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Ecology and Demographics of Chinook Salmon in the Chena River

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ABSTRACT:

The goal of this work was to improve our understanding of the way ecological processes regulate population size and generate annual variability in the abundance of Chinook salmon, (*Oncorhynchus tshawytscha*), returning to the Chena River. We measured relationships between environmental variables and biological responses, including baseline nutrient levels, ecosystem metabolism, primary production, benthic and drifting densities of juvenile Chinook food resources (aquatic and terrestrial invertebrates), feeding rates and foraging behavior of juvenile Chinook salmon, and the effects of flow, temperature, and food abundance on Chinook growth, condition, and abundance. We developed new 3-D video methods to analyze the fine-scale behavior of juvenile Chinook, and used them to study territoriality within schools of these fish, one of the behavioral mechanisms underlying potential density dependence. Most of the field measurements, depending on study component, occurred between 2007-2010. Statistical models (Random Forests) indicated that discharge and length of time between high water events were the most important factors measured for predicting stream metabolism rates. Discharge was also identified as the most important variable for predicting benthic macroinvertebrate density and biomass. Primary production rate peaked at intermediate discharge, respiration rate was lowest at the greatest time since last high water event, and benthic macroinvertebrate density was lowest at high discharge rates. Phosphorus concentration was low throughout the summers, while nitrogen concentration was more variable; the ratio of nitrogen to phosphorus ranged from 27:1 to 172:1, suggesting that phosphorus may have been limiting primary production. Terrestrial invertebrate infall, drift, and juvenile Chinook diet varied widely through the summers (May-Sept) of 2008 and 2009. Drift was comprised of 33% terrestrial and 67% aquatic invertebrate mass, while juvenile Chinook diet contained 19% terrestrial, 80% aquatic, and 1% unidentifiable invertebrate mass. Proportion of terrestrial invertebrate mass consumed increased through summer and, at times, comprised up to 39% of total diet. Low similarity of invertebrates in diet and infall, and diet and drift suggested that fish were, in part, prey-selective, selecting hymenopterans and chironomid midges (Diptera). In both years, prey mass consumed and discharge varied inversely, but no correlation was found between proportion of terrestrial invertebrates consumed and discharge. However, the two sampling dates with the highest proportion of terrestrial invertebrates consumed occurred shortly after a 60-year flood, indicating that terrestrial invertebrates may be important during rain and associated high water. Feeding trials in 2009 indicated fish may not always be limited by food however, rather their growth controlled by temperature. We also observed that these fish frequently capture and spit out an unexpectedly high amount of drifting, inedible detritus, and analyzed the effect of this distraction on their potential growth and competition. The above findings regarding ecological processes informed the development and interpretation of models relating spawner abundance to recruitment in light of major ecological effects. These models showed that stream discharge was very important to Chinook recruitment in the Chena River; there were distinctly more recruits per spawner in years with low to medium discharge than in years with extended periods of high discharge. Patterns in recruitment data and our ecological findings suggest that this pattern arose from positive effects of low to medium flow on productivity and foraging conditions, as opposed to acute mortality from floods.

Keywords: Chena River, Chinook salmon, competition, diet, feeding behavior, feeding trials, foraging ecology, growth, invertebrate, nutrients, primary production, stream metabolism, territoriality

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INTRODUCTION:

The goal of this work was to improve our understanding of the way ecological processes regulate population size and generate annual variability in the abundance of adult Chinook salmon, (*Oncorhynchus tshawytscha*), returning to the Chena River, an important salmon spawning stream in the Middle Yukon drainage. Chinook salmon populations in the Yukon River drainage have a stream-type life history (Healey 1991). Adults spawn in July and August, fry emerge from the gravel the next spring, juveniles rear in freshwater for the summer, over-winter in freshwater, and migrate to the ocean the following spring. Density dependent mortality that regulates population size of these stream-type Chinook salmon populations may act in freshwater, rather than in the marine environment. Support for this conclusion comes from studies of other anadromous salmonids that rear in streams as juveniles, including coho salmon, *Oncorhynchus kisutch* (Holtby and Scrivener 1989; Hartman and Scrivener 1990), steelhead trout *Oncorhynchus mykiss*, (Ward and Slaney 1993; Ward 1996), brown trout, *Salmo trutta*, (Elliott 1989, 1993, 1994), and Atlantic salmon, *Salmo salar*, (Gibson 1993; Jonsson et al. 1998). The reason that published data demonstrating freshwater density dependent mortality is lacking for Chinook salmon is probably a consequence of the fact that they typically rear in relatively large rivers which makes the necessary fieldwork difficult.

The research on other species suggests the mortality that regulates the abundance of Chinook salmon is the consequence of competition for space and/or food during the summer months that juveniles spend rearing in freshwater (Chapman 1962, 1966; Mason and Chapman 1965; Grant and Kramer 1990; Grant 1993; Elliott 1994; Milner et al. 2003; Nislow et al. 2000). If this is the case then the shape, or curvature, of the stock-recruitment curve will be determined by the relationship between fry abundance at the beginning of the summer, and the intensity of density dependent mortality later that summer (see Elliott 1994). The population size, indicated by the scaling the x and y -axes of the stock-recruitment curve, will be determined by the quantity of rearing habitat and the density of fish in this habitat, after density dependent mortality has acted.

When the environmental conditions that affect density dependent and density independent mortality early in the life history are relatively stable, and data collection is precise, stock-recruitment data can fit a Ricker curve quite closely (Elliott 1994; Fig. 1). This is important to recognize because it demonstrates how the stock-recruitment curve can provide a valuable and necessary benchmark against which to measure the influence of environmental factors on population dynamics (Elliott et al. 1997).

Study goals: Our goals can be expressed in relation to the most common graphical representation of salmon population dynamics; a Ricker curve plotted through a scattered set of data points, along with the replacement line that indicates equilibrium population size (Fig. 2). Our goals were 1) to get a better understanding of the ecological processes that produce the density dependence responsible for the curvature of the stock recruitment curve (if there were no density dependent mortality the plot relating the number of recruits per spawner to the number of spawning fish would be horizontal, which it is not); 2) provide a better understanding of the ecological processes responsible

for the number of fish in the population. This could be thought of as the “carrying capacity” or “productive capacity” of the habitat for Chinook salmon. Variations in carrying capacity can be visualized by varying the magnitude of the numbers used to scale the x - and y -axes of the stock-recruitment curve, and 3) get a better understanding of the way annual and longer-term variability in important ecological processes generates scatter around the stock-recruitment curve.

OBJECTIVES:

- 1) Determine whether density dependent mortality is due to i) competition for spawning habitat or ii) competition between juveniles during summer rearing.
- 2) Determine the timing of competitive bottlenecks that might generate density dependent mortality of fish during the summer rearing period.
- 3) Determine whether competition for food is responsible for density dependent mortality in freshwater.
- 4) Determine the influence of stream flow, and other environmental variables, on the productivity and availability of the food consumed by juvenile fish.
- 5) Use modeling and data from objective 4 to predict how seasonal flow patterns will affect the density of juveniles at the end of the summer.
- 6) Determine how food abundance and water temperature interact to influence growth rate, energy reserves, and marine survival.
- 7) Use a retrospective analysis to investigate the way environmental conditions influence the number of adults that survive to spawn.
- 8) Use results from objective 7 to refine the stock-recruitment analyses to account for the effects of environmental conditions on recruitment.

Project objectives met

The first step in meeting the objectives was to collect relevant data on environmental variables expected to influence growth and production of Chinook salmon. We successfully measured seasonal (spring-summer-fall) dynamics of stream discharge, stream temperature, stream nutrients (N, P, DOC), primary production, stream ecosystem respiration, prey density and composition, Chinook salmon feeding rates and growth, foraging success, territoriality behavior, and feeding profitability. We conducted an experimental feeding study to investigate competition during the summer rearing season (part of Obj 1), and to determine if competition for food is occurring (Obj 2 and 3). Time and resource constraints prevented us from measuring competition for spawning habitat (Obj 1). For objectives 2, 3 and 6 we collected and analyzed length data, but due to

analytical costs did not analyze energy reserves (part of Obj 6). Objectives 4-5 were accomplished by measuring food abundance, and tied to Objective 8. For Objectives 7, we investigated some specific mechanisms linking environmental conditions to recruitment (specifically, the effects of fine drifting debris and territoriality on foraging success under varying stream discharge levels). For Objective 8, we constructed stock-recruitment models for the Chena incorporating significant effects of stream discharge on rearing juveniles, and some lesser effects of discharge and temperature on spawning adults or incubating eggs. Data on discharge, water chemistry, prey densities, feeding habits, fish condition, growth and indices of competition have been analyzed and published in three M.S. graduate student theses and one Ph.D. dissertation, and their results presented below. Two manuscripts have been published, four manuscripts submitted to journals, and two more to be submitted later this year from this study (see pages 67-70 of this report, under Deliverables).

In a nutshell, we found that the Chena River is highly oligotrophic, and primary production appears to be limited by P, and not by N. N:P ratios were much higher than 20 through both sampling seasons. Benthic densities of invertebrates varied widely, appearing to be in part controlled by flow. Drifting prey (terrestrial and aquatic invertebrates) also varied widely across summers and between years, and at times appeared related to flow, but the correlation was weak at best. Juvenile Chinook diets through the summers both years showed that both terrestrial prey (influenced more by flow) and aquatic prey are important sources of food, and predation by fishes affected by flow. (See appendices A and B for detailed reporting.)

The second step was to understand how these environmental drivers directly or indirectly affect juvenile Chinook in the Chena River, and to incorporate pertinent environmental data into the stock-recruitment analysis for Chena River Chinook.

The results of our experimental food supplementation suggested that juvenile Chinook salmon were not food limited during the summer 2009 study period. However, anecdotal information from 2008 when fish densities were greater suggested fish may be under food resource constraints. Because fish condition was the same in both supplemented and control sites, we concluded that temperature is likely setting the limit on fish growth, not food, at least during the one year (2009) we were reliably able to measure fish growth. We used a simple individual based bioenergetics approach to estimate size of juvenile Chinook salmon at the end of their first summer residency using actual and hindcasted water temperature data to estimate fish length from the 1981 brood year forward. We used estimates of return of adults per spawner from a stock recruit analysis conducted by the Alaska Department of Fish and Game to determine whether a relationship between water temperature, freshwater growth, and marine survival exists in the Chena River. We did not find evidence that marine survival is correlated with freshwater growth; however, we did find evidence suggesting that growth during the freshwater rearing period may be related to food availability following years when adult escapement is high.

In addition to our inferences about competition based on supplementation experiments, our ongoing work on foraging behavior has provided some preliminary insights on the mechanisms of competition on the scale of individual groups of fish. Juvenile Chena Chinook salmon overwhelmingly feed in schools ranging from ten up to hundreds of individuals, yet they often maintain individual territories within these schools. Nothing like this juxtaposition of aggregation and territoriality has been previously studied in the ecological literature we searched, so it represents a valuable study system for some of the general concepts in ecology. The ubiquity of schooling behavior suggests that survival is highly dependent on an individual's ability to feed and grow in close proximity to its competitors. The strength and causes of density dependence in the population may depend on the degree to which strong competitors in each school monopolize the food drifting into it. We have collected the data and developed some new mathematical techniques to analyze this question. This work has also highlighted fine drifting debris as an unexpected environmental variable of considerable importance to juvenile Chinook salmon feeding behavior and growth, and probably to drift-feeding fishes in general. It may affect competition by limiting the ability of dominant individuals to monopolize resources, allowing more individuals to grow, but more slowly. These effects would be mediated by the density of drifting debris, which is correlated with flow and may provide another link between seasonal flow patterns and fish growth.

METHODS:

Study area

We conducted this study on the Chena River in interior Alaska, USA. The Chena River is a clear-water river that flows 241 km from its headwaters in the foothills west of Fairbanks, to the confluence with the Tanana River, a tributary of the Yukon River. The watershed is approximately 5,200 km² and includes five major tributaries: North Fork, West Fork, South Fork, East (Middle) Fork, and Little Chena River (Fig. 3). Since 1968, mean annual discharge at the U.S. Geological Survey (USGS) Two Rivers gauging station, located 145 km upstream of the mouth of the river, has been approximately 20 m³s⁻¹ and daily mean flows ranged from 0.6 to over 496 m³s⁻¹. Peak discharge typically occurs in early summer, though high flow can occur at any time the river is free of ice. Urban development exists along the lower 40 km of the river, while the upper portions remain relatively undeveloped. As such, the Chena River has a natural flow regime and is virtually free of human development along most of its length.

We worked at four study sites located within the middle section of the river, an area roughly 75 km long that supports the majority of the juvenile salmon that rear in the river during the summer. The upper two sites, Site 1 and Site 2, were located 131 km upstream of the mouth of the river (N 64 53.909', W 146 38.271') and 123.5 km upstream of the mouth of the river (N 64 52.847', W 146 43.360'), and the lower two sites, Site 3 and Site 4, were located 88 km upstream of the mouth of the river (N 64 49.052', W 147 06.273') and 84 km upstream of the mouth of the river (N 64 48.253',

W 147 07.901') (Figure 3). Sites were selected based on accessibility and suitability for sampling techniques; we selected sites that included a long run where we could deploy a data logger just upstream of a riffle big enough to allow for sampling of benthic macroinvertebrates using a Surber sampler.

I. Flow, temperature, chemistry, stream ecosystem metabolism, and benthic prey.

Sampling regime

We sampled river water and benthic macroinvertebrates at the four study sites once every other week when the river was free of ice from June through late September in 2008, and from May through mid-September in 2009. Thus, there were eight sampling dates per study reach in 2008 and ten sampling dates per study reach in 2009. Continuous data loggers were maintained at all four sites throughout the study periods each year.

Environmental variables

We measured dissolved oxygen, water temperature, turbidity, and photosynthetically active radiation (PAR) using Hydrolab® DS5 Water Quality Multiprobe data loggers (Hach Environmental, Loveland, Colorado, USA). The data loggers recorded an instantaneous reading for each parameter every 15 min during deployment, from which we computed daily means. PAR data was limited to Site 1, Site 3, and Site 4 in 2008 and Site 2 and Site 3 in 2009; thus, we averaged PAR data among those sites, and used the mean of the site values for each day in our subsequent data analyses. Though this meant that there was no inter-site variation in the PAR data, the day-to-day variation in PAR values exceeded the variation in PAR values between sites (data not shown). High flow limited site accessibility at times, and that, along with equipment failure, meant that the length of data logger deployment time varied between years and among sites, but was commonly between 60 and 115 days.

To prevent data loggers from becoming damaged during deployment, we wrapped each one in flexible packaging foam and placed it inside a custom-built protective case that consisted of an aluminum pipe set into a five-gallon pail filled with cement, which was anchored to the riverbed. We anchored each case approximately two meters from the riverbank and in about one meter of water. Each PAR sensor was mounted on top of the aluminum pipe, and thus was not subject to shading by the pipe or the rest of the protective case.

Data loggers were maintained every other week by removing the data logger from its case, cleaning off any debris, macroinvertebrates, and biofilm, downloading data files, changing batteries, and re-calibrating the loggers. The data loggers were not re-calibrated after June in 2008 because the calibration procedure did not appear to be working correctly. In 2009, the data loggers were re-calibrated in the field every other week. None of the data loggers exhibited data-drift in a consistent direction

throughout the summer in 2009. It is likely that data-drift was similarly unbiased in direction in 2008.

Mean daily discharge for each site was obtained from the nearest USGS gauging station. We also calculated the time since last high water event as a second discharge metric. A high water event was defined as flow greater than or equal to $50 \text{ m}^3 \text{ s}^{-1}$. This value was chosen based on visual inspection of hydrographs from past years; we determined that using this threshold would typically result in the occurrence of four to five “high water events” per year in the Chena River. Dates directly prior to high water events when the hydrograph was already rising were not included in the time since last high water event, as these days were considered the preliminary days of the next high water event.

We collected one water sample at each site every other week. Water samples were filtered through $0.7\text{-}\mu\text{m}$ Whatman glass microfibre filters and stored in high-density polyethylene bottles in a cooler in the field; they were frozen upon return to the lab. Water chemistry analysis was performed by the Cooperative Chemical Analytical Laboratory (Oregon State University, Corvallis, Oregon, USA) using APHA methods (APHA, 2005). Water samples were analyzed for soluble reactive phosphorus (SRP; detection limit: 0.001 mg L^{-1}), nitrate plus nitrite ($\text{NO}_3^- \text{-N} + \text{NO}_2^- \text{-N}$; detection limit: 0.001 mg L^{-1}), ammonium ($\text{NH}_4^+ \text{-N}$; detection limit: 0.010 mg L^{-1}), and dissolved organic carbon (DOC; detection limit: 0.05 mg L^{-1}). The ratio of dissolved inorganic nitrogen to soluble reactive phosphorus (DIN:SRP) was calculated as the atomic ratio of $\text{NO}_3^- \text{-N} + \text{NO}_2^- \text{-N} + \text{NH}_4^+ \text{-N}$ to SRP.

Ecosystem metabolism

We estimated ecosystem metabolism rates at each site using a single-station diel oxygen method (Odum, 1956). We recorded dissolved oxygen concentration and percent saturation at 15-min intervals using data loggers (see previous section). We used these data, together with the temperature data recorded at the same time, to estimate daily mean GPP and ER, using the nighttime regression technique (Marzolf et al., 1994, 1998; Young & Huryn, 1998). Metabolism estimates were made using a spreadsheet entitled “Microsoft® Excel model to calculate ecosystem metabolism”, which is available from the Cawthron Institute in Nelson, New Zealand (<http://www.cawthron.org.nz/coastal-freshwater-resources/downloads.html>). Estimates of GPP rate were made at 15-min intervals using a derivative of the following equation:

$$dO/dt = \text{GPP} - \text{ER} - (k \cdot D)$$

Where dO/dt is the rate of change in dissolved oxygen concentration ($\text{gO}_2 \text{ m}^{-3} \text{ sec}^{-1}$), GPP is gross primary production ($\text{gO}_2 \text{ m}^{-3} \text{ sec}^{-1}$), ER is ecosystem respiration ($\text{gO}_2 \text{ m}^{-3} \text{ sec}^{-1}$), k is the reaeration coefficient (sec^{-1}), and D is the oxygen deficit (or surplus) in the river (i.e., the difference between the measured oxygen concentration and the value at 100% saturation; $\text{gO}_2 \text{ m}^{-3}$). We measured dissolved oxygen concentration and calculated the oxygen deficit based on those measurements and simultaneous

measurements of temperature. We employed the nighttime regression technique to estimate ER rate and the reaeration coefficient.

The night-time regression technique allows one to estimate reaeration and ER from the oxygen concentrations recorded in the dark; during the night-time, the change in oxygen concentration over time is equal to the product of the reaeration coefficient and the oxygen deficit, plus the rate of ER. Thus, by regressing the change in oxygen concentration over time against the oxygen deficit, it is possible to estimate the reaeration coefficient (the slope of the regression line), and the ER rate (the y-intercept of the regression line). This technique assumes that ER and reaeration are constant across the day and night (Kosinski, 1984; Young & Huryn, 1996).

We validated nighttime regression estimates (and the assumption that night length was long enough to enable the use of this technique at a sub-arctic latitude) using a daytime regression technique (Kosinski, 1984) on a selection of data. The day-time regression technique is similar to the night-time regression method in that one can estimate reaeration and ER rate by using the oxygen record to build a regression; it is different in that it requires above-canopy PAR data, because GPP is assumed to be a function of light level (Kosinski, 1984). We used PAR data collected by the University of Alaska Fairbanks at Poker Flat Research Range (N 65 7.080', W 147 25.920'; about 50 km from study sites), and stored by the UV-B Monitoring and Research Program of the United States Department of Agriculture (http://uvb.nrel.colostate.edu/UVB/da_queryPar.jsf) to approximate above-canopy PAR at our study sites on the Chena River. We also verified that possible relationships between metabolism rates and river discharge were not simply an artifact of reaeration changing with discharge by calculating the Spearman correlation between the reaeration coefficient and river discharge rate.

A tracer gas method is the most accurate way to determine reaeration in a river. There are also numerous empirical equations that can be used to estimate the reaeration coefficient (k). Because the Chena River is up to 60 m wide and up to 5 m deep in the sampled reaches, tracer gas experiments are unfortunately unfeasible; in addition, previous studies have shown that empirical equations vary greatly in their under or overestimation of k (Genereux & Hemond 1992, Young & Huryn, 1999). The method used in this study to estimate k (the night-time regression technique) provides a measure of the strength of the estimation in the form of an R^2 value. In this study, the mean strength of the regression equation for estimating k (mean $R^2 \pm$ SD) was 0.83 ± 0.14 . Metabolism rates for days when R^2 was less than 0.4 were not recorded.

Metabolism estimates were calculated in volumetric units and converted to areal units by multiplying GPP and ER rates by mean reach depth. We measured mean reach depth at each site on four or five dates throughout the 2008 field season by taking five measurements across each of five transects located up to 500 m above each site. We estimated mean reach depth for each day throughout the field seasons at each site by regressing mean reach depth measurements against discharge rates reported by the

USGS gauging station closest to each site. We used the 2008 regressions to estimate daily mean reach depths in 2008 and 2009.

We calculated the mean daily GPP estimates at each site for the week prior to benthic macroinvertebrate sampling to use in the benthic macroinvertebrate analysis.

Benthic macroinvertebrates

We collected two replicate benthic macroinvertebrate samples from riffle habitat at each site every other week, except when we were unable to because of high water (twice at Site 3 and once at all other sites in 2008, and once at Sites 3 and 4 in 2009). We collected the samples with a 500- μm , 0.1 m² Surber sampler and preserved them in the field in 80% ethanol. In the lab, we sorted, counted, measured (to the nearest 0.5 mm), and identified (to family) the macroinvertebrates. We estimated their biomass via published length-weight regressions (Uye, 1982; Meyer, 1989; Burgherr & Meyer, 1997; Kawabata & Urabe, 1998; Benke et al., 1999; Johnson & Strong, 2000; Sabo et al., 2002; Baumgartner & Rothhaupt, 2003; Gruner, 2003; Miyasaka et al., 2008; M. Wipfli, unpubl. data). We calculated the mean benthic macroinvertebrate density and biomass between replicate samples.

In addition to our broader benthic macroinvertebrate data analyses (described below), we tested for relationships between benthic Heptageniidae density, as well as benthic Heptageniidae biomass, and the rate of GPP during the week prior to benthic macroinvertebrate sampling. We chose to use Heptageniidae density and biomass as an indicator of scraper density and biomass, as this functional feeding group is most likely to rely on algae as a major food source (Cummins et al., 2008), and because it was common throughout the sampling reaches. Of the families we observed in our benthic macroinvertebrate samples, Heptageniidae was the only one in which most members are scraping macroinvertebrates (Waltz & Burian, 2008); all other families we observed that include scrapers also include members of other functional feeding groups as well.

Data analysis

We used the Random Forests statistical procedure for data analyses. Random Forests is a statistical modeling method that can be used for regression analyses to describe relationships between variables (Breiman, 2001; Cutler et al., 2007). Output includes partial dependence plots, which are x-y plots that display the predicted relationship between two variables after removing the effects of the other variables included in the model (Elith et al., 2008). Partial plots represent the predicted relationship between two variables, rather than the actual relationship; thus, care should be taken when interpreting them as they may appear to over-state confidence in the depicted relationship. We chose to use this statistical approach instead of a more traditional technique such as generalized linear models because the environmental variables in our study were highly collinear (data not shown). High collinearity violates one of the key assumptions of linear modeling; Random Forests, however, has no such

assumption (Cutler et al., 2007). To develop our Random Forests models, we used the R program RFmodelSel, which was designed for building Random Forests classification or regression models. The regression model selection criteria in this program are: greatest percent variation explained, smallest mean squared error, and smallest number of parameters (Murphy et al., 2010).

We log-transformed the GPP data to improve the symmetry of their distribution; the transformation normalized the data and reduced clumping. The rest of the metabolism data did not require transformation. The metabolism models included PAR, turbidity, temperature, discharge, days since last high water event, ordinal date, year, and site as possible predictor variables. We also developed alternative metabolism models that did not include year and site as possible predictor variables (though they did include all other variables listed above). These metabolism models were developed to determine how much variation in the metabolism data was explained by the environmental variables alone.

We used two-sided Spearman correlations to test for relationships between nutrient concentrations and metabolism metrics instead of including the nutrient data in the Random Forests models. We used this approach because we had daily nutrient concentrations for eight dates in 2008 and ten dates in 2009 rather than daily concentrations throughout the field seasons. We also used two-sided Spearman correlations to test for relationships between representative scraper populations, benthic Heptageniidae density, as well as benthic Heptageniidae biomass, and the rate of GPP during the week prior to benthic macroinvertebrate sampling. We developed separate Random Forests models for benthic macroinvertebrate density and biomass. We included GPP rate, discharge, ordinal date, year, and site as possible predictor variables in initial models, but in the final versions we included only discharge, ordinal date, year, and site. We left GPP rate as a possible predictor variable out of the final models because it was not identified as an important predictor variable in the original models and because doing so allowed us to include dates that were missing GPP rates in the data analysis. We conducted all analyses using R, a free statistical package available online (R Development Core Team, 2008).

II. Chinook prey density and juvenile foraging.

Site selection

Two study reaches were selected that contained the largest concentrations of juvenile Chinook salmon in summer. Sampling occurred at two sites in the upstream reach and two in the lower reach. The study sites were located at river bends with a large proportion of root wads, fallen trees, and mats of woody debris which provided ample quality habitat for juvenile Chinook salmon. Sites ranged from 214 to 530 m long. We measured the width of the river in each site at five evenly distributed points, and the average river wetted width ranged from 30 to 43 m.

Sampling scheme

We sampled invertebrate infall, drift, and juvenile Chinook salmon diet approximately every other week from 6 June to 25 September 2008 and from 12 May to 15 September 2009, for a total of eight sampling events each summer. We continuously measured water temperature with data loggers at each site during both summers (Hobo Water Temp Pro v2, Onset Corp, MA and Hach Environmental Hydrolab DS5 Water Quality Sonde, CO). We obtained stream discharge data from USGS gauging stations at Hunts Creek (near sites 1 and 2) and Moose Creek Dam (near sites 3 and 4).

Field Methods

Terrestrial invertebrate infall

We sampled invertebrate infall with floating pan traps at our four study sites for a 24-h period preceding each diet sampling event. Pan traps were designed to catch invertebrates falling into the stream; they consisted of a black plastic pan (34.3 x 29.2 x 13.3 cm) filled with ~5 cm water and 2-3 drops of dish soap to break the surface tension to prevent invertebrates from escaping. Each pan trap was floated within a blue insulation foam frame. We placed four traps at each site for a total of 16 possible samples per sampling date. Traps were placed on the cut bank side of the river in locations where juvenile Chinook salmon were observed. Traps were tethered with nylon cord to overhanging tree limbs, vegetation, or woody debris approximately 0.5-1.0 m from the cut bank. After the 24-h deployment, the contents of each pan were sieved through a 250- μ m mesh and stored in at least 80% ethanol. For our analysis, we calculated terrestrial invertebrate infall, aquatic invertebrate infall (adult winged forms), and total invertebrate infall (both terrestrial invertebrates and adult winged forms of aquatic invertebrates) by calculating the biomass and number of each category of invertebrates that fell into the traps per sampling date and site.

Terrestrial invertebrates in drift

Invertebrate drift was collected for a 24-h period concurrent with pan trap sampling. We placed one drift net at each site in 2008 and two in 2009. Each drift net (250- μ m mesh) was attached to a circular pipe (13-cm diameter) anchored 30 cm below a floating rectangle of blue insulation foam. The entire drift float was tethered to overhanging branches or large woody debris approximately 0.5-3.0 m from the bank. At the end of the 24-h sampling period, we collected the nets, brought them to the lab, and stored each drift sample in 80% ethanol. We measured stream flow at the mouth of the pipe before and after nets were placed in the river with a flow meter (Marsh-McBirney Flo-Mate 2000, Hach, CO) to estimate the amount of water flowing through the net over the 24-h period. We estimated drift per cubic meter of water per date by dividing the biomass and number of invertebrates caught in the drift net by the mean stream discharge for the 24-hour sampling period. In our analysis, we used the mean invertebrate biomass (per cubic meter of water per date), the source type (terrestrial vs. aquatic), and the percent source type in each sample.

Terrestrial invertebrates ingested by juvenile Chinook salmon

We trapped fish and collected their stomach contents 24 hours after the end of drift and terrestrial infall sampling to reduce the effects of disturbance on fish due to sampling for prey availability. Fish were captured on two consecutive days between 10:00 and 16:00. We used dip nets and seines to catch fish because minnow traps were not effective in the beginning of the summer (May to mid-July); from mid-July through September, we used baited minnow traps to capture fish. In 2008, we measured fish fork length to the nearest 1 mm; in 2009, we measured fish fork length, again to the nearest 1 mm, as well as fish weight, to the nearest 0.1 g. To collect stomach contents, fish less than 40 mm long were sacrificed and preserved in 80% ethanol, with an incision in their stomachs to prevent further digestion or degradation of the stomach contents. Fish greater than 40 mm were anaesthetized with MS-222 (tricane methanesulfonate), and stomach contents were collected by gastric lavage with a 10-ml pipette and preserved in 80% ethanol (Meehan & Miller, 1978). Once diet sampling was complete, we transferred the fish to a holding tub until they recovered and swam normally, and then returned them to the location of capture.

We calculated the biomass, number, and frequency of invertebrates consumed per fish by sampling date and site, and the proportion of the diet that was terrestrial or aquatic (mg invertebrates dry mass / mg total dry mass). Over both summers, we only had five empty stomach samples. These five were included in our analysis and results. The juvenile Chinook salmon in this study were consistently growing throughout the summer, on average about 5 mm every two weeks (Table 1). We standardized biomass consumed by fish length and found the same patterns and statistical results as when using the non-length standardized values. Thus for conciseness and clarity, we are only presenting the values of biomass and proportions consumed. The index of relative importance (*IRI*) was calculated to determine which invertebrate taxa were most important to the juvenile Chinook diet in each sampling year. *IRI* is a compound index that combines the percent number, mass, and frequency of each taxon to calculate an importance ranking (Pinkas *et al.*, 1971; Liao *et al.*, 2001). *IRI* was calculated with the equation:

$$IRI = (\% N + \% M) \times (\% F)$$

where *N* is the percent by number, *M* is the percent by mass, and *F* is the percent of frequency of occurrence.

Laboratory Procedures

For invertebrate infall samples, specimens were identified to order except for those that have both aquatic and terrestrial members such as Coleoptera, Diptera, Hemiptera, and Lepidoptera, which were identified to family level. For the diet and drift samples, invertebrates were identified to the nearest convenient taxonomic group (primarily family). Drift samples were sieved through a 1mm sieve and then subsampled down to 1/16 of the original sample, while still maintaining a minimum of 500 invertebrates per sample. All invertebrates were counted, measured by length,

and categorized as either aquatic or terrestrial based on larval origin (Wipfli, 1997). Dipterans in the following families were assumed to be aquatic: Ceratopogonidae, Chironomidae, Empididae, Psychodidae, and Tipulidae. All adult and larval stages of aquatic insects were excluded from the terrestrial source category (Wipfli, 1997). We estimated invertebrate dry mass (mg) using length-weight regressions (Rogers *et al.*, 1976; Uye, 1982; Meyer, 1989; Sample *et al.*, 1993; Hodar, 1996; Burgherr & Meyer, 1997; Hodar, 1997; Kawabata & Urabe, 1998; Benke *et al.*, 1999; Johnson & Strong, 2000; Sabo *et al.*, 2002; Baumgärtner & Rothhaupt, 2003; Gruner, 2003; Miyasaka *et al.*, 2008; Wipfli, unpublished data)

Statistical Analysis

We used a repeated measures analysis of variance (rm ANOVA) with date as the repeated measures factor to test for significant differences by site, date, and year of invertebrate mass by source. An rm ANOVA was conducted for infall, drift, and juvenile Chinook diet. Invertebrate infall and diet data were $\ln(x+1)$ transformed, while drift data were fourth root transformed to meet the assumptions of normality and variance of the ANOVA. We used a Bonferroni correction of $\alpha = 0.05 / 3 (= 0.017)$ to account for testing multiple hypotheses (mass of terrestrial, aquatic, and total invertebrates) from the same data set. Since using a Bonferroni correction increases the risk of committing a type II error, we reported p -values of $\alpha = 0.10 / 3 = 0.033$ as marginally significant.

Pearson's correlation coefficient was used to test whether the total mass consumed and the proportion of terrestrial prey consumed was positively or negatively associated with sampling date. Pearson's correlation coefficient was also used to test the association between total and the proportion of terrestrial prey mass consumed and the environmental variables of stream discharge and temperature, as well as the relationship between discharge and water temperature. For the Pearson's correlations using discharge and water temperature, we used the mean daily discharge and mean water temperature for each sampling date. We used a Bonferroni correction of $\alpha = 0.05 / 3 (= 0.017)$ to take into account the multiple comparison between 2008, 2009, and the combination of both years. P -values of $\alpha = 0.10 / 3 = 0.033$ were reported as marginally significant.

To determine whether juvenile Chinook salmon consumed invertebrate prey according to their availability, we conducted a multidimensional scaling (MDS) ordination (McCune & Grace, 2002; Brodeur *et al.*, 2010). We used the MDS ordination to visualize the similarities in invertebrate composition data between infall, drift, and juvenile Chinook salmon diet. We created two different ordinations based on a Bray-Curtis dissimilarity matrix of the mean proportion by mass of the top 95% invertebrate taxa and life stage per sample type (i.e., infall, drift, or diet), date, and year. We did not use site as a variable because we were concerned with prey consumption and availability as a whole, and not site-to-site variability. Each point on the ordination represents the combination of sample type-date-year. Sample points plotted closer together have greater similarity in invertebrate community composition.

The first ordination included all invertebrate taxa, while the second ordination included only terrestrial taxa. In the second ordination, we only used sampling dates where terrestrial invertebrates were present. An ordination with stress less than 0.20 was considered to be suitable for interpretation; a stress value is comparable to standard deviation (McCune & Grace, 2002; Brodeur *et al.*, 2010). We then used a similarity percentage (SIMPER) analysis on both ordinations to determine the percent dissimilarity between invertebrate community composition of diet compared to drift, and diet compared to infauna. Two sample points which share no species have a very high dissimilarity, and two sample points which share the same species in similar abundances have a low dissimilarity (Clarke, 1993). We also used SIMPER on both ordinations to determine which prey taxa accounted for the largest difference in the invertebrate community composition between comparisons of infauna to diet and drift to diet. The repeated measures ANOVAs were done using SAS[®] software, version 9.1 of SAS System for Windows (SAS Institute Inc., Cary, NC, USA). Pearson's correlation coefficient tests were done using R, an open-source statistical program (R Core Development Team). The MDS ordination and SIMPER analysis were done using the PRIMER v6 software (Clarke, 1993). Hereafter all means are reported as mean \pm standard error (SE).

III. Chinook growth modeling, abundance, density dependence.

Site selection

Eight research sites were chosen using a randomized plot design. Four upstream sites (US1-4) were located between 64.864021N, -146.782157W, and 64.892929N, -146.648643W and four downstream sites (DS1-4) were located between, 64.790316N, -147.162720W and 64.822348N, -147.074728W. We identified suitable sites in early May 2009, based on the presence of large woody debris accumulation throughout the water column. These sites were typically located on the cut banks of the river and were considered edge habitats, with complex cover composed of rootwads and debris. Sites were between 10-20 m long. All sites were velocity shelters; a boundary between the site and the main river was visible as a current shear line (Beechie *et al.* 2005). Rootwads and debris jams were the most abundant cover at all sites, but some also had undercut banks, live forbs and grasses, and mats of floating detritus. Site substrates were composed of sand and gravel or cobble. Water temperature was recorded hourly using HOBO[®] data loggers (Onset Corporation, Bourne, MA, USA) suspended from instream large woody debris and weighted to the streambed. The uppermost site was randomly chosen to either be control or supplemental food. The remaining sites alternated between control and fed sites, to ensure that appropriate distances between fed sites were such that migration to fed sites from control would be unlikely.

Supplemental feeding

Supplemental feeding was performed using custom designed feeders from TEC Industrial Inc. (Rochester, MN, USA). Feeders were installed at the upstream end of supplemented sites in early June 2009. Feeders continuously added food to each site,

at the rate of ~750g/day. This amount of food was 10 times the maximum rations that 75 fish with mean weight of 7g and 80mm would require to feed at maximum rations at ideal temperatures for growth (Sagar and Glova 1988), providing a super abundance of food available to fish at each site. Food introduced was a slow sinking salmon fry feed (Silver Cup Fish Feed, Murray, UT, USA). During our first study season of 2008 we observed that juvenile Chinook salmon readily consumed the supplemental food. Feeders were continually powered through a deep cell battery kept charged by solar panels. Feeders were refilled with food on a weekly basis.

Mark-Recapture, fish condition, and mass frequency distribution

To estimate fish abundance at our research sites, to collect data for estimating fish condition, and to plot sub-population mass frequency distribution, we conducted a series of independent mark-recapture experiments. Sampling was designed to estimate abundance at each site during three periods (July, August, and September 2009). Each experiment consisted of three capture events conducted over three consecutive days. Ten Gee-type minnow traps (23 x 45 cm, 0.6 cm wire mesh, 2.5 cm diameter opening) baited with salmon roe were set out at each of the sites, and allowed to soak from 2-5 hours. Captured fish were placed in a bucket of river water, anesthetized with tricaine methanesulphonate (MS-222) until they lost equilibrium. Then we measured fork length to the nearest mm and weight was measured to the nearest 0.01 g using a Pescola spring scale. Next, event and site specific marks were implanted on each fish using visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington). Marks consisting of up to three colors were made on their anal fin, caudal fin, adipose fin, or on their bodies, using one or two color combinations for each capture. After marking, fish were returned to a bucket of river water until they recovered and released back into the same site. Marks were made on the first and second day of each experiment. On the third day, fish lengths and weights were taken, and the fish were inspected for previous marks.

Length Data

We gathered juvenile Chinook salmon length data over the summer in 2009 via underwater videography at eight sites; four upstream sites (US1-4) were located between 64.864021N, -146.782157W, and 64.892929N, -146.648643W and four downstream sites (DS1-4) were located between, 64.790316N, -147.162720W and 64.822348N, -147.074728W. The video recording system consisted of two Sony 480 Exview Microcams mounted to a lightweight aluminum rod; underwater footage was recorded using two Sony HC32 digital recorders. When we first arrived at a site, we visually identified where fish were located within the site before introducing the camera into the water to record video of fish and of the calibration object (a 3-D grid of dots on a clear polycarbonate cube) for 3-D measurements. Approximately 10 minutes of video were recorded at each site, for each session. Once video was recorded, we used the freely available software program VidSync 1.2 (vidsync.sourceforge.net; Neuswanger, pers. comm.) to estimate fish length from the video. Video from the cameras was uploaded into the VidSync program and footage

from paired cameras was synchronized. Using video of the calibration object, the software calculated 2D-to-2D projective transformations from the screen coordinates of both videos to two surfaces of the cube. For each measurement of a fish's head or tail, we clicked the object and the software calculated a line through two surfaces to represent the line-of-sight from the camera. It then intersected the lines from both cameras to triangulate the position of a fish's head or tail in 3-D, and calculated the length of a fish based on the 3-D distances between its head and tail. We tested the accuracy of measurements by measuring the length of known objects in our videos; additionally, the mean and variance in the length distributions collected by video methods were not significantly different from those collected by minnow traps during the same period of time ($t = 0.0476$, d.f. = 29.689, $p = 0.9624$).

We also recorded fish lengths while conducting mark-recapture abundance estimates. Sampling was designed to estimate abundance at each site during three periods (July, August, and September 2009). Ten Gee-type minnow traps (23 x 45 cm, 0.6 cm wire mesh, 2.5 cm diameter opening) baited with salmon roe were set out at each of the sites and allowed to soak for 2-5 hours. Captured fish were placed in a bucket of river water and anesthetized with tricaine methanesulphonate (MS-222®) until they lost equilibrium. Then we measured fork length to the nearest mm, and mass was measured to the nearest 0.01 g using a Pescola® spring scale.

A concurrent study provided information on fish diet described above in the section titled *Chinook prey density and juvenile foraging*. Sampled fish were measured for length (nearest mm), and fish mass (nearest 0.1 g) was also measured.

We found historical length data from 1981, 1982, 1995 and 1996 from two theses. The length data for years 1981 and 1982 were from juvenile Chinook salmon sampled during the summer rearing period and were collected using standard minnow traps and common sense minnow seines at 8 sites, located upstream from the mouth of the Chena River at river kms 9.6, 35, 42, 71, 124, 134, 148, and 188 (Walker 1983). For the purpose of our study, we excluded the Badger Slough (35 km) and Nordale Road (42 km) sites because of skew in the data caused by capturing age 1+ juvenile Chinook salmon. The 1995 and 1996 data came from spring sampling efforts on outmigrating smolt, primarily sampled by a rotary screw trap, but also with minnow traps, beach seines, and a modified incline plane trap (Daigenault 1997). Three sampling sites (upper, middle, and lower) were located near the Moose Creek Dam, which is 71 km from the mouth of the Chena River. Although the 1995 and 1996 data were collected from outmigrating salmon we considered using it to compare our model prediction of end of first growing season length because it is typically strongly correlated with early smolt lengths; Bradford et al. (2001) showed that growth slowed considerably over winter for juvenile Chinook salmon, and winter growth for Arctic grayling is <10% that of summer growth (Roguski and Schallock 1967). However, Bradford et al. (2001) also found that early season growth in May and June before smoltification was significant, with mass of the fish doubling, and mean length increasing 18mm before outmigration. After further investigation of the historical data, we decided to exclude the 1995 smolt data, because of small sample size and

because observed length was much greater (10-20 mm) than any other years' actual or predicted length. We believe this is because the sampling was conducted later in the 1995 study season in order to increase sample size, and the fish likely experienced rapid growth in length in the short open water period before the sampling occurred. We used only length data from 1996 for comparisons of observed to predicted length, because of earlier sampling dates, consistent sampling techniques and higher sample size in that year.

Temperature Data

During 2009, average daily water temperature was calculated from hourly measurements made at each site using HOB0® data loggers (Onset Corporation, Bourne, MA, USA) suspended from instream woody debris and weighted to the streambed. We obtained additional water temperature data collected by the United States Geological Survey (USGS) at the Hunts Creek gauging station near Two Rivers, 64.860006°N, -146.803319°W, (USGS 14593400). Hourly water temperature data were available from 11 September 2006 forward. Air temperature data were collected from the Fairbanks International Airport, 64.815°N 147.85639°W, by the Alaska Climate Research Center, part of the Geophysical Institute at the University of Alaska Fairbanks. The USGS has been collecting stream discharge data since 1967 from the Chena River, near Two Rivers gauging station, 64.902758°N, -146.356972°W, (USGS 15493000).

For years when instream water temperature data were not available, we used a model for predicting water temperature based on air temperature and discharge (van Vliet et al. 2011)

$$Tw = \mu + \frac{\alpha - \mu}{(1 + e^{\gamma(\beta - T_{air})})} + \frac{\eta}{Q} + \varepsilon,$$

$$\text{with } \gamma = \frac{4 \tan \theta}{\alpha - \mu}$$

where μ = lower bound of water temperature (°C); α = upper bound of water temperature (°C); γ = measure of the slope at inflection point (steepest slope) of the S-shaped relation (°C⁻¹); β = air temperature at inflection point (°C); η = fitting parameter (°C m³ s⁻¹); Tw = water temperature (°C); T_{air} = air temperature (°C); Q = river discharge (m³ s⁻¹); ε = error term (°C); and $\tan \theta$ = slope at inflection point (-).

To apply this equation, we used Mathematica (Wolfram Research, Inc. 2008) to use a long time series of daily air temperature data available from the Fairbanks International Airport and daily discharge data from the USGS gauging station on the Chena River near Two Rivers, AK (USGS 15493000), available since October 1, 1967, and water temperature from the USGS gauging station at Hunts Creek since September 2006. During the period that all data series overlapped (2006-2011), we

calculated a regression to estimate water temperature based on air temperature at the airport and discharge and used that regression to generate a complete water temperature time series.

Water temperatures tend to lag behind air temperature (Erickson and Stefan 2000; Jeppesen and Iversen 1987; Webb et al. 2003), and, because of this, a lag effect was incorporated into the regression analysis (van Vliet et al. 2011). For the Chena River we found that water temperature was most correlated with air temperature from the previous day. We ran linear and non-linear models to predict water temperature, in addition to models with air temperature and discharge alone (both variables squared, or with just one squared). Using ANOVA and ranking the models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002), the model with air temperature squared alone was best. Discharge was relevant, but barely; it accounted for very little of the variance, and the discharge parameter was not significant ($p = 0.25$).

Data Analysis

Fish condition

To investigate indicators of competition, we explored the effects of supplemental feeding on individual mass at length. To meet assumptions of normality, we log-transformed our data. Linear mixed effects models (Pinheiro et al. 2008) were used in the 'nlme' package version 3.1-89 in the R programming environment (R Development Core Team 2008), with fixed treatment effects, and random site effects to evaluate the effects of supplemental feeding on individual fish condition:

$$\log_{10}(M) = \alpha_t + \beta_t * \log_{10}(L) + a_s + b_s * \log_{10}(L) + \varepsilon_{ts},$$

where M is the fish response, mass of juvenile Chinook salmon at length, L. α_t and β_t are the slopes and intercepts for the treatment (fixed) effect, a_s and b_s are the slopes and intercepts for the site (random) effect, and ε are errors.

Indices of Competition

We plotted mass-frequency distributions for all sampled fish at each site during each sampling event, except at the farthest downstream site (DS4), due to low sample size. Plots were made using the 'lattice' program in the R programming environment (Sarkar 2008) on a scale from 0 to 10 grams, using 50 bins to distribute proportions of the population. Distributions were examined for skew to investigate potential density-dependence. We also calculated the Gini coefficient, a measure of inequality, for each site and event (Weiner and Solbrig 1984; Keeley 2001). The Gini coefficient is a number between 0 and 1, with higher numbers indicating more inequality in the data. Coefficients were calculated using the 'reldist' package version 1.595 of the R programming environment (Handcock and Morris 1999). We used a repeated measures analysis of variance (rm ANOVA) with sampling event as the repeated measure to test for significant differences in the Gini coefficients

between treatments and through time. The rm ANOVA was done using IBM SPSS Statistics 19 (SPSS Inc. 2010).

Abundance estimates

In addition to visualizing local subpopulation effects of mass distribution, we gathered abundance and count data at each of the sites. For the mark-recapture experiment study design and analysis, specific conditions must have been set for estimates up abundance to be considered unbiased (Seber 1982). For each research site during each 3-day experiment, we assumed equal catchability for all animals within a single day capture event, that marking did not affect an animal's probability of being recaptured, and that sampling each day was instantaneous. We assumed that animals retained their tags throughout the 3-day experiment and that all tags were read properly. We also assumed that survival rates were the same for marked and unmarked animals and between each sampling occasions. Finally, we assumed that the study area was closed to immigration and emigration during the course of each 3-day experiment. An experiment on juvenile Chinook salmon from the Fraser River found mortality for tagged fish to be low (1.6%), and retention of elastomer tags to be 100% after 3 months (Bradford et al. 2001).

Abundance estimates for each of the sampling events were conducted in program MARK (White and Burnham 1999) for closed population capture-recapture models (Otis *et al.* 1978). The closed capture model is based on the full likelihood parameterization with three types of parameters; p_i is the probability of first capture, c_i is the probability of recapture, and N is abundance. We input data into the program using the LLL encounter history format. Three models were run for each of the study sites to estimate abundance: In the model descriptions, $(.)$ = a constant parameter, and (t) = a time varying parameter.

$$\begin{aligned} N, p(.) &= c(.) \\ N, p(t) &\equiv c(t) \\ N, p(.), c(.) \end{aligned}$$

All models were ranked using AIC_c , and we selected our 'best' model based on the model with the lowest AIC_c score. All sites ranked $N, p(t) \equiv c(t)$ as the best model, and we used that model to estimate abundance (N) and standard errors.

We estimated catch per unit effort (CPUE) for each of our trapping days. Where catch was the total number of fish caught at each sampling event, and effort was the number of minnow traps multiplied by the number of minutes fished. We used Spearman's rank correlation ρ to investigate the correlation between abundance estimates and total CPUE.

Growth Modeling

We investigated growth over time using Generalized Additive Models (GAM) (Wood 2006) in the 'mgcv' package version 3.1-89 in the R programming

environment (R Development Core Team 2008). For all models we investigated the growth patterns, measured in terms of length, by date. We estimated each model on two levels; by reach (upstream vs. downstream) and with full models fit with all sites. Our first model type was relatively simple, and examined the growth by site or reach. This model assumed the same growth pattern at each site, but a fixed difference in length between sites (i.e., a growth curve shifted up or down). We also fit a model that allowed for different growth patterns by site and reach, and ranked the models using AIC. Δ AIC suggested that the more complex model with different growth curves for each site was the best fit for the data. To compare differences between sites, we refit the GAM using a polynomial with 5 d.f., which was roughly equivalent to our estimated degrees of freedom in our ‘best’ GAM model and ran pairwise comparisons between all sites.

Bioenergetics

To test the hypothesis that temperature regulates growth of juvenile Chinook salmon rearing in the Chena River, we used a simple individual based model from Rasmussen and From’s (1991) rainbow trout bioenergetics model to predict the growth of a single rainbow trout through different temperature histories. Bioenergetics models are useful tools; one way they can be used is to detect poor growth by comparing measured length to predicted length under optimal conditions (maximum rations) and they can be used to identify factors that limit growth (e.g., food, space, and predation). We used the Rasmussen and From model because the required parameters have not yet been established for Chinook salmon, because it is parameterized to a more closely related stream salmonid in the same genus (*Oncorhynchus*) than other available bioenergetics models (e.g., genus *Salmo*, Elliott et al. 1995), and because it was parameterized for fish in a similar size range experiencing similar temperatures. This model was derived for rainbow trout on pellets, however, it showed no significant difference in parameters between dry and wet pellets (From and Rasmussen 1984), suggesting that the parameters are not overly sensitive to food type. Larsson and Berglund (1998) found in Arctic char *Salvelinus alpinus* that the relationship between growth and temperature was not significantly different between food pellets and live *Neomysis* food. The main difference between food sources is that the maximum ration (i.e. the maximum amount of food a fish is able to consume) on wild food is much smaller, around 0.3x the maximum pellet ration, averaged over all fish of all sizes in one productive stream studied (Rasmussen, pers comm.). We suspect this is caused by both the lower energy density of wild food and the practical limitations of drift-feeding. The model we used takes this pellet-to-wild-food multiplier as an adjustable parameter for determining the maximum daily ration.

We input mean daily water temperature data into the model for the period of the summer growing season when mean water temperature was above 4°C. For our first application of the model, we averaged daily mean water temperature data collected *in situ* at each of our sites in 2009, to get a daily mean temperature for upstream and downstream reaches. For brood years 2007-2009, we also ran the model using

temperature data collected by the USGS at Hunts Creek. For brood years 1981-2006, we input hindcasted temperature data into the model.

We compared the model output length and weight with observed fish length and weight data collected during 2009 to determine how well it predicted growth throughout the freshwater rearing season at upstream and downstream sites. The model did not predict end of season Chinook weight accurately, which may be due to species differences for which the model was parameterized; however, the model did accurately predict length. Using actual and hindcasted temperature data from Hunts Creek, we predicted the length of juveniles at the end of the freshwater rearing season given maximum wild rations, approximately where the first annulus would be deposited on their scales for brood years 1981-2009. We compared predicted to actual length of juveniles at the end of their first summer using data we collected during our 3-year study, as well as fish length data from Chena River salmon found in the literature for years 1981, 1982, and 1996.

Survival

To examine the relationships between smolt size, temperature, and survival of salmon, and to determine whether there is a positive correlation between smolt size and the productivity of a brood year (in terms of recruits per spawner), we used estimates of recruits per spawner for years 1986-2002 from the Alaska Department of Fish and Game stock recruitment analysis (Matthew Evenson, ADF&G, pers. comm.) and regressed these on predicted smolt size estimated using the Rasmussen and From (1991) bioenergetics model.

IV. Foraging analyses, mechanisms of competition, and recruitment.

Development of video methods

Analyzing the fine-scale behavior of schools of dozens of fish required major improvements to the 3-D video analysis technology pioneered by Hughes and Kelly (1996). We designed an untethered, wide-angle stereo video camera system that could be placed within inches of groups of juvenile Chinook salmon inside tight logjams, and record their behavior with enough detail to resolve the outcomes of most foraging attempts and enough 3-D precision to resolve feeding territories and measure individual lengths. We also created software with a sufficiently streamlined workflow to process thousands of these measurements, a volume of data that would have been impossible using earlier technology. This Mac OS 10.7+ application, called VidSync, is written for the Cocoa environment in the Objective-C language, and is available as an open-source download from <http://vidsync.sourceforge.net>.

Although the main contribution of VidSync is its unprecedented ease and speed of use, it also combines a novel collection of mathematical methods uniquely suited for studying fish behavior. The original method of Hughes and Kelly (1996) used

polynomial fitting to link the 2-D coordinates from each video screen to a common 3-D coordinate system defined by a calibration box called a quadrat. We instead use the more robust method of normalized Direct Linear Transformation (nDLT; Hartley and Zisserman 2004), which greatly increases the volume of viewing space in which we can make accurate measurements. We combine nDLT with the Brown-Conrady model (Brown 1966) for reducing the accuracy-breaking radial and decentering distortion inherent to wide-angle lenses and underwater filming.

We also developed a protocol for filming fish effectively, considering both the specific requirements of our analysis system and general principles for gathering clear footage underwater. We compiled all these contributions – hardware, software, and field protocol – into a methodological paper for widespread use, because of their broader effectiveness and application.

Gathering and analyzing video data

We collected video footage opportunistically in the upper Chena (throughout the area in between the Moose Creek Dam and the Middle Fork / North Fork confluence) from June through September in 2008, 2009, and 2010. The majority of usable footage came in 2010, reflecting our improvements to our methods. We are using VidSync to measure, categorize, and catalog the foraging and competitive interactions of each fish during a selected sample from each video. We analyzed the 5 videos with the highest visual quality for analyses of foraging attempt outcomes and territoriality.

For each selected video segment, we recorded data for each fish that provided an adequate view of its foraging attempts. We followed each fish one-by-one throughout the segment, recording the position and outcome of each of its foraging attempts.

Effect of drifting detritus

We categorized the outcomes of each observed foraging attempt in a way that provides insight into whether the attempt was focused on debris or food. We noted whether the particle was pursued without capture, captured and expelled from the mouth (colloquially, “spit out”), or captured and ingested. Each category was further subdivided to keep track of some events with ambiguous interpretations (such as those in which a captured particle appeared to be spit out based on a characteristic mouth motion, but the particle was not visible as it was ejected).

Because our findings suggested that most foraging attempts focus on debris, we amended our goals to include examining several implications of this effect on foraging theory and models for drift-feeding fishes in general. We also used these results to examine the validity of the common technique of using foraging attempt rate as a proxy for ingestion rate and fitness.

Territoriality and the mechanisms of competition

Tracking all the foraging attempts of each fish in the visible portion of a school allowed us to map feeding territories for those individuals. The 3-D video measurement system also measured water velocity and the position of the surface, bottom, and cover, effectively producing a complete map of the habitat and the behavior of the fish within it.

We constructed feeding territories by taking into account every foraging attempt – whether on debris or potential food – by each fish. These points were used to generate a mathematical representation of each territory as a kernel density estimate (KDE), a smooth-fit 3-D function representing the probability of the fish foraging within a given area. Although KDEs are in very widespread use for studying large animal territoriality in 2-D, ours was their first application in 3-D, which required some novel extensions to the 2-D mathematical techniques for estimating territory size and overlap.

By combining KDE-based territory estimates with foraging rates and knowledge of the water velocity gained by tracking passive particles through the video, we estimated the effect of each fish's foraging on its neighbors, especially those downstream. By looking at the relationship between territory size, territory spacing, relative territory position, and foraging attempt / ingestion rate, we can learn about how the foraging behavior and success of individuals is affected by the presence and positions of competitors. This portion of our work is still being finalized.

Stock-recruitment analysis

We considered three stock-recruitment models, including the Ricker model and three extensions of the Ricker model that included environmental factors. Two extensions added only the median June to September daily stream discharge: in one model, this was a simple linear factor, and in the other, it was incorporated as a nominal variable as a “high flow” or “low flow” year, with those two categories separated by a threshold defined by an adjustable parameter. The third, most complex extended model included a nominal discharge effect and also included a nominal effect of the maximum flood peak and number of degree-days during the pre-winter spawning and incubation period (July 20 to October 25).

RESULTS:

I. Flow, temperature, chemistry, stream ecosystem metabolism, and benthic prey.

Environmental variables

Environmental conditions (water temperature, turbidity, PAR, and river discharge) were similar among the study sites, but varied between years; in particular, water temperature and PAR were higher in 2009, while river discharge was lower. In both

2008 and 2009, $\text{NH}_4^+\text{-N}$ and SRP concentrations were low (at times below the detection limits), while $\text{NO}_2^-\text{-N}+\text{NO}_3^-\text{-N}$ and DOC concentrations were more variable throughout the summer (Fig. 4). For dates when SRP was detectable, DIN:SRP ratios ranged from 33:1 to 172:1 in 2008, and from 27:1 to 143:1 in 2009.

Ecosystem metabolism

Pearson's correlations showed that both the night-time and day-time regression techniques for estimating metabolism rates produced highly correlated estimates (GPP: Pearson $r = 0.90$, $n = 370$, $P < 0.001$; ER: Pearson $r = 0.63$, $n = 370$, $P < 0.001$), but we chose to report night-time regression estimates in order to include our full data-set in our analyses rather than just the sub-set. Metabolism rates were significantly higher when estimated using the night-time regression technique, by $0.07 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for GPP, and by $1.03 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for ER (GPP: paired $t(369) = -3.76$, $P < 0.001$; ER: paired $t(369) = -7.12$, $P < 0.001$). A two-sided Spearman correlation showed that reaeration coefficient value was not correlated with river discharge rate ($n = 539$, $\rho = -0.047$, $P = 0.274$).

GPP rates ranged from 0.08 to $9.35 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, and ER rates ranged from 1.58 to $42.05 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$; overall, river ecosystem metabolism rates were variable throughout the two field seasons and between sites, but in general both GPP and ER rates were higher at Site 1 than at the other three study sites (Fig. 5). The variables included in the Random Forests model for GPP explained 75% of the variance in the data, and the model identified site as the overall most important variable, followed by discharge. Turbidity, PAR, ordinal date, year, and temperature were approximately equal in importance, and the final variable that the model identified was time since last high water event (Fig. 6a). The variables included in the alternative Random Forests model for GPP (i.e. the model that did not include year and site as possible predictor variables) explained 63% of the variance in the data.

The variables included in the model for ER explained 52% of the variance in the data, and the model indicated that site was the overall most important variable. Ordinal date, PAR, and time since last high water event were identified as the next most important variables, with approximately equal importance, and temperature was also identified as important (Fig. 6b). The variables included in the alternative Random Forests model for ER (i.e. the model that did not include year and site as possible predictor variables) explained 31% of the variance in the data.

PAR was ranked third in importance for predicting GPP rate, along with several other variables; the partial dependence plot for PAR showed that GPP rate had a positive relationship with PAR values below approximately $0.3 \text{ mEs}^{-1}\text{m}^{-2}$; at PAR intensities above this threshold, GPP rate remained constant (Fig. 7a). In addition, PAR was ranked as the second most important variable for predicting ER rate, along with two other variables; the partial dependence plot for PAR showed that there was a positive relationship between ER rate and PAR values below approximately $0.5 \text{ mEs}^{-1}\text{m}^{-2}$; at PAR values above this threshold, ER rate remained constant (Fig. 7b).

Discharge was identified as the second most important variable for predicting GPP rate, and the partial dependence plot for discharge showed that GPP rate peaked at intermediate discharge (Fig. 8a). For ER rate, discharge was not identified as an important predictor. However, time since last high water event, an alternative measure of discharge, was tied with other variables as the second most important predictor for ER rate; the partial dependence plot for time since last high water event indicated that ER rate was lowest at the greatest time since last high water event (Fig. 8b). Two-sided Spearman correlations, with a family-wise alpha of 0.05 for each year, revealed no significant relationships between metabolism rates and nutrient concentrations.

Benthic macroinvertebrates

Benthic macroinvertebrate density ranged from 7 to 1012 # indiv. m⁻² and biomass ranged from 1 to 146 mg m⁻²; overall, both were variable throughout the two field seasons and between sites. Chironomidae was the most commonly encountered benthic macroinvertebrate taxon at Sites 2, 3, and 4, in both 2008 and 2009 (representing 60%, 51%, and 45% of individuals at Sites 2, 3, and 4 in 2008, and 42%, 52%, and 53% of individuals in 2009), while Simuliidae was the dominant benthic macroinvertebrate taxon at Site 1 during both years (representing 45% of individuals in 2008, and 31% of individuals in 2009). Other commonly encountered taxa at the four sites included Heptageniidae, Ephemerellidae, Hydracarina, Nemouridae, Chloroperlidae, and Oligochaeta.

The variables included in the Random Forests model for benthic macroinvertebrate density explained 58% of the variance in the data, and the model indicated that discharge was the overall most important variable, followed by ordinal date and year, which were approximately equal in importance (Fig. 9). The partial dependence plot for discharge showed that benthic macroinvertebrate density was lowest at high discharge rates (Fig. 10). The variables included in the alternative Random Forests model for benthic macroinvertebrate density (i.e. the model that did not include year and site as possible predictor variables) explained the same amount of the variance in the data (58%).

The variables included in the model for benthic macroinvertebrate biomass explained 39% of the variance in the data, and the model identified discharge as the overall most important variable, followed by ordinal date and year, which were approximately equal in importance, and finally by site (Fig. 9). The variables included in the alternative Random Forests model for benthic macroinvertebrate biomass (i.e. the model that did not include year and site as possible predictor variables) explained 27% of the variance in the data.

GPP rate was not identified as an important predictor for either benthic macroinvertebrate density or biomass in the preliminary Random Forests models. Two-sided Spearman correlations showed that GPP was not correlated with benthic

Heptageniidae density ($n = 38$, $P = 0.401$) or benthic Heptageniidae biomass ($n = 38$, $P = 0.693$).

II. Chinook prey density and juvenile foraging.

Terrestrial invertebrate infall

Four sites within the same study reach described above were used for this part of the study as well. In 2008, terrestrial invertebrate infall mass peaked during late August (8/12), whereas, in 2009, terrestrial infall peaked earlier in late June (6/22) and then again mid-August (8/18, Figure 11). The mass of adult-winged aquatic and terrestrial invertebrate infall generally followed similar patterns within summer in both 2008 and 2009. In 2008, terrestrial invertebrate infall ranged from 6-51 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ with a mean of 17 ± 5 mg dry mass $\text{m}^{-2} \text{d}^{-1}$. In 2009, terrestrial invertebrate infall ranged from 0-72 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ with a mean of 33 ± 8 mg dry mass $\text{m}^{-2} \text{d}^{-1}$. Terrestrial infall mass was significantly higher in 2009 than 2008, varied significantly by sampling date, and marginally by date*year (rm ANOVA, year: $P = 0.003$, sampling date: $P < 0.001$; date*year: $P = 0.018$), but not by site. The top five taxa by mass of terrestrial invertebrate infall in 2008 were adult Hymenoptera, followed by adult Collembola, Araneae, Hemiptera, and Coleoptera Staphylinidae. The top five taxa by mass for terrestrial invertebrate infall in 2009 included the same taxa as in 2008, but in a different order with adult Coleoptera Staphylinidae having the highest mass, followed by adult Hymenoptera, Araneae, Collembola, and Hemiptera.

Contribution of terrestrial invertebrates in the drift

In 2008, terrestrial invertebrates in the drift peaked in early June (6/11) and then again in mid-August (8/12), whereas in 2009 the mass of terrestrial invertebrates was variable and had peaks in each month (Figure 12). The greatest peak of terrestrial invertebrate drift (8/12) was concordant with the greatest peak of terrestrial invertebrate infall, but in 2009 the peaks of terrestrial infall and drift did not consistently match (Figs. 11 and 12). However in the beginning of both summers, there was an initial peak of aquatic invertebrate drift primarily made up larval chironomids (Diptera), although this first peak was almost two weeks later in 2009 than in 2008 (Fig. 12).

In 2008, terrestrial invertebrate drift ranged from 0.01-0.4 mg dry mass m^{-3} , had a mean of 0.12 ± 0.04 mg dry mass m^{-3} , and was $20 \pm 6\%$ of the invertebrate drift (Fig. 12). During 2009, terrestrial invertebrates drift ranged from 0.01-0.24 mg dry mass m^{-3} , had a mean of 0.07 ± 0.02 mg dry mass m^{-3} , and was $27 \pm 6\%$ percent of the drift. Unlike terrestrial infall, terrestrial drift did not vary significantly by date nor was significantly higher in 2009 than in 2008. Furthermore, terrestrial drift did not vary seasonally in a similar manner both years (rm ANOVA, date*year: $P = 0.004$). In the 2008 drift, the top five terrestrial taxa by mass were adult Hymenoptera, followed by adult Hemiptera, Diptera in the families Xylophagidae and Sciaridae, and Araneae. In

the 2009 drift, the top five terrestrial taxa by mass were adult Hymenoptera, followed by adult Hemiptera, Coleoptera Staphylinidae, Araneae, and Lepidoptera.

Contribution of terrestrial invertebrate prey to juvenile Chinook diet

We sampled juvenile Chinook salmon for stomach contents, obtaining a total of 360 samples ($n = 118$ in 2008, $n = 233$ in 2009) from fish 28-87 mm in length. Both summers, juvenile Chinook consumed a low mass of aquatic and terrestrial prey in the beginning of the summer and then consumed an increasing but variable mass throughout the rest of the season (Fig. 13). In 2008, juvenile Chinook consumed terrestrial invertebrates in a range of 0.05 - 3.67 mg dry mass fish⁻¹, with a mean 1.4 ± 0.4 mg dry mass fish⁻¹. In 2009, juvenile Chinook once again consumed a similar terrestrial invertebrate mass ranging from 0 - 3.30 mg dry mass fish⁻¹; however, with a lower annual mean of 0.75 ± 0.26 mg dry mass fish⁻¹. Although marginally significant, juvenile Chinook consumed more terrestrial invertebrate mass in 2008 than in 2009 (rm ANOVA, $P = 0.028$). This was also reflected in the proportion of their total diet made up by terrestrial invertebrates, with terrestrial invertebrates making up $24 \pm 4\%$ of total juvenile Chinook diet in 2008 versus $16 \pm 4\%$ in 2009. Consumption of terrestrial invertebrates varied significantly by site and date (rm ANOVA, site: $P < 0.001$; date: $P < 0.001$), and varied marginally by year and by the site between years (rm ANOVA, year: $P = 0.028$; year * site: $P = 0.028$).

Juvenile Chinook consumed a wide range of invertebrate prey, consisting of 16 orders and at least 47 families. Using the calculated IRI to determine the importance of differing taxa to juvenile Chinook diet, we found that chironomids (Diptera) in all their life stages (larva, pupa, and adult) as well as chloroperlids (Plecoptera) ranked in the top five most important taxa for both 2008 and 2009. Two terrestrial taxa ranked in the top ten most important taxa consumed per year: adult Hymenoptera and Araneae in 2008, as well as adult aphids (Hemiptera) and hymenopterans in 2009.

During both summers, the proportion of terrestrial invertebrates in the diet was initially low, generally increased throughout the season (Fig. 14), and was positively correlated to sampling date (Pearson's correlation; 2008: $r = 0.35$, $P < 0.001$; 2009: $r = 0.36$, $P < 0.001$). In 2008 on two different sampling dates (8/13 and 8/27), terrestrial invertebrates made up 39% of the total diet (Figure 14). These two dates with the highest proportion of terrestrial invertebrates consumed in the total diet followed a 60-year flood that peaked on July 31 with a discharge of $250.1 \text{ m}^3 \text{ s}^{-1}$, a twelve-fold increase from the mean annual flow. In 2009, the largest proportion of terrestrial invertebrates consumed that year occurred in late August with terrestrial invertebrates making up 38% of the total diet.

Relationship between infall, drifting invertebrates, and predation by fishes

The first ordination comparing aquatic and terrestrial invertebrate availability (via infall and drift) to consumption by juvenile Chinook resulted in clustering by sample type (Fig. 15). Clustering by sample type, i.e. infall, drift, and diet, signified that

invertebrate community composition was more similar in abundance and composition by sample type rather than across samples types, dates, or years. This also signified that there was low overlap between the invertebrate community represented in the comparisons of infall to diet and diet to drift. Juvenile Chinook diet and drift had approximately 23-28% similar taxa and abundance levels (SIMPER, mean percent dissimilarity of invertebrate composition: 77% in 2008 and 72% in 2009). SIMPER determined that hymenopterans in 2008 and adult chironomids in 2009 contributed the most dissimilarity between invertebrate composition of juvenile Chinook diet to drift. In both summers, juvenile Chinook consumed a higher proportion of both hymenopterans and adult chironomids than the proportion of either available in the drift. Additionally in both summers, black fly larva (Diptera: Simuliidae) and water mites (Acari: Hydracarina) were highly abundant by proportion in the drift. Yet, juvenile Chinook consumed black fly larva at levels lower than their availability, and rarely consumed water mites.

Juvenile Chinook diet and invertebrate infall also had low total overlap with 22-27% similar taxa and abundance levels (SIMPER, mean percent dissimilarity of invertebrate composition: 78% in 2008 and 73% in 2009). Both in 2008 and 2009, adult chironomids contributed the most dissimilarity between diet to infall, with a higher proportion of adult chironomids in infall samples than in juvenile Chinook diet. Adult aquatic stoneflies (Plecoptera) also contributed to the dissimilarity between diet and infall, with a higher proportion of adult stoneflies in infall than in juvenile Chinook diet. As a whole, juvenile Chinook diet had a low, but comparable overlap with both drift and infall (SIMPER, mean percent dissimilarity of 2008 and 2009 combined, diet to drift: 74% and diet to infall: 75%).

When examining only terrestrial taxa in the second ordination, diet and drift samples loosely clustered with some overlap. This signified greater overlap of terrestrial invertebrate composition and quantity between diet and drift (Figure 6-b). Terrestrial infall had some overlap with the terrestrial invertebrate composition and abundance of diet and drift, but did not cluster with them (Fig. 15). SIMPER analysis determined that in both years Hymenoptera was the taxon that contributed the most dissimilarity between diet to drift and diet to infall. In 2008, the proportion of hymenopterans was higher in both drift and infall than in the juvenile Chinook diet. However in 2009, the proportion of hymenopterans in the diet was slightly higher than the proportion in drift and almost twice as much as the proportion in the infall. The percent dissimilarity of terrestrial taxa between diet to drift was lower than the percent dissimilarity between diet to infall in both years (respectively, 2008: 65% vs. 70%; 2009: 51% vs. 77%), indicating that terrestrial invertebrates consumed by juvenile Chinook were more closely represented by terrestrial invertebrates in the drift than in infall samples. This lack of overlap between infall and diet was primarily due to differences in levels of abundance between sample types, not differences in terrestrial invertebrate taxa.

Effects of discharge and stream temperature on predation by juvenile Chinook

Total prey mass consumed was negatively correlated with river discharge in 2009 and both years combined, but was negligibly correlated in 2008 (Pearson's correlation; 2008: $r = -0.10$, $P = 0.29$, 2009: $r = -0.35$, $P < 0.001$; combined: $r = -0.23$, $P < 0.001$). The proportion of terrestrial prey mass consumed was negligibly correlated with discharge in 2008 and in both years combined, but had a marginal negative correlation with discharge in 2009 (Pearson's correlation; 2008: $r = 0.05$, $P = 0.65$; 2009: $r = -0.14$, $P = 0.02$, combined: $r = 0.07$, $P = 0.17$).

Total invertebrate prey mass consumed was positively correlated with water temperature for 2009 and both years combined, and had a non-significant positive correlation in 2008 (Pearson's correlation; 2008: $r = 0.09$, $P = 0.38$; 2009: $r = 0.26$, $P < 0.001$; combined: $r = 0.22$, $P < 0.001$). The proportion of terrestrial prey mass consumed was not significantly correlated with water temperature in either 2008 or 2009, but had a marginal negative correlation with the water temperature of both years combined (Pearson's correlation; 2008: $r = -0.13$, $P = 0.18$; 2009: $r = 0.03$, $P = 0.65$; combined: $r = -0.11$, $P < 0.04$). In addition, water temperature and discharge were negatively correlated for each individual year and both years combined (Pearson's correlation; 2008: $r = -0.25$, $P = 0.01$; 2009: $r = -0.51$, $P < 0.001$; combined: $r = -0.47$, $P < 0.001$).

III. Chinook growth modeling, abundance, density dependence.

Fish condition

During the 2009 study season, we did not find a significant effect of supplemental feeding on individual growth, condition, or subpopulation level abundance. The linear mixed effects model used to test the effects of supplemental feeding on individual fish condition found no significant difference in fish condition between fed and unfed treatment sites ($p = 0.30$) (Table 1), and the plots of log-transformed mass (g) on length (mm) regressions suggested no difference between treatments (Fig. 16).

Density dependence

Mass frequency distributions showed similar size inequalities for all treatment sites across all dates, between both upstream and downstream reaches (Figs. 17 and 18). Gini coefficients were not significantly different between treatments (rm ANOVA, $F_{1,6} = 1.778$, $p = 0.23$), but did lessen through time (rm ANOVA, $F_{1,6} = 12.000$, $p = 0.013$).

Abundance estimates

Due to low recapture at upstream sites, estimates of juvenile Chinook population abundance could only be calculated at sites DS1-3 (Table 2). After the first sampling event, DS4 had insufficient captures to calculate an abundance estimate. Abundance estimates for DS1 were similar for both events (Fig. 19). We observed a significant increase in abundance from July to August at DS2, but not between August and September. DS3 abundance was nearly identical for July and August, but was

slightly larger in September. CPUE (Table 2) and abundance were strongly correlated ($S = 4$, $p = 0.0005$, $\rho = 0.95$, correlation coefficient = 0.97). Because they were strongly correlated, we used CPUE as a proxy for abundance at our sites where we were unable to estimate abundance because of low numbers of recaptured fish.

Growth modeling

Considering the growth in length at each site by date using a polynomial, the trend in length was highly significant ($r^2 = 0.91$, $F_{8,304} = 391.8$, $p < 0.001$). Using pairwise comparisons, all upstream and downstream sites were significantly different from each other ($p < 0.001$). In the upstream reach, the furthest upstream site was significantly less than all other sites ($p < 0.001$), the rest were not significantly different ($p > 0.168$). In the downstream reach, DS1 was not significantly different from any of the other sites ($p > 0.187$). DS3 was significantly less than DS2 ($p < 0.001$), and DS4 was significantly greater than DS3 ($p < 0.001$), but DS2 and DS4 were not significantly different ($p = 0.658$) (Fig. 20).

Bioenergetics

Using temperature data collected *in-situ*, Rasmussen and From's (1991) bioenergetic model worked well to predict length of juvenile Chinook salmon based on maximum wild rations during the 2009 summer growing season. There was a strong correlation between predicted and observed growth in both upstream and downstream reaches ($r^2 = 0.95$ and 0.93 , respectively) (Fig. 21).

Using temperature data from Hunts Creek, we were able to predict fish length at the end of the summer rearing season for years 1981-2009. Of 18 observations of fish length from 6 years of data, the predicted length was encompassed by the confidence interval of observed length in 4 observations. From 2007-2008, using actual water data from the Hunts Creek USGS gauging station, our predicted length was within 2 standard errors of observed length at the end of the summer growing season, and, in 2009 predicted length was within 2 standard errors of observed length for 1 of our 4 comparisons (Table 1). Using the hindcasted temperature data from Hunts Creek, predicted growth was 1.1 – 3.1 mm less than observed growth of smolt during 1996 (Daignault 1997). In 1981 and 1982, predicted growth was greater than observed for all sites by as much as 17 mm (Walker 1983).

Survival

Estimated smolt length was not correlated with recruits per spawner ($r^2 = 0.049$, $p = 0.39$). The relationship between recruits per spawner and growing degree-days and mean summer temperature were also not significant ($r^2 = 0.047$ and 0.0005 respectively, and $p = 0.39$ and 0.93 , respectively).

IV. Foraging analyses, mechanisms of competition, and recruitment

Video methods

Our video hardware and field filming protocol were both refined to a state of reliable performance, as evidenced by the much larger percentage of usable videos collected in our final year of filming (2010) than in any of the previous years. The unrestrictive mathematical methods used in VidSync contributed to our ability to film useful video in the tight spaces characteristic of juvenile Chinook salmon habitat in the Chena.

The VidSync software offers a dramatically faster work process than previous 3-D video measurement software, and has allowed us to measure several hundred foraging attempts in a day. It would allow thousands of simpler measurements that require less judgment-based discernment, such as length or position measurements. Multiple people have been trained to use it in less than an hour, and users familiar with its predecessors regard VidSync as easier to use. In addition to the improved speed and ease of use, VidSync also showed sub-millimeter measurement accuracy within the distance range relevant to fish in our study.

We have submitted a paper detailing these advances to the Canadian Journal of Fisheries and Aquatic Sciences.

Effect of drifting detritus

Our results from this analysis suggest that only 9% of foraging attempts appear to lead to ingesting prey, while the remaining attempts are spent in pursuit and rejection of debris. These rejections are approximately evenly split between those in which the fish captures an item but expels it, and those in which it invests time to pursue the item but decides not to capture it. Figure 22 shows the combined results from the categorization of 401 foraging attempts by 12 fish over a period of 20 minutes on August 14, 2009. A comparable pattern was measured in four other video clips shot under different conditions, and this was representative of behavior observed qualitatively under a much broader range of conditions. Some groups spent up to 25% of their total foraging time pursuing and handling debris, corresponding to an equal reduction in expected net energy intake.

Territoriality and the mechanisms of competition

We developed several new mathematical and graphical methods for analyzing feeding territories in 3-D, and applied them to the spatial foraging data (Figures 23-25).

Many juvenile Chinook salmon in the Chena maintained and defended individual territories, even while clustered together in a school or shoal. To our knowledge, this was the first formal observation in ecology of feeding territoriality observed simultaneously with aggregation behavior, and it was also the first observation of 3-D territories (some located directly above or below others). No relationships were evident between foraging success and aggression or territorial position among

individuals, but the great variation in these variables suggests some differences might not have been detectable.

Stock-recruitment analysis

The basic Ricker model left much variation in recruitment unexplained for Chena Chinook salmon (Fig. 26). However, the residuals of the log recruits per spawner from this model were strongly related to flow by a variety of metrics (Fig. 27), suggesting that in general high-flow years yield poor recruitment, while low- to medium-flow years yield good recruitment. A Ricker model modified with a single flow effect explained much more variation (Fig. 28). The explanatory power of this model was further improved (Fig. 29) by incorporating two marginally statistically significant, but ecologically very plausible effects: a linear effect of the number of degree-days (an index of temperature) from the beginning of spawning until winter, and a nominal negative effect of very severe floods during that period that could destroy redds.

We were interested in determining whether the strong discharge effect was a result of productivity-related ecological mechanisms acting over a long time period, or whether it was due to acute negative effects of specific floods. We looked for correlations of recruitment with maximum flood peak during the juvenile rearing summer, and with flashiness (the total length of the hydrograph line for the year if it were stretched out straight) and the coefficient of variation of daily discharge. We also looked at each of these variables during the specific times of vulnerability, such as the first two weeks the fish are emerging from the gravel. None of these factors were strongly related to recruitment, suggesting that prolonged flow regime effects (probably linked to overall productivity and foraging conditions) were most important.

DISCUSSION:

I. Flow, temperature, chemistry, stream ecosystem metabolism, and benthic prey.
[These data have been compiled into one manuscript published in Hydrobiologia, 2013]

Metabolism and PAR

GPP rate increased with increasing PAR intensity and then plateaued at light saturation. We also found an unexpected increase and plateau in ER rate with increasing PAR intensity. Light availability has been identified as an important factor influencing GPP rate, but it generally does not directly influence ER rate because processes that contribute to ER are not necessarily photosynthetic processes (Young et al., 2008). However, ER rate and light intensity may appear to be related if algae are responsible for a substantial proportion of the ER occurring in the river, a condition that can occur in well-lit streams and rivers (Bunn et al., 1999; Young et al., 2008). Due to its sub-arctic location, the Chena River is well-lit during the summer

months, when our study occurred; thus, a large portion of the ER occurring in the river may have been due to algal activity.

Metabolism and discharge

Our results supported the hypothesis that GPP rate is greatest at intermediate river flow in the Chena River. GPP rate was greatest at discharge values between base flow and approximately $28 \text{ m}^3 \text{ s}^{-1}$. At higher discharge rates, GPP rate declined; this was likely because increased flow is associated with decreased light availability and increased water velocity. GPP rate has been shown to decline in response to decreased light availability and increased turbidity (Izagirre et al., 2008), both of which occur during flooding; GPP rate also declines during flooding as a result of reduced algal biomass due to abrasion caused by high water velocity (Young et al., 2008). Intermediate river flow may represent a balance between the positive effects of nutrient inputs (Stevenson, 1990) and the negative effects of decreased light availability and increased water velocity.

We hypothesized that ER rate is also greatest at intermediate river flow in the Chena River; however, we did not find evidence to support this. In fact, the Random Forests model for ER did not identify discharge as an important predictor of ER rate. The model did, however, identify time since last high water event as an important predictor. ER rate tended to be greatest at the shortest time since last high water event, and as the time since last high water event lengthened, ER rate fell. ER rate may have been highest directly following a high water event because floods are associated with increased nutrient and organic matter inputs (Stevenson, 1990; Roberts et al., 2007).

One of the ways in which discharge affects GPP rate is through abrasion of algal biomass. Abrasion due to high flow typically does not affect ER rate to the same extent because a substantial portion of ER can occur in the hyporheic zone, where respiring microbes are protected from abrasion (Fellows et al., 2001). This may be one explanation for why discharge was not identified as an important predictor of ER rate in the Chena River. Furthermore, if most ER occurs in the hyporheic zone and is therefore unaffected by abrasion during floods, we would expect that ER rate would not be low directly following a flood (contrary to what we would expect for GPP rate).

Metabolism and nutrients

We did not find any evidence to support our hypothesis that both GPP and ER rates are highest at greatest nutrient concentrations in the Chena River. We found no relationships between GPP rate and any of the nutrients measured in either year, nor any relationships between ER rate and any of the nutrients measured in either year.

In our study, we were not aware of any major human-caused increases or decreases in nutrient concentrations throughout the field seasons. We found that NH_4^+ -N and SRP

concentrations were low throughout the study (at times below the detection limits), while NO_2^- -N+ NO_3^- -N concentration was somewhat higher. In addition, the DIN:SRP ratios were well above the threshold for phosphorus limitation (Cai et al., 2008), suggesting phosphorus may have been one of the factors limiting metabolism in the Chena River.

If phosphorus was limiting metabolism, primary producers would have taken up any available phosphorus immediately, and therefore phosphorus would no longer be detectable in the water. This could explain why we did not find a correlation between metabolism rates and soluble reactive phosphorus (SRP) concentration. In addition, if phosphorus, rather than nitrogen, was limiting metabolism, then metabolism rates would not have responded to variation in nitrogen concentration in the river. Although we observed moderate changes in NO_2^- -N+ NO_3^- -N concentration throughout the field seasons, we did not find any correlations between metabolism rates and NO_2^- -N+ NO_3^- -N, suggesting that nitrogen was always available in abundance relative to phosphorus.

Our water chemistry results suggest that phosphorus, rather than nitrogen, may have been limiting metabolism in the Chena River, although we did not conduct nutrient-limitation studies; this is consistent with the results of a study on nutrient concentrations in the Chena River conducted in 2005-2006 (Cai et al., 2008). Long-term phosphorus fertilization of the Kuparuk River, an arctic river in northern Alaska, resulted in increases in metabolism rates, chlorophyll *a* concentrations, and fish growth rates (Slavik et al., 2004), suggesting that phosphorus was one of the factors limiting GPP, with effects that transferred up through the food web and affected multiple trophic levels.

Benthic macroinvertebrates and GPP rates

Our results did not support the hypothesis that benthic macroinvertebrates are more abundant and larger during or following periods of the highest rates of GPP in the Chena River. We expected that benthic macroinvertebrates would be more abundant and their biomass would increase following periods of high GPP because algal activity drives GPP rate and is an important food source for stream macroinvertebrates (McCutchan & Lewis, 2002), but the benthic macroinvertebrate Random Forests models did not identify GPP as an important variable for predicting benthic macroinvertebrate density or biomass. In addition, two-sided Spearman correlations showed that GPP was not correlated with benthic Heptageniidae density or benthic Heptageniidae mass. This finding suggests that the results of the Random Forests models were not simply an artifact of including all functional feeding groups in the models. Because scraping macroinvertebrates, of which Heptageniidae is one example (Waltz & Burian, 2008), are the functional feeding group most likely to rely on algae as a major food source (Cummins et al., 2008), we expected that this group would be most likely to show a relationship with GPP. However, GPP rates were not correlated with either Heptageniidae density or biomass.

One explanation for detecting no relationships between benthic macroinvertebrate density or biomass and GPP rate may be that benthic macroinvertebrate density responds to changes in GPP rate on an annual scale rather than a seasonal one. Our study included data from only two years, which is not enough time to test such a hypothesis. Past research, however, has indicated that benthic macroinvertebrate density can increase in response to additional food resources in as short as 17 days (Wipfli et al., 1999), suggesting that this explanation is not likely. Studies conducted in Alaska that have found an increase in benthic macroinvertebrate abundance following an increase in food resources (such as a natural salmon spawning event or an experimental salmon carcass addition, which can lead to increased biofilm chlorophyll *a* levels and ash-free dry mass) typically have much greater, and sustained, increases in food resources than we saw naturally occurring in the Chena River during our study (Wipfli et al., 1998; Wipfli et al., 1999; Tiegs et al., 2009). This could explain why we did not find a relationship between benthic macroinvertebrates and GPP rate; perhaps an increase in food resources has to be large, as well as sustained, to have an observable effect on benthic macroinvertebrates. However, another explanation may be that a longer time lag than the one we used (i.e., longer than one week) was necessary to observe an effect on benthic macroinvertebrates.

Benthic macroinvertebrates and discharge

We found evidence to support our hypothesis that benthic macroinvertebrates are least abundant during high flows. Our Random Forests model identified discharge as the most important variable for predicting benthic macroinvertebrate density, and the accompanying partial dependence plot showed a negative relationship between benthic macroinvertebrate densities and discharge rates above approximately $20 \text{ m}^3 \text{ s}^{-1}$. Though this rate of flow is well below the threshold of $50 \text{ m}^3 \text{ s}^{-1}$ that we used to categorize substantial high water events in our analysis, it appears to be the threshold for ecologically significant floods, at least in the case of benthic macroinvertebrates.

Extreme hydrologic events, such as floods and droughts, typically result in reduced benthic macroinvertebrate abundance (Konrad et al., 2008). In the case of flooding, as water velocity increases, benthic macroinvertebrates are more likely to leave the river bed because of the hydraulic stress they are experiencing. As more benthic macroinvertebrates begin to drift, fewer remain on the river bed (at least in the riffle habitats that we sampled); thus, following high discharge rates that promote drifting, benthic macroinvertebrates are less abundant.

Inter-site variability

Our models identified site as the most important variable for predicting GPP and ER rates. This suggests that there was some environmental factor or factors that differed among the study sites that we did not capture in our environmental measurements; in addition, there could have been environmental factors that did not differ among the study sites that we were unable to measure, which could account for the percentage of

variation in the data that the models could not explain. During both 2008 and 2009, GPP and ER rates were substantially higher at the furthest up-river site (Site 1) than at the other three study sites. There are several possibilities that could account for the difference in metabolism rates between Site 1 and the other sites. Site 1 is separated from the other three sites by a major tributary (the South Fork of the Chena River); this separation could lead to ecological differences between the sites that could influence metabolism rates such as differences in pH levels (Niyogi et al., 2002; Young et al., 2008), differences in the size and stability of river-bed substrate (Young et al., 2008), or differences in hyporheic connectivity (Fellows et al., 2001), none of which were measured in this study.

Another set of factors that could account for the difference in metabolism rates between our study sites is differences in benthic macroinvertebrate density, biomass, or community composition. Benthic macroinvertebrate density and biomass did not differ between the study sites in the same pattern as the difference in metabolism rates (i.e. Sites 2, 3, and 4 similar, and all different from Site 1); however, benthic macroinvertebrate community composition did differ in that fashion. Simuliidae was the most common taxon at Site 1 in both years, while Chironomidae was the most common taxon at the other three sites in both years. Members of the Simuliidae family generally belong to the collector-filterer functional feeding group (Adler & Currie, 2008), while members of the Chironomidae family generally belong to the collector-gatherer, collector-filterer, or predator functional feeding groups (Ferrington et al., 2008). The differences in their methods of collecting food and relative abundance at the study sites could affect the amount and quality of biofilm at the study sites, which in turn may have led to the differences in metabolism rates that we observed.

Another feature that could have influenced metabolism rates at our study sites was spawning salmon. When adult salmon return to their natal streams and rivers to spawn, the result is an influx of marine-derived nutrients in the form of fish carcasses, eggs, and metabolic waste (Gende et al., 2002). Our results suggest that phosphorus may have been limiting metabolism in the Chena River; thus, if our study sites experienced different densities of spawning salmon, we would expect those sites with a higher number of spawning salmon to have higher rates of metabolism as well. Aerial surveys conducted during the late summer in 2005 and 2007 indicate that salmon redds, or areas where female salmon deposit their eggs, were more abundant near Site 1 than at locations near our other three study sites; furthermore, the area where redd density peaked was up-river of all of our study sites (S. Decker, unpubl. data). Though the aerial surveys were conducted prior to the present study, the consistency between the two years suggests that salmon redds were likely more abundant near Site 1 than near our other three study sites during the years of our study. The higher rates of metabolism that we observed at Site 1 could have been a result of increased nutrient availability due to the proximity of spawning salmon.

We found that both GPP and ER rates increased with PAR up to a point, and then leveled off. The relationship between ER rate and PAR suggests that a substantial

portion of the ER occurring in the Chena River may be due to algae. We also found that metabolism did not increase with increasing nitrogen concentrations, perhaps because metabolism may have been limited by phosphorus availability. GPP rate was highest at intermediate discharge rate, and discharge was the most important variable for predicting GPP rate with the exception of site. ER rate was highest directly following high water events, and declined with increasing time since last high water event.

Though site was most important for predicting metabolism rates, it was not identified as particularly important in our benthic macroinvertebrate models. Similarly, periods of high GPP rate did not appear related to increased benthic macroinvertebrate density and biomass, perhaps because of the lack of periods with a high and sustained rate of GPP during our study. The benthic macroinvertebrate models both indicated that discharge was the most important variable for predicting densities and biomass, and benthic macroinvertebrate density was lowest at the highest discharge rates.

In conclusion, river discharge rate and length of time between high water events were the most important of the environmental factors that we studied for predicting changes in basal food web resources in the Chena River. In addition, our results suggest that phosphorus may have been limiting GPP in the river. These findings have important implications for river management because management schemes invariably cause changes to discharge rates and flow regimes, and added development within a watershed typically increases nutrient loading. The effects of these changes can cascade through the food web of a river through the impact they have on resources at the base of the food web, such as metabolism rates and benthic macroinvertebrates.

II. Chinook prey density and juvenile foraging. *[These data have been compiled into one manuscript which will be submitted to Freshwater Biology in summer 2013]*

Availability of terrestrial invertebrates via infall and drift

Terrestrial invertebrate infall in the Chena River was highly variable throughout the summer and between years, showing no consistent pattern between the two years of our study. However within each summer, we observed a similar pattern by date between the mass of aquatic and terrestrial invertebrates, even though the life history (e.g. hatches, number of generations per summer, and emergence dates) are presumably different between these two distinct categories. That we observed both aquatic and terrestrial invertebrates following the same pattern of infall into the Chena suggests that climate (i.e. wind patterns, air temperature, humidity, and precipitation) may have greater control on invertebrate infall than an individual taxon's life history. Also related to climate, we observed higher terrestrial invertebrate infall in 2009 relative to 2008. This could be due to lower air temperatures in 2008. On average near the Chena River, the air temperature in May-September was 2.5° C cooler in 2008 than in 2009. Previous research documented

increasing air temperatures coinciding with an increase in quantity of invertebrates entering streams (Nelson, 1965; Edwards & Huryn, 1995; Romero *et al.*, 2005).

The mean terrestrial infall for both summers (25 ± 5 mg dry mass $\text{m}^{-2} \text{d}^{-1}$) was on the low end compared to published values of summer terrestrial infall, ranging from 1.3 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ in a small New Zealand pasture stream to a high of 112 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ in the Horonai Stream in Japan (Baxter *et al.*, 2005). A study of small coniferous streams in southeast Alaska found a mean terrestrial infall of 37 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ (Wipfli 1997). Another study, also in Alaska, found a mean terrestrial infall of 83.3 mg dry mass $\text{m}^{-2} \text{d}^{-1}$ in small to mid-size coniferous streams (Allan *et al.*, 2003). Several plausible ecological mechanisms could explain the low mean terrestrial infall mass into the Chena River compared to other lotic systems. One of the reasons we found decreased terrestrial inputs per unit area may be due to the Chena River being a larger river system than the streams in the previously mentioned Alaskan studies. The river continuum concept predicts that allochthonous inputs decrease per unit area as one heads downstream because of the increased volume of water relative to the stream edge, which most likely would result in decreased allochthonous inputs per unit area (Vannote *et al.*, 1980; Polis *et al.*, 1997; Baxter *et al.*, 2005). A study in Virginia that examined the difference in terrestrial infall rate in different order (e.g. size) streams found that a 2nd order stream site had over 5 times the mean mass of infall than a 6th order river site (Cloe & Garman, 1996). Another possible reason could be due to our sample design of leaving our pan traps out for only one day, which resulted in the potential for missing pulses of terrestrial infall. In other terrestrial infall studies conducted in Alaska, pan traps were left out for one to two weeks (Wipfli, 1997; Allan *et al.*, 2003). We chose to collect infall samples over a relatively short 24 h period to avoid disturbance from regular motor boat traffic since we were concerned about our pan traps getting swamped.

Drift of terrestrial invertebrates was highly variable by date and year, and we found few consistent or discernible patterns within two years of sampling. Both summers we saw an early season peak in terrestrial and aquatic invertebrate drift which may have been related to invertebrate life cycles or thermal mechanisms such as a number of degree days, water, and air temperature (Mason & Macdonald, 1982; Brittain & Eikeland, 1988). Terrestrial invertebrates composed approximately 24% of the total drift for both years. Yet, on occasion, the mean mass of terrestrial invertebrate drift nearly equaled the mean mass of aquatic invertebrate drift. The relative proportion of terrestrial invertebrate drift was comparable to other studies conducted in temperate streams which showed similar trends that at times terrestrial invertebrates contributed as high or greater mass to the drift than aquatic invertebrates (Cloe & Garman, 1996; Romaniszyn *et al.*, 2007). In temperate zones, terrestrial invertebrate drift is known to peak in availability during the summer (Cloe & Garman, 1996; Bridcut, 2000).

Terrestrial invertebrates as prey for juvenile Chinook

The quantity of terrestrial invertebrates in the diet of juvenile Chinook varied throughout the summer, with a mean of $19 \pm 3\%$ terrestrial invertebrate mass

consumed in both summers combined. Late in the summer, terrestrial invertebrates comprised up to 38% of the total diet on several dates. In small streams, juvenile salmonid diet has been found to consist of up to 50%-72% terrestrial invertebrates of the prey mass consumed (Wipfli, 1997; Nakano *et al.*, 1999b; Eberle, 2007). Although the highest proportion of terrestrial invertebrates consumed was lower in the Chena than in many smaller streams, the reality that terrestrial invertebrates contributed up to 39% of the total juvenile Chinook diet is notable because of the magnitude and since few studies have examined the importance of terrestrial invertebrates for juvenile fish in mid-size or large rivers (Baxter *et al.*, 2005; Paetzold *et al.*, 2008).

Juvenile Chinook consumed more terrestrial invertebrates towards the end of the summer season. Higher consumption of terrestrial invertebrates has been observed in late summer and fall in Oregon, West Virginia, Kamchatka, and Idaho (Romero *et al.*, 2005; Webster & Hartman, 2005; Eberle & Stanford, 2010; Rosenberger *et al.*, 2011). The increase in terrestrial invertebrate consumption in the Chena may have been due to decreased aquatic invertebrate availability in 2008 since the increase in terrestrial invertebrate consumption coincided with an overall decrease in drifting aquatic invertebrate mass. However, we did not see this pattern in 2009 where a late summer increase in terrestrial invertebrate consumption occurred, even though a decrease in drifting aquatic invertebrate mass was not observed. The increase in terrestrial invertebrate consumption could also be due to increased gape size of the fish with summer growth and, therefore, a greater ability to capture large forms of prey such as terrestrial invertebrates (Elliott, 1994). Terrestrial invertebrates are recognized to be a larger and higher energy food source than aquatic invertebrates, and drift feeding fish are known to preferentially select large prey (Edwards & Huryn, 1996; Nakano *et al.*, 1999b). An increase in terrestrial invertebrate consumption could be important bioenergetically as summer is when fish store fat and increase body size, which is important for overwinter survival (Reimers, 1963; Mason, 1976). Larger body length and rapid growth in juvenile salmonids have been found to increase overwinter survival and most likely lead to increased marine survival (Quinn & Peterson, 1996; Ruggerone *et al.*, 2009). Thus, terrestrial prey may provide an important energy subsidy at a critical stage for survival.

The terrestrial invertebrates that were important prey items for juvenile Chinook in the Chena River were adult Hymenoptera, Araneae, and aphids (Hemiptera). An outbreak of aphids in 2009 (Gutierrez, personal observation) was reflected in the infall traps, the drift, and in the diet, suggesting that juvenile Chinook can capitalize and respond to incidents of high abundances of terrestrial invertebrates. Still, the main staple of the juvenile Chinook diet were chironomids in all their life stages. A study investigating the diet of juvenile Chinook smolts in a nearby Alaskan river (the Salcha River) reported finding that chironomids were the main prey item consumed early in the season as well (Loftus & Lenon, 1977).

Relationship between invertebrate infall, drift, and predation by fishes

The composition of invertebrate taxa in the infall and drift did not match well with the composition of prey consumed by juvenile Chinook salmon. The mean percent dissimilarity between drift and diet, and infall and diet was 74% and 75%, respectively, suggesting that neither sampling method collected invertebrates that overlapped completely with the juvenile Chinook diet. This makes sense as infall samples primarily catch terrestrial and winged adult aquatic invertebrates, while drift samples theoretically mimic what invertebrates are drifting in the river, but may be excluding terrestrial invertebrates floating on the water surface and may be composed of invertebrates post fish-selection (i.e. the fish already consumed invertebrates out of the drift). However, the ordination comparing only terrestrial invertebrates showed a higher overlap between invertebrates in the drift and diet rather than invertebrates in the infall. This suggests that terrestrial invertebrates in the juvenile Chinook diet were more closely related in quantity and composition to terrestrial invertebrates in the drift than those captured by the pan traps.

SIMPER analysis of all invertebrates consumed determined that adult chironomids and hymenopterans were the taxa that had the most dissimilar proportions between diet to drift and diet to infall. In the diet to drift comparison for both 2008 and 2009, juvenile Chinook consumed a greater proportion of chironomids and hymenopterans than were in the drift implying selectivity for these taxa and that these taxa might have been consumed before entering the drift. These results support our findings from the IRI analysis which showed that chironomids and hymenopterans were in the top six most important taxa consumed by juvenile Chinook in both years. Our SIMPER results comparing diet to infall showed a larger proportion of chironomids in the infall samples than the proportion consumed which suggests that juvenile Chinook consumed adult chironomids at a lower proportion than was falling in, although this difference could be an artifact of the sampling method. Pan traps may collect higher proportions of certain taxa such as winged Diptera and thus might suggest a higher availability in the environment than is actually there (Edwards & Huryn, 1995; Wipfli, 1997). Another possible bias in a comparison between a predator and its potential prey is that the comparison assumes that the collection methods are spatially and temporally compatible. By site and date, the drift nets were set out at different distances from the riverbank depending on woody debris presence and river discharge, e.g. when discharge was high we anchored the drift nets closer into the bank due to water velocity being too fast where we had previously placed the drift nets at lower discharge. Yet, the infall traps were consistently set out at the same distance from the bank over the course of the study. Indirectly, the constantly changing distance of the drift nets may have better mimicked the opportunistic foraging habits of juvenile fish.

Our SIMPER analysis of only terrestrial invertebrates consumed placed Hymenoptera as the taxa that had the most dissimilar abundance between diet to drift and diet to infall. By IRI, the importance of Hymenoptera was rated 6th out of the top 10 most important taxa for both 2008 and 2009. Several diet studies have recently documented one or two species of terrestrial invertebrates as being particularly important for the diet of fish in their region. Studies in West Virginia streams noted the importance by

mass of adult terrestrial Lepidoptera in the diet of brook trout (Webster & Hartman, 2005; Utz & Hartman, 2007), as well as the Coleopteran family Scarabaeidae by bioenergetic estimates (Utz *et al.*, 2007). In California during March through July, terrestrial Isopoda was identified as the taxa with the highest proportion mass in the diet of juvenile steelhead trout (Rundio & Lindley, 2008). In our study, we documented through the measure of mass, as well as IRI and SIMPER analysis, that adult hymenopterans are one of the most important terrestrial invertebrate prey items for juvenile Chinook salmon in the Chena River.

Effects of discharge and stream temperature on predation by juvenile Chinook

Stream temperature and discharge had variable influences on juvenile Chinook predation. Total mass consumed by juvenile Chinook was not correlated with river discharge in 2008, but was negatively correlated in 2009 and both years combined. A negative correlation between total mass consumed and discharge indicates that, at high discharge, fish are consuming a lower mass of invertebrates, and vice versa. Yet, high discharge also increases the availability of benthic and aquatic invertebrates, which may result in more prey available to fish (O' Brian & Showalter, 1993; Romaniszyn *et al.*, 2007). High discharge, however, may pass threshold levels at which physical factors begin to scour the stream bed causing a delayed decrease in aquatic invertebrate availability and taxonomic richness, as well as a decrease in prey consumption (Scrimgeour & Winterbourn, 1989; Quinn & Hickey, 1990; Perry *et al.*, 2003). In addition, high discharge can cause increased turbidity, and high turbidity has been shown to reduce fish's consumption of available prey (Berg *et al.*, 1985). In the Chena River, spates of high discharge may have caused a temporary decrease in aquatic invertebrate availability and reduced juvenile Chinook's ability to detect and capture prey leading to our result of a negative correlation between total mass consumed and discharge.

Particularly high discharge and flood events may increase terrestrial invertebrate infall by increasing the wetted perimeter of a riverbank and sweeping terrestrial invertebrates into the river by overland flow (Layzer *et al.*, 1989; Edwards & Huryn, 1995). Although we found no significant correlation between the proportion of terrestrial invertebrates consumed and discharge, our study found that the two sampling dates with the highest proportion of terrestrial invertebrates consumed by juvenile Chinook occurred after a late summer 60-year flood in 2008. A possible explanation for this is that a high discharge threshold was reached, and the flood may have scoured the streambed, decreasing the amount of aquatic invertebrates, which may have caused the juvenile Chinook to switch to terrestrial prey. Several studies suggested that fish may switch to terrestrial invertebrates when aquatic invertebrate abundance or mass are low (Cloe & Garman, 1996; Nakano & Murakami, 2001; Romero *et al.*, 2005). A comparison between terrestrial invertebrate availability in both summers reveals that the mass of terrestrial infall and the proportion of terrestrial invertebrates in the drift were higher in 2009 than in 2008. Thus, availability was higher in 2009 than in 2008, but a greater mass of terrestrial invertebrates was consumed in 2008. One potential explanation is that the 60-year

flood in 2008 may have caused an increase in the yearly mean of terrestrial invertebrates consumed. This is circumstantial evidence as we were not able to sample diet, infall, or drift during the flood since the discharge was too high for sampling. However, this indicates that terrestrial invertebrates may not only be more important later in the summer, but also after high discharge events.

We also evaluated stream temperature as a possible factor of how important terrestrial invertebrates are to juvenile Chinook, as fish are known to have higher metabolic needs and consume greater amounts as temperature increases (Elliott, 1994). Our results support this: we found a positive correlation between water temperature and mean mass consumed for 2008 and 2009, and for both years combined. However, when we examined the relationship between proportion of terrestrial invertebrates consumed and water temperature, we found no significant correlation in each individual year and a negative correlation for both years combined. Our results also showed a strong negative correlation between river discharge and water temperature. The negative correlation between terrestrial invertebrates consumed and water temperature may have been driven by the inverse relationship between water temperature and discharge. When water temperature dropped due to periods of high discharge, the scouring of the stream bed may have led to a decrease in aquatic invertebrate abundance and therefore an increase in the proportion of terrestrial invertebrates consumed.

Conclusions

Terrestrial infall, drift, and predation by juvenile Chinook in the Chena River were highly variable by date and by season. The diet of age-0+ juvenile Chinook salmon was primarily made up by aquatic invertebrates, largely all life stages of chironomids. Adult hymenopterans were the most important terrestrial prey for juvenile Chinook, which also capitalized in 2009 on an increased availability of aphids. This illustrates the link between riparian forests, the invertebrates they support, and the flow of terrestrial prey into rivers that subsidizes the prey base for aquatic consumers, in this case, fish. Terrestrial invertebrate consumption by juvenile Chinook in the Chena River should not be discounted as the percent of prey mass consumed reached up to 38% on three different sampling dates. Our study indicates that both aquatic and terrestrial invertebrates are important prey resources for juvenile Chinook salmon in the Chena River, with terrestrial prey ingestion increasing through the summer and potentially after periods of high discharge. As terrestrial prey subsidies can be a key food source for stream fish, it is important to understand what may drive the variability of terrestrial infall, drift, and consumption by fish.

III. Chinook growth modeling, abundance, density dependence. [This information has been compiled into two manuscripts submitted as companion papers to *Transactions of the American Fisheries Society* in summer 2013]

Fish condition

Fish condition at sites that received supplemental food wasn't significantly different from control sites in this study. This did not support our hypothesis that fish at supplemental sites would have a better Fulton's condition factor, K , than fish at control sites. This result suggests that juvenile Chinook salmon did not experience density dependent interactions, and it did not appear that they were food limited, at least during 2009. We did not see population level effects occurring either, or population level effects explaining the null effect on individual growth.

Density dependence and abundance estimates

The homogeneity we observed in individual growth did not suggest density dependent interactions were occurring. Alternatively, we may have been able to infer density dependent interactions if populations at control sites decreased throughout the summer and remained stable at supplemental food sites. However, our ability to make such an inference was compromised by our inability to estimate abundance at many of the sites. Over the course of the summer, many of our sites likely experienced recruitment, but we were not able to estimate abundance at our upstream sites due to low capture and recapture numbers, which in addition to low population size, may have occurred because of inefficient closure of the site over the three day sampling event. At our downstream sites, population abundance was similar across all months, except for substantial recruitment at the DS2 site between July and August.

Although we were able to satisfy the closure assumption and estimate population abundances over a 3-day period at three of our downstream sites, there was evidence of the population being open over a longer time period. We documented a few instances of Chinook salmon migrating between sites. We observed migrations of tagged fish in both upstream and downstream directions, but our sample size was small ($N=6$). However, because sampling design did not sample outside of research sites, we have no data as to the scale or frequency of movements. Conversely, we also had evidence of site fidelity by a few marked fish in nearly all sites, both in fed and unfed treatments over the course of the three sampling periods.

Seasonal fluctuations in both the supply of food and the availability of space for feeding during the first summer interact to determine the productivity of stream reaches (Nislow et al. 2000). The DS2 site, which had a relatively high density of juvenile Chinook salmon and experienced significant recruitment between June and July, was located at the outside edge of a meander bend. It had apparent low velocity, and large amounts of birch woody debris buildup throughout its depths. A study by Beechie et al. (2005) looked at habitat types and their use by juvenile salmonids in large rivers, and found that Chinook and coho salmon were most abundant in channel margins, where velocities were low and cover more abundant. We had a site with similar characteristics as DS2 during the 2008 field season, with lower velocities and substantial woody debris, just off of the main channel. Both of these sites proved to be 'super sites' with the highest fish presence of all sites throughout the season. However, during a large flooding event in 2008, the debris jam was reorganized, and

flows appeared to be modified through the site. We monitored this site throughout the 2009 season again. Though the habitat structure was still similar, flows appeared different, though they were never quantified. The site was no longer supporting large populations of juvenile salmon. We captured and observed between 13 and 17 fish during sampling events in June, July, in August (Site US2) during 2009. During the 2008 season, we consistently saw large numbers of fish at this site, and on one occasion where we attempted enumerations, visually observed over 120 fish. In addition to considering food availability in the abundance and growth of juvenile Chinook salmon, habitat availability may prove an interesting area for further research.

The mass frequency distributions of fish at all sites and sampling events were nearly normally distributed, and did not indicate inequalities. This method of looking at competition has proved effective in other studies, particularly in work conducted by Mason (1976) and Keeley (2001). Mason tested whether food or space set the limitation on juvenile coho production in streams, especially in the summer months. The results of Mason's study indicated that food was the limiting factor of juvenile coho salmon productivity. Mason experimentally manipulated the density of coho/m² in 6 stream reaches from 1-9 fish/m², and then supplemented food to some of the sections. By increasing food availability, Mason (1976) was able to increase fish densities to 6 -7 times above naturally occurring densities. Supplemental food also normalized the length frequency distributions of the fish. The initial stocking density of coho had a slight right skew, the final size distribution of coho in the unsupplemented site had a strong right skew, which is indicative of competition, whereas the final size distribution in the site receiving supplemental food had normal size distribution. Skew in the distributions suggests inequitable distribution of food through interference competition. Considering figures 17 and 18, most of our data has a slight right skew or a normal distribution, however, analysis of the Gini coefficient suggests similar inequalities in all sites, and the skew is not isolated to one treatment type. The relative normality of our distributions is likely because the fish were not experiencing competition for food. The sites were likely below saturation levels due to territory size, because of presumed high quality available habitat along the length of the river, and sufficient food abundance throughout the river.

Keeley (2001) showed how density dependence regulates population size in steelhead trout, through mortality, growth and emigration by experimentally manipulating food availability, density, and the possibility of emigration as well. Across treatments, fish size increased with increased food abundance, and decreased with increased stocking density. Density dependence operated by reducing growth and increasing mortality as a population reached carrying capacity. In treatments allowed to emigrate, inequalities in growth and mortality continued to regulate population size, but there was a reduction in their effects. The results of Keeley's work found that while both food and space are important factors in shaping the demography of stream salmonid populations, that neither appeared to limit salmonid abundance exclusively. Within our experiment, had competition for food been occurring to the level to cause density dependent effects, we believe we would have detected it.

While anecdotal, we did observe different trends during summer 2009 than in summer 2008. During the 2008 field season, we did observe a greater abundance of fish at food-supplemented sites during some of our trial feeding runs that appeared to remain at the sites, where declines were observed at un-supplemented sites. Also, the number of fish at all sites was higher. However, during our 2007 pilot and 2008 season we tested fish enumeration methods that required no fish handling (snorkel surveys, grid point sampling and line transects utilizing underwater videography, and visual counts), but were unable to get estimates of abundance that could be used to compare between the two years.

In addition to the appearance of lower numbers of juveniles in 2009, the salmon run of 2008 was lower than the previous year (Brase 2011), and there was also a 60-yr flood two weeks after the peak spawning, causing major scouring of the river bed, both of which could contribute to the numbers of juveniles rearing in the Chena River to be less in 2009 than 2008 (Lapointe et al. 1999). If the numbers of fish rearing in the Chena River is low, there would be less likelihood for resource limitation to have a measurable effect on their growth.

Other possible reason that we may not have seen effects of supplemental feeding during the summer, may be speculated upon drawing from other research conducted in the Chena River during 2009. In addition to there likely being a lower number or recruits due to lower spawners over the previous year, there may have been increased amount of food available to the rearing juveniles over the previous summer (this report). Using study sites within the same upstream and downstream reaches as our study, student Gutierrez measured invertebrate infall (adult aquatic and terrestrial invertebrates), prey sources for juvenile salmon, using floating pan traps, and also measured drift (section II, this report). Invertebrate infall differed between the two years. In 2008, the mean terrestrial infall was $17 \pm 5 \text{ mg dry mass m}^{-2}\text{d}^{-1}$ and in 2009 the mean terrestrial infall was higher, $33 \pm 8 \text{ mg dry mass m}^{-2}\text{d}^{-1}$. Drift was slightly different between the two years, in 2008, the mean total drifting invertebrate dry mass was $0.6 \pm 0.2 \text{ mg m}^{-3}$ and in 2009, the mean total dry mass was $0.5 \pm 0.04 \text{ mg m}^{-3}$. Gutierrez found that there was greater infall in 2009 than in 2008, but slightly greater drift in 2008 than in 2009, however, neither of these results were significant. The combination of lower spawner abundance, leading to less recruits, and slight increases in food availability from terrestrial infall are both factors that likely contributed to not observing density dependent interactions during the 2009 field season.

The synthesis of our results lead us to reject the hypotheses that Chinook salmon in the Chena River exhibit density dependent interactions due to competition for food resources. During summer 2009, juvenile Chinook salmon likely were not experiencing food limitation. However, this is likely due to interannual variability of many factors, including habitat, spawner abundance, and food availability, occurring within the river, topics which deserves further observation and study, as evidence of limitation was present, but not substantiated during the 2008 field season.

Bioenergetics and growth modeling

Our primary goal in this study was to investigate if temperature or food availability was the primary factor limiting growth of juvenile Chinook salmon in the Chena River. Density-dependence is often assumed the most important biological mechanism for both individual fish condition and overall production of fish populations; a thermal limitation to growth would instead imply that food and space were readily available to juvenile fish and other, density-independent factors may be more important in limiting juvenile production. A bioenergetics model (Rasmussen and From 1991) assuming maximum wild rations worked well to predict growth of juvenile Chinook salmon in 2009 (Figure 1). Only in 1980 and 1981 (Walker 1983) were observed lengths less than predicted by the bioenergetics model (Table 1); for all other years of data, the predicted length was greater (i.e. 1996, 2009) or within 2 standard errors of observed length (i.e. 2007, 2008). Walker (1983) noted in his thesis that the 1980 and 1981 escapements of Chinook salmon in the Chena River were the highest in recent years (Fred Anderson, ADF&G, pers. comm.) and stated that those high escapements probably resulted in high densities of juvenile Chinook salmon the following year. Unfortunately, mark-recapture and counting tower estimates of escapements of adult salmon on the Chena River were not initiated until 1986, so we do not have a metric to compare the runs in 1980 and 1981. Conversely, the runs in 2006-2008 were three of the lowest seven escapements since run estimates have been made, and, in the rearing years following the 2006-2008 escapements (2007-2009), the bioenergetics model effectively predicted growth (i.e. 2007-2008) or underestimated growth (i.e. 2009) on maximum wild rations, which suggests that density-dependent interactions were not occurring. In 1981 and 1982, our bioenergetics model predicted growth only when reduced rather than maximum rations were assumed (Table 2). This implies potential for food limitation in the Chena River, but only during high-escapement periods, though it does not preclude the importance of other density-dependent factors such as space and feeding territory. Our results imply temporal dynamics in the importance of density-dependent processes; in years when Chinook salmon runs were average or low, density-independent factors (e.g., floods during spawning or scouring spring flows) may have overwhelmed the potential for density-dependence, and juvenile Chinook salmon growth was limited only by river temperature.

Observed growth of individual fish along the Chena River was not uniform due to spatial variability in thermal regimes along the Chena River, both at the reach scale (e.g., upstream versus downstream reaches) and at the site scale (e.g., sites within an upstream or downstream reach). Because of this, temperature influences on average length of a cohort at outmigration may be better predicted and inferred at whole-reach scales (Walker 1983; Gutierrez 2011). Further, interannual variability in temperatures and density-dependent processes implies predictions are most valid if made on a cohort-by-cohort basis, factoring in run size, thermal conditions, and the length of the growing season. However, if investigating spatial variability in growth potential within a single cohort is the focus of the study, a full thermal profile of the

river will be required; very subtle differences in thermal regimes resulted in differential observed growth among river locations.

Our secondary goal in this study was to examine if there was a positive relationship between predicted growth of juvenile Chinook salmon during their freshwater period and the productivity of a brood year in terms of recruits per spawner. Our study did not detect such a relationship; however, this may be due to our assumption of maximum potential growth (i.e., no food limitation) for estimating fish length. A limitation in testing our bioenergetics model is its low sample size – data for actual end of season lengths were available for only 5 years. Further, our ability to validate our model was only for those years of low escapement ($n=3$), when food limitation was unlikely. A bioenergetics model that modifies ration based on escapement size would be possible if additional data were available; we recommend sampling juvenile Chinook salmon at the end of the first summer rearing season to determine average cohort length. A long-term data set of this kind would be relatively inexpensive to obtain and would allow for an effective test of whether juvenile length at the end of the first growing season significantly affects overall marine survival on a cohort-by-cohort basis. This is certainly not a given; some years of high escapement in the Chena River have been followed by high returns, which indicates that, even if density-dependent interactions are negatively affecting overall growth of juvenile Chinook salmon in freshwater, this does not, in turn, negatively affect their marine survival. Research suggests that it is in the marine life stage that population-level controls take place, which limits our potential to make marine survival predictions based on individual traits during their freshwater phase (Beamish and Mahnken 2001).

In a dynamic system like the Chena River, we anticipate but do not always account for variability in ecological processes that regulate the demographic characteristics and abundance of juvenile salmon. Numerous and highly dynamic processes over a large area (i.e., oceanic conditions, weather, flooding, adult returns, habitat quality, and food availability) make this task difficult. This is certainly the case for our study; we were unable to observe consistent evidence of either density-independent or density-dependent processes on freshwater growth of juveniles. However, our bioenergetics model showed potential for testing the assumption of density-dependence on a cohort-by-cohort basis, a powerful tool for predicting and understanding demographic processes within the Chena River population and beyond.

IV. Foraging analyses, mechanisms of competition, and recruitment. [These data comprise four manuscripts, two submitted to journals in May 2013 and two in summer 2013.]

Video methods

The video technology we developed was essential to our discoveries about juvenile Chinook salmon foraging behavior and competition. It allows us to observe behavior

in more detail, and more accurately, than previous video methods, and we can measure data much faster, therefore measuring a much larger quantity of this type of data than has been possible before.

These video methods offer some general advantages for the study of fish behavior, and for the accurate remote measurement of basic quantities like length in fish that are too sensitive (e.g., endangered Devil's Hole Pupfish) or too inaccessible (e.g., deep sea) to capture and measure manually. Most behavioral studies on salmonids are based on a single observer's real-time interpretation of fleeting events, usually concerning a single focal individual and its actions. Video creates a reviewable record so others can verify behavioral interpretations, and so an observer can review events repeatedly (and in slow motion) to clarify the outcome. This capability was critical to our analysis of foraging attempt outcomes in relation to debris. Video also makes it possible to measure the simultaneous behavior of dozens of individuals, providing information on their interactions as a group that would not be available from observing one animal at a time. This is critical to our study of competition, in which the competitive environment for each fish must take into account depletion of food by all upstream fish simultaneously.

Our primary contribution is to make the advantages of video more available for behavioral studies by making the measurement process much faster, easier, and more practical. There was previously no software to enable the sort of efficient 3-D measurement and data annotation and organization required for a study like ours, and for many similar behavior studies. Our methods and software are already being used separately by colleagues in New Zealand, the Seychelles, and Argentina, with others expressing interest.

Effect of drifting detritus

Only about 9% of prey capture attempts by juvenile Chinook salmon in the Chena appear to lead to ingestion. Of the items fish captured in their mouths, 85% were subsequently expelled. This number is far higher than what any previous study has measured. Biro et al. (1996) and McLaughlin et al. (2000) measured the same statistic for juvenile brook trout in still water, and found, respectively, that 7% and 20% of items captured subsurface were spit out. Our study is the first to examine the question in flowing water – an advance made possible by our video technology developments. It makes sense that we observed far more items spit out in flowing water, because there is more suspended debris, and the fish have less time to inspect each item visually before capturing it.

Both previous studies were concerned mainly with the use of foraging attempt rate as a proxy for energy gain and fitness. Like them, our study backs the conclusion that foraging attempt rate is a questionable proxy for fitness because attempt rate does not necessarily predict ingestion rate. Our study is the first to also consider the opportunity cost of being distracted by debris while other potential food drifts by. Higher levels of debris should decrease the optimal water velocity for drift-feeding,

increase the minimum size of prey in the diet, and decrease overall prey capture rate. Debris may also lessen the effects of competition, because the upstream fish in a group will miss some food that passes by them, creating opportunities for downstream individuals. This could help explain why these fish feed in schools.

Overall, our study suggests that drifting debris is a “new” environmental variable with as much potential importance to juvenile Chinook salmon as other factors like flow, turbidity, and substrate. This is likely to hold true for juvenile salmonids and other drift-feeding fish in moving water in general. The importance of the effect depends on the amount of debris of the same size as the fish’s prey, making it particularly relevant to juvenile salmonids during the very early life stages when density dependent competition is most likely to create a competitive bottleneck for the population size.

Territoriality and the mechanisms of competition

Based on our preliminary analysis and qualitative examination of remaining video data, we can conclude that juvenile Chinook salmon are often territorial. We have also observed that they are overwhelmingly found in schools in or around complex large woody debris, probably in response to the threat of avian predation. While territoriality is very common in salmonids, it has not been previously recorded on a fine spatial scale comparable to the short distances between fish in these schools. This juxtaposition of two behaviors often treated as polar opposites – territoriality and schooling – is apparently new to the study of ecology, as is the examination of 3-D territoriality in general. Our ongoing work to understand this territorial behavior, as well as its relationship to food and drifting debris abundance, should shed light on the mechanisms by which food abundance may limit population size and contribute to density dependence.

Stock-recruitment analysis

We found an exceptionally strong relationship between juvenile Chinook salmon recruitment and median stream discharge. This relationship was strongest when discharge was considered over the full summer growing season (May through September), not in any critical periods. There were no strong relationships with variables associated with single catastrophic floods, except for marginally significant evidence that the largest floods do some damage to eggs still in the redds. In a nutshell, recruitment is high when juveniles are rearing in generally low to average discharge years, and recruitment is poorer when the juveniles experience extended periods of high water.

That this effect is strongest when considered across the whole summer and that no acute flood effects on juveniles were evident both suggest that the mechanism behind the strong discharge effect involves basal productivity and foraging conditions. The primary productivity and fish prey (invertebrate) abundance elements of this study both indicated that the Chena was most productive at low to medium discharges, and

the fish behavioral components showed that fine debris in the water (correlated with discharge) should reduce fish energy intake. Consistent with this observation, the diet samples also showed reduced foraging success at high flows.

General conclusions and observations

Our anecdotal observations during four summers in the field have clarified some important aspects of juvenile Chinook ecology that were not a part of individual study components.

First, large, complex woody debris is extremely important habitat. As numerous other studies have noted, particularly in coastal rivers of the Pacific Northwest, large woody debris is important as a refuge from predators, a substrate for food production, a mechanism for pool formation, and a buffer to create low-velocity flow refuges for feeding in food-rich fast-water environments. In the Chena, the overwhelming majority of juvenile Chinook salmon were found with areas where large woody debris held many pieces of more complex, small woody debris in place, and they retreat to this wood as cover when spooked. Good areas include large logjams, large rootwads, and areas along the bank where large trees have fallen across the stream as “sweepers.” A large logjam may support thousands of juvenile Chinook salmon throughout the summer. There seem to be relatively fewer fish around small rootwads and sweepers in the stretches of river that have such logjams, perhaps suggesting a preference for the logjams. However, some reaches (such as downstream of river km 90) contain no large logjams, and the fish there associate more with complexes of sweepers. It is not clear whether logjams contribute to producing more fish, or simply concentrate the production into a smaller area. However, we found very few fish in areas lacking both types of cover, and we think it is likely that Chinook production would suffer if any future action reduced the river’s capacity to produce and retain large and complex wood.

This finding raises some concern about the removal of large wood from the river at the Moose Creek Dam after large floods. During our systematic abundance survey in our pilot field season in 2007, we found much lower densities of fish at sites below the dam than above it. This may be caused by the lower density of large wood in the river, although other potential causes such as food, predation, and spawning habitat may also prevent substantial production from that reach. It would be worthwhile for future studies to investigate the potential for increased production in the lower reach if more wood were allowed to pass the dam (for example, by pushing it back into the river during medium-high water events, rather than trucking it away).

Second, we observed that the population of juveniles declines noticeably from June into September, with the sharpest drop in abundance from mid June to early July. This suggests that competitive bottlenecks may be acting on the juvenile population, and density dependent processes are most likely to be influential during the first few weeks after emergence. The fish become exceptionally hard to find in late September, but they are still captured in minnow traps, suggesting that their behavior changes

dramatically as winter approaches and they no longer use the same habitat in the same way.

Finally, fish densities and prey abundances varied substantially between years, suggesting that what may be limiting one year may be different than the next. During summer 2009, juvenile Chinook salmon likely were not experiencing food limitation. However, this is likely due to interannual variability of many factors, including habitat, spawner abundance, and food availability, occurring within the river, topics which deserves further observation and study, as evidence of limitation was present, but not substantiated during the 2008 field season.

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DELIVERABLES:

Website: <http://www.chenakings.org/>

Annual progress reports: Submitted to ADF&G every year of project.

Theses:

Benson, E.R. 2010. Environmental variation and whole stream metabolism in an interior Alaska river. Masters thesis, University of Alaska Fairbanks.

Gutierrez, L. 2011. Terrestrial invertebrate prey for juvenile Chinook salmon: Abundance and environmental controls in an interior Alaska River. Masters thesis, University of Alaska Fairbanks.

Perry, M.T. 2012. Growth of juvenile Chinook salmon (*Onchorhynchus tshawytscha*) as an indicator of density-dependence in the Chena River. Masters thesis, University of Alaska Fairbanks.

Dissertation:

Neuswanger, J.N. 2014. Using new 3-D video methods to investigate roles of debris and territoriality in the foraging behavior and recruitment of juvenile Chinook salmon. Ph.D. Dissertation, University of Alaska Fairbanks.

Presentations:

Perry, M.T., M.S. Wipfli, N.F. Hughes, J.R. Neuswanger, A.E. Rosenberger, and M.J. Evenson. 2012. Retrospective analysis of juvenile Chinook salmon in an Interior Alaska River: Insight into marine survival and density dependence. Alaska Chapter American Fisheries Society Annual Meeting, Kodiak, AK, 21-26 Oct.

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a subdrainage of the Yukon River, Alaska. North American Benthological Society annual meeting, Grand Rapids, MI, 17-22 May.

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Gutierrez, L., M.S. Wipfli, A.L. Blanchard, N.F. Hughes, and E.C. Green. Terrestrial invertebrate prey for juvenile Chinook salmon: Abundance and environmental controls in an interior Alaska River. In revision for *Freshwater Biology*.

Neuswanger J., M.S. Wipfli, A.E. Rosenberger, N.F. Hughes. Measuring fish and their habitats: Versatile 2-D and 3-D video techniques with user-friendly software. Submitted to the *Canadian Journal of Fisheries and Aquatic Sciences*.

Neuswanger J., M.S. Wipfli, A.E. Rosenberger, N.F. Hughes. 2014. Mechanisms of drift-feeding behavior in juvenile Chinook salmon and the role of inedible debris in a clear water Alaskan stream. *Environmental Biology of Fishes*. In press.

Perry, M.T., M.S. Wipfli, N.F. Hughes, J.R. Neuswanger, A.E. Rosenberger, M.J. Evenson. Response to *in-situ* supplemental feeding of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Chena River, Alaska. Submitted to *Transactions of the American Fisheries Society*.

Perry, M.T., M.S. Wipfli, N.F. Hughes, J.R. Neuswanger, A.E. Rosenberger, M.J. Evenson. Restrospective analysis of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in an Interior Alaska River; Insight into marine survival and density dependence. Submitted to *Transactions of the American Fisheries Society*.

Two more Neuswanger et al. manuscripts to be submitted summer 2014.

PROJECT DATA SUMMARY:

We collected several types of data on the primary productivity and benthic invertebrate biomass of the Chena River in relation to flow, including nutrient concentrations, primary production, stream metabolism, and benthic macroinvertebrates, all stored in Microsoft Excel files.

We collected a detailed database of invertebrate prey availability, including both drifting invertebrates and terrestrial invertebrate infall. Most specimens were identified to family or order level. Data were collected approximately bi-weekly throughout 2008 and 2009. These data were all compiled together in a Microsoft Access database with detailed metadata on collection methods.

Data on fish diets, abundance, and length frequencies were also collected bi-weekly or monthly through 2008 and 2009, and are stored in Excel.

Video data of fish feeding behavior were collected from 2008 to 2010 and stored in original form as disk images of the camera hard drives, as well as in compressed Quicktime movie format (H264 codec) for viewing and analysis. These data are hundreds of gigabytes in size and cannot currently be practically posted online. Specific behavioral analyses of several videos are stored in the .VSC file format of the open source VidSync software we developed (<http://vidsync.sourceforge.net>), making these analyses repeatable and extensible.

Stock-recruitment data from the Alaska Department of Fish and Game were not collected specifically for this project, but were used for some analyses.

Data are kept by Dr. Mark Wipfli, Institute of Arctic Biology, University of Alaska, Fairbanks. 907-388-9544, mwipfli@alaska.edu

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PRESS RELEASE:

Scientists at the University of Alaska Fairbanks, in collaboration with the Alaska Department of Fish and Game, recently completed a multi-year study on the ecology of the Chena River Chinook salmon, aiming to understand how freshwater forces potentially contribute to Chinook salmon population fluctuations. The work was funded by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative, to investigate a well-known salmon population with weak recent runs similar to many other Alaska rivers. Previous research has shown that salmon returns often depend on what happens to the young fry during the first few months after they emerge from eggs in the spawning gravel. Therefore, the researchers studied young juvenile Chinook salmon in the Chena River as they grew from one to three inches long during their first summer of life, prior to migrating out to the Bering Sea the following spring. They found several links between

river conditions and the growth and survival of juvenile Chinook salmon. Their data suggest that the recent decline in the Chena River Chinook salmon run may be, in part, reliant on climate variability.

The researchers began work in 2007 to establish that the main habitat for juvenile Chinook salmon in the Chena stretches from the Moose Creek Flood Control Dam up to the intersection of the North and Middle Forks of the Chena near “third bridge” on Chena Hot Springs Road. The researchers collected juvenile salmon, which were released unharmed, for stomach samples and weight measurements, and collected other data on fish size and feeding behavior without touching the fish, using 3-dimensional video measurement techniques they pioneered for this study. They also collected a variety of data on the abundance of both aquatic and terrestrial invertebrates, which the fish eat, and the chemistry of the river’s ability to produce food for those invertebrates – the base of the food chain.

The researchers also analyzed population data from the Alaska Department of Fish and Game, comparing it to the USGS record of water levels in the Chena River at Two Rivers. This comparison showed that Chinook salmon fared much better when the summer they spent in freshwater in the Chena had low to medium stream flow instead of consistently high flow. The data suggested that juvenile salmon are resilient to the effects of occasional major floods, even in their earliest weeks, but the population suffers when moderately high water persists for long periods of time throughout the summer.

The data these researchers collected on juvenile Chinook salmon and their prey suggest that prolonged periods of high water could negatively affect Chinook returns. The food web productivity of the river—its ability to produce food for the invertebrates the fish eat—declined sharply at above-average stream flows, possibly as a result of less light reaching the stream bottom due to increased depth and turbidity. This may mean there is less food in the river overall during years with prolonged periods of high water. High water also increased the amount of debris in the river, which the researchers showed distracts the attention of feeding fish and reduces their ability to detect actual prey. This behavioral observation was corroborated by stomach samples showing that the fish ate less food during periods of high water.

Overall, the research showed that high stream flows negatively affect both the river’s production of food and the ability of the fish to capture food. This result probably explains why the population data shows that the Chena River Chinook salmon population does when the juveniles experience low to medium flow in the river during their first summer. This natural variation may also provide evidence why this population has declined recently – the Chena has experienced an unusual number of high flow years over the past decade. The trend and ecological factors this study highlighted for the Chena are now being investigated in various ways for other streams throughout Alaska, to see whether the Chena results may help explain the broader negative trend in Chinook salmon populations.

TABLES AND FIGURES:
(following pages)

Table 1. Sample statistics for length and weight analyses from Chena River sites, summer 2009.

Site	Sampling Event	n	Fork length (mm)	Weight (g)		Fulton's K	
			Mean (SE)	Mean (SE)		Mean (SE)	
US1	July	13	53.3 (1.1)	1.5 (0.1)		1.00	(0.02)
	August	44	70.9 (0.7)	3.5 (0.1)		0.97	(0.02)
	September	48	77.8 (0.7)	5.0 (0.1)		1.05	(0.01)
US2	July	17	53.6 (1.1)	1.6 (0.1)		0.99	(0.03)
	August	13	71.8 (1.6)	3.7 (0.3)		0.98	(0.02)
	September	16	81.5 (1.0)	5.4 (0.2)		0.99	(0.03)
US3	July	7	56.0 (2.8)	1.9 (0.3)		1.00	(0.04)
	August	31	72.2 (0.7)	3.5 (0.1)		0.93	(0.02)
	September	63	78.8 (0.5)	4.7 (0.1)		0.96	(0.01)
US4	July	20	56.6 (1.0)	1.9 (0.1)		1.00	(0.02)
	August	101	75.0 (0.4)	4.1 (0.1)		0.97	(0.01)
	September	121	79.7 (0.5)	5.2 (0.1)		1.01	(0.01)
DS1	July	19	55.2 (1.0)	1.8 (0.1)		1.04	(0.03)
	August	44	70.6 (0.7)	3.6 (0.1)		1.01	(0.02)
	September	26	81.7 (0.9)	5.7 (0.2)		1.03	(0.02)
DS2	July	113	56.2 (0.4)	1.8 (0.0)		1.00	(0.01)
	August	245	71.4 (0.3)	3.7 (0.2)		1.02	(0.04)
	September	178	80.7 (0.3)	5.4 (0.1)		1.02	(0.01)
DS3	July	42	54.1 (0.7)	1.5 (0.1)		0.94	(0.01)
	August	19	67.1 (1.1)	3.1 (0.2)		1.01	(0.02)
	September	57	77.5 (0.6)	4.8 (0.1)		1.02	(0.01)

Table 2. Abundance estimates \pm standard error (SE) of juvenile Chinook salmon at three sites in the downstream reach. Total CPUE across all sampling days for all sites, summer 2009.

Site	Sampling Event	n	Abundance (SE)		Total CPUE
US1	July	13	-	-	6.92
	August	44	-	-	9.29
	September	48	-	-	9.67
US2	July	17	-	-	5.03
	August	13	-	-	2.16
	September	16	-	-	3.49
US3	July	7	-	-	0.33
	August	31	-	-	4.84
	September	63	-	-	42.9
US4	July	20	-	-	3.03
	August	101	-	-	27.8
	September	121	-	-	11.74
DS1	July	19	-	-	1.15
	August	44	100	(-30.63)	4.56
	September	26	86	(-50.85)	3.94
DS2	July	113	175	(-24.14)	8.21
	August	245	693	(-110.57)	52.02
	September	178	756	(-175.48)	39.77
DS3	July	42	80	(-22.77)	3.15
	August	19	74	(-65.03)	2.7
	September	57	159	(-48.18)	12.09

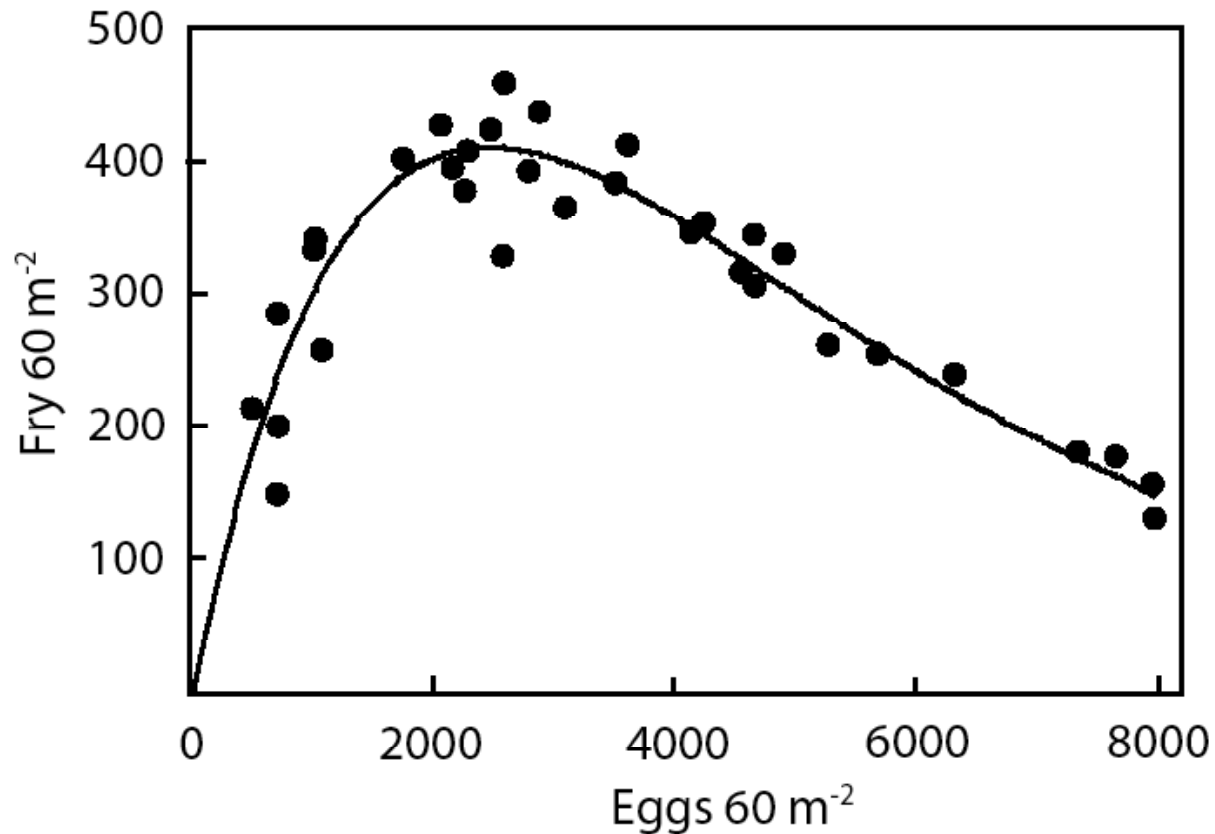


Figure 1. Relationship between egg density and the density of trout parr aged 0+ years in May/June for anadromous brown trout in a 60 m² section of Black Brows Beck (redrawn from Elliott 1994). These data demonstrate how closely stock-recruit data can fit a Ricker curve when sampling error and annual environmental variation are small. Black Brows Beck is a small stream approximately 0.5 m wide.

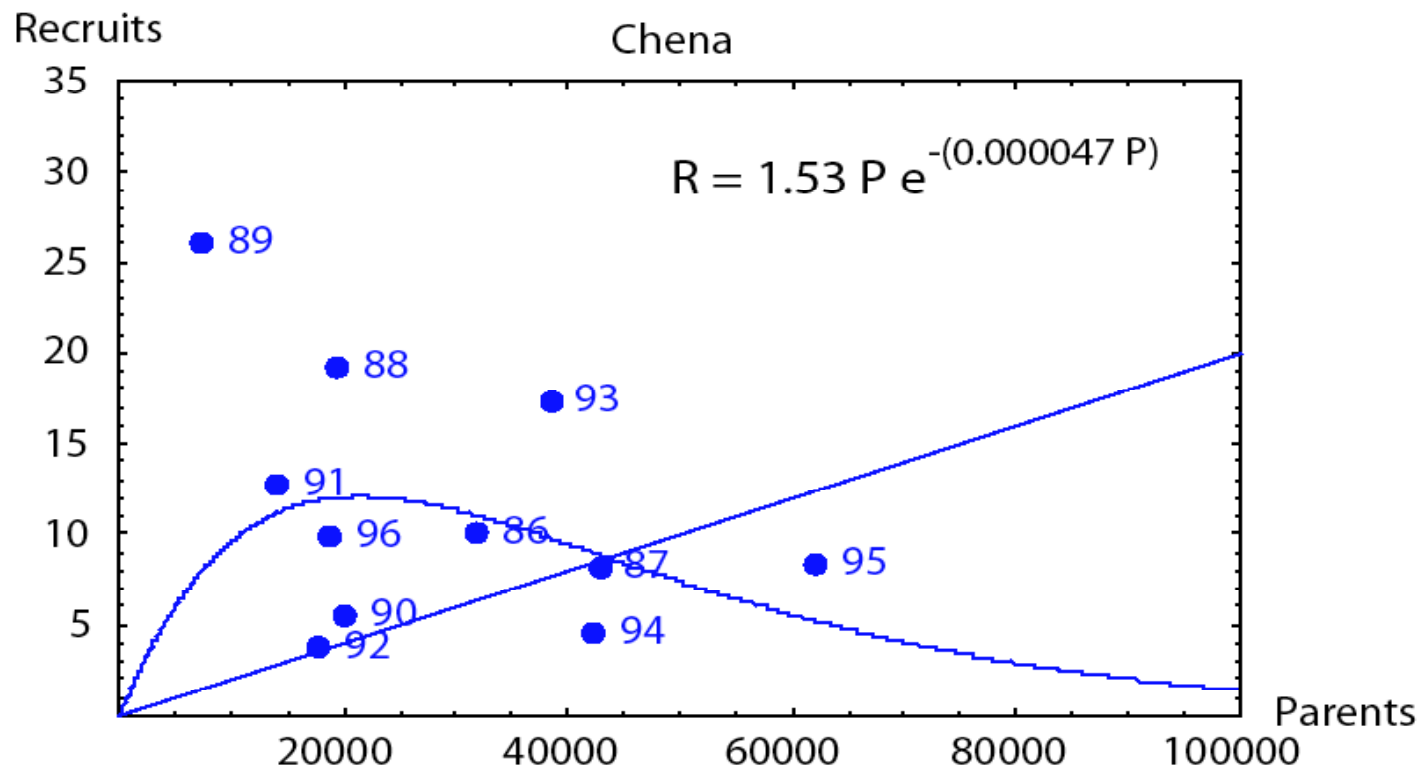


Figure 2. Ricker curve fitted through the stock-recruitment data for Chena River Chinook salmon. Units for Parents are thousands of eggs, units for Recruits are numbers of returning progeny (thousands). Data points are labeled by brood year. The equation for the parameterized Ricker model is shown on the plot. We have added a "ballpark" replacement line for reference purposes assuming a 0.02% egg-adult survival rate at equilibrium population size.

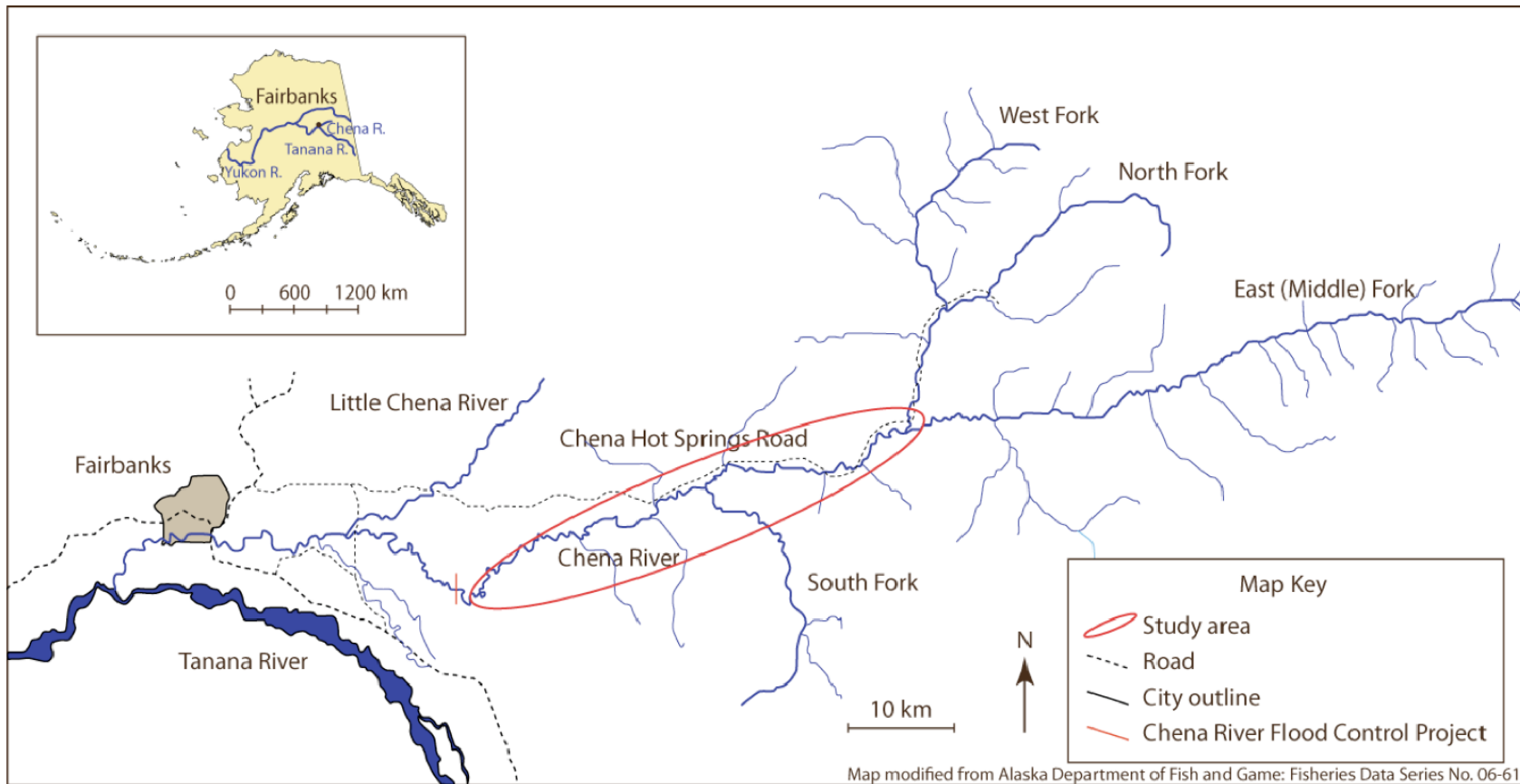


Figure 3. Location of study.

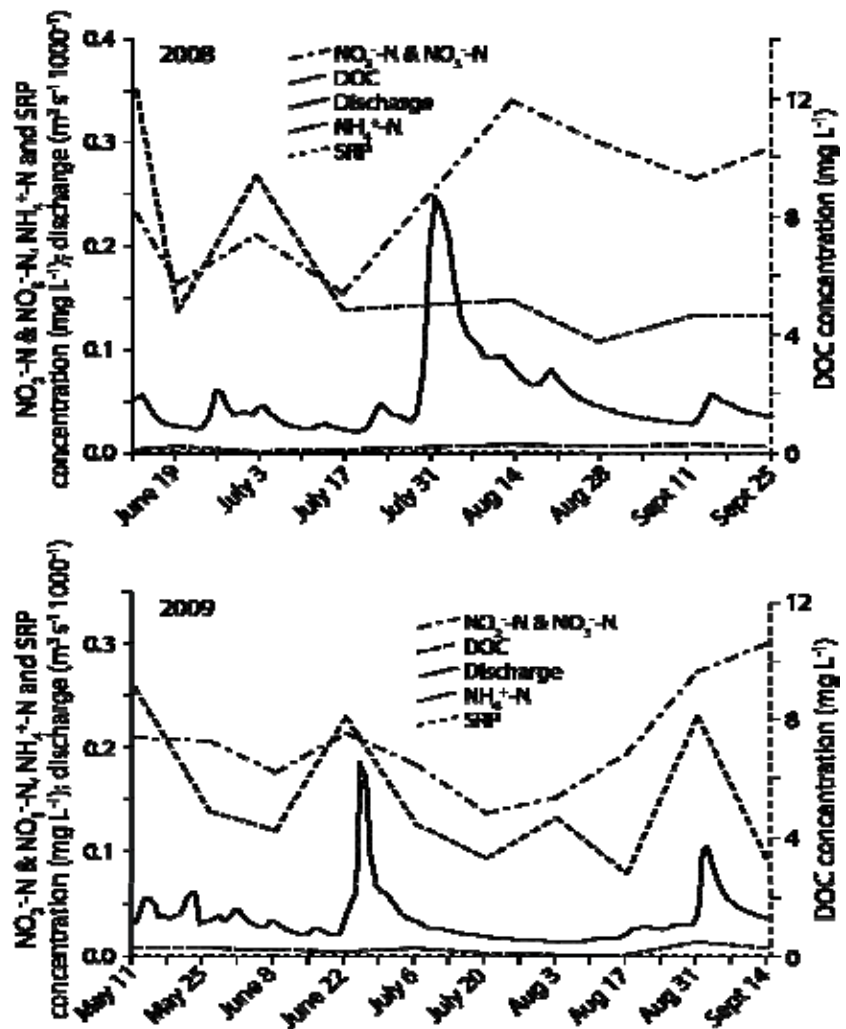


Figure 4. Nutrient concentrations and mean daily discharge rate in the Chena River, Alaska, USA, throughout the summers of 2008 (upper panel) and 2009 (lower panel). Data are mean values among the four study sites. Nutrients measured include: nitrite and nitrate nitrogen ($\text{NO}_2^- \text{--N}$ and $\text{NO}_3^- \text{--N}$), ammonia nitrogen ($\text{NH}_4^+ \text{--N}$), soluble reactive phosphorus (SRP), and dissolved organic carbon (DOC).

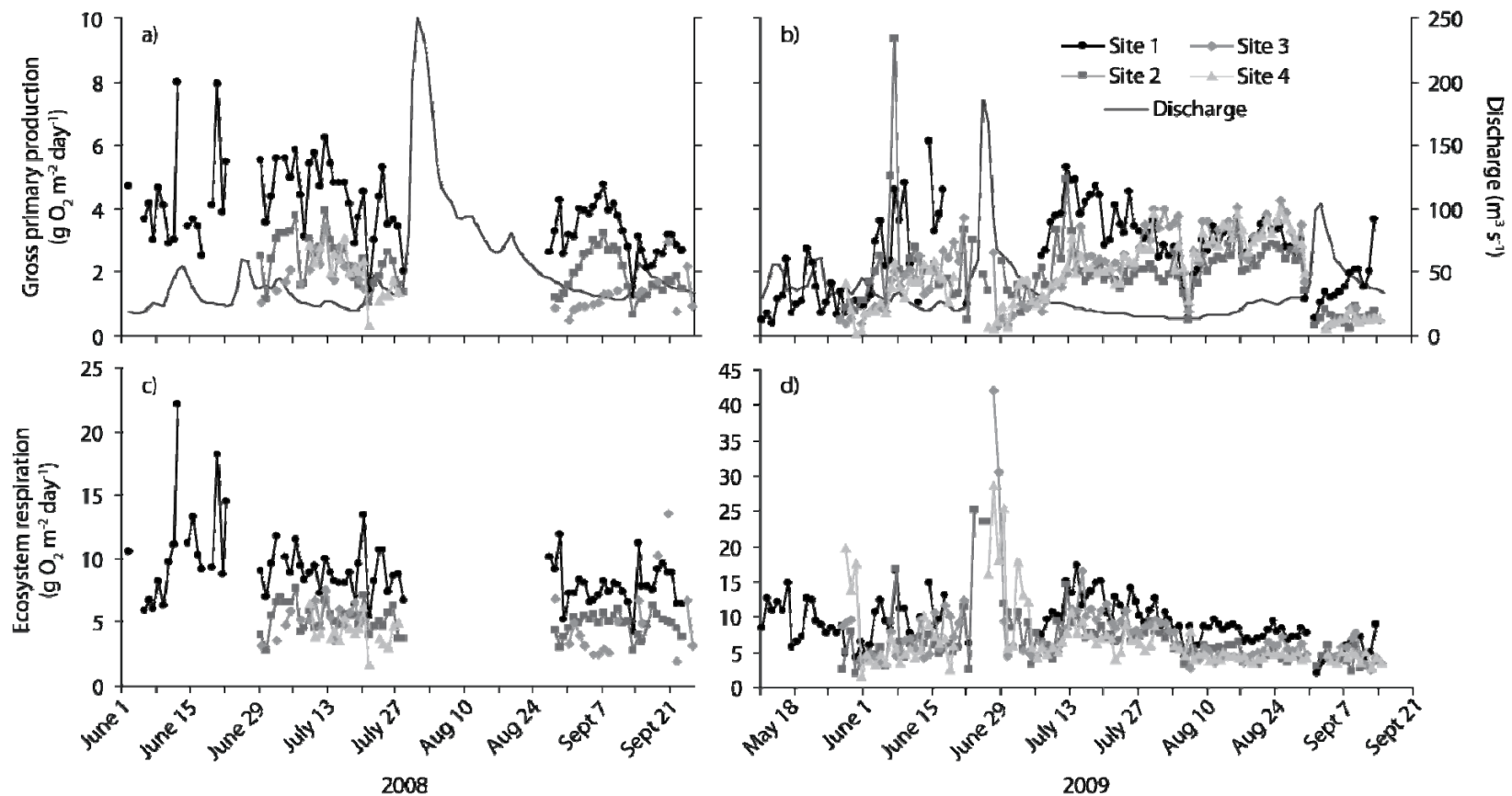


Figure 5. Gross primary production and river discharge rates in (a) 2008 and (b) 2009, and ecosystem respiration rates in (c) 2008 and (d) 2009 at four sites in the Chena River, Alaska, USA. Gaps represent dates during which data were unavailable due to equipment failure or site inaccessibility.

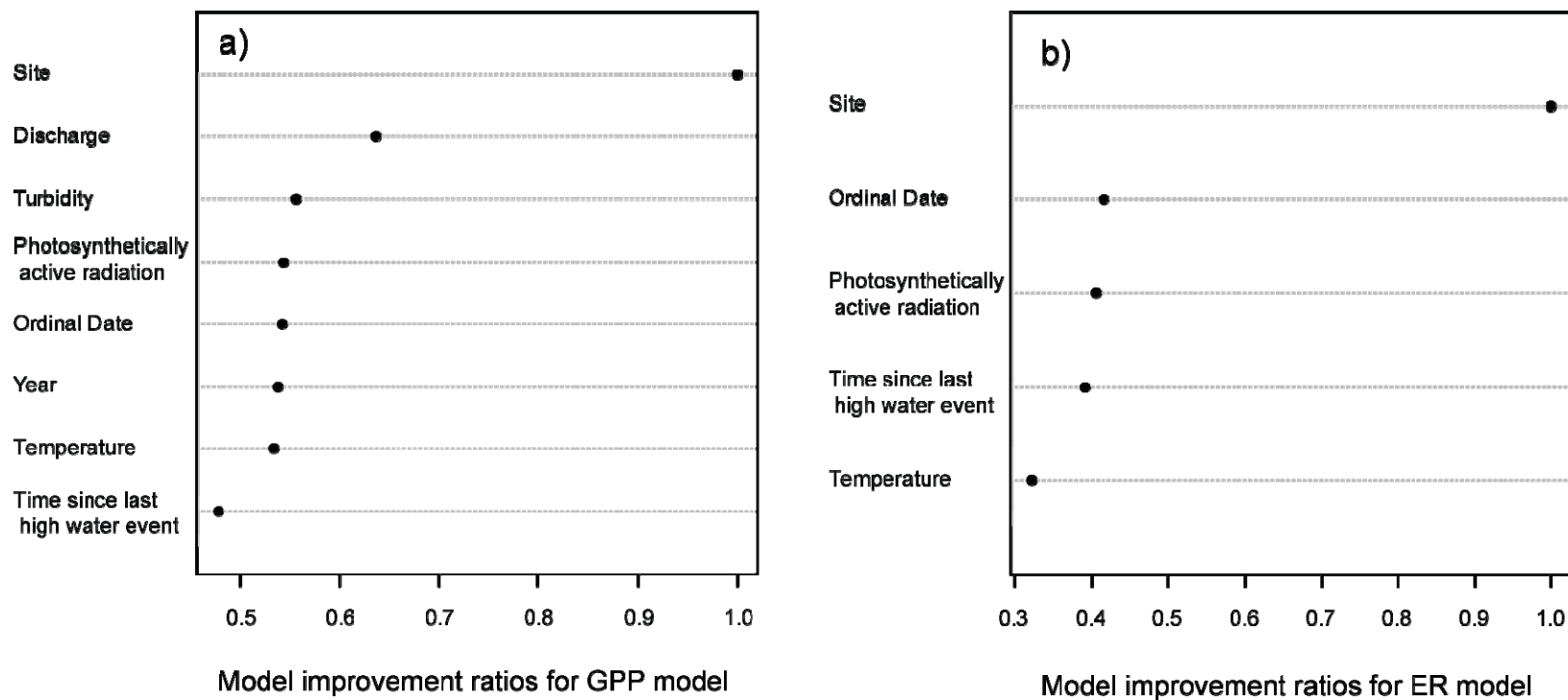


Figure 6. Model improvement ratios and variable importance rankings for (a) gross primary production rate (GPP) and (b) ecosystem respiration rate (ER) Random Forests models in the Chena River, Alaska, USA, 2008-2009. The GPP model explains 75% of the variation in GPP rates in the Chena River and the ER model explains 52% of the variation in ER rates. If site and year are not included as predictor variables in the models, the GPP model explains 63% of the variation in GPP rates, and the ER model explains 31% of the variation in ER rates.

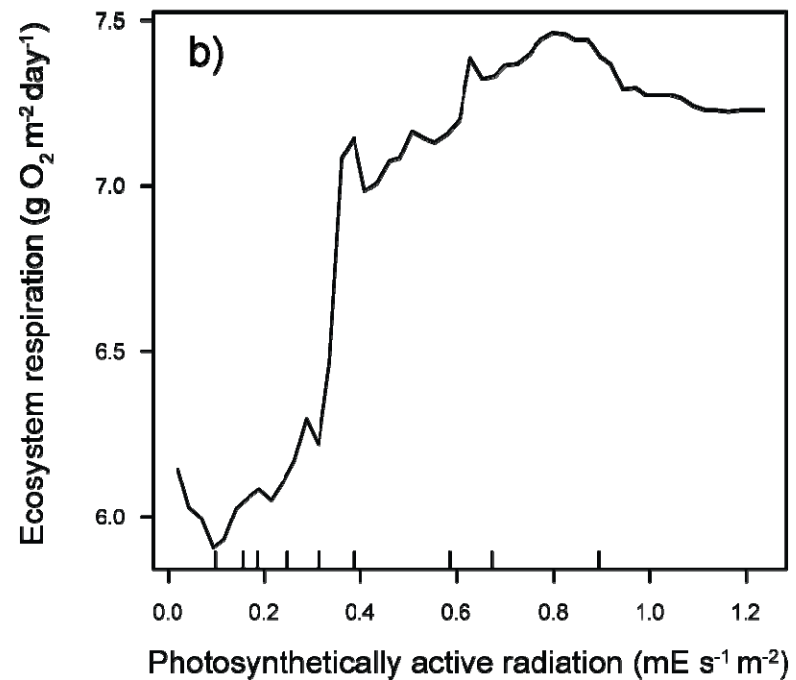
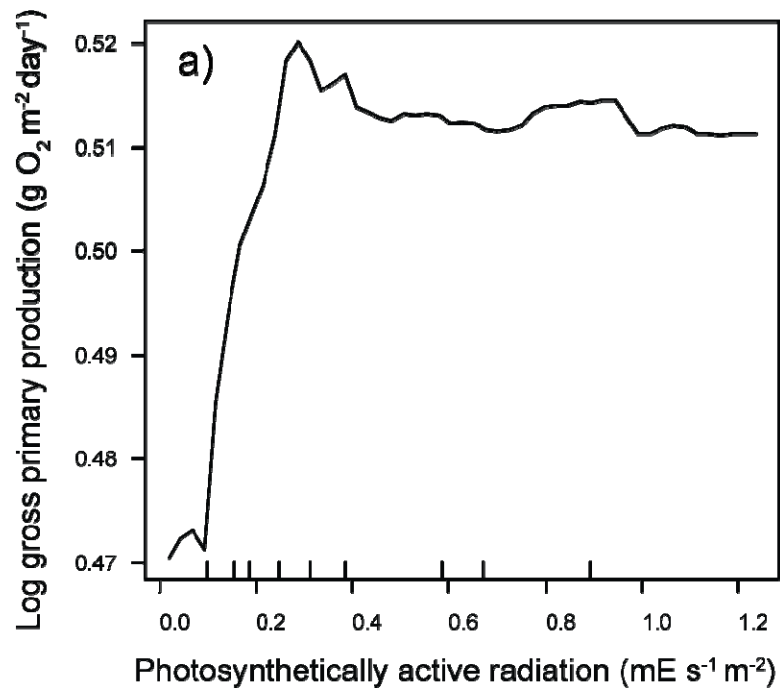


Figure 7. Effects of photosynthetically active radiation (PAR) on (a) primary production rate and (b) respiration rate in the Chena River, Alaska, USA, 2008-2009. These partial dependence plots show the influence of PAR on primary production rate and respiration rate with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axes represent deciles of data.

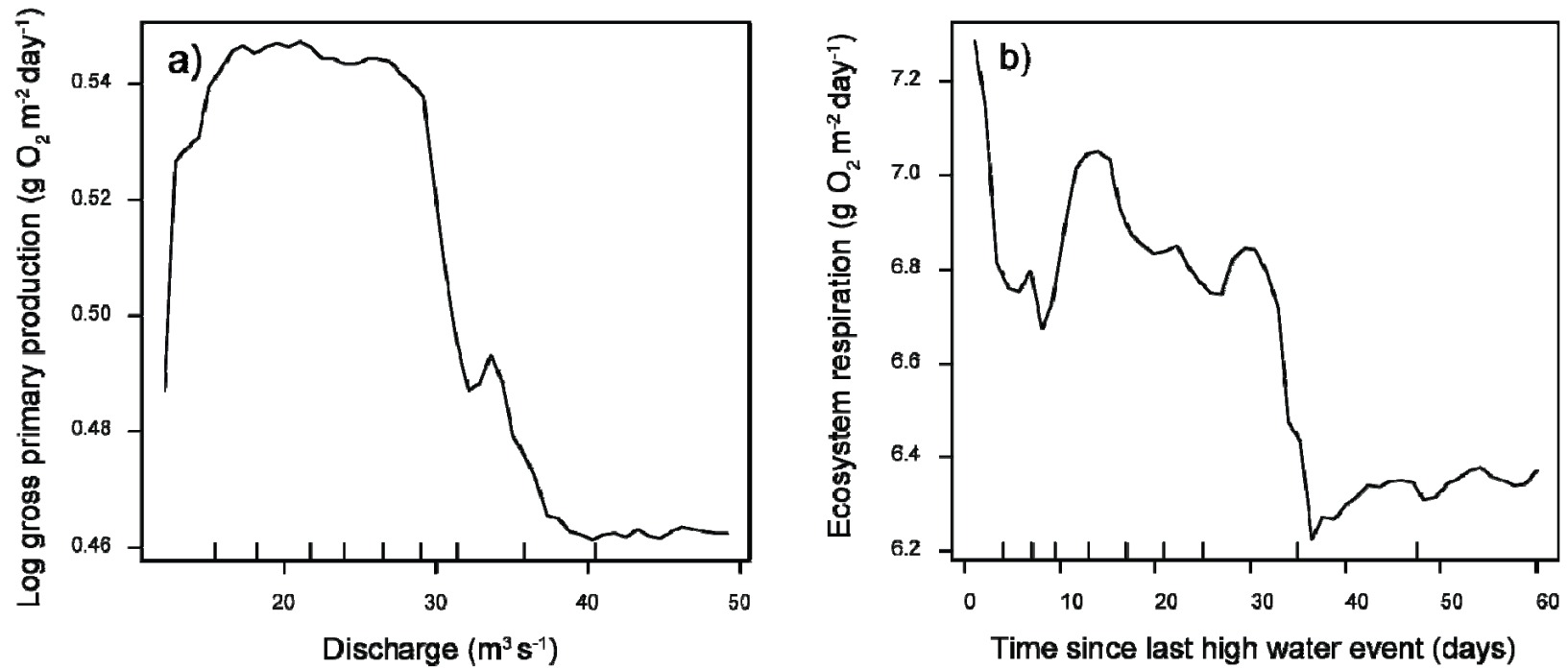


Figure 8. (a) Effect of discharge on primary production rate, and (b) effect of time since last high water event on respiration rate in the Chena River, Alaska, USA, 2008-2009. These partial dependence plots show the influence of discharge or time since last high water event on the metabolism metric with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axes represent deciles of data.

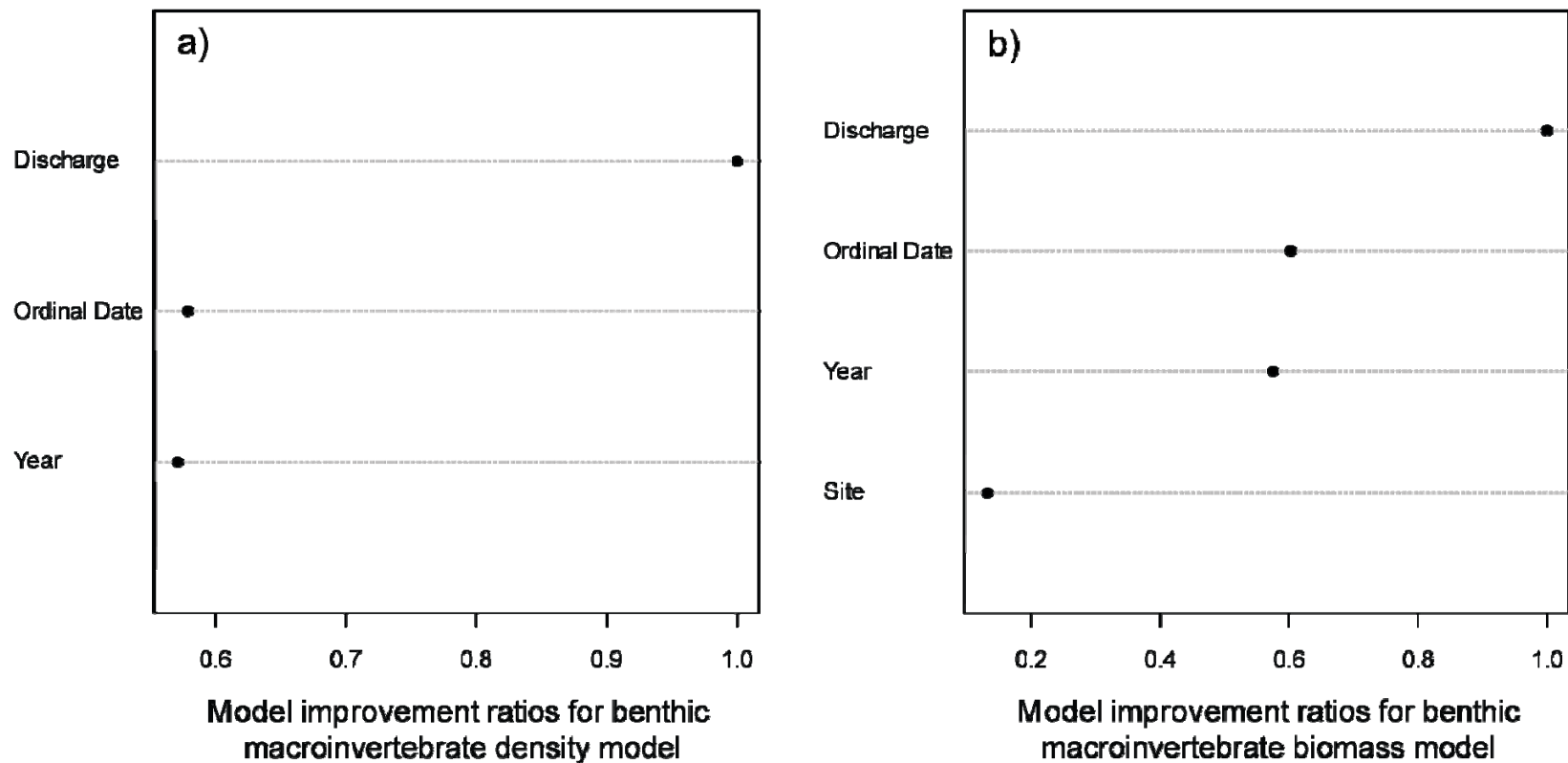


Figure 9. Model improvement ratios and variable importance rankings for (a) benthic macroinvertebrate density and (b) benthic macroinvertebrate biomass Random Forests models in the Chena River, Alaska, USA, 2008-2009. The density model explains 58% of the variation in benthic macroinvertebrate densities in the Chena River, and the biomass model explains 39% of the variation in benthic macroinvertebrate biomass. If site and year are not included as predictor variables in the models, the density model explains the same amount of the variation in benthic macroinvertebrate densities (58%), and the biomass model explains 27% of the variation in benthic macroinvertebrate biomass.

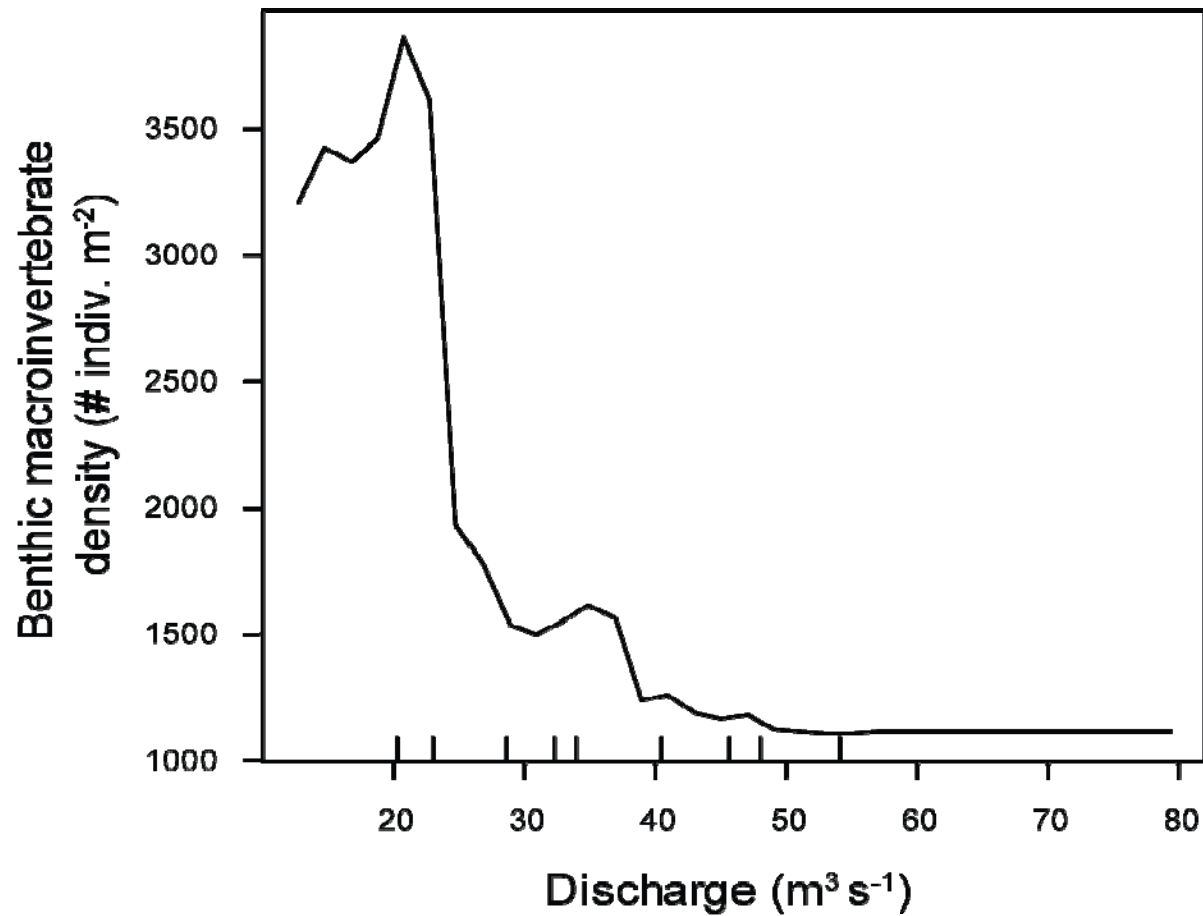


Figure 10. Effect of discharge on benthic macroinvertebrate density in the Chena River, Alaska, USA, 2008-2009. This partial dependence plot shows the influence of discharge on benthic macroinvertebrate density with the effects of all other variables removed. Inward-facing vertical dash marks on the x-axis represent deciles of data.

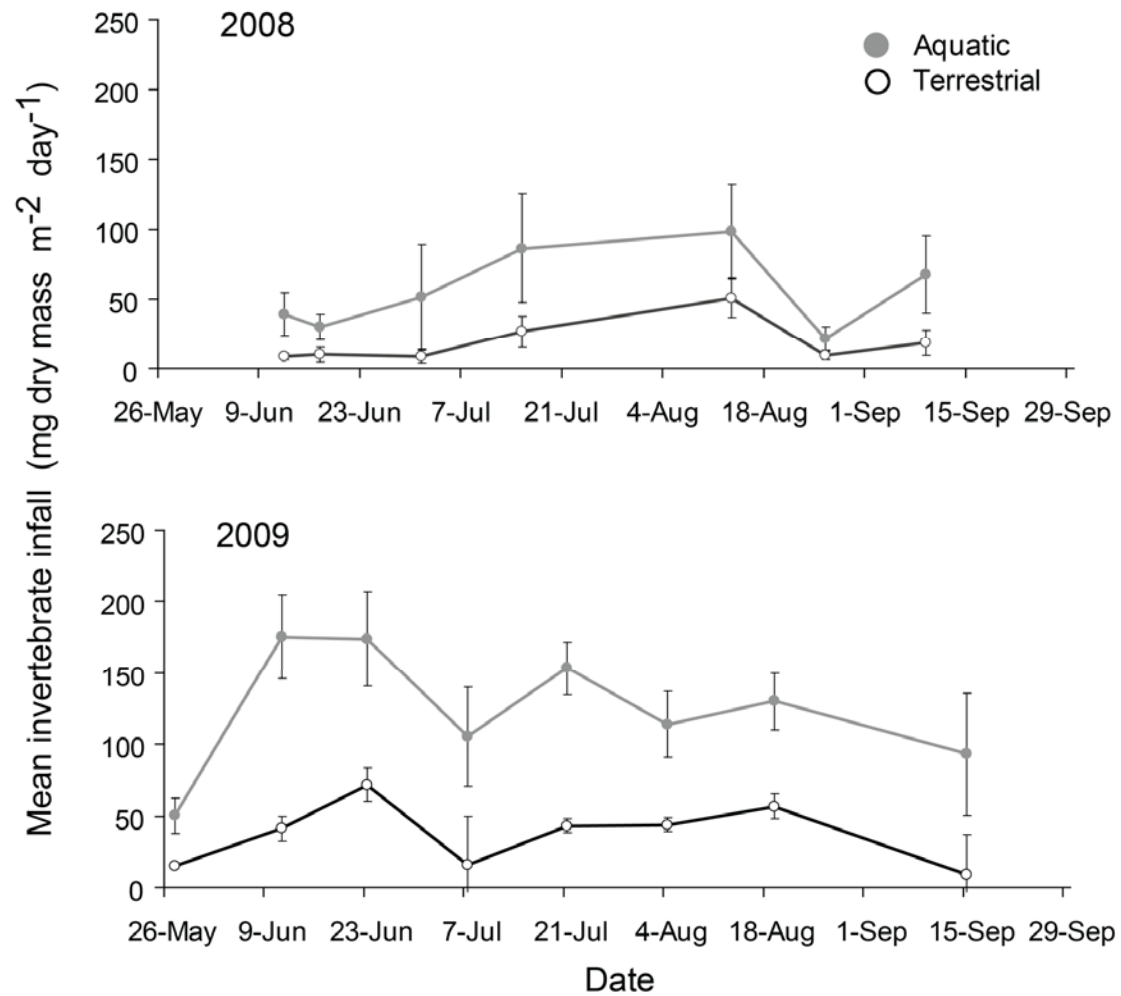


Figure 11. Invertebrate infall (mean \pm SE) by origin source (aquatic and terrestrial) into the Chena River, Alaska during the summers of 2008 and 2009.

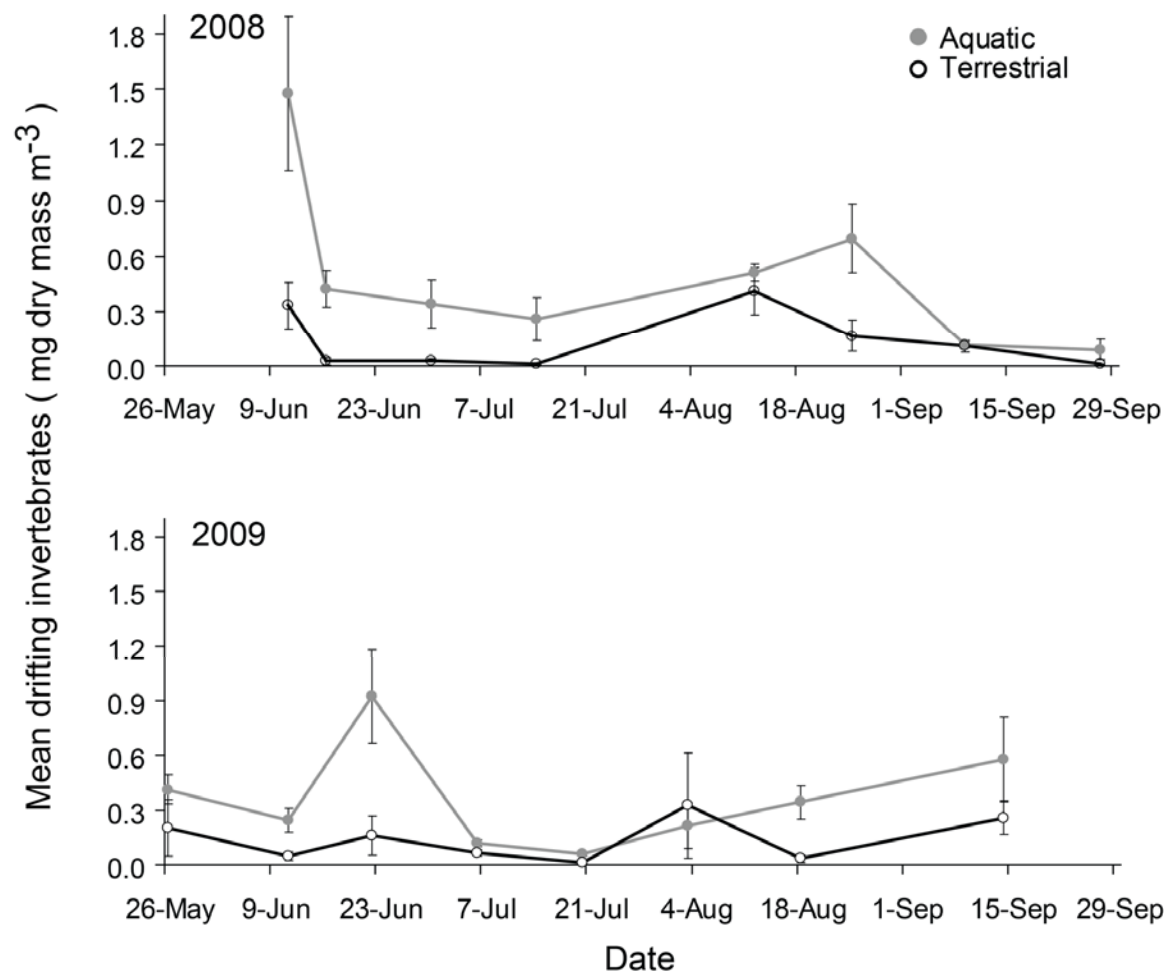


Figure 12. Drifting invertebrates (mean \pm SE) by origin source (aquatic and terrestrial) in the Chena River, Alaska during the summers of 2008 and 2009.

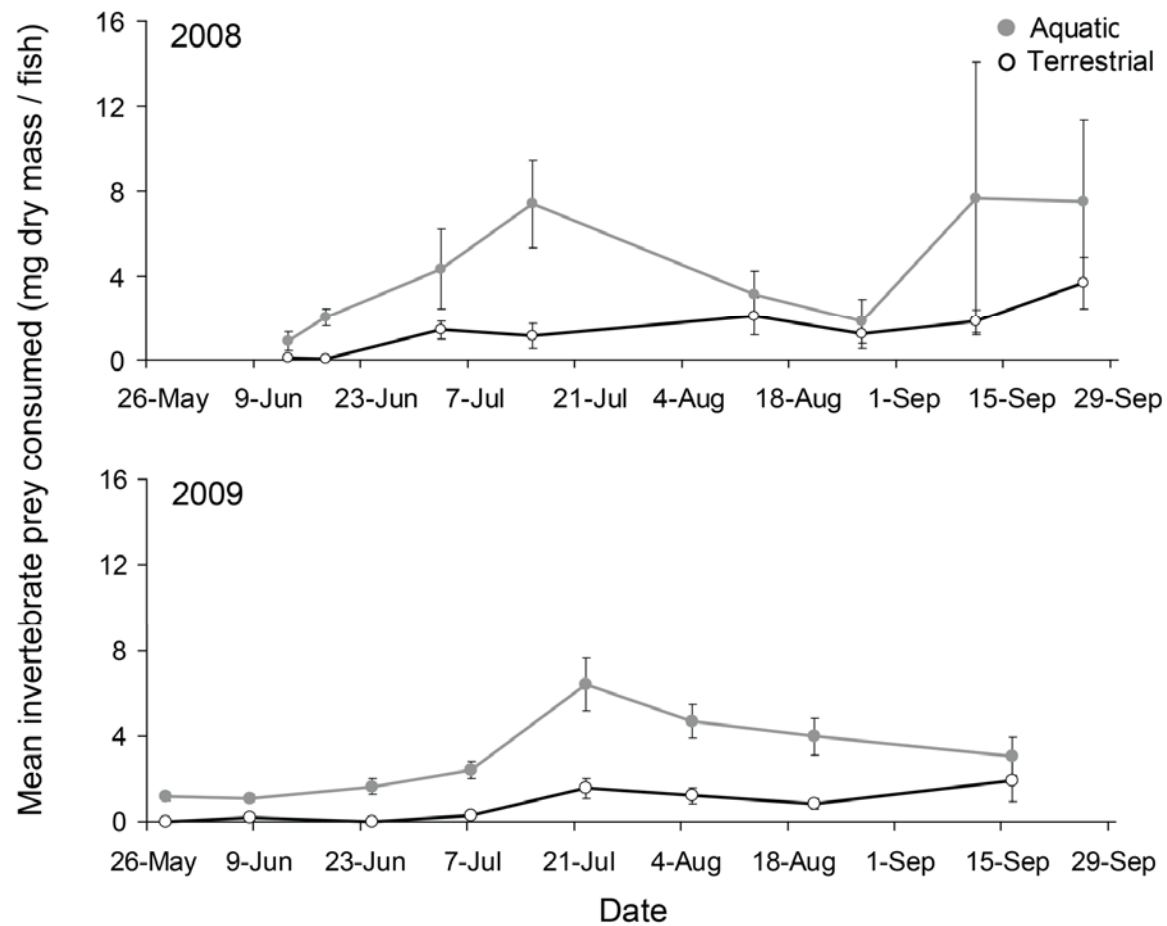


Figure 13. Prey mass consumed (mean \pm SE) by juvenile Chinook salmon broken down into origin source (aquatic and terrestrial) in the Chena River, Alaska during the summers of 2008 and 2009.

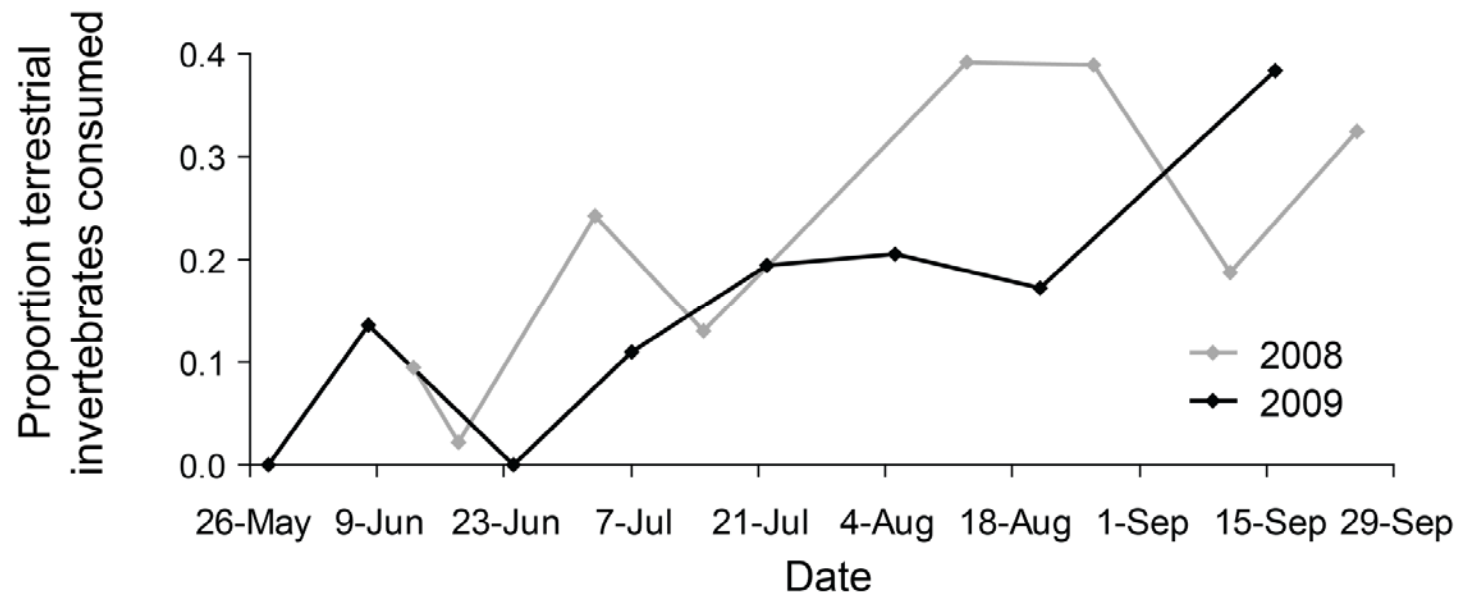


Figure 14. Proportion terrestrial invertebrates consumed by juvenile Chinook salmon in the Chena River during the summers of 2008 and 2009.

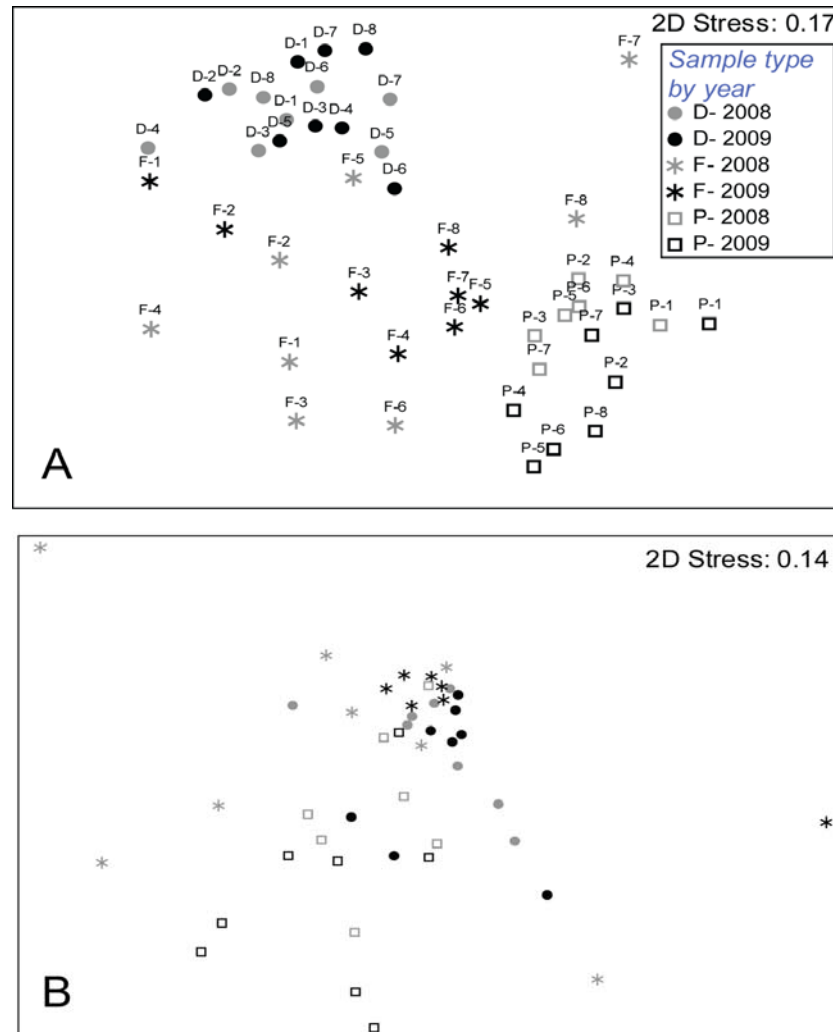


Figure 15. Multidimensional scaling ordination of the mean proportion by mass of the top 95% invertebrate families and life stages for each sample date in the Chena River, Alaska during the summers of 2008 and 2009. Sample type refers to F = fish diet, D = invertebrate drift, P = invertebrate infall; sample date 1-8 represents each of 8 sampling events between May-September.

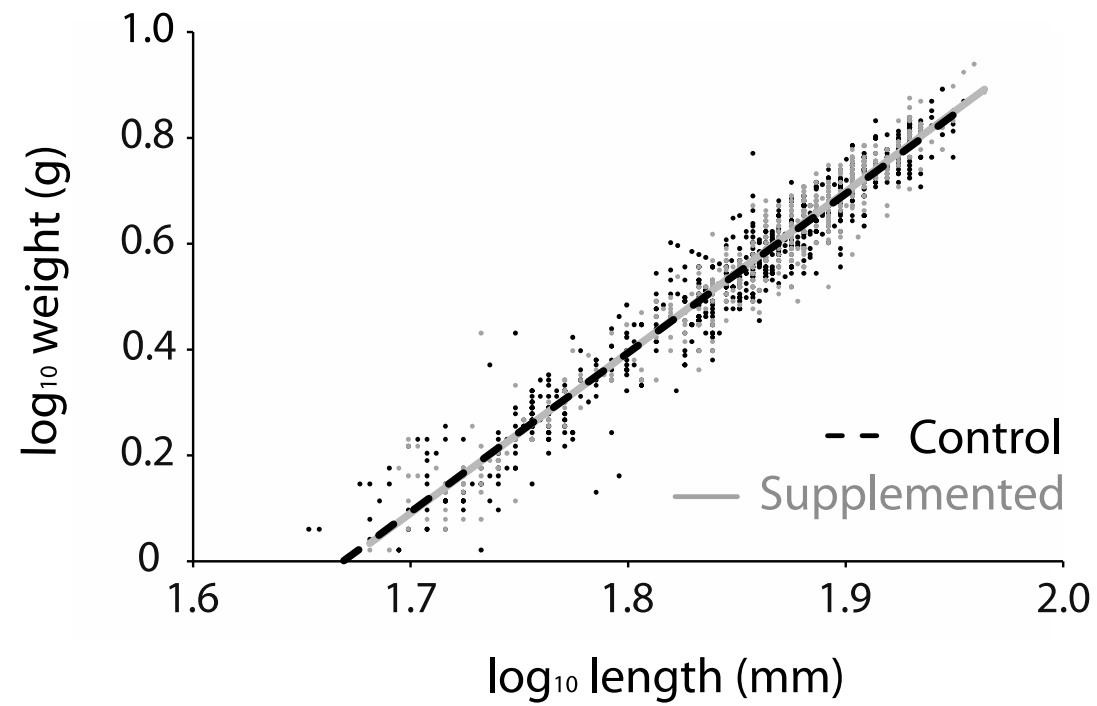


Figure 16. Regression of log transformed weight and length for all Chinook salmon in control and supplemented food sites.

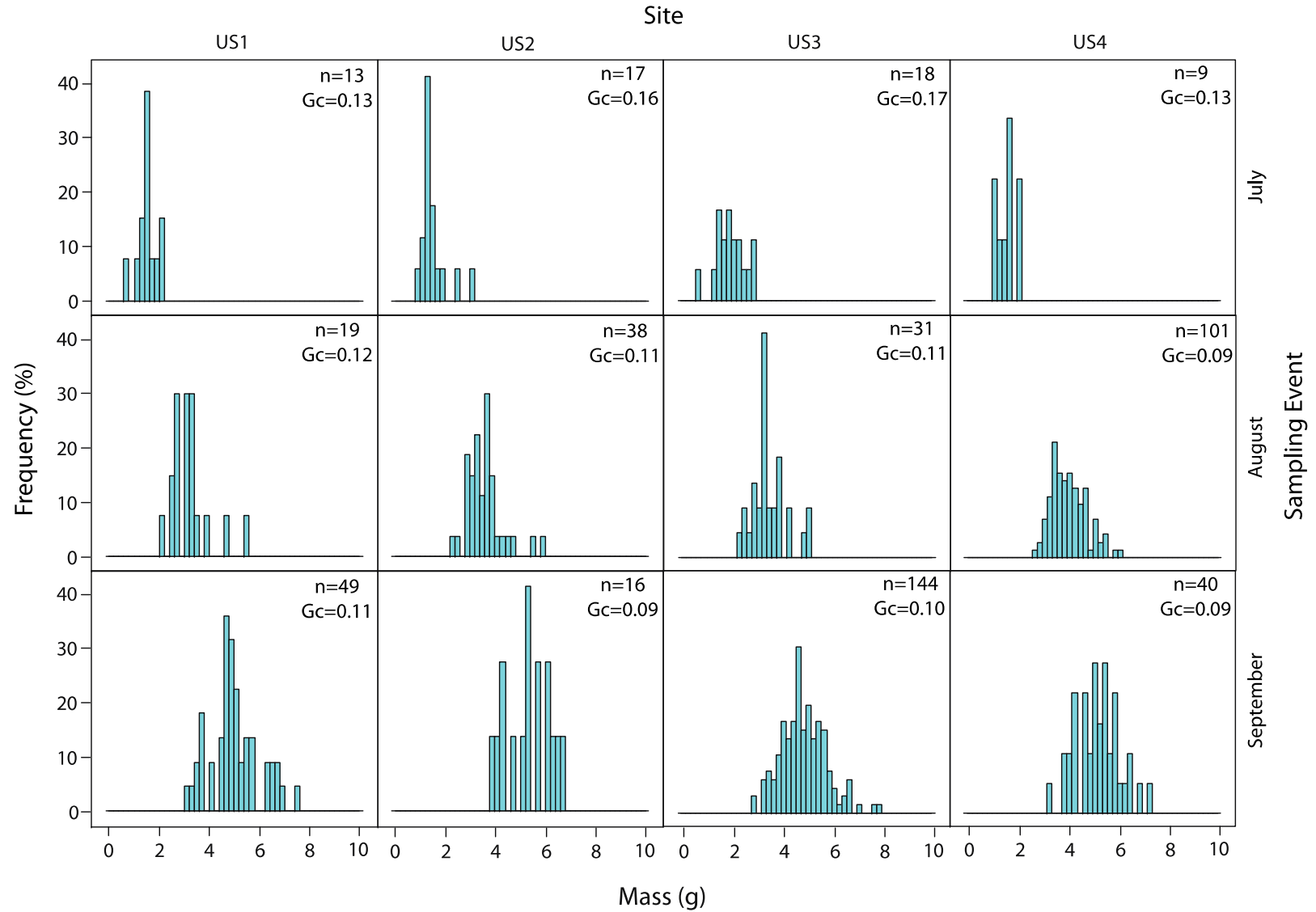


Figure 17. Mass frequency distributions of Chinook salmon at upstream sites, July-September. In the upper right hand of each plot is the sample size used to make the plot, as well as the Gini coefficient for that sampling event.

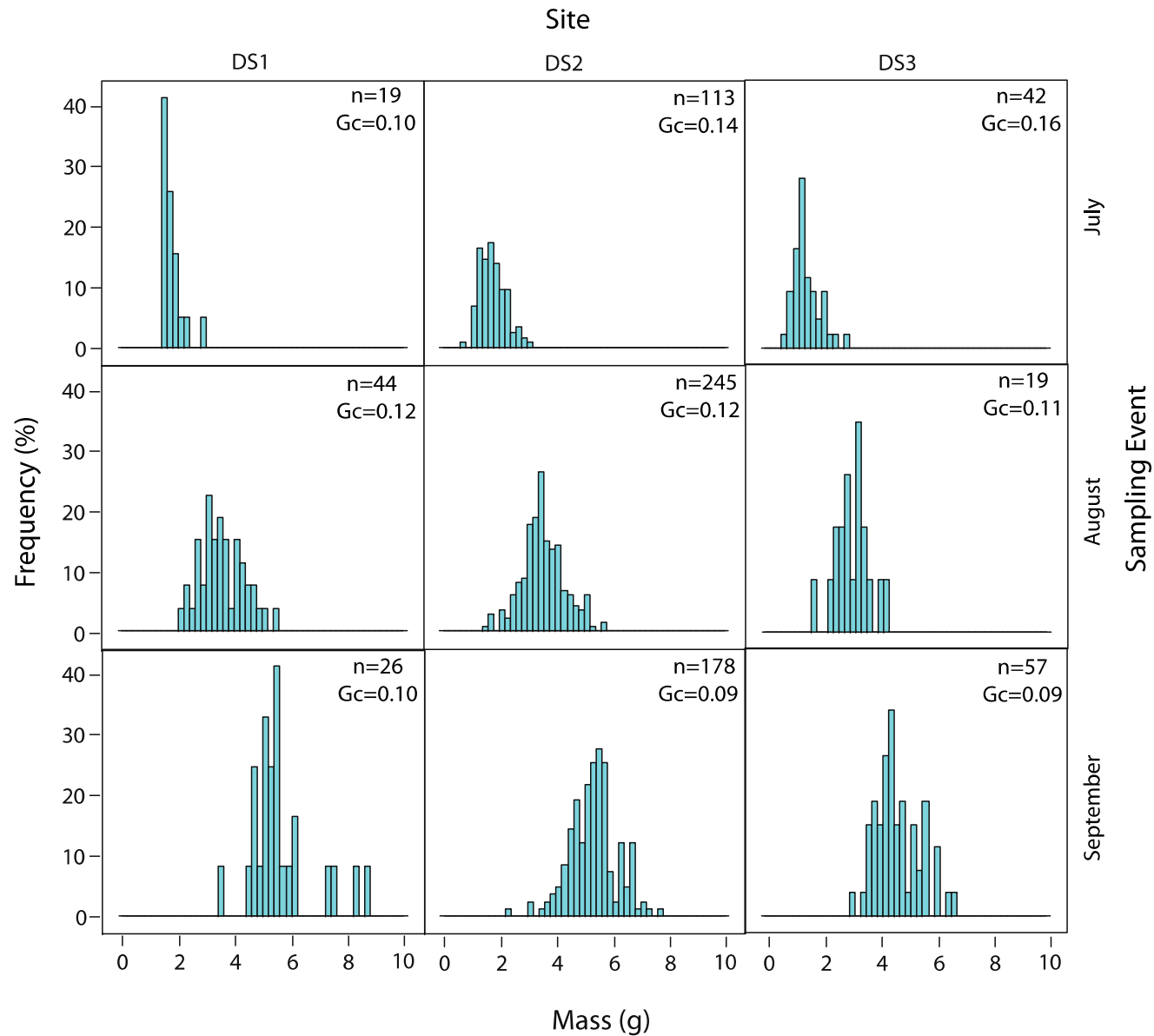


Figure 18. Mass frequency distributions of juvenile Chinook salmon at downstream sites, July-September. In the upper right hand of each plot is the sample size used to make the plot, as well as the Gini coefficient for that sampling event.

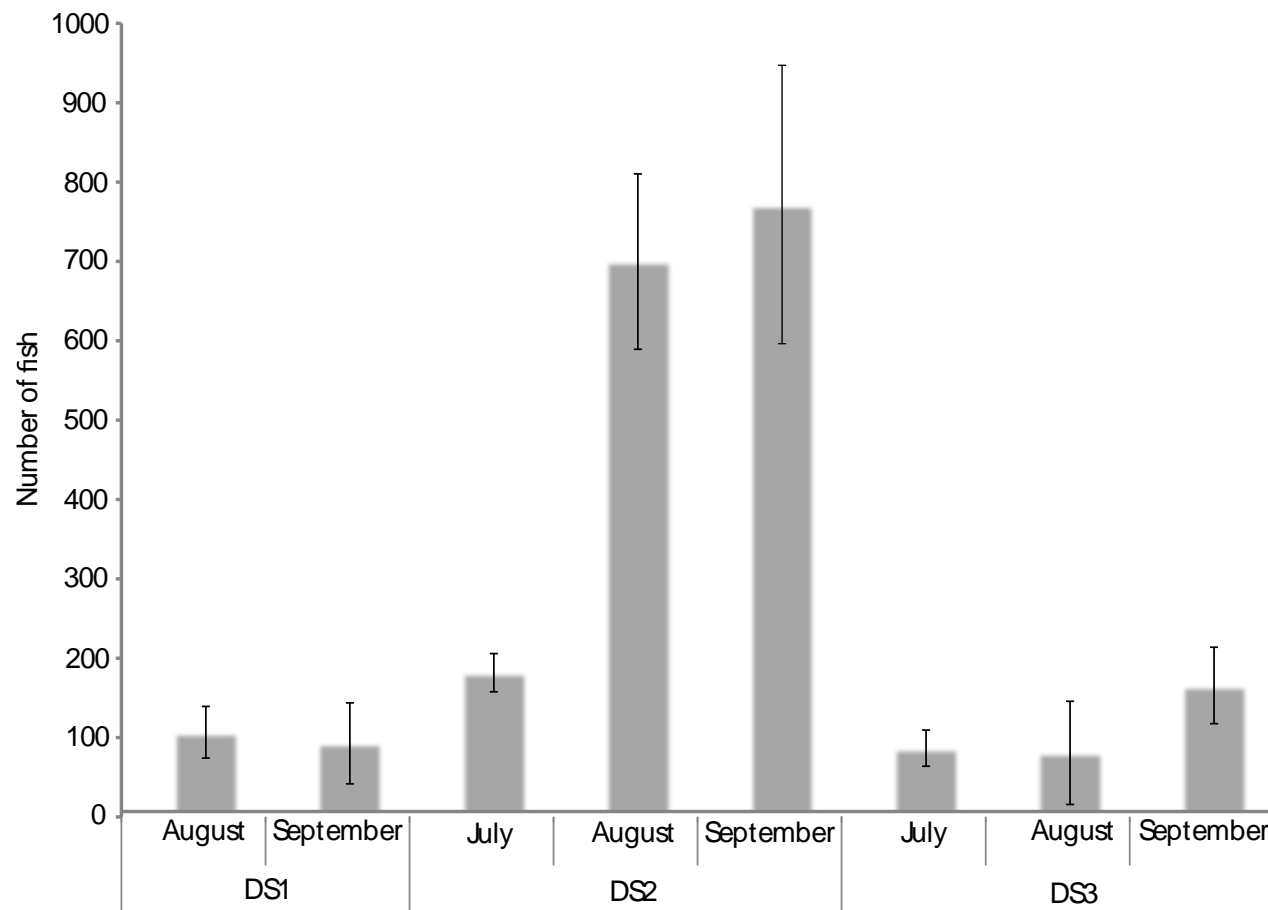


Figure 19. Abundance estimates of juvenile Chinook salmon at three sites in the downstream reach, summer 2009. The error bars represent standard errors.

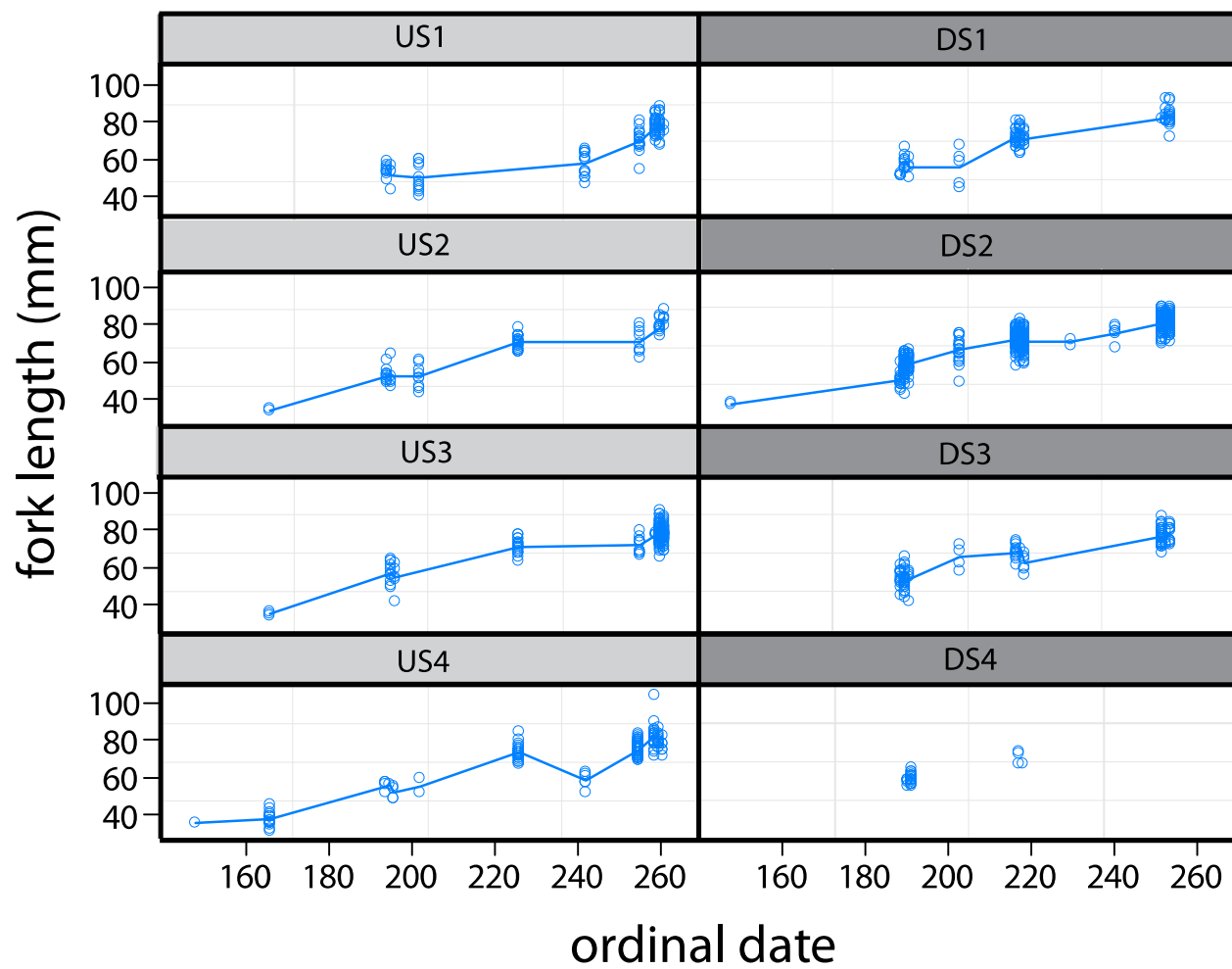


Figure 20. Fork length (mm) of juvenile Chinook salmon at ordinal date for all sites, summer 2009.

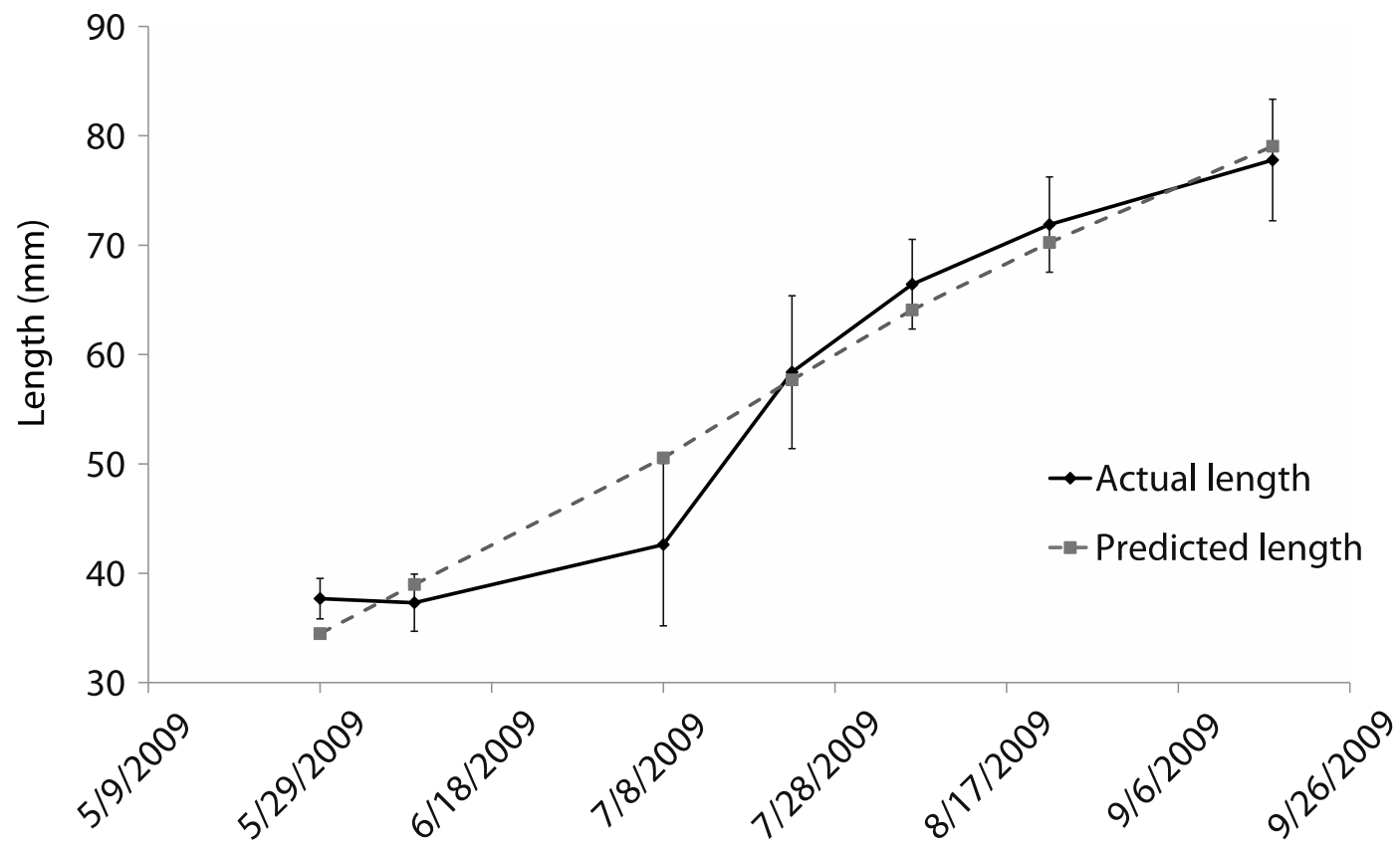


Figure 21. Actual length and predicted length of juvenile Chinook salmon. Error bars represent 1 standard deviation. Predicted length was within one standard deviation of actual length 82% of the time.

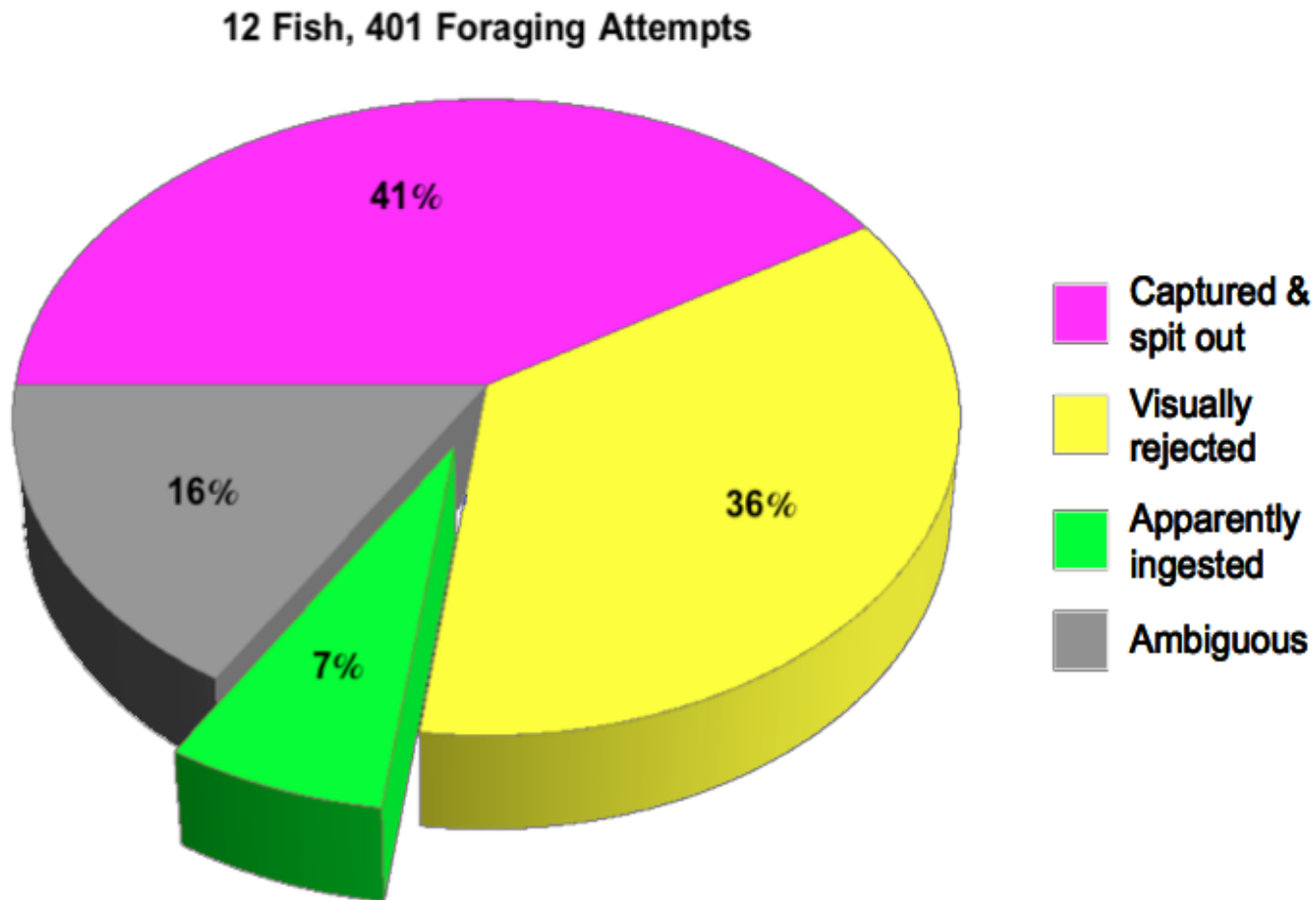


Figure 22. Example of foraging outcomes by juvenile Chinook salmon, Aug 14, 2009.

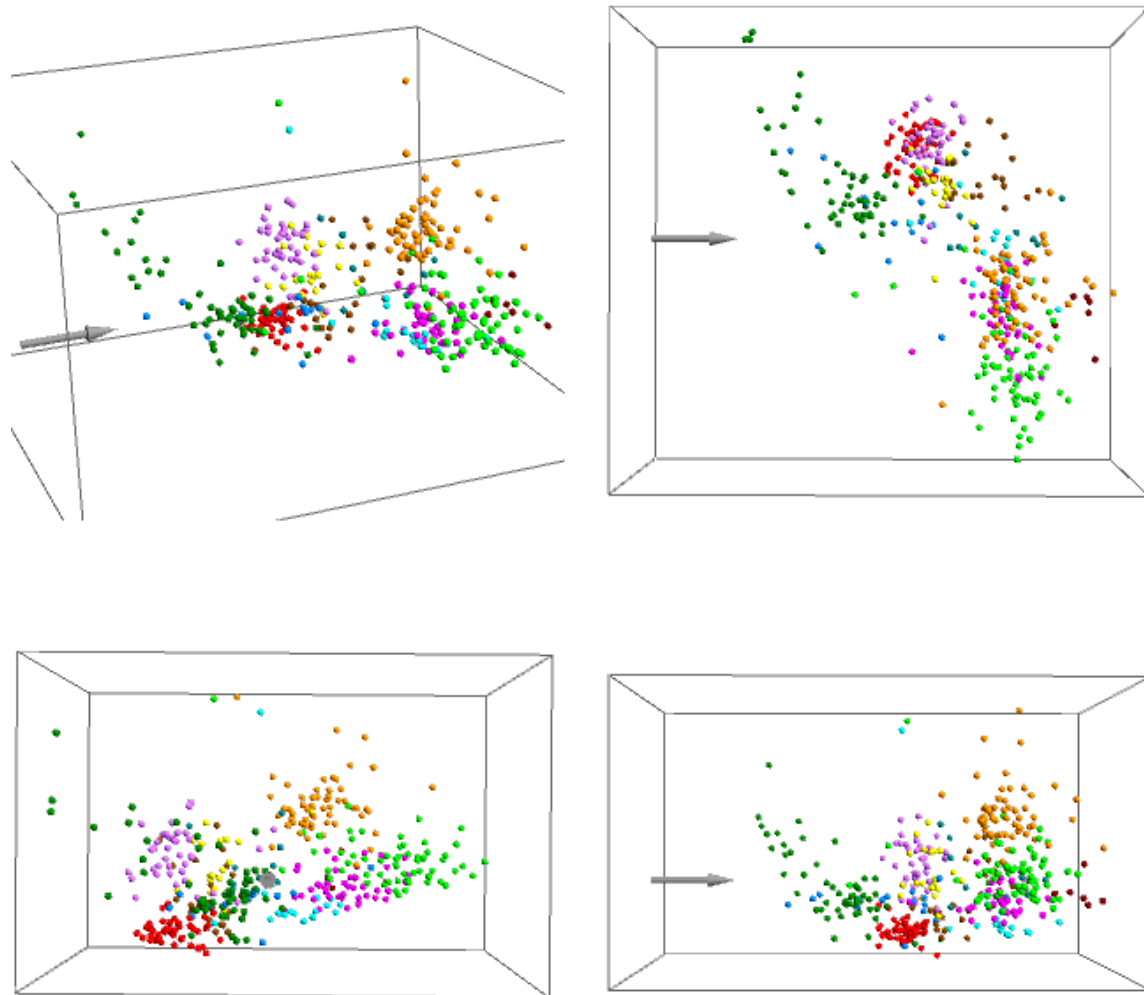


Figure 23. Foraging attempt locations of 12 juvenile Chinook salmon observed for 20 minutes. Clockwise from top left: Oblique angle view, top view, camera side view, view from upstream. The gray arrow shows the direction of flow from the upstream end of the school. Each color designates a different fish.

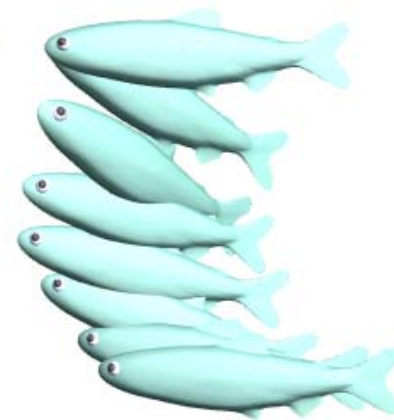
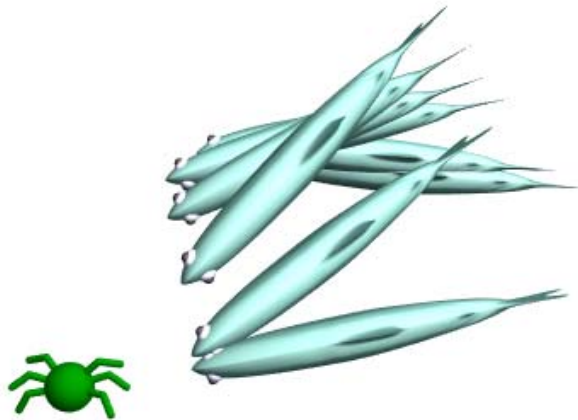


Figure 24. 3-D reconstruction of a juvenile Chinook salmon prey capture maneuver as viewed from three different angles, and traced in the original video. Such reconstructions are useful for evaluating potential energy expended to investigate potential prey, including debris.

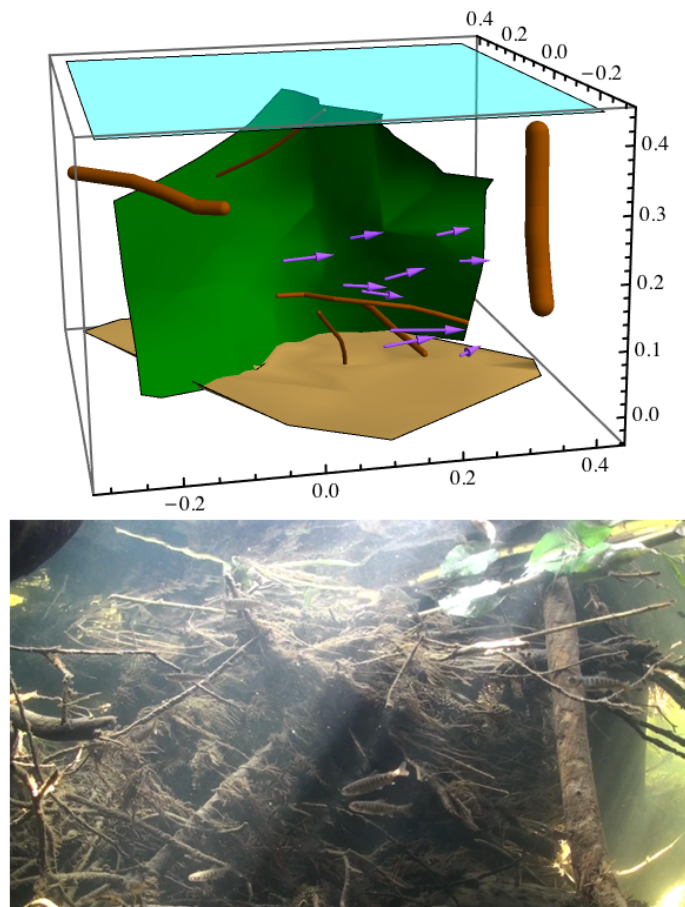


Figure 25. 3-D reconstruction of juvenile Chinook salmon habitat (above) and the habitat represented (below). The brown tubes represent logs, the blue and tan surfaces represent the surface and bottom, the green surface represents the boundary of the dense cover in the background, and the purple arrows are water velocity vectors calculated by tracking drifting debris particles. This reconstruction demonstrates how VidSync allows a digital recreation of the fish's habitat, making it possible to know the depth, distance-to-cover, and water velocity at each fish's position at all times during behavioral observations.

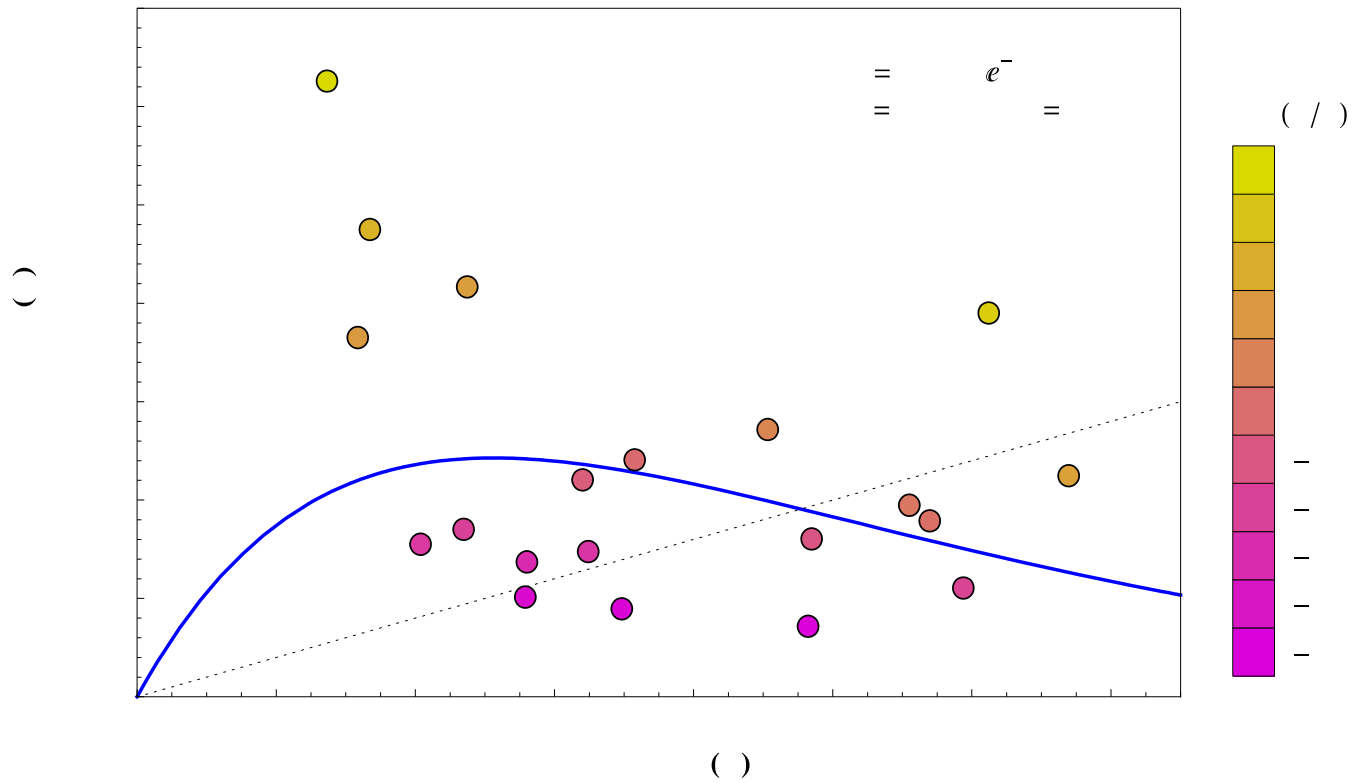


Figure 26. **Basic Ricker model for the Chena River, 1986-2005.** The points are color coded by residual, in order to clarify the correspondence with the annual flow regimes in Figure 2. The dotted black replacement line indicates the level of 1 recruit per spawner.

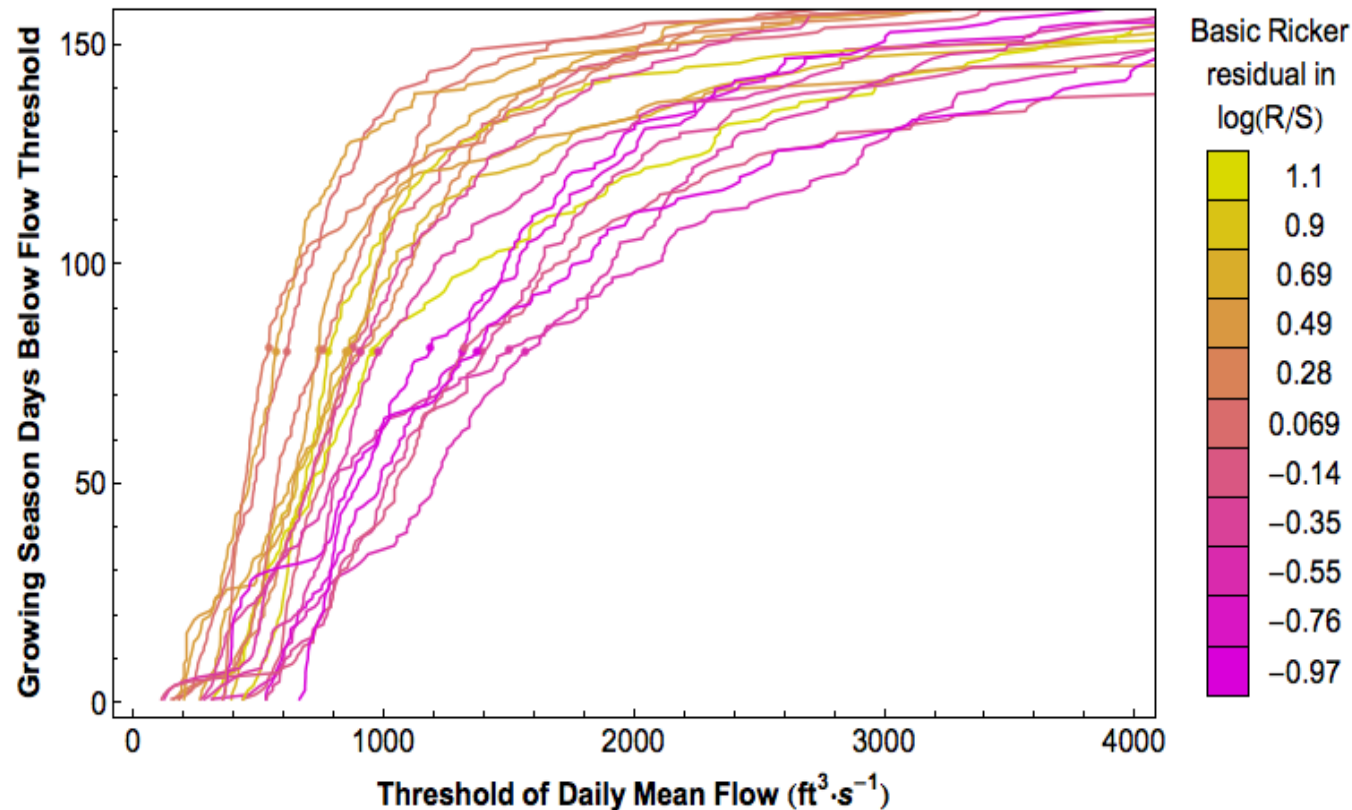


Figure 27. **Annual flow histories and Chinook salmon productivity for the Chena River.** Each line represents flow during the freshwater rearing summer for a particular year class of fish, colored according to the residuals from the basic Ricker model for that year in Figure 1. Yellow represents productive Chinook salmon years (more recruits per spawner than predicted by the model), grading into purple for poor years. The vertical axis shows the number of days above each threshold from April 26th, the median date of spring break-up, until September 30th, when the river typically begins to freeze. We selected these dates a priori as the “summer growing season,” the dates at which the river is not covered with ice and may be somewhat productive (even if the Chinook alevins have not yet emerged). Lines high on this graph represent generally low-flow years, and lower lines, high-flow years. Small dots mark the median flow for each year, illustrating that quantiles of flow can be viewed as horizontal transects of this graph.

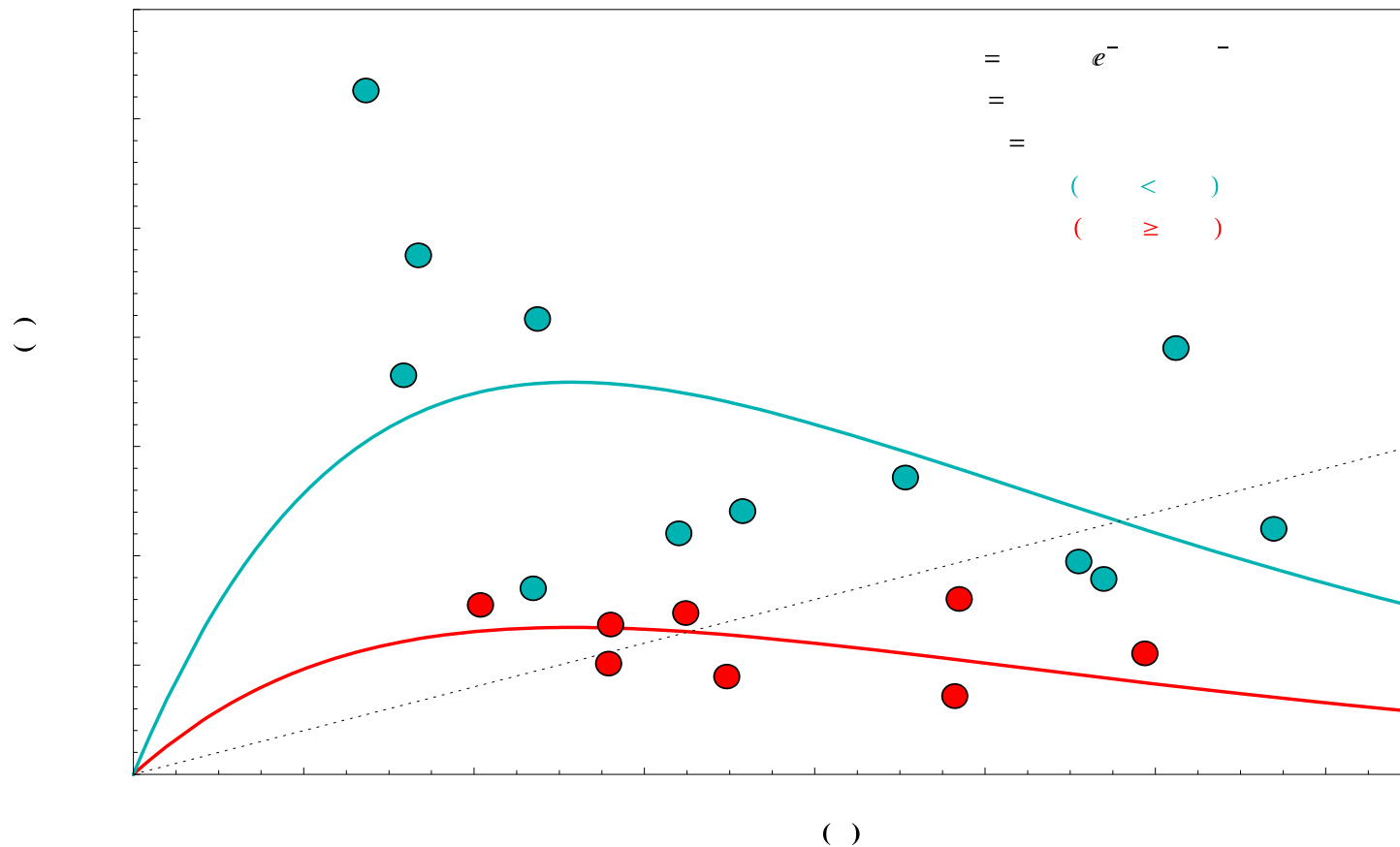


Figure 28. **Nominal flow effect generalized Ricker model fit to Chena River stock-recruitment data for 1986 to 2005.** The two curves for high and low flow years are calculated as part of the same linear regression model with flow as a nominal variable.

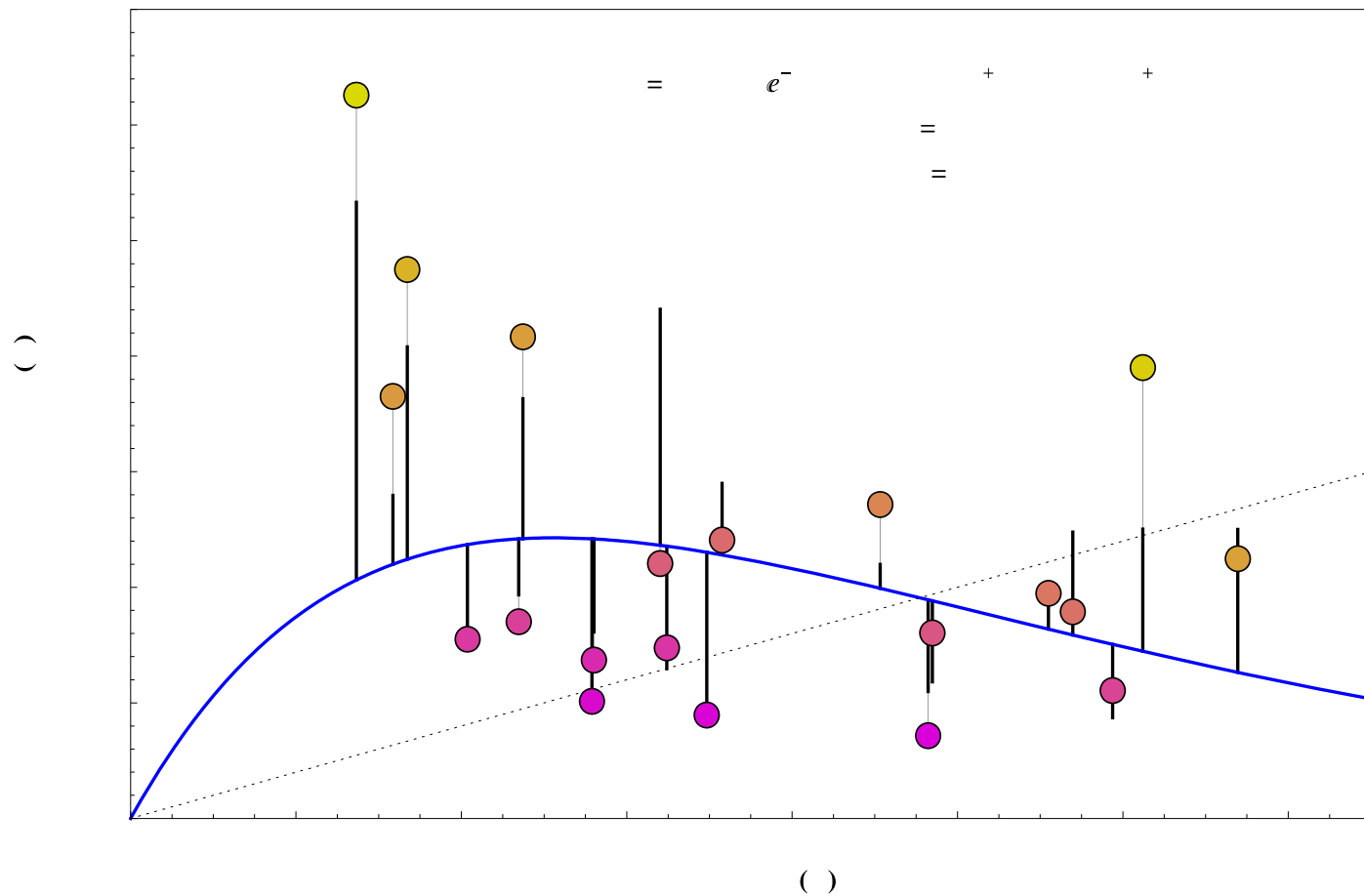


Figure 29. **The most detailed generalized Ricker model for Chena River stock-recruitment data from 1986 to 2005.** The blue line is the standard Ricker model curve, and the dark extensions represent the additional variability explained by our generalized model that incorporates three environmental variables (Q50 – median flow, and GDDSPI and MAXSPI – growing degree days and maximum flood peak during spawning and incubation).