwater stream, whereas no such relationship existed in the surface-water stream. Diet or temperature could explain this pattern, in addition to other factors that were not measured in this study. For example, prey energy density may be greater at colder temperatures (Cavaletto and Gardner 1999), so the fish in the groundwater stream may have consumed a better diet even though diet composition did not differ between streams. Furthermore, recent work indicates that lipid content is higher in young-of-year salmonids at colder temperatures (McMillan et al. 2012) and in individuals with lower metabolic requirements (Sloat and Reeves 2014).

Results of this study in combination with our previous work on hatching and emergence of young-of-year Coho Salmon in our study system (Campbell 2017, Campbell et al. 2019) provide unique insights into linkages between events in the life cycle of salmon and spatio-temporal environmental variability. In the streams studied here, these conditions appear to lead to a synchronous hatch and emergence time between streams (Campbell et al. 2019). Following that point in the life cycle, fish are reared in very different environments in each stream. Young-of-year Coho Salmon in the surface-water stream experienced relatively warm temperatures, and fish in the groundwater stream experienced colder temperatures and greater availability of macroinvertebrate prey. As with fry emergence, the effects of this environmental variability are not apparent as differences in growth and body size of individuals between streams. Finally, differences we observed in fish condition near the end of the growing season point to important gaps in our understanding of processes that drive condition vs growth.

This research provides insights into the phenology of Coho Salmon and the complexities of growth dynamics that emerge when considering spatio-temporal axes of variability in the environment (Ward 1989, Crozier et al. 2008, Wainwright and Weitkamp 2013, Schindler et al. 2015). Our work emphasizes the importance of understanding local variability and small environmental changes on fish growth dynamics (Potter et al. 2013), in addition to larger changes that may lead to wholesale shifts in species distributions or localized extinctions (Schindler et al. 2008, Bottom et al. 2009). We need novel ways to synthesize our knowledge about environmental effects on fish to best manage healthy populations in a changing climate (Penaluna et al. 2018, Flitcroft et al. 2019). Understanding these details involves a host of challenges, but it also provides crucial insights into the complex interplay of processes that can allow species, such as salmon, to be more resilient in the future.

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