

1 **Impact Statement**

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

7 **Abstract**

8 Climate change is affecting the distribution and productivity of Pacific salmon
9 throughout their range. At high latitudes, warmer temperatures have been associated
10 with increased freshwater growth of juvenile salmon, but it is not clear how long this
11 trend will continue before further warming leads to reduced growth. To explore the
12 potential influence of climate warming on juvenile Chinook and Coho Salmon summer
13 growth rates in southcentral Alaska, we coupled bioenergetics models with temperature
14 sensitivity models for streams across the Kenai River watershed. We measured diet (n
15 = 772 stomachs) and growth (n = 3,791 weight/length values) under current conditions
16 and used published air temperature projections to model growth for the 2030-2039 and
17 2060-2069 decades. We estimated direct effects of climate warming on juvenile growth
18 (body mass at the end of May–Sept. study period) will be primarily negative, ranging
19 from +5.1% to -22.8% relative to a 2010-2019 baseline. Estimated effects depended on
20 age cohort, feeding rate, and climate scenario. However, an extended growing season
21 from warming could mitigate or offset predicted reductions in growth during midsummer.
22 Our results illustrate how diverse habitats are expected to produce variation in the
23 magnitude of climate effects throughout juvenile salmon rearing environments.

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 a climate trend will have neither unidirectional or homogenous effects on the wider ecosystem (Schindler et al. 2008; Lynch et al. 2016; Jones et al. 2020).

Among stream-rearing Pacific salmon, growth rates of Chinook *O. tshawytscha* and Coho *O. kisutch* Salmon 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 one (for Chinook Salmon) or one to two (for Coho Salmon) years 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 addition, in subarctic regions of interior Alaska, warmer stream temperatures have been associated with increased juvenile growth of both Chinook (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 (southcentral 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 juvenile Chinook and Coho Salmon summer growth rates 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 to parameterize 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) and physical factors (flow regime (Poff et al. 1997), water quality, and habitat connectivity) that affect fish growth, but allow for modeling changing conditions that are otherwise difficult to address. To address the uncertainty of future conditions we used a suite of climate and

feeding rate scenarios for simulation inputs. Our approach allowed us to estimate change in mass at the end of the summer growing season relative to baseline scenarios. We anticipated that the three geomorphically distinct focal tributaries and main stem would exhibit unique thermal regimes and feeding patterns and that juvenile Chinook and Coho Salmon would display distinct patterns in growth rates 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 juvenile Chinook and Coho Salmon rearing habitat, 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: a) characterized feeding rates and thermal conditions that contribute to differences in current growth rates and b) used growth simulations to characterize expected juvenile summer growth rates in different habitat types under future climate change scenarios. We anticipated 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 nearby yet distinct habitats we aimed to better understand how juvenile salmon productivity may respond to climate change in the context of diverse habitats.

Materials & 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 ten sites within the Kenai River watershed. Based on these field data, we simulated juvenile growth during summer under current conditions using coupled stream temperature models and bioenergetic 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 bioenergetic 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 southcentral 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 three tributaries of the Kenai River in 2015 and 2016: Beaver Creek (lowland), Russian River (montane), and Ptarmigan Creek (glacial), and the Kenai River main stem (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 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 - 1000 m), high gradient, and glacially influenced (7% ice coverage in 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 results gained from this study may be relevant to the broader region.

Field Sampling

Stream Temperature

We acquired water ($n=14$ sites) and air ($n=11$ sites) temperature data from an array of HOBO® Temp Pro v2 loggers deployed during summers 2015 and 2016, U.S. Geological Survey (USGS) stream gauge stations at Soldotna (station ID 15266300) and Cooper Landing (station ID 15258000; USGS 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 in (Mauger et al. 2015). Supplemental Information Section A describes site locations, methods used to ensure

sites were representative of local environs using channel transects, equipment calibration, and logger check procedures.

Juvenile Salmon Capture

We sampled juvenile Chinook ($n = 1,145$) and Coho Salmon ($n = 2,646$) within the lower, middle, and upper extent of their documented habitat (Reimer 2013) in each of the three focal tributaries (Figure 2). We also sampled sites in the mainstem 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 terrain prevented access. We sampled fish from main channel and off-channel habitat at each site. Sites were visited approximately monthly (31 ± 5 days, mean \pm SD) throughout May to August 2015 and May to September 2016 (summarized in Supplemental Information Section B, Figure B1). Coordinates for the fish sampling sites are listed in the supplementary information (Table S1). At each fish sampling event we used a handheld YSI® 556 Multi-parameter instrument or Cooper-Atkins AquaTuff Instant Read® thermocouple to record water temperatures (°C).

We used Gee® minnow traps baited with salmon eggs to capture juvenile salmon, an effective method for 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 to 20 traps at water depths of 15 to 45 cm, ensuring sites were undisturbed by foot traffic so as not to alter the community of invertebrates normally available as juvenile salmon prey. We set the

traps for 2 to 4 hours per set. We ensured that all salmon eggs used as bait were commercially sterilized or disinfected with a ten-minute soak in a 1/100 Betadyne solution prior to use.

We anesthetized captured juvenile salmon prior to measurement and diet sampling by submersion in a 20 to 40 mg/L eugenol (AQUI-S™) bath for 2 to 3 minutes. Once individuals exhibited a total loss of equilibrium, we removed them from the bath and measured fork length (FL) to the nearest mm and weighed to the nearest 0.1 g. We allowed fish to recover in aerated water until equilibrium was fully regained and retained them in-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*; Rainbow Trout; *O. mykiss*). We released all fish near the point of capture when daily sampling was complete.

For a subset of juvenile Chinook ($n = 219$) 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 and 16 Coho Salmon with $FL \geq 50$ mm (Supplementary information 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 fish ≥ 50 mm FL in the field and flushed gut contents out of the mouth using gastric lavage technique with a modified syringe (Culp et al. 1988) into a 250 μ m sieve. We preserved gut contents in a minimum of 70% ethanol in a Whirl-Pak bag.

184

185 *Juvenile Salmon Age and Growth*

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

191 We quantified the growth of juvenile salmon in sampling strata with adequate
192 sample sizes of stream-rearing parr. We excluded age-2 Coho Salmon and age-1
193 Chinook Salmon from our analyses as these cohorts were anticipated to be almost
194 exclusively pre-smolt outmigrants (Shields and Dupuis 2017) and sample sizes were
195 small. Sample size for juvenile Chinook and Coho Salmon was variable across
196 sampling events (range = 1 to 168 individuals per species/age cohort), due in part to the
197 patchy distribution of fish across the landscape. We excluded iterations of $n < 3$
198 observations when segregated by age, species, and sample event due to small sample
199 size. We also excluded cases where the mean fish weight declined between sampling
200 events, suggesting outmigration of larger individuals (2 of 55 cases). After applying
201 these inclusion standards, 72% (108/150) of the total possible combinations of sample
202 event, age, and species remained.

203 We examined the temporal and spatial scales at which fish growth patterns could
204 be segregated and compared. First, we explored the possibility of grouping and
205 averaging data from sites within each study watershed. We observed significant
206 differences in daily mean temperature (Jun 1 to Aug 20) among sites within two of the

four watersheds (the montane and main stem) ($p < 0.05$, Kruskal-Wallis) and 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 6th, the earliest day for a final site visit among both years and all sites) was selected as the response metric for which to compare among future scenarios. See Supplemental Information Section D for further details on linear mixed modeling methods and results.

We investigated if summary thermal metrics from Jun 1st to Aug 6th (mean, minimum, maximum, and 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). Further, Alaska water quality regulations specify 15°C as a temperature of concern for growth and propagation of fish (ADEC 2020).

Juvenile Salmon Diet

We examined stomach content samples under 4.0x dissecting microscopes. Distinguishable invertebrates ($n = 8,879$) were identified to family level or the lowest taxon feasible ($n = 112$ taxon / life stage combinations identified) and body lengths were measured to the nearest 1.0 mm (Merritt and Cummins 1996). We estimated 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 in a sample, we assumed that the head and thorax represent 1/3 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 (Chipps and Garvey 2007). We determined dry mass of individual invertebrates using the allometric formula

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

where W is the total dry body mass, L is the total body length, and a and b are constants (Ricker 1973). We derived 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 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 captured in this study (B.E. Meyer, unpublished data). We converted prey item dry mass to wet mass using the relationships published by McCarthy (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. We grouped juvenile fish prey items in with the salmon eggs prey

category. We assigned energy density values to the six prey categories using literature references (Table 2) for use in bioenergetics modeling.

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 using 2015 and 2016 field data, we used 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 ($\Delta^{\circ}\text{C } T_w / ^{\circ}\text{C } T_a$), a metric quantifying the average change in stream temperature per 1 °C change in air temperature, 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 temperature for each week of the 2015-2016 study periods that had < 30% of observations missing and fit 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 >20°C where 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

a period of days with observations common to all sites and years (June 1st to Aug. 20th), with the exception of the Lower Russian River site, for which earliest available water temperature data in 2015 was June 22nd.

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

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

where m and b are the site-specific slope and intercept values (Table S4, supplementary data). We used monthly decadal mean downscaled air temperatures published by Scenarios Network for Arctic and Alaska Planning based on the mean of the five best-performing global climate models for Alaska as daily input values for the periods of May to September 2010-2019, 2030-2039, and 2060-2069 under the RCP 6.0 (mid-range CO₂ emissions) and RCP 8.5 (rapid increase CO₂ emissions) scenarios (Walsh et al. 2008; IPCC 2014; SNAP 2014). To investigate performance of the stream temperature models, we regressed mean monthly water temperatures observed in 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 summers 2015-2016 as inputs. We performed a simulation for each cohort (i.e., unique iteration of sampling site, year, fish species, and fish age) fit 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 pooling 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, 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 we used to fit simulations included a) the mean feeding rate under current conditions, b) +20% of mean feeding

rate, and c) -20% of mean feeding rate, intended to represent low, medium, and high feeding rate scenarios.

Future salmon growth was projected from May 26th to Sept 4th. 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 6th) 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 26th 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, 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 x 2 climate scenarios x 3 feeding rate scenarios x 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 juvenile Chinook Salmon growth in laboratory and field settings (Madenjian et al. 2004). Plumb and Moffitt (2015) found that Stewart and Ibarra's (1991) parameters overestimate the metabolic consequences

of higher temperatures on sub-yearling Chinook Salmon, so recent studies have employed modified temperature-dependent consumption parameters for both species when simulation temperatures were $>18^{\circ}\text{C}$ to minimize parameter error (Davis et al. 2019). However, none of the daily water temperature inputs in our simulations were $>18^{\circ}\text{C}$, thus the Stewart and Ibarra (1991) parameters were employed for all simulations. Previous efforts with bioenergetics modeling with Alaskan juvenile Chinook Salmon found the Stewart and Ibarra (1991) parameters better suited to describe growth than the Plumb and Moffit (2015) parameters (Falke et al. 2019). We verified that our response variable, simulated mean weight on August 6th, corresponded with observed or linearly interpolated values (Simulated Mean Weight = $0.39 + 0.97(\text{Observed Mean Weight})$, $r^2 = 0.9$), suggesting that our model was able to represent the growth patterns found in our empirical observations. For input parameters not measured directly in the field, data pertaining to juvenile Chinook and Coho Salmon energetics were obtained from values included with Fishbioenergetics 4.0 software (Deslauriers et al. 2017). Indigestibility values of 17% and 3% were assigned, respectively, to invertebrate and fish diet items (Beauchamp et al. 2007).

Results

Fish Capture

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

Water Temperature

Observed water temperatures ranged from 5.3°C to 19.6°C with a mean \pm SD of 12.3°C \pm 2.2°C during the set of days with data common to both years of field data (June 1 to August 20) (Figure 3). Overall, sites in the montane watershed had the highest mean water temperature (13.3 \pm 2.4°C, mean \pm SD), followed by the lowland (12.6 \pm 1.7°C, mean \pm SD), glacial (11.8 \pm 1.6°C, mean \pm SD), and mainstem (11.1 \pm 2.4°C, mean \pm SD) 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 (slope of 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 temperature ($n = 10$ sites, coefficient of determination = $-0.08 + 0.83 \times \text{Sensitivity}$, $r^2 = 0.47$, $P < 0.05$). The glacial watershed exhibited notably lower air-water sensitivity and correlation than the other watersheds, which were generally higher (Figure 4). Sensitivity values ranged from 0.64 to 0.74 at sites in the lowland watershed, 0.45 to 0.67 in the montane watershed, 0.20 to 0.32 in the glacial watershed, and 0.68 to 0.72 in the main stem. Correlation values ranged from 0.61 to 0.70 in the lowland watershed,

0.19 to 0.48 in the montane watershed, 0.04 to 0.17 in the glacial watershed, and 0.20 to 0.35 in the main stem. Linear model parameters for regressions used to estimate air-water sensitivity at each site are reported in supplementary information (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 °C (Figure 5). The greater range of values in the observed water temperatures relative to the projected arose from the difference in temporal scale of the two datasets, with observed water temperature measurements made at 15-minute 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 difference from the observed 2015-2016 summer water temperatures, with an overall mean absolute difference of 0.3 \pm 1.22°C (mean \pm SD). Correlations between projected and observed monthly mean water temperatures ranged from r^2 = 0.22 - 0.95 among sites. Mean projected monthly water temperature differed only slightly between the mid-range and rapid-increase scenarios (absolute difference = 0.2 \pm 0.0°C, mean \pm SD).

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 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 mean change in water temperature

relative to 2010-2019 ranged 0.2°C to 1.8°C among sites and decades, while under the mid-range emission scenario the range was 0.1°C to 1.1°C.

Juvenile Salmon Diet

A total of 13,723 individual items were identified from 772 diet samples. Among the 11,983 diet items recognizable as individual organisms, 8,879 of them were identifiable as specific taxa, and the remainder were assigned as "Unknown Invertebrate" without a wet mass estimate or assigned energy value. Terrestrial and marine subsidies (terrestrial invertebrates and salmon eggs) composed >40% of the overall diet by wet mass in eight of twelve iterations of watershed, species, and age (averaged between both years, Table 2 and 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 at August 6th) by age and species varied markedly across sites and years (Figure 7). Basic thermal metrics at each temperature logger site (mean, maximum, and minimum temperature, and frequency of 0.25-hourly temperature observations >15°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 direct effects of climate warming was negative in almost all cases, with a mean of -4.91 ± 0.3 % and ranging from +5.1% to -22.8% 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 three cohorts (of 21 total) 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 relative to the 2010-2019 time period under most climate and feeding rate scenarios modeled in this study. These results suggest climate warming over the next 10-50 years could reduce juvenile Chinook and Coho Salmon summer growth rates 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 through fall) will decline, because 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 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 were intermediate relative to other well-studied salmon systems such as the warmer Columbia River system (Chang and Psaris 2013) or 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. 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 upstream of our sampling sites (Lisi et al. 2013).

Water temperature logger data collected at mainstem sites is 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, 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% to 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 were overall close to the observed values in terms of mean difference ($0.30 \pm 1.22^{\circ}\text{C}$, mean \pm SD). The approach of using of 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 have limited accuracy (Arismendi et al. 2014).

Glacial melt will likely moderate the influence of warming air temperatures in our study systems even well in to 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. While the watersheds in Southeast Alaska above a threshold of >30% glacial coverage saw cooling as a result of glacial melt, the two glacial-influenced watersheds in this study (Ptarmigan Creek and main stem Kenai River, 7% and 14% ice coverage respectively) are well below 30% glacial coverage.

Future research will continue to improve stream temperature model accuracy, 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 in long-term changes in sensitivity relationships (Klein et al. 2005; Bliss et al. 2014; SNAP 2014).

Juvenile Salmon Growth Under Future Warming Scenarios

Juvenile Chinook and Coho Salmon summer growth rates 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 (Sept. 4th) decreased in future decades in nearly all climate and feeding rate scenarios. In our simulations, a net decrease of growth relative to 2010-2019 outcomes implies 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 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 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 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 future trends in these processes are 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 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 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 juvenile Chinook and Coho Salmon growth rate 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 estimates of growth using field-based estimates of food consumption and water temperature experience, incorporating data across a large and diverse watershed and incorporating 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) 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 hydrodynamic, bioenergetics, and net energy intake approaches 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 Plumb and Moffitt's (2015) bioenergetics parameters, which generally estimate higher temperature values for 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, 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 which found warming temperatures generally increased growth rates of juvenile Sockeye Salmon *O. nerka*, resulting in earlier outmigration 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, smaller size could act as a cue to extend 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 outmigration while juvenile Coho Salmon typically spend one to two years (Quinn 2018; Oke et al. 2020). If a shift in growth rates associated with climate change affects age class structure and migration timing, as observed for Bristol Bay Sockeye Salmon populations, these effects may be more recognizable in Coho Salmon with their more variable freshwater life history than in Chinook Salmon. As to whether age classes could be gained or lost is difficult to predict, it is not known if 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 to understand 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 the direct effects of 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 also highly sensitive to air temperature. However, the question remains 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 food resources that juvenile Chinook and Coho Salmon rely on, 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 heterogenous, interconnected portfolio of habitat types and the varied life histories they support (Schindler et al. 2010; Justice et al. 2017; Thompson et al. 2019).

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