

ARTICLE

Landscape characteristics influence projected growth rates of stream-resident juvenile salmon in the face of climate change in the Kenai River watershed, south-central Alaska

Benjamin E. Meyer¹  | Mark S. Wipfli² | Erik R. Schoen³  | Daniel J. Rinella⁴ | Jeffrey A. Falke¹

¹Alaska Cooperative Fish and Wildlife Research Unit, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

²U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

³International Arctic Research Center, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

⁴U.S. Fish and Wildlife Service, Anchorage Conservation Office, Anchorage, Alaska 99503, USA

Correspondence

Benjamin E. Meyer
Email: ben@kenaiwatershed.org

Present address

Benjamin E. Meyer, Kenai Watershed Forum, Soldotna, Alaska 99669, USA

Abstract

Objective: Climate change is affecting the distribution and productivity of Pacific salmon throughout their range. At high latitudes, warmer temperatures have been associated with increased freshwater growth of juvenile salmon, but it is not clear how long this trend will continue before further warming leads to reduced growth. To explore the potential influence of climate warming on juvenile Chinook and Coho Salmon summer growth rates in southcentral Alaska, we coupled bioenergetics models with temperature sensitivity models for streams across the Kenai River watershed.

Methods: We measured diet ($n = 772$ stomachs) and growth ($n = 3,791$ weight/length values) under current conditions and used published air temperature projections to model growth for the 2030–2039 and 2060–2069 decades.

Result: We estimated direct effects of climate warming on juvenile growth (body mass at the end of May–September study period) will be primarily negative, ranging from +5.1% to –22.8% relative to a 2010–2019 baseline. Estimated effects depended on age cohort, feeding rate, and climate scenario. However, an extended growing season from warming could mitigate or offset predicted reductions in growth during midsummer.

Conclusion: Our results illustrate how diverse habitats are expected to produce variation in the magnitude of climate effects throughout juvenile salmon rearing environments.

KEYWORDS

early life history, physiology, riparian and stream

INTRODUCTION

Climate change is driving shifts in water temperature regimes throughout the range of Pacific salmon *Oncorhynchus* spp., but effects on freshwater rearing habitat are context specific and difficult to predict (Crozier and Zabel 2006; Schindler and Hilborn 2015). Even within Alaska, at the northern end of the Pacific salmon

distribution, increasing water temperature may be driving contractions in the distribution of thermally suitable rearing habitat in low-elevation, low-gradient drainages (Mauger et al. 2017) while simultaneously providing new opportunities for salmon in previously cold-limited areas (Schoen et al. 2017). Diverse landscapes can mediate the effects of broader climate signals on anadromous fish habitat in ways that depend on local geography, thus ensuring

that a climate trend will have neither unidirectional nor homogeneous effects on the wider ecosystem (Schindler et al. 2008; Lynch et al. 2016; Jones et al. 2020).

Among stream-rearing Pacific salmon, the growth rates of Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* may be especially sensitive to shifts in freshwater thermal regimes due to their longer freshwater residency times. In Alaska, these fish typically reside in streams for 1 year (Chinook Salmon) or 1–2 years (Coho Salmon) before migrating to sea (Quinn 2018). Freshwater growth rate is relevant because larger smolt size can influence age at marine entry, which in turn drives age structure and population stability (Cline et al. 2019), and growth is often positively correlated with marine survival (Henderson and Cass 1991; Ruggerone et al. 2009). In subarctic regions of interior Alaska, warmer stream temperatures have been associated with increased juvenile growth of both Chinook Salmon (Falke et al. 2019) and Coho Salmon (Armstrong et al. 2010). However, it is unclear whether this pattern holds in more temperate regions with historically warmer thermal regimes, such as the Gulf of Alaska region, or how long it will persist before further warming leads to reduced growth (Mauger et al. 2017; Shaftel et al. 2020). The effects of warming vary across geomorphically diverse watersheds, adding further complexity to how juvenile salmon growth responds to climate warming (Lisi et al. 2015).

Chinook Salmon populations in the Kenai River (south-central Alaska) support famed sport, commercial, and subsistence fisheries. These populations have experienced low productivity since 2005 (Fleischman and Reimer 2017), leading to harvest restrictions and closures as well as stimulating interest into past, present, and future drivers of growth and survival. In this study, we used a scenarios analysis informed by contemporary field data to explore how the summer growth rates of juvenile Chinook and Coho salmon may respond to rising air temperatures across the Kenai River watershed's diverse landscape. We measured water temperatures, juvenile salmon growth, and diet patterns in three geomorphically distinct sub-basins and in the main stem during the summer rearing periods of 2015 and 2016. We used these data for parameterizing air–water sensitivity and bioenergetics models to project changes in future summer growth under different climate and consumption scenarios (Hanson et al. 1997; Mohseni et al. 1998; Deslauriers et al. 2017). Fish bioenergetics models describe growth as a function of temperature and food ration and do not include other biological factors (stream productivity, predation, disease, and competition) or physical factors (flow regime [Poff et al. 1997], water quality, and habitat connectivity) that affect fish growth, but they allow for the modeling of changing conditions that are otherwise difficult to evaluate. To address

Impact Statement

As climate change warms water temperatures in salmon-bearing Gulf of Alaska watersheds over the next century, juvenile Chinook and Coho salmon that feed at lower rates and live in low-elevation tributaries are likely to see the greatest decreases in their summer growth rate.

the uncertainty of future conditions, we used a suite of climate and feeding rate scenarios for simulation inputs. Our approach allowed us to estimate the change in mass at the end of the summer growing season relative to baseline scenarios. We anticipated that three geomorphically distinct focal tributaries and the main-stem Kenai River would exhibit unique thermal regimes and feeding patterns and that juvenile Chinook and Coho salmon would display distinct patterns in growth rates that are attributable in part to these differences.

Our broader goals were to (1) illustrate how diverse landscapes filter the effects of climate change (Griffiths et al. 2014) on the rearing habitat of juvenile Chinook and Coho salmon, (2) characterize how juvenile growth rates in different freshwater habitats respond to a common regional climate signal, and (3) project how these varied responses may influence future growth. To accomplish these goals, we (1) characterized feeding rates and thermal conditions that contribute to differences in current growth rates and (2) used growth simulations to characterize expected juvenile summer growth rates in different habitat types under future climate change scenarios. We anticipated that the largest changes in summer growth under future warming climate scenarios would be observed at sites with the highest air–water temperature sensitivity. By identifying spatial and temporal patterns in variables that influence growth in proximate yet distinct habitats, we aimed to better understand how juvenile salmon productivity may respond to climate change in the context of diverse habitats.

MATERIALS AND METHODS

Overall approach

We measured air temperature, water temperature, and the growth rates and diet composition of juvenile Chinook and Coho salmon during May–September 2015 and 2016 at 10 sites within the Kenai River watershed. Based on these field data, we simulated juvenile growth during summer under current conditions using coupled stream

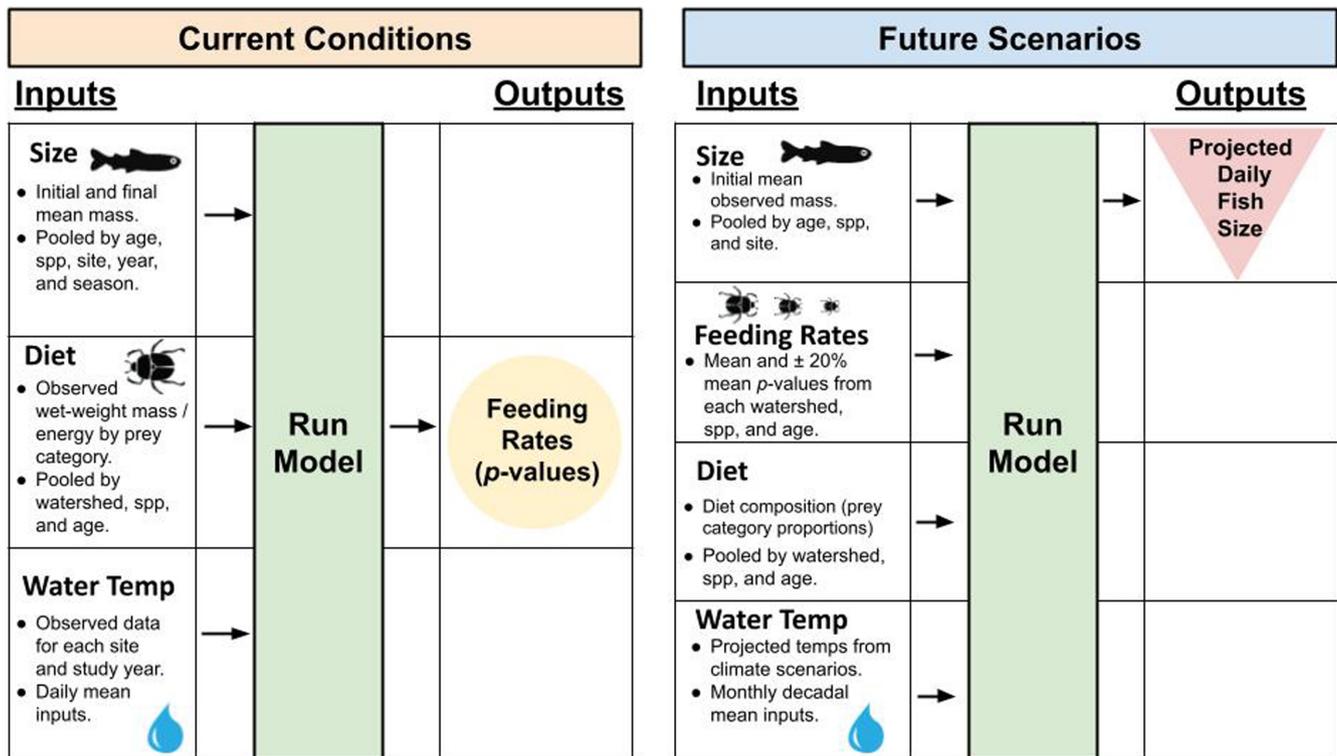


FIGURE 1 Schematic of inputs and outputs used in bioenergetics modeling to estimate fish growth under future climate and growth scenarios. Field data from the years 2015–2016 were used as inputs in season-length bioenergetics simulations of growth under current summer conditions, and feeding rate (p -value; or proportion of theoretical maximum consumption) estimates were the output. Next, future simulations were fitted to a range of consumption scenarios that were scaled relative to these current feeding rates. Water temperature (temp) inputs for future scenarios were based on empirical air–water sensitivity relationships and air temperature projections from downscaled climate models.

temperature models and bioenergetics models (Figure 1). We then compared the relative changes in growth from a 2010–2019 baseline period to those projected under various future temperature and feeding rate scenarios for the 2030–2039 and 2060–2069 decades. The stream temperature model generated monthly stream temperatures, which were input as daily values to a bioenergetics model that predicted the daily growth rate and size of idealized juvenile Chinook or Coho salmon. Our model used field-based empirical inputs for food, temperature, and fish size across geographically diverse habitats within the Kenai River watershed, emphasizing the diversity of food and water temperature conditions across space and time.

Study area

The Kenai River drains an area of 5,568 km² in south-central Alaska, running 182 km west from the Kenai Mountains and emptying into Cook Inlet near the city of Kenai (Figure 2). The watershed supports some of Alaska's most intensively managed and harvested salmon populations, including commercial, sport, subsistence, and personal-use fisheries. We conducted

field sampling in the Kenai River main stem and in three tributaries of the Kenai River during 2015 and 2016: Beaver Creek (lowland), Russian River (montane), and Ptarmigan Creek (glacial; Table 1). The lowland tributary is characterized as low elevation (21–65 m), low gradient, and dominated by wetlands. The resulting longer water residence time coupled with early season snowmelt was anticipated to produce higher daily mean water temperatures and to result in high sensitivity to air temperature (Mauger et al. 2017; Wells and Toniolo 2018). In contrast, the glacial tributary is characterized as high elevation (166–1,000 m), high gradient, and glacially influenced (7% ice coverage in the watershed; Table 1). The resulting low water residence time coupled with late-season snowmelt and glacial melt throughout the summer was anticipated to produce lower average water temperatures and lower sensitivity to air temperature. The montane tributary was intermediate in these attributes. The geography of the Kenai River watershed encompasses the range of watershed types found throughout the Gulf of Alaska catchment area (Sergeant et al. 2020); thus, the results gained from this study may be relevant for the broader region.

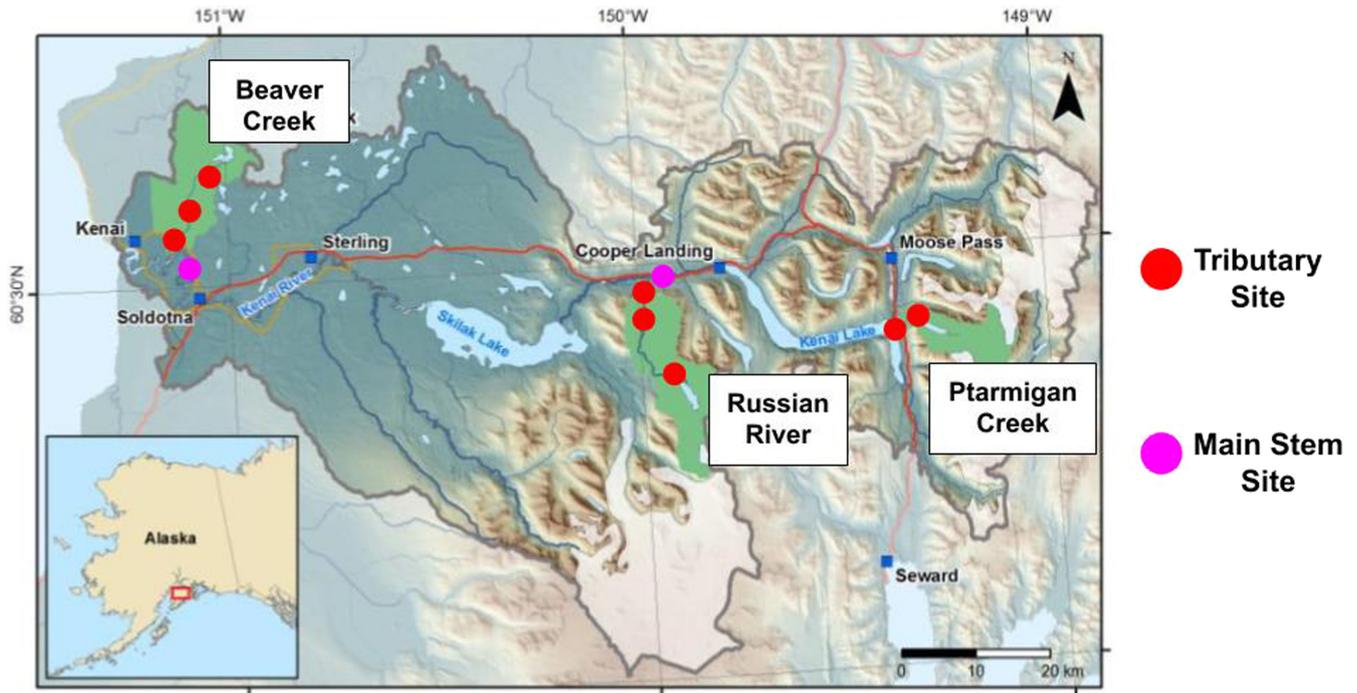


FIGURE 2 Map of the Kenai River watershed, Alaska, with study tributaries and fish sampling sites highlighted. The map is modified from Schoen et al. (2017).

TABLE 1 Landscape characteristic values for the main-stem Kenai River, Alaska, and tributaries, as derived from a U.S. Geological Survey 1-m digital elevation map (U.S. Geological Survey 2016). Overall Kenai River watershed values are from Benke and Cushing (2005).

Watershed	Elevation at mouth (m)	Ice cover in watershed (%)	Confluence with main-stem Kenai River (km)	Average gradient (%)	Watershed area (km ²)	Total length (km)
Lowland (Beaver Creek)	21	0	17	2	157	58
Montane (Russian River)	106	<1	121	9	163	90
Glacial (Ptarmigan Creek)	166	7	165	14	86	43
Main stem (Kenai River)	0	14	NA	23	5,200	132

Field sampling

Stream temperature

We acquired water temperature ($n = 14$ sites) and air temperature ($n = 11$ sites) data from an array of HOBO Temp Pro v2 loggers that were deployed during the summers of 2015 and 2016, U.S. Geological Survey stream gauge stations at Soldotna (station 15266300) and Cooper Landing (station 15258000; U.S. Geological Survey 2021), and National Weather Service archives for the Kenai Airport. Water and air temperature data were collected at a minimum of three sites per tributary and two sites in the main stem along a longitudinal gradient

from lower to upper reaches. We employed best practices and standards for collection of temperature time series as described by Mauger et al. (2015). Supplemental Information Section A (available in the online version of this article) describes site locations, methods used to ensure that the sites were representative of local environs using channel transects, equipment calibration, and logger check procedures.

Juvenile salmon capture

We sampled juvenile Chinook Salmon ($n = 1,145$) and Coho Salmon ($n = 2,646$) within the lower, middle, and

upper extents of their documented habitat (Reimer 2013) in each of the three focal tributaries (Figure 2). We also sampled sites in the main-stem Kenai River above the mouths of Beaver Creek and the Russian River (Figure 2). Fish sampling efforts were constrained to a 200-m length of stream centered around each water temperature logger site and were modified if fish capture success was low or if terrain prevented access. We sampled fish from main-channel and off-channel habitat at each site. Sites were visited approximately monthly (mean \pm SD = 31 ± 5 days) throughout May–August 2015 and May–September 2016 (summarized in Supplemental Information Section B, Figure B1). Coordinates for the fish sampling sites are listed in Table S1. At each fish sampling event, we used a handheld YSI 556 Multi-parameter Instrument or a Cooper-Atkins AquaTuff Instant Read thermocouple to record water temperatures ($^{\circ}$ C).

To capture juvenile salmon, we used Gee minnow traps baited with salmon eggs, which is an effective method for the passive capture of juvenile salmonids in pools and moving water in Alaska (Magnus 2006). Eggs were enclosed in perforated containers to prevent consumption but permit scent to escape. We suspended 12–20 traps at water depths of 15–45 cm, ensuring that the sites were undisturbed by foot traffic so as not to alter the community of invertebrates that were normally available as juvenile salmon prey. The traps were deployed for 2–4 h/set. We ensured that all salmon eggs used as bait were commercially sterilized or disinfected with a 10-min soak in a 1/100 Betadine solution prior to use.

We anesthetized captured juvenile salmon prior to measurement and diet sampling by submersion in a 20–40-mg/L eugenol (AQUI-S) bath for 2–3 min. Once individuals exhibited a total loss of equilibrium, we removed them from the bath, measured FL to the nearest millimeter, and recorded weight to the nearest 0.1 g. We allowed fish to recover in aerated water until equilibrium was fully regained, and we retained them in the stream in a mesh basket to prevent same-day recaptures. We identified, recorded, and released all non-target fish species (e.g., Slimy Sculpin *Cottus cognatus* or Rainbow Trout *O. mykiss*). We released all fish near the point of capture when daily sampling was complete.

For a subset of juvenile Chinook Salmon ($n = 219$) and Coho Salmon ($n = 553$), we sampled scales and stomach contents to determine age and diet composition for bioenergetics models. At each monthly site visit, we aimed to sample up to 16 juvenile Chinook Salmon and 16 Coho Salmon with FLs of 50 mm or greater (Table S2). All sizes of juveniles were included in size measurements to enable recording of representative size frequency data, and fish smaller than 50 mm FL represented a small fraction of age-0 fish.

We randomly selected 50-mm FL and larger fish in the field, and the gut contents were flushed out of the mouth and into a 250- μ m sieve by using a gastric lavage technique with a modified syringe (Culp et al. 1988). We preserved the gut contents in a minimum of 70% ethanol in a Whirl-Pak bag.

Juvenile salmon age and growth

We aged scales from the same fish that were selected for stomach content analysis and used this information along with length–age relationships to assign an age to each individual fish (Quist et al. 2012). Methods for aging scales and predicting the age-cohort for salmon without aged scales are outlined in Supplemental Information Section C.

We quantified the growth of juvenile salmon in sampling strata with adequate sample sizes of stream-rearing parr. We excluded age-2 Coho Salmon and age-1 Chinook Salmon from our analyses, as these cohorts were anticipated to be almost exclusively presmolt out-migrants (Shields and Dupuis 2017) and sample sizes were small. Sample size for juvenile Chinook and Coho salmon was variable across sampling events (range = 1–168 individuals per species/age-cohort), due in part to the patchy distribution of fish across the landscape. We excluded iterations involving less than three observations when segregated by age, species, and sample event due to small sample size. We also excluded cases in which the mean fish weight declined between sampling events, which suggested out-migration of larger individuals (2 of 55 cases). After applying these inclusion standards, 72% (108/150) of the total possible combinations of sample event, age, and species remained.

We examined the temporal and spatial scales at which fish growth patterns could be segregated and compared. First, we explored the possibility of grouping and averaging data from sites within each study watershed. We observed significant differences in daily mean temperature (June 1–August 20) among sites within two of the four watersheds (the montane and main-stem watersheds; Kruskal–Wallis test: $p < 0.05$), and we elected to retain all sites as segregated locations in further analyses.

To select an appropriate growth metric, we used a linear mixed-effects approach. The metric of final weight (mean weight on August 6, the earliest day for a final site visit among both years and all sites) was selected as the response metric for comparison among future scenarios. See Supplemental Information Section D for further details on linear mixed modeling methods and results.

We investigated whether summary thermal metrics from June 1 to August 6 (mean, minimum, and maximum

temperatures and the frequency of daily mean temperature values $> 15^{\circ}\text{C}$) were associated with final size at the scale of individual cohort (i.e., a unique fish age, species, and sampling site) and year. We examined the 15°C threshold because temperatures exceeding this value during the juvenile rearing phase have been associated with reduced salmon growth rates (Richter and Kolmes 2005) and reduced Chinook Salmon population productivity in south-central Alaska (Jones et al. 2020). Furthermore, Alaska water quality regulations specify 15°C as a temperature of concern for growth and propagation of fish (Alaska Department of Environmental Conservation 2020).

Juvenile salmon diet

We examined stomach content samples under $4.0\times$ dissecting microscopes. Distinguishable invertebrates ($n = 8,879$) were identified to the family level or the lowest feasible taxon ($n = 112$ taxon–life stage combinations identified), and body lengths were measured to the nearest 1.0 mm (Merritt and Cummins 1996). We estimated the lengths of partially digested prey based on intact individuals of the same taxon that appeared similar in size (Wipfli 1997). When intact individuals of the taxon were absent from a sample, we assumed that the head and thorax represented one-third of the total length of partially digested prey (Gonzales 2006). Diet items that we could not positively attribute to ingestion of prey (e.g., exoskeletons,

separated insect wings or legs, empty Trichoptera casings, and head capsules unidentified to genus) were recorded but not included in diet proportions.

We characterized diet proportions in terms of mass, the most applicable metric for energy flow and food web studies (Chippis and Garvey 2007). We determined the dry mass of individual invertebrates by using the allometric formula

$$W = aL^b, \quad (1)$$

where W is the total dry body mass, L is the total body length, and a and b are constants (Ricker 1973). We derived the length–mass regression constants a and b and percent dry mass values from a database of over 100 genera with values published in existing literature and from a study of Alaskan stream invertebrates (Meyer 2019). For juvenile fish prey items, we used regression constants from the length–weight relationship developed from age-0 Coho Salmon that were captured during this study (B. E. Meyer, unpublished data). We converted prey item dry mass to wet mass using the relationships reported by McCarthy et al. (2009). We summarized diet composition using the following six categories: (1) immature aquatic invertebrates, (2) terrestrial invertebrates, (3) adult aquatic invertebrates, (4) salmon eggs, (5) non-salmon fish eggs, and (6) invertebrates of unknown origin. Juvenile fish prey items were grouped with the salmon eggs prey category. Using literature references (Table 2), we assigned energy density values to the six prey categories for use in bioenergetics modeling.

TABLE 2 Diet proportion inputs used for bioenergetics modeling in projected climate scenarios. Numerical values below prey categories are energy density (J/g) estimates from the literature sources indicated in the footnotes.

Drainage	Salmon species	Age	Fish eggs (5,235 J/g) ^a	Immature aquatic invertebrates (3,365 J/g) ^b	Terrestrial invertebrates (5,250 J/g) ^b	Adult aquatic invertebrates (4,225 J/g) ^b	Salmon eggs (9,000 J/g) ^c
Lowland (Beaver Creek)	Chinook	0	0.00	0.46	0.02	0.52	0.00
	Coho	0	0.00	0.53	0.03	0.44	0.00
	Coho	1	0.04	0.50	0.07	0.39	0.00
Montane (Russian River)	Chinook	0	0.00	0.35	0.02	0.18	0.45
	Coho	0	0.01	0.46	0.04	0.38	0.12
	Coho	1	0.00	0.47	0.05	0.43	0.04
Glacial (Ptarmigan Creek)	Chinook	0	0.00	0.73	0.09	0.17	0.00
	Coho	0	0.00	0.13	0.03	0.10	0.74
	Coho	1	0.05	0.59	0.14	0.16	0.06
Main stem (Kenai River)	Chinook	0	0.00	0.68	0.04	0.27	0.02
	Coho	0	0.00	0.10	0.27	0.10	0.53
	Coho	1	0.00	0.82	0.00	0.07	0.12

^aBeauchamp et al. (1989).

^bMcCarthy et al. (2009).

^cArmstrong (2010).

Projected future trends in water temperature and salmon growth

Stream temperature

We used published projections of air temperature along with our field data on air and water temperature to estimate future water temperatures for use in bioenergetics simulations (Figure 1). For the simulations based on 2015 and 2016 field data, we used the observed daily mean water temperatures. For water temperatures in scenarios involving projected air temperatures and varied feeding rates, we used projected air temperatures and observed air–water sensitivity. We calculated air–water sensitivity ($\Delta^{\circ}\text{C } T_{\text{Water}} / ^{\circ}\text{C } T_{\text{Air}}$), a metric quantifying the average change in stream temperature (T_{Water}) per 1°C change in air temperature (T_{Air}), for each water temperature logger site associated with a fish sampling site ($n = 10$; Mohseni et al. 1999). We calculated weekly mean values of air and water temperatures for each week of the 2015–2016 study periods that had $<30\%$ of observations missing, and we fitted a linear regression for each site using the weekly mean values from both years. We used a linear relationship because streams in cool climates like the Kenai Peninsula rarely experience temperatures greater than 20°C , as evaporative cooling effects flatten out the air–water temperature relationship (Mohseni et al. 1998). We selected weekly mean temperatures rather than a shorter time interval because a weekly time scale allows for integration across daily fluctuations in factors that influence temperature, such as high precipitation or drought, and generally produces better correlations (Erickson and Heinz 2000). We developed the sensitivity relationships from the period of days with observations common to all sites and years (June 1–August 20), with the exception of the lower Russian River site, for which the earliest available observation of water temperature data in 2015 was June 22.

For daily water temperature inputs in the scenarios modeling, we used projected water temperatures derived from site-specific air–water temperature sensitivity relationships based on 2015–2016 field data. We used down-scaled projections of mean monthly air temperatures as inputs following the linear formula

$$T_{\text{Water}} = m(T_{\text{Air}}) + b, \quad (2)$$

where m and b are the site-specific slope and intercept values (Table S4). Monthly decadal mean down-scaled air temperatures published by the Scenarios Network for Arctic and Alaska Planning (SNAP) based on the mean of the five best-performing global climate models for Alaska were used as daily input values for May–September in 2010–2019, 2030–2039, and 2060–2069 under the RCP

(representative concentration pathway) 6.0 (mid-range CO_2 emissions) and RCP 8.5 (rapid-increase CO_2 emissions) scenarios (Walsh et al. 2008; Intergovernmental Panel on Climate Change 2014; Scenarios Network for Alaska and Arctic Planning 2014). To investigate performance of the stream temperature models, we regressed mean monthly water temperatures that were observed during the 2015–2016 field season against those that were predicted for the same time period by each model using SNAP data inputs.

Projected juvenile salmon growth

We used a two-step modeling process to estimate projected effects of shifting water temperature regimes on juvenile salmon summer growth (Figure 1). First, we modeled salmon growth and consumption under current conditions using field data from the summers of 2015–2016 as inputs. We performed a simulation for each cohort (i.e., unique iteration of sampling site, year, fish species, and fish age) fitted to mean initial and final weights for intervals between sequential site visits throughout the summer growing season. We summarized diet composition inputs in terms of mean proportion by weight of each diet item category (Table 2). We calculated diet proportions segregated at the scale of watershed, age, and species while pooling samples across individual sites, years, and sampling events. We used the coarser spatiotemporal scale for diet inputs because gastric lavage samples provide a “snapshot” of diet intake, and the pooling of diet samples reduces the influence of random variability on diet composition model inputs (Chipps and Garvey 2007). For daily food inputs, simulations used constant diet proportions and energy density values throughout each simulation. The output of these simulations was an estimated feeding rate that was expressed in terms of a proportion (p -value) of the theoretical maximum consumption rate under the observed conditions (Jobling 1994).

Second, we simulated salmon growth rates under a range of potential future scenarios of climate warming and feeding rates. We used the feeding rates estimated from the simulations of current conditions to generate three feeding rate scenarios per cohort for modeling future growth (Table S3). The three rates that we used to fit the simulations included (1) the mean feeding rate under current conditions, (2) a 20% increase in the mean feeding rate, and (3) a 20% decrease in the mean feeding rate, intended to represent low, medium, and high feeding rate scenarios.

Future salmon growth was projected from May 26 to September 4. The start date was the earliest day of available fish weight data common to all sites and fieldwork years, and the end date was calculated as the earliest final

fish sampling event (August 6) plus an additional 30 days to include the remaining summer season. Starting weight for each scenario simulation was the mean weight (either observed or linearly interpolated) on May 26 from the simulations of current conditions.

We estimated the direct effects of climate warming on growth in terms of the percent change in final body weight relative to the 2010–2019 simulations. We used Fish Bioenergetics 4.0 in R Shiny, which allows users to simulate fish growth based on the Wisconsin bioenergetics model (Hanson et al. 1997; Deslauriers et al. 2017). The model treats growth rate as the net balance from energy intake (food consumption) minus energy costs (metabolism, activity, and digestion).

To address the uncertainty of future conditions (Ney 1993), we used a suite of climate and feeding rate scenarios for growth simulation inputs. We performed a total of 378 unique growth simulations (21 cohorts \times 2 climate scenarios \times 3 feeding rate scenarios \times 3 decadal periods). We used Stewart and Ibarra's (1991) bioenergetics parameter values for both species, which were adapted for Chinook Salmon from a bioenergetics model for Coho Salmon. Although these parameters were originally calibrated for adult fish, they have accurately predicted the growth of juvenile Chinook Salmon in laboratory and field settings (Madenjian et al. 2004). Plumb and Moffitt (2015) found that Stewart and Ibarra's (1991) parameters overestimated the metabolic consequences of higher temperatures for subyearling Chinook Salmon; therefore, to minimize parameter error, recent studies have employed modified temperature-dependent consumption parameters for both species when simulation temperatures are greater than 18°C (Davis et al. 2019). However, none of the daily water temperature inputs in our simulations exceeded 18°C; thus, the Stewart and Ibarra (1991) parameters

were employed for all simulations. Previous bioenergetics modeling efforts with Alaskan juvenile Chinook Salmon found that the Stewart and Ibarra (1991) parameters were better suited to describe growth than the Plumb and Moffitt (2015) parameters (Falke et al. 2019). We verified that our response variable, simulated mean weight on August 6, corresponded with observed or linearly interpolated values (simulated mean weight = $0.39 + 0.97$ [observed mean weight], $r^2 = 0.90$), suggesting that our model was able to represent the growth patterns found in our empirical observations. For input parameters that were not measured directly in the field, data pertaining to juvenile Chinook and Coho Salmon energetics were obtained from values included with Fish Bioenergetics 4.0 (Deslauriers et al. 2017). Indigestibility values of 17% and 3% were assigned to invertebrate and fish diet items, respectively (Beauchamp et al. 2007).

RESULTS

Fish capture

Age-0 Chinook Salmon and age-0 and age-1 Coho Salmon were captured throughout the study area (Table 3), with juvenile Chinook Salmon being relatively sparse compared to juvenile Coho Salmon in tributaries, whereas in the main stem Chinook Salmon were more commonly captured (Table S2).

Water temperature

Observed water temperatures ranged from 5.3°C to 19.6°C (mean \pm SD = $12.3 \pm 2.2^\circ\text{C}$) during the set of

TABLE 3 Overall summary of fish size, weight, and FL values (mean \pm SD). Coho Salmon were captured in greater numbers than Chinook Salmon in all watersheds except the main-stem Kenai River. This table summarizes the overall catch results found in Table S2.

Watershed	Salmon species	Age	Mean FL (mm)	Mean weight (g)	N
Lowland (Beaver Creek)	Chinook	0	54.3 \pm 6.9	1.9 \pm 0.8	203
	Coho	0	57.5 \pm 10.1	2.3 \pm 1.3	257
	Coho	1	82.2 \pm 11.7	6.7 \pm 2.8	1,132
Montane (Russian River)	Chinook	0	56.2 \pm 9.4	2.2 \pm 1.1	102
	Coho	0	53.9 \pm 7.8	1.9 \pm 0.9	821
	Coho	1	77.4 \pm 12.4	5.6 \pm 2.7	219
Glacial (Ptarmigan Creek)	Chinook	0	70.9 \pm 7.7	4.1 \pm 1.2	30
	Coho	0	61.1 \pm 8.4	2.6 \pm 1.1	92
	Coho	1	82.6 \pm 11.4	6.6 \pm 2.8	292
Main stem (Kenai River)	Chinook	0	55.8 \pm 8.4	2.1 \pm 0.9	840
	Coho	0	48.3 \pm 4.9	1.3 \pm 0.4	276
	Coho	1	79.6 \pm 14.3	6.1 \pm 3.1	11

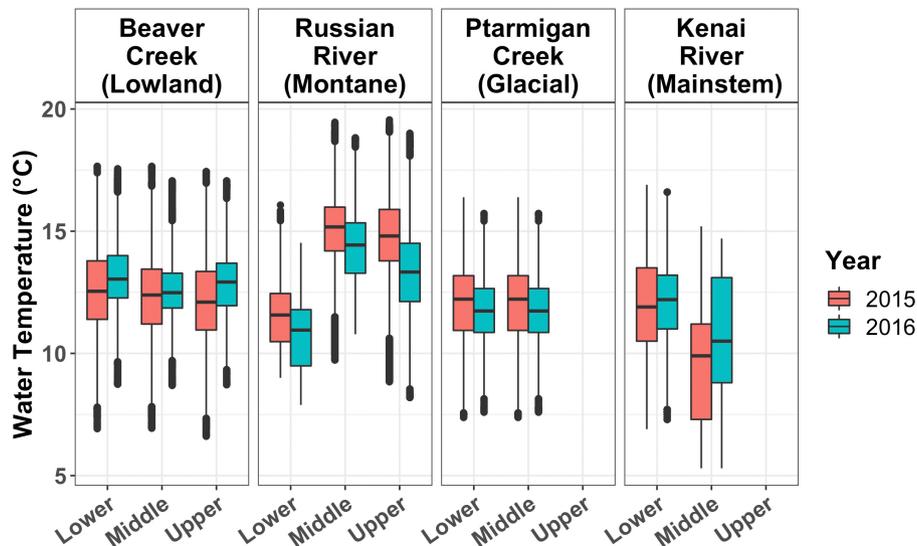


FIGURE 3 Observed water temperatures by site and year (observations at 0.25-h intervals) for the lower, middle, and upper reaches of each watershed. Water temperatures shown include those from the subset of time with data common to all sites and years (June 1–August 20). The horizontal line within each box represents the median temperature, the lower and upper limits of each box correspond to lower and upper quartiles, the vertical lines correspond to minimum and maximum observations, and the points represent outliers.

days with data common to both years of fieldwork (June 1–August 20; Figure 3). Overall, sites in the montane watershed had the highest mean water temperature (mean \pm SD = $13.3 \pm 2.4^\circ\text{C}$), followed by the lowland ($12.6 \pm 1.7^\circ\text{C}$), glacial ($11.8 \pm 1.6^\circ\text{C}$), and main-stem ($11.1 \pm 2.4^\circ\text{C}$) drainages. Instantaneous temperature exceeded 15°C at all sites at least once, though daily mean values exceeded 15°C only at the middle and upper montane sites. Mean water temperatures across all sites were not consistently higher or lower in 2015 than in 2016 (Figure 3).

Observed air–water sensitivities

Air–water temperature sensitivity (i.e., the slope of the air–water temperature relationship) was highest in the lowland tributary and lowest in the glacial tributary and main stem, with the montane tributary exhibiting intermediate values. Sites with higher air–water sensitivities generally had higher correlations (r^2 values) between observed air and water temperatures ($n = 10$ sites; coefficient of determination [r^2] = $-0.08 + 0.83 \times \text{sensitivity}$; $r^2 = 0.47$; $p < 0.05$). The glacial watershed exhibited notably lower air–water sensitivity and correlation values than the other watersheds, which generally had higher values (Figure 4). Sensitivity values ranged from 0.64 to 0.74 at sites in the lowland watershed, from 0.45 to 0.67 in the montane watershed, from 0.20 to 0.32 in the glacial watershed, and from 0.68 to 0.72 in the main stem. Correlation values ranged from 0.61 to 0.70 in the lowland watershed, from 0.19 to 0.48 in the montane watershed, from 0.04 to

0.17 in the glacial watershed, and from 0.20 to 0.35 in the main stem. Linear model parameters for regressions that were used to estimate air–water sensitivity at each site are reported in Table S4.

Projected water temperatures

Decadal monthly mean projected water temperatures from air–water temperature sensitivity models for the 2010–2019 decade ranged from 6.2°C to 15.3°C (mean \pm SD = $11.1 \pm 1.9^\circ\text{C}$; Figure 5). The greater range of values in the observed water temperatures relative to the projected temperatures arose from the difference in temporal scale of the two data sets, as observed water temperature measurements were made at 15-min intervals, while projected water temperatures were monthly decadal means.

Projected water temperatures generated using the 2010–2019 decadal mean air temperature inputs showed minimal systematic differences from the observed 2015–2016 summer water temperatures, with an overall mean absolute difference \pm SD of $0.30 \pm 1.22^\circ\text{C}$. Correlation values (r^2) between projected and observed monthly mean water temperatures ranged from 0.22 to 0.95 among sites. Mean projected monthly water temperature differed only slightly between the mid-range and rapid-increase scenarios (absolute difference: mean \pm SD = $0.2 \pm 0.0^\circ\text{C}$).

The magnitude of projected change under future climate scenarios was generally smallest in the glacial watershed and largest in the main-stem and lowland watersheds (Figure S1). Projected water temperatures increased by

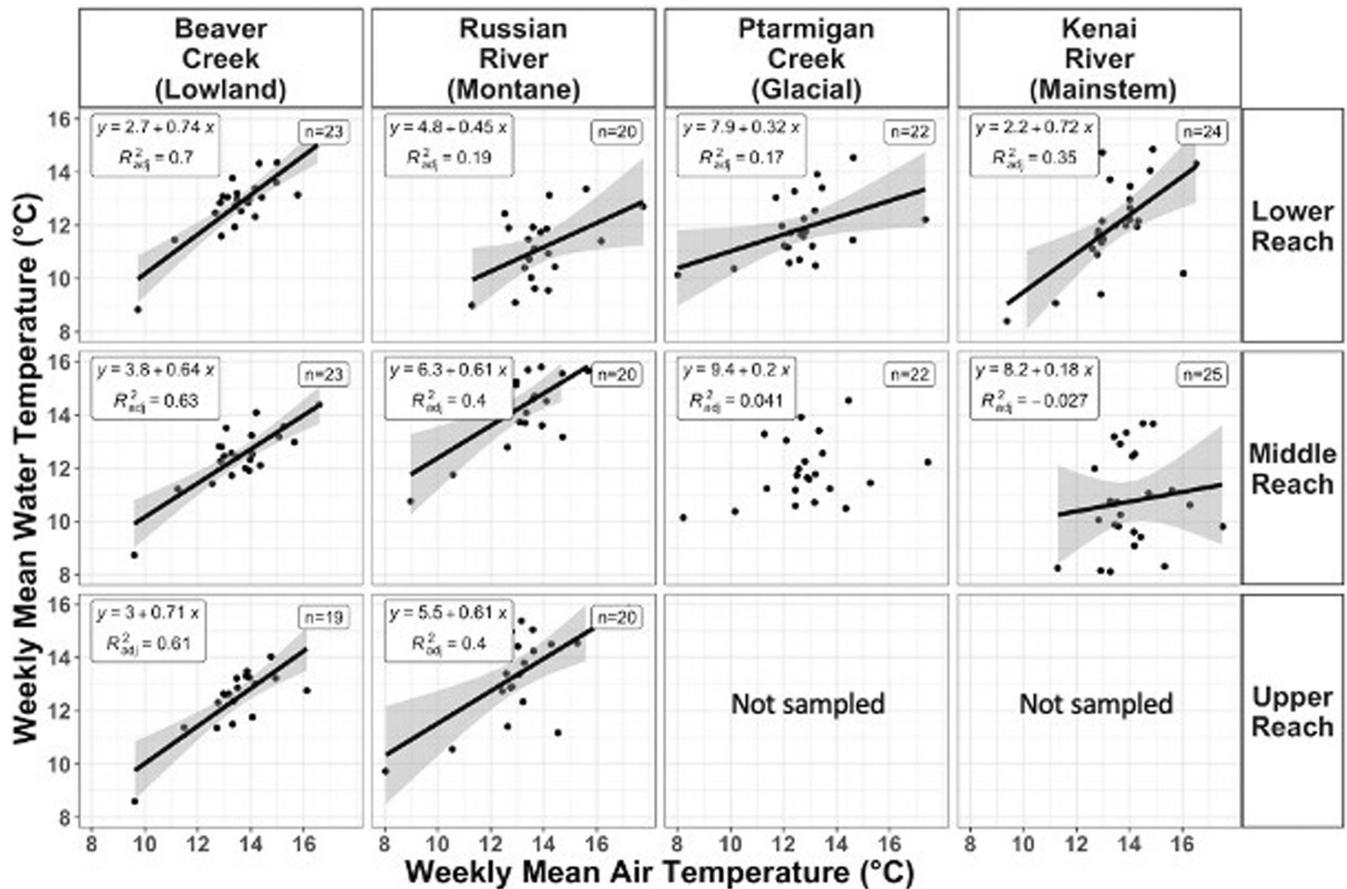


FIGURE 4 Linear regressions fitted to weekly mean air and water temperature values for each site (lower, middle, and upper reaches of each study watershed). Statistically significant relationships ($p < 0.05$) are shown with a trend line (solid black line) and 95% confidence band (gray shaded area). Adjusted R^2 (R^2_{adj}) values are provided. Model output and estimates for individual regressions are available in Table S4.

a greater magnitude under the rapid-increase climate scenario than under the mid-range scenario at all sites (Figure S1). Under the rapid-increase emissions scenario, the mean change in water temperature relative to 2010–2019 ranged from 0.2°C to 1.8°C among sites and decades, while under the mid-range emission scenario the range was 0.1–1.1°C.

Juvenile salmon diet

In total, 13,723 individual items were identified from 772 diet samples. Among the 11,983 diet items that were recognizable as individual organisms, 8,879 of them were identifiable as specific taxa and the remaining items were classified as “unknown invertebrates” without a wet mass estimate or assigned energy value. Terrestrial and marine subsidies (terrestrial invertebrates and salmon eggs) composed over 40% of the overall diet by wet mass in 8 of 12 iterations of watershed, species, and age (averaged between both years; Table 2; Figure 6). Fish smaller than 60 mm FL did not consume salmon eggs or unidentified fish eggs.

Juvenile fish were rare as a prey item (5 of 8,879 identifiable items).

Observed juvenile salmon growth

The final size of salmon parr (mean mass on August 6) by age and species varied markedly across sites and years (Figure 7). Basic thermal metrics at each temperature logger site (mean, maximum, and minimum temperatures and the frequency of 0.25-h temperature observations $> 15^\circ\text{C}$) were not predictive of final size (all r^2 values < 0.01 ; $p > 0.05$).

Projected juvenile salmon growth under future scenarios

The projected summer growth response of juvenile salmon to the direct effects of climate warming was negative in almost all cases, with a mean \pm SD of $-4.91 \pm 0.3\%$ and ranging from +5.1% to -22.8%

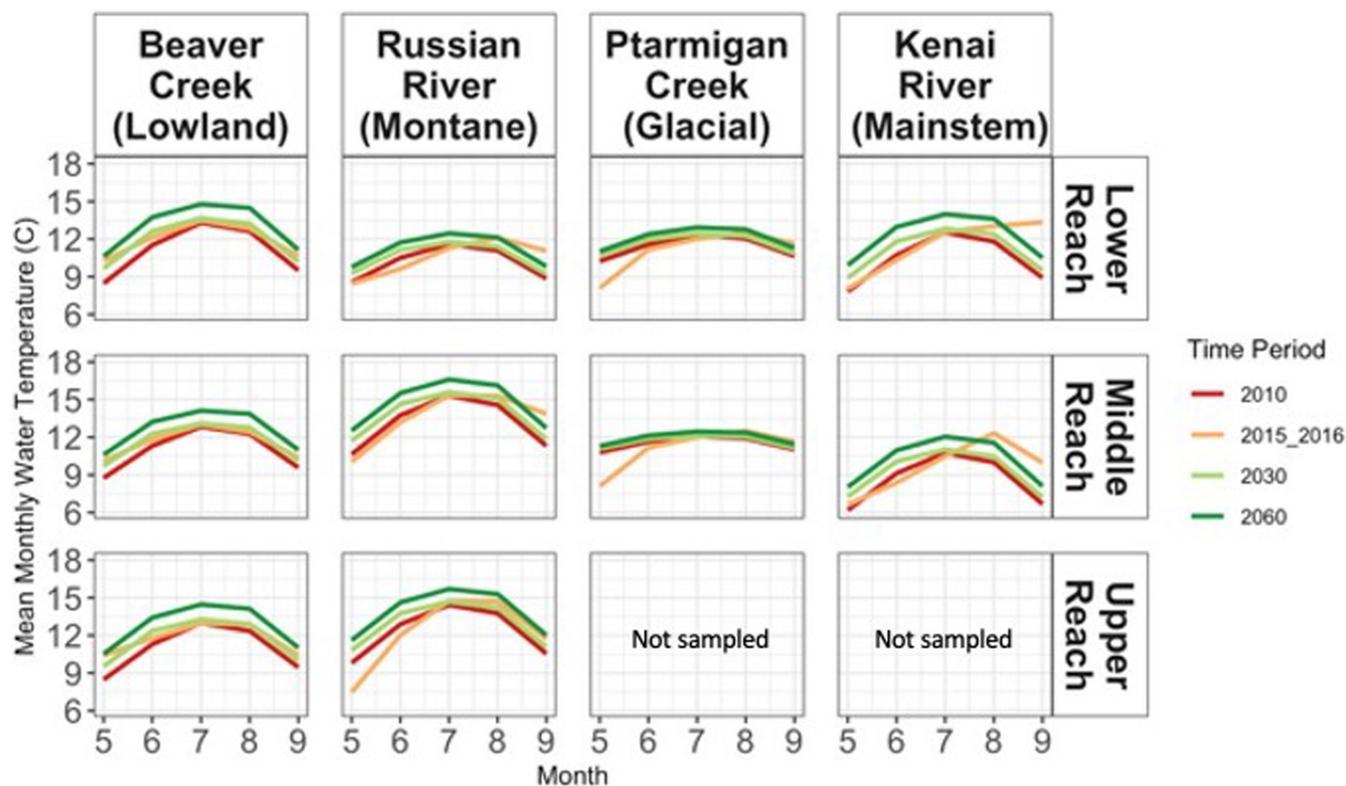


FIGURE 5 Observed and modeled water temperatures ($^{\circ}\text{C}$; monthly means for May–September) for each site and period. Modeled monthly mean temperature values shown are from the RCP 8.5 (rapid-increase CO_2 emissions) scenario. Monthly means were not significantly different between the RCP 6.0 (mid-range CO_2 emissions) and RCP 8.5 climate scenarios (Wilcoxon rank-sum test: $W = 12,971$, $p = 0.46$), so only the RCP 8.5 scenario is shown here. For growth simulations, monthly decadal average values were input at a daily time step.

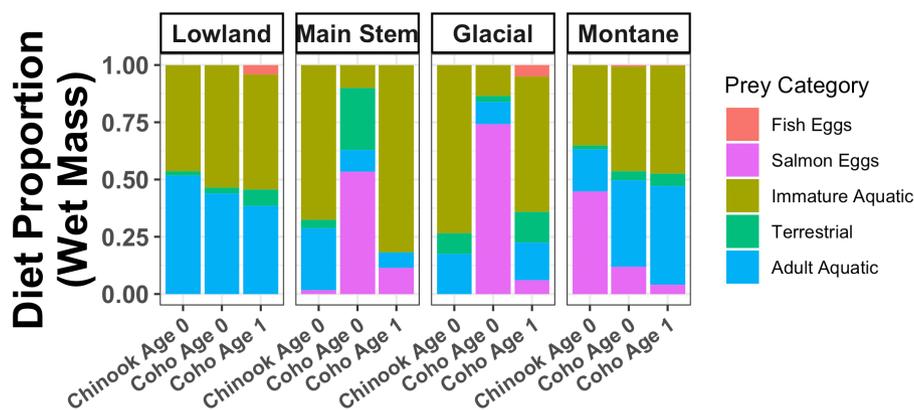


FIGURE 6 Overall diet proportions segregated by cohort (age and salmon species) and drainage (lowland = Beaver Creek; main stem = Kenai River; glacial = Ptarmigan Creek; montane = Russian River). Prey category values were calculated from mean wet mass ($n = 772$ stomachs). Immature aquatic, terrestrial, and adult aquatic are invertebrate categories.

among decades across cohorts, feeding rate scenarios, and climate scenarios (Figure 8). Nearly all cohorts saw a decrease in final mass under at least one future scenario relative to the 2010–2019 simulations, and 3 of the 21 total cohorts exhibited at least one future scenario in which fish mass increased (Table S5). For most cohorts, increased feeding rate (+20%) scenarios generally produced a smaller magnitude of

response relative to low feeding rate scenarios (–20%; Figure 8).

DISCUSSION

Juvenile salmon mass at end of the summer simulation period was projected to decline by the 2030s and 2060s

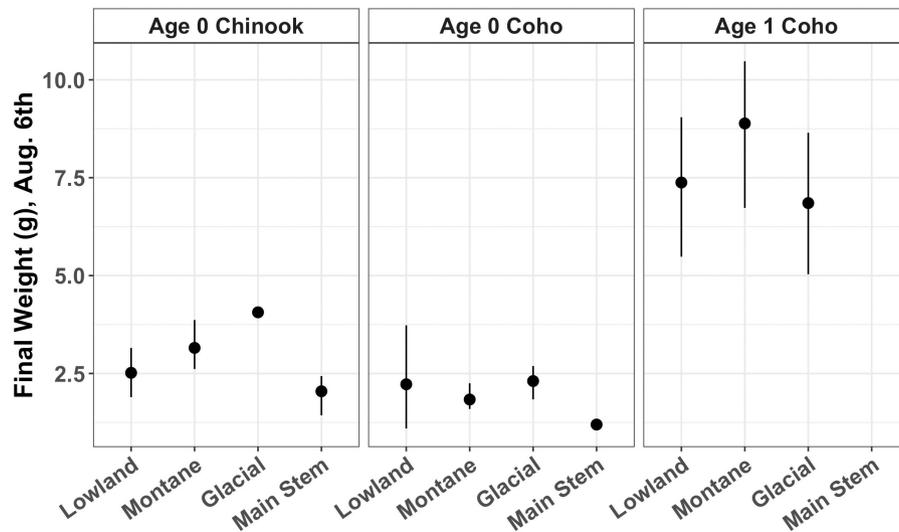


FIGURE 7 Final mean size (g) on August 6 for juvenile salmon populations by age and species from 2015 and 2016 data (watersheds: lowland = Beaver Creek; montane = Russian River; glacial = Ptarmigan Creek; main stem = Kenai River). Error bars indicate the maximum and minimum values for all years and cohorts within a drainage. Error bars are not visible when the range of minimum and maximum values is small and obscured behind the point.

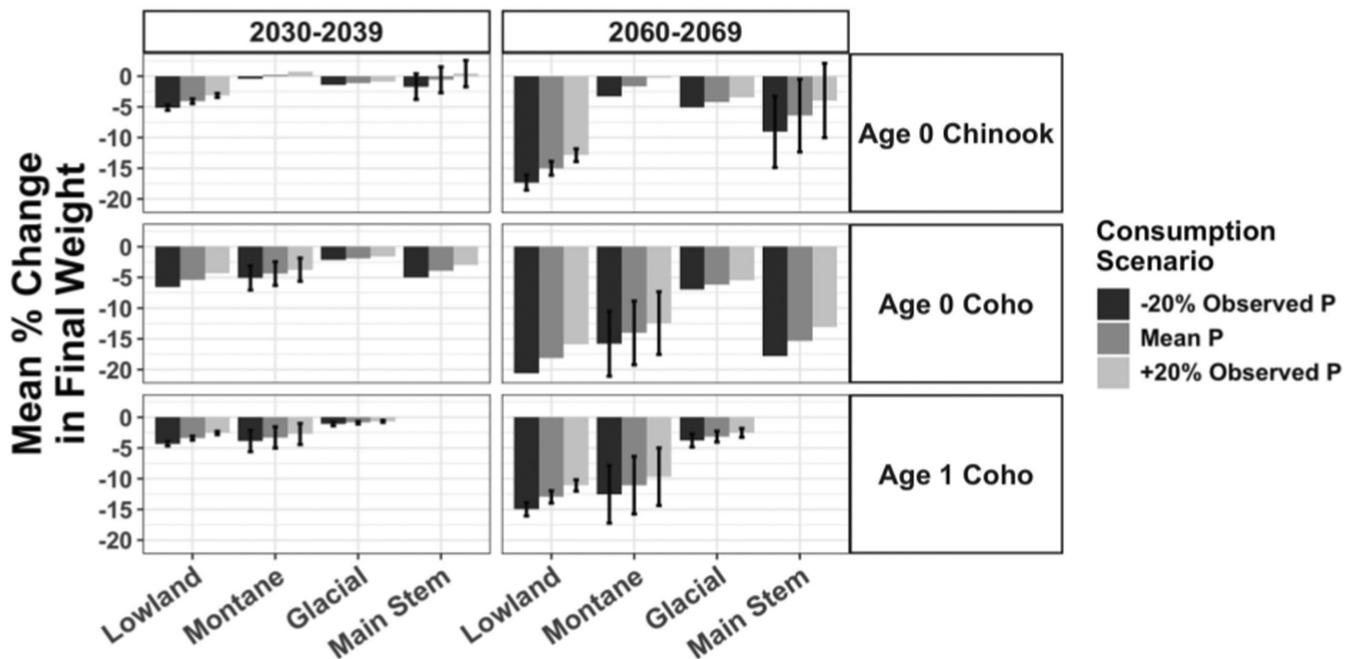


FIGURE 8 Mean change in simulated juvenile salmon size at the end of summer (September 4) in 2030–2039 and 2060–2069 relative to 2010–2019 based on RCP 8.5 emissions scenarios, ranging from +2.6% to –23.3%. Consumption scenarios indicate the mean or $\pm 20\%$ of the observed feeding rate (p = proportion of theoretical maximum consumption). Error bars are SDs among multiple sites within a watershed (lowland = Beaver Creek; montane = Russian River; glacial = Ptarmigan Creek; main stem = Kenai River). Absence of error bars indicates that only one site within a watershed had sufficient population data to perform simulations. See [Table S5](#) for complete results of the percent change in simulated size relative to 2010–2019.

relative to the 2010–2019 time period under most of the climate and feeding rate scenarios modeled in this study. These results suggest that climate warming over the next 10–50 years could reduce the summer growth rates of juvenile Chinook and Coho salmon across a wide diversity

of habitat types, even if salmon are able to substantially increase their feeding rates. However, this result does not necessarily indicate that fish mass at the end of the full growing period (spring–fall) will decline, as an extended growing season could compensate for some of the

reduced growth during summer (Armstrong et al. 2021). No existing models can predict the responses of complex systems to climate change with certainty (Schindler and Hilborn 2015); instead, our goals were to project the likely responses of juvenile salmon among distinct environments to plausible future climate scenarios and to highlight the degree of variation in responses to a regional climate signal.

Temperature effects

Observed water temperatures

The range of summer temperatures observed in our study was intermediate relative to those in other well-studied salmon systems, such as the warmer Columbia River system (Chang and Psaris 2013) or the generally cooler Bristol Bay systems (Lisi et al. 2013). Surprisingly, our montane tributary was on average slightly warmer than the lowland system, though this could be an artifact of specific site locations (i.e., the presence of lakes) rather than overall means throughout the watersheds. A more detailed reach-scale spatial stream network model will reveal more detailed stream temperature patterns throughout the region (Ver Hoef et al. 2006; Isaak et al. 2014). The glacial tributary in our study was generally warmer than other glacial systems studied in Southeast Alaska (Fellman et al. 2014), which could be attributable to warming effects of the large lake that was situated upstream of our sampling sites (Lisi et al. 2013).

Water temperature logger data collected at main-stem sites are commonly used to interpret biological effects on juvenile salmonid populations, but a growing body of evidence suggests that main-channel water temperatures do not fully encompass their actual thermal experience (Limm and Marchetti 2009; Armstrong et al. 2013; Huntsman and Falke 2019). For example, juvenile Coho Salmon consume sources of abundant, energy-dense foods, such as salmon eggs (Armstrong et al. 2013) or benthic macroinvertebrates (Baldock et al. 2016), in cool habitats and then return to warmer off-channel habitats to optimize metabolism. Despite these and other well-documented examples of behavioral thermoregulation, it remains unclear whether it is the exception or the rule among stream-rearing juvenile salmon at high latitudes.

Projected future water temperatures

Monthly mean water temperature in future time periods saw increases proportional to site-specific sensitivity values, with both sensitivity and air-water temperature

correlation generally decreasing with increasing stream gradient and glacial influence. Our models simulated monthly mean water temperatures with 23–94% accuracy for observed 2015–2016 monthly mean water temperatures, with lower accuracy at higher-elevation sites, consistent with previous work in the Cook Inlet region (Mauger et al. 2017; Shaftel et al. 2020). Although correlation values are lower at some of our study sites, the predicted temperatures overall were close to the observed values in terms of mean difference (mean \pm SD = $0.30 \pm 1.22^\circ\text{C}$). The approach of using monthly decadal averages masks the effects of some phenomena that influence thermal regime, such as a drought periods resulting in warmer water temperatures. However, the time scale is appropriate for our model inputs because more granular time scales of stream temperature projection have been shown to exhibit limited accuracy (Arismendi et al. 2014).

Glacial melt will likely moderate the influence of warming air temperatures in our study systems even well into the 2060–2069 period (McGrath et al. 2017), but cooler thermal summer regimes resulting from glacial melt, as has been seen in some Southeast Alaska streams (Fellman et al. 2014), are an unlikely outcome of ongoing climate warming. Although Southeast Alaska watersheds above a threshold of 30% glacial coverage saw cooling as a result of glacial melt, the two glacially influenced watersheds in this study (Ptarmigan Creek: 7% ice coverage; main-stem Kenai River: 14% ice coverage) are well below 30% glacial coverage.

Future research will continue to improve the accuracy of stream temperature models, potentially accounting for a suite of factors beyond the scope of this study, including glacial and snow melt (Cline et al. 2020), interaction with groundwater, flow and discharge rates, solar radiation, wind, and humidity (Arismendi et al. 2014). Non-stationary processes that shift the proportions of a watershed's input sources through time, such as drying wetlands, shifts in precipitation trends, or glacial retreat, will be of consequence for long-term changes in sensitivity relationships (Klein et al. 2005; Bliss et al. 2014; Scenarios Network for Alaska and Arctic Planning 2014).

Juvenile salmon growth under future warming scenarios

Summer growth rates of juvenile Chinook and Coho salmon primarily responded negatively to increased projected water temperatures, even in most scenarios that simulated increases in feeding rates. Projected responses to future scenarios varied by site and among cohorts in proportion to the magnitude of change in water temperature. Final simulated size at the end of the summer

(September 4) decreased in future decades in nearly all climate and feeding rate scenarios. In our simulations, a net decrease of growth relative to the 2010–2019 outcomes implies that there is a greater proportion of days in the simulation period with mean water temperature further away from the cohort's optimal temperature.

Our results pertain specifically to the direct effects of warming during the summer period. We found decreasing summer growth rates in most scenarios, but two future trends could compensate for the decrease in growth rates that we found in our simulated results. First, longer growing seasons with earlier ice-out dates and later freeze-up dates (Brown et al. 2018) and the resulting extended period of opportunity for growth could offset the simulated losses. Second, increased productivity in invertebrate communities could result in increased food abundance and could allow for higher growth rates even if water temperatures diverge further from optimum. Alternatively, a future *reduction* in resource availability coupled with warming could result in “metabolic meltdown,” leading to even larger reductions in growth than our models projected (Huey and Kingsolver 2019). Modeling of future trends in these processes is beyond the scope of this work, although our simulations do incorporate a potential increase or decrease in invertebrate production with our feeding rate scenarios. Caution is warranted in the use of simple physiological models as a mechanistic basis for projecting fish size under rising temperature scenarios (Lefevre et al. 2018). Our results support a broad expectation of reduced summer growth across a variety of plausible future conditions. The boundaries of our approach highlight the need for year-round monitoring over multiple years to identify biotic and abiotic controls on juvenile salmon productivity (Brady 2020).

Recognizing the strengths and limitations of bioenergetics-based approaches is important for their interpretation. The model accounts for the fact that the water temperature threshold value at which the growth rate of juvenile Chinook and Coho salmon begins decreasing (T_{opt}) depends both on fish mass and feeding rate and is not fixed (Brett et al. 1969; Beauchamp et al. 2007). A strength in our use of the bioenergetics model is that it allows for estimation of growth using field-based estimates of food consumption and water temperature experience, incorporating (1) data across a large and diverse watershed and (2) the substantial natural variation in diet and body mass across distinct environments. A strength of our study is that the simulations incorporate observed fish size and observed feeding rate data from a diverse selection of cohorts and environments, emphasizing the heterogeneous response of a temperature-dependent process across diverse landscapes. Absent from the bioenergetics model are hydrodynamic effects, including ways in which

turbidity and water velocity affect drift-feeding behavior and movement, competition with conspecifics, predation, and others. Additionally, the bioenergetics parameters from Stewart and Ibarra (1991), which were employed in our model, are borrowed from a population in the warmer Great Lakes region; thus, it is likely that our simulations represent an underestimate of the actual proportion of days in which daily mean temperatures exceed T_{opt} for our study populations. Spatially explicit habitat modeling approaches that incorporate hydrodynamics, bioenergetics, and net energy intake show promise in assessing habitat quality to help inform conservation management (Carmichael 2019; Falke et al. 2019).

Our results differ from some other studies modeling the effect of rising water temperature on juvenile salmon growth. Fullerton et al. (2017) instead projected increasing growth rates for juvenile Chinook Salmon under future warmer temperature regimes throughout a diverse set of simulated watersheds. The differing result may be partially attributable to their use of the Plumb and Moffitt (2015) bioenergetics parameters, which generally estimate higher temperature values for the metabolic optimum, rather than the Stewart and Ibarra (1991) parameters employed here. Other modeling efforts by Beer and Anderson (2011), like our study, found that results vary by ecoregion, with rising mean temperature contributing to increased growth in streams that presently experience cool temperatures but decreasing juvenile growth in already-warm streams.

Implications of our results differ from other recent work in a cool tributary of the Yukon River, located at the northern edge of the species' range, which found increased growth of juvenile Chinook Salmon under warmer conditions (Falke et al. 2019). Our results also differ from those observed in Bristol Bay, where warming temperatures generally increased the growth rates of juvenile Sockeye Salmon *O. nerka*, resulting in earlier out-migration timing and contributing to a simplification of population age-class structure (Cline et al. 2019). If reduced summer growth rates ultimately decrease the size of juvenile salmon at the end of summer growing seasons, then smaller size could act as a cue for the fish to extend their freshwater residency.

Chinook and Coho salmon have different life histories, and differential impacts associated with climate change are anticipated as a result. In Alaskan streams, juvenile Chinook Salmon typically spend one full year in freshwater prior to out-migration, while juvenile Coho Salmon typically spend 1–2 years in freshwater (Quinn 2018; Oke et al. 2020). If a shift in growth rates associated with climate change affects age-class structure and migration timing, as was observed for the Bristol Bay Sockeye Salmon populations (Cline et al. 2019), these effects may be more

recognizable in Coho Salmon, with their more variable freshwater life history, than in Chinook Salmon. Whether age-classes could be gained or lost is difficult to predict; it is not known whether slower-growing fish would produce a greater proportion of parr that rear for an additional year before smoltification. Applying annual data on smolt age-class structure could be a valuable source of information for understanding how climate change is affecting Kenai River salmon populations (Tobias and Willette 2010).

In summary, the simulations in this study indicate that across a variety of habitats, climate-driven temperature increases over the next 20–50 years will have the direct effect of reducing summer growth rates for juvenile Chinook and Coho salmon, particularly in watersheds that are also highly sensitive to air temperature. However, the question remains regarding whether other climate-driven environmental changes that also affect growth, such as an extension of the spring and fall shoulder seasons or changes in productivity of the food resources upon which juvenile Chinook and Coho salmon rely, might either compound or compensate for these losses or even enhance future growth rates. Also uncharacterized is the degree to which populations may adapt to these changing conditions either through modified habitat use or natural selection (Crozier et al. 2008; Armstrong et al. 2013). Our results illustrate how landscape settings produce a diverse set of responses to climate change, emphasizing the value of conserving a heterogeneous, interconnected portfolio of habitat types and the varied life histories that they support (Schindler et al. 2010; Justice et al. 2017; Thompson et al. 2019).

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of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

Data is available for download from Knowledge Network for Biocomplexity (KNB) at <https://knb.ecoinformatics.org/view/doi:10.5063/F1Q52MZF>.

ETHICS STATEMENT

All research activities were authorized through an Alaska Department of Fish and Game aquatic resource permit (SF2015-191 and SF2016-158) and approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (720490-4).

ORCID

Benjamin E. Meyer  <https://orcid.org/0000-0002-2751-5958>

Erik R. Schoen  <https://orcid.org/0000-0001-8301-6419>

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