

Title: Diversity of stream thermal regimes in Bristol Bay and implications for juvenile salmon growth potential

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Introduction

Bristol Bay produces the world's largest and most valuable wild salmon runs, averaging 38.7 million fish annually (20-year average 1991-2010; Jones et al. 2013) with an economic value of \$1.5 billion (2010 estimate, Knapp et al. 2013). The region produces about half of the world's sockeye salmon supply and is recognized for its large Chinook salmon runs. Bristol Bay salmon populations represent both economic and food security (Jones et al. 2013) to Alaskans. The high productivity of Bristol Bay salmon populations is due in part to habitat diversity, including thermal diversity, across the region.

Climate change is causing altered thermal regimes in freshwater ecosystems, including warmer minimum and maximum temperatures and a lengthening of the open-water season (Jones et al. 2017). In recent years, scientists have observed that changes in thermal regimes are accelerating juvenile salmon growth rates in the Bristol Bay region (Schindler et al. 2005, Rich, et al. 2009) and altering life-history diversity for sockeye salmon in Lake Aleknagik and Lake Iliamna (Cline et al. 2019). Changes in juvenile growth are likely due to longer duration of warmer temperatures during the summer growth period and increased availability of food resources. However, much uncertainty exists regarding impacts of thermal regime shifts on lake- and stream rearing salmon populations in the Bristol Bay region.

A collaborative water temperature monitoring network in the Bristol Bay region created an opportunity to investigate year to year variation in thermal regimes and its effect on the growth potential for stream-rearing salmon (Mauger and Troll 2014). Here, we use a regional dataset to evaluate the implications of recent observed temperatures for salmon. We will investigate how thermal regimes within streams have influenced the growth potential of stream-rearing salmon in the Bristol Bay region and observed ecological shifts which have occurred in response to changing thermal regimes (e.g., age-class structure). The main objectives of this project were to: (1) characterize thermal regimes of streams in the Bristol Bay region as they relate to salmon life-history diversity; (2) evaluate differences of thermal regimes within and among watersheds/populations; and (3) model the effects of changing thermal regimes on juvenile salmon growth potential for distinct populations in the Bristol Bay region. The objective of this project is to better understand how these shifting mosaics of salmon growth potential are influenced by rapidly changing thermal regimes across the region. Additionally, thermal regimes and growth models for 2019 (the hottest summer on record in Alaska) were used as a case study for how future climate change may impact growth rates and life-history diversity of salmon

populations in the Bristol Bay region. Ultimately this modeling approach develops hypotheses of temperature effects on juvenile salmon growth and population dynamics that can be tested in the future with empirical datasets from the region.

Methods

Study Area

The Bristol Bay region encompasses the Togiak (12,367 km²), Wood River (3,541 km²), Nushagak Bay (5,436 km²), Upper (13,024 km²) and Lower Nushagak River (7810 km²), Mulchatna River (11,120 km²), Lake Clark (8,976 km²), Iliamna (18,530 km²), Egegik (7,185 km²), and Naknek (9,708 km²) watersheds, delineated by USGS HUC8 boundaries (Figure 1). These watersheds cover the Kuskokwim Mountains, Bristol Bay Lowlands, Alaska Peninsula, Lime Hills, and Ahklun Mountains ecoregions (Nowacki 2001).

Although all five Pacific salmon species are found in the Bristol Bay region, this project focuses on Chinook and coho salmon, given their strong reliance on stream habitat for rearing and spawning.



Figure 1. Map of study region and temperature monitoring sites with inset map showing study location in the southwestern portion of Alaska. HUC 8 watersheds are outlined and labeled by name, and temperature monitoring sites are colored by the organization responsible for

data collection and management.

Temperature Data Collection

Data were collected at 124 streams and rivers in the Bristol Bay region: Wood River (51), Lake Clark (17), Mulchatna River (14), Lake Iliamna (10), Togiak (10), Naknek (7), Upper Nushagak River (6), Lower Nushagak River (5), Nushagak Bay (3), and Egegik Bay (1). These temperature monitoring sites were maintained by a number of organizations, including the University of Alaska Anchorage's Alaska Center for Conservation Science, the U.S. Fish and Wildlife Service's Togiak National Wildlife Refuge and Alaska Region Office of Subsistence Management, Cook Inletkeeper, Levelock Village Council, Nondalton Tribal Council, New Koliganek Village Council, Dave & Kim Egdorf's Western Alaska Sport Fishing Camp, Bear Trail Lodge, Copper River Lodge, Aleknagik Traditional Council, Iliamna Village Council, Bristol Bay Native Association, New Stuyahok Traditional Council, University of Alaska Fairbanks Bristol Bay Campus, National Park Service's Southwest Alaska Inventory and Monitoring Network and Lake Clark National Park, U.S. Geological Survey, and the University of Washington's Alaska Salmon Program. The temperature data used for this analysis were compiled as part of a larger project funded by the Alaska Sustainable Salmon Fund investigating thermal sensitivity of watersheds in Bristol Bay, Kodiak, Prince William Sound, Cook Inlet, and the Copper River watershed. Those data have been archived on Zenodo and can be accessed for download and reuse (Larson et al. 2024b). Sites ranged from having 1 to 18 years of summer temperature monitoring. In total, there were 789 site-year combinations in the entire temperature dataset. Of the 124 sites, there were 23 sites with 10 or more years of data, identified as being long-term monitoring sites.

Overall, sampling sites were distributed across all HUC8s in the Bristol Bay region (Figure 1), with a high concentration in the Wood River drainage (51 sites) and the lowest number in Egegik Bay (1 site). The majority of data collection occurred between 2015 and 2019, when a temperature monitoring network was active in Bristol Bay, but data used for this study span from 2001 to 2020 (Figure 2A). Study sites were broadly representative of the stream sizes in the region, although smaller headwater streams were overrepresented (2nd and 3rd order) and larger systems (4th, 5th, and 9th order) were underrepresented relative to their proportional distribution on the landscape (Figure 2B).

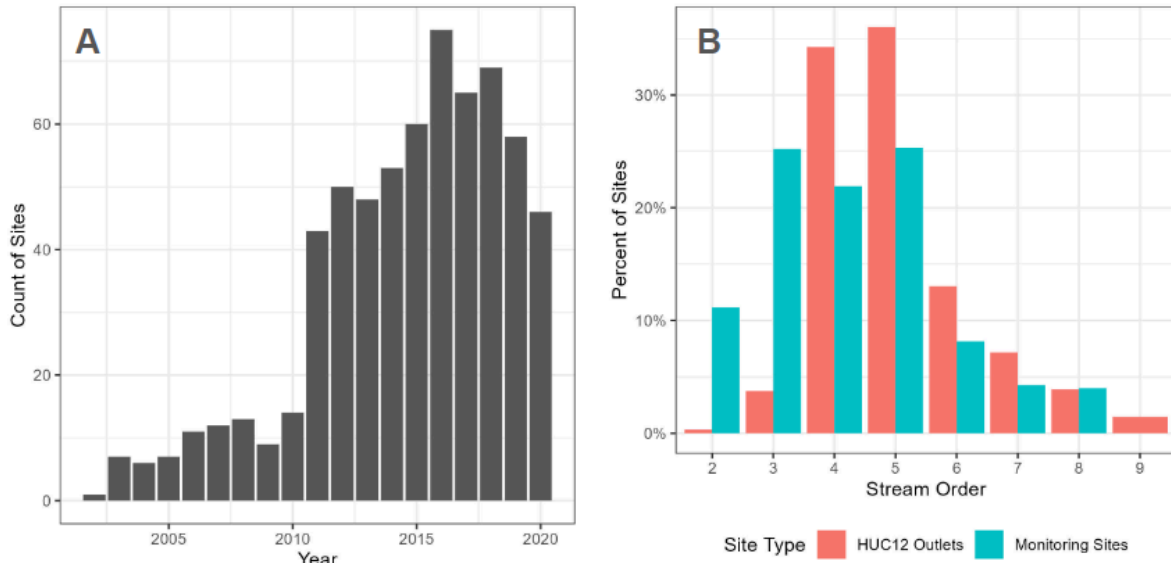


Figure 2. Distribution of temperature monitoring sites in Bristol Bay, based on (A) years where data was collected and (B) stream order of both HUC12s in the region and of monitoring sites.

Temperature Data Analysis

All analyses were conducted in R. We reviewed all stream temperatures from the summer months for data quality and anomalous or suspect data were flagged and excluded from further analysis, following suggestions in Mauger et al. (2015). Temperature data anomalies can occur when temperature loggers become exposed to air during low flows or buried by sediment during floods. Exposure to air was determined by comparing logger temperatures to nearby NOAA Global Historical Climatology Network air temperatures. In cases where duplicate loggers were deployed, those logger temperatures were compared to each other to determine if burial had occurred. Continuous temperature measurements were then summarized into daily means, minimums, and maximums for analysis.

Temperature metrics were calculated generally following methods in Shaffel et al. 2020, with the inclusion of minimum temperature and mean temperature to select metrics that have implications for year round growth of juvenile salmon and are not redundant (pairwise correlations of less than 0.8). The 11 temperature metrics used in this study are briefly described in Table 1. These same temperature metrics were used in a parallel study exploring thermal sensitivities of salmon habitats in Bristol Bay, Kodiak Island, Cook Inlet, Copper River, and Prince William Sound watersheds (Larson et al. 2024a). Data from that study were used to compare Bristol Bay thermal regimes to other salmon-bearing regions in southern Alaska by comparing distributions of temperature metrics.

Table 1. Temperature metrics used to describe and differentiate thermal regimes in the Bristol Bay region.

Category	Abbreviation	Description	Units
Magnitude	MWMT	Maximum 7-day moving average of maximum daily temperatures	°C
Magnitude	Min. Temp	Minimum daily temperature	°C
Magnitude	Mean Temp.	Mean daily temperature	°C
Variability	Range	Maximum daily range	°C
Variability	Var.	Variance of daily maximum temperatures	°C ²
Frequency	Sum. 13	Number of days greater than 13 degrees Celsius	Count
Frequency	Sum. 18	Number of days greater than 18 degrees Celsius	Count
Duration	Dur. 13	Duration of longest warm event above 13 degrees Celsius	Days
Duration	Dur. 18	Duration of longest warm event above 18 degrees Celsius	Days
Timing	Tim. MWMT	Timing of maximum 7-day moving average of maximum daily temperatures	Julian day
Timing	Tim. Max. Daily	Timing of maximum daily temperature	Julian day

For long term monitoring sites (10 or more years of data), Mann-Kendall tests and Sen's slope estimates were performed on time series at each site to determine if there was a trend over time in three thermal metrics crucial for juvenile salmon growth and survival (Mean Temp., MWMT, and Tim. MWMT). For this analysis, time series were constrained to the summer months (June through August) to account for seasonal differences in available data. The 'trend' package in R was used for these analyses (Pohlert 2023).

Juvenile Salmon Modeling

To explore the potential implications of changing river and stream temperature regimes for juvenile salmon growth, we simulated the growth potential of juvenile coho and Chinook salmon using a bioenergetics model. The goals of this analysis were to compare thermal constraints on growth across the Bristol Bay region and among years with different climatic conditions. We used the model to simulate growth potential, or the body weight that an age-0 salmon could potentially achieve during the summer months under the thermal regimes measured in each site year, assuming it consumed primarily invertebrate prey across a range of typical feeding rates.

This approach integrates the “thermal experience” of a juvenile salmon during the growing season. The bioenergetics model ran on a daily time step, so we summarized temperature measurements at each site in each year as a time series of daily mean values to input into the model.

We implemented the bioenergetics simulations in Fish Bioenergetics 4.0 v1.1.5 (Deslauriers et al. 2017), using physiological parameters for Chinook and coho salmon summarized by Stewart and Ibarra (1991). In prior studies of Alaska Chinook and coho salmon, these parameters have produced bioenergetics model results that better align with field data than alternative parameter sets (see Falke et al. 2019 and Meyer et al. 2023 for details). We used the design file function to facilitate running large numbers of simulations in a scripted, repeatable analysis. The growth potential simulations generally followed the methods described by Meyer et al. (2023) with the following differences. Simulations ran from June 1 to August 31 and were restricted to site-years with available temperature data for those start and end dates. When necessary, missing temperature data between the start and end points were filled by linear interpolation.

In addition to temperature, food quality and feeding rate are also key determinants of salmon growth rates (Beauchamp 2009, Brett et al. 2011, Railsback 2022). We assumed that juvenile salmon consumed a diet of invertebrates with an energy density of 3500 kJ/g, based on diet analysis of juvenile coho salmon in the Wood River drainage (Armstrong et al. 2010). This estimate was a slightly lower quality diet than has been reported for juvenile Chinook and coho salmon feeding on a combination of aquatic and terrestrial invertebrates in other parts of Alaska (Falke et al. 2019, Meyer et al. 2023), and this assumption may have made our growth potential estimates conservative.

To explore how variation in feeding rates, which were unknown, might influence the growth potential results, we simulated growth under 3 feeding rate scenarios, in terms of the proportion of their theoretical maximum consumption rate (pC_{max}): 30% (low), 45% (typical), and 60% (high). This range encompassed the range of long-term feeding rates estimated in other bioenergetics studies of juvenile coho and Chinook salmon in Alaska that were fit to empirical growth data (Falke et al. 2019, Meyer et al. 2023). The model produced end-of-summer growth potential estimates that generally aligned with the range of juvenile coho salmon body masses observed in the Wood River drainage of Bristol Bay (e.g., Armstrong et al. 2010, D. E. Schindler and J. L. Carter unpublished data). We recognize that salmon can achieve higher feeding rates for short periods (e.g. when gorging on pulsed subsidies such as salmon eggs, Armstrong et al. 2010). Such pulsed resource opportunities are spatially patchy and temporally short-lived, and we did not attempt to simulate them for this study, lacking diet data from most site years. However, the range of long-term feeding rates (pC_{max} values) reported by Meyer et al. (2023) were determined using empirical growth rates of age-0 Chinook and coho salmon sampled throughout the Kenai River drainage, many of which consumed salmon eggs opportunistically. Thus, we expected our simulation results to be broadly indicative of the thermal constraints on growth of juvenile salmon that feed primarily on invertebrates and opportunistically on salmon eggs in Bristol Bay streams. We interpreted the growth potential results as most useful for

making relative comparisons among hydrologic units, sites, and years, rather than as precise estimates of growth rates at any given site year.

Results

Thermal Diversity in Bristol Bay

Overall, temperatures varied widely both within and across watersheds in the Bristol Bay region and across sampling years (Figures 3 and 4). The timespan of this study included a historically hot summer in 2019, when many river systems experienced extended durations of temperatures above 18 degrees Celsius, which causes thermal stress for migrating adult coho and Chinook salmon (Bowen et al. 2020, von Biela et al. 2022).

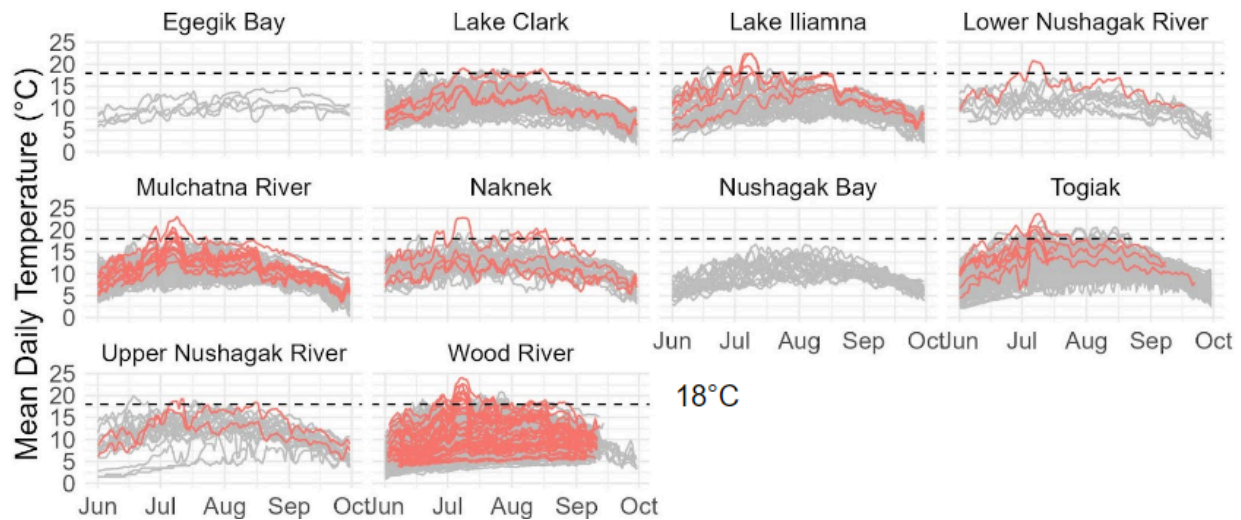


Figure 3. Mean daily temperatures across the summer over all sampled years, broken out by HUC8 watershed. 2019 years are shown in red, all other years are depicted in gray. The horizontal dashed line demarcates the 18 degree Celsius threshold of thermal stress for adult migrant coho and Chinook salmon.

Overall, the study region encompasses streams with a diverse array of thermal regimes (Figure 4). Maximum weekly mean temperatures ranged from 5.4 degrees Celsius (Little Togiak Creek, monitored by University of Washington) to 26.2 degrees Celsius (Idavain Creek, monitored by the National Park Service Southwest Alaska Inventory and Monitoring Network). Mean temperatures ranged from 3.5 degrees Celsius (Little Togiak Creek) to 17.6 degrees Celsius (Nichols Creek, monitored by Togiak National Wildlife Refuge). More than half of the site year combinations had no days above 18 degrees Celsius, although one site (Nichols Creek) experienced 64 days with a mean temperature above 18 degrees Celsius. Maximum temperatures and mean temperatures were lowest in the Wood River watershed, and were highest in the Upper Nushagak (Figure 4). Both the Upper Nushagak and Togiak watersheds had many sites that experienced multiple days above 18 degrees Celsius (Figure 4).

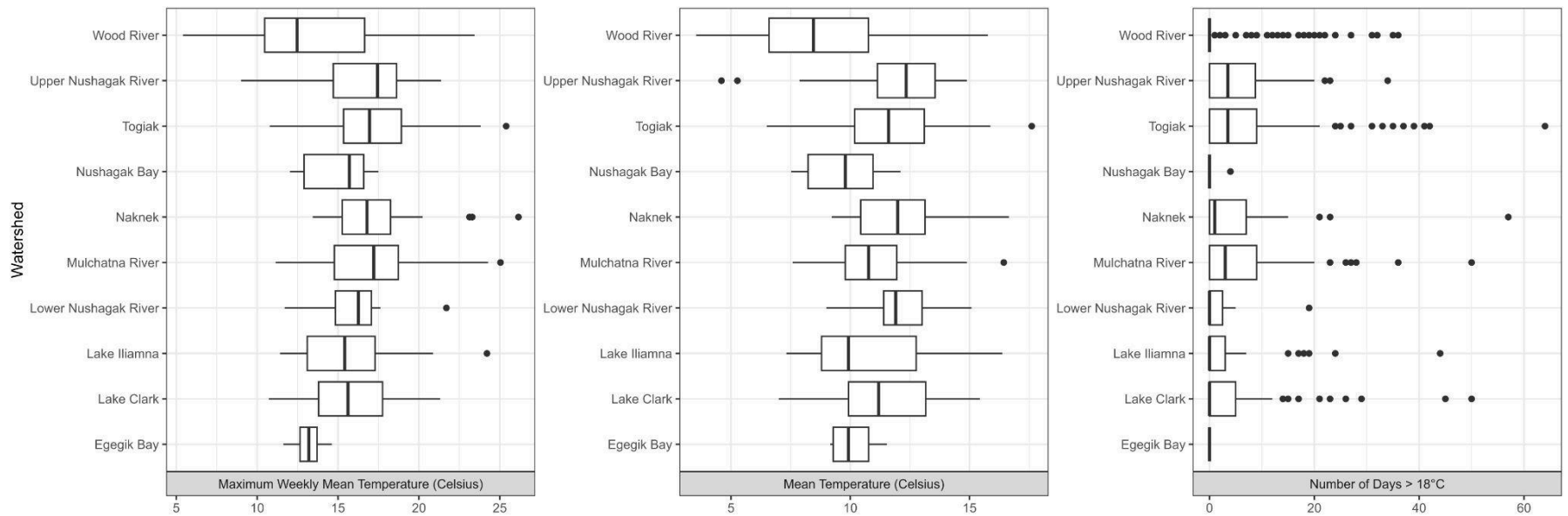


Figure 4. Distributions by HUC8 drainage of temperature metrics most relevant for juvenile salmon growth potential. Maximum weekly mean temperature shown at left, mean temperature in the middle, and number of days above 18 degrees Celsius at right.

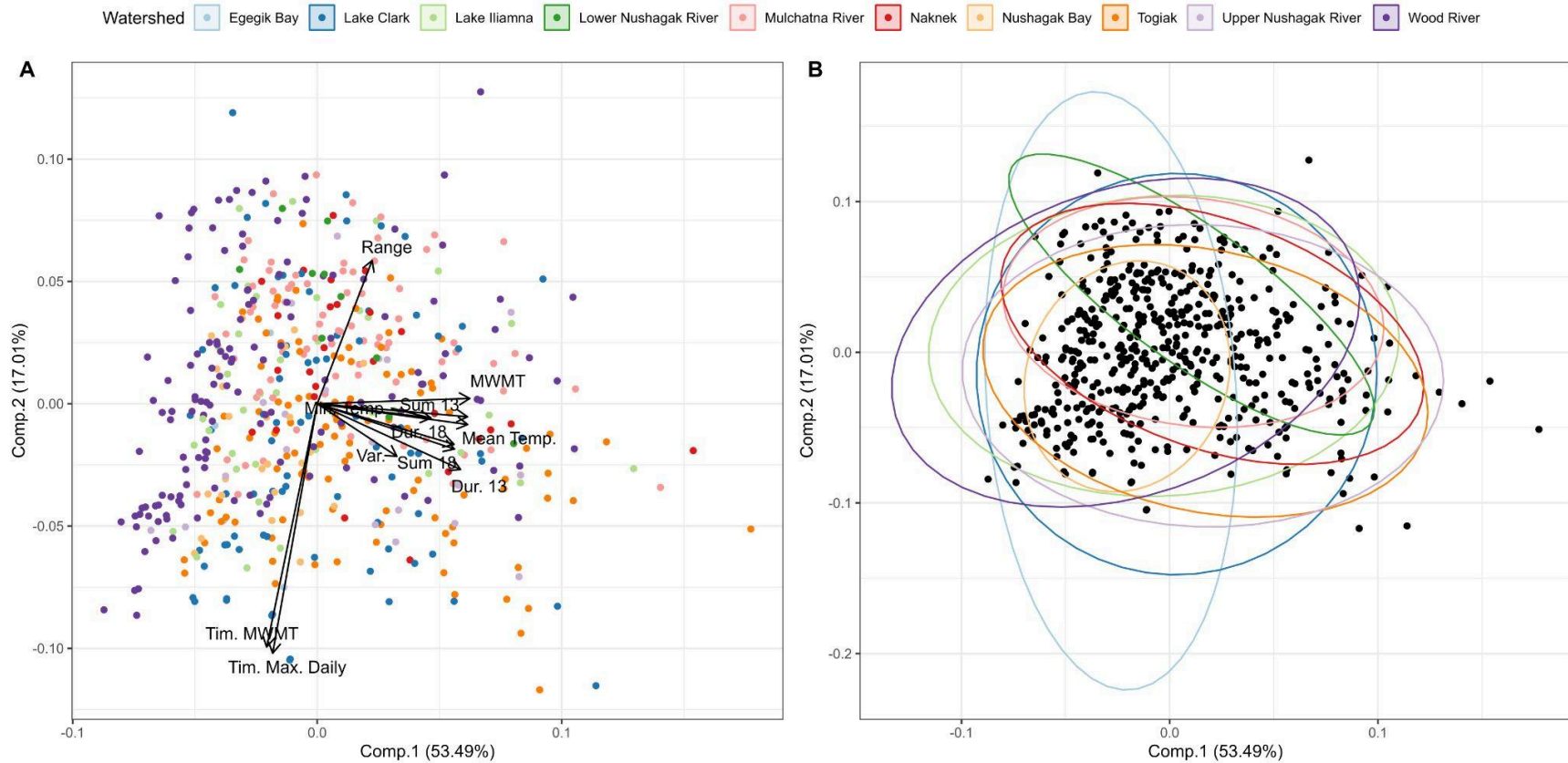


Figure 5. Ordination of 11 temperature metrics by HUC 8 watershed in the Bristol Bay region with each point representing a site and year combination with (A) loadings of temperature metrics and points colored by watershed, and (B) fitted ellipses by watershed. The included temperature metrics are maximum weekly mean temperature, mean temperature, timing of maximum daily temperature, timing of maximum weekly mean temperature, number of days above 13 degrees Celsius, number of days above 18 degrees Celsius, duration of longest warm event above 13 degrees Celsius, duration of longest warm event above 18 degrees Celsius, minimum temperature maximum daily range, and the variance of daily maximum temperatures.

Ordination showed more variation within watersheds than across watersheds, with watersheds not clearly differentiating from each other based on the 11 selected temperature metrics (Figure 5). However, there were some key differences among watersheds. For example, Nushagak Bay and the Lower Nushagak River had sites that had more similar thermal regimes, compared with other watersheds. Egegik Bay appears to be differentiated from the other watersheds, but that is largely driven by the low number of sites in that watershed. Generally, temperatures tend to peak around mid-July, although maximum weekly mean temperatures can occur anywhere from early June to late August (Figure 6).

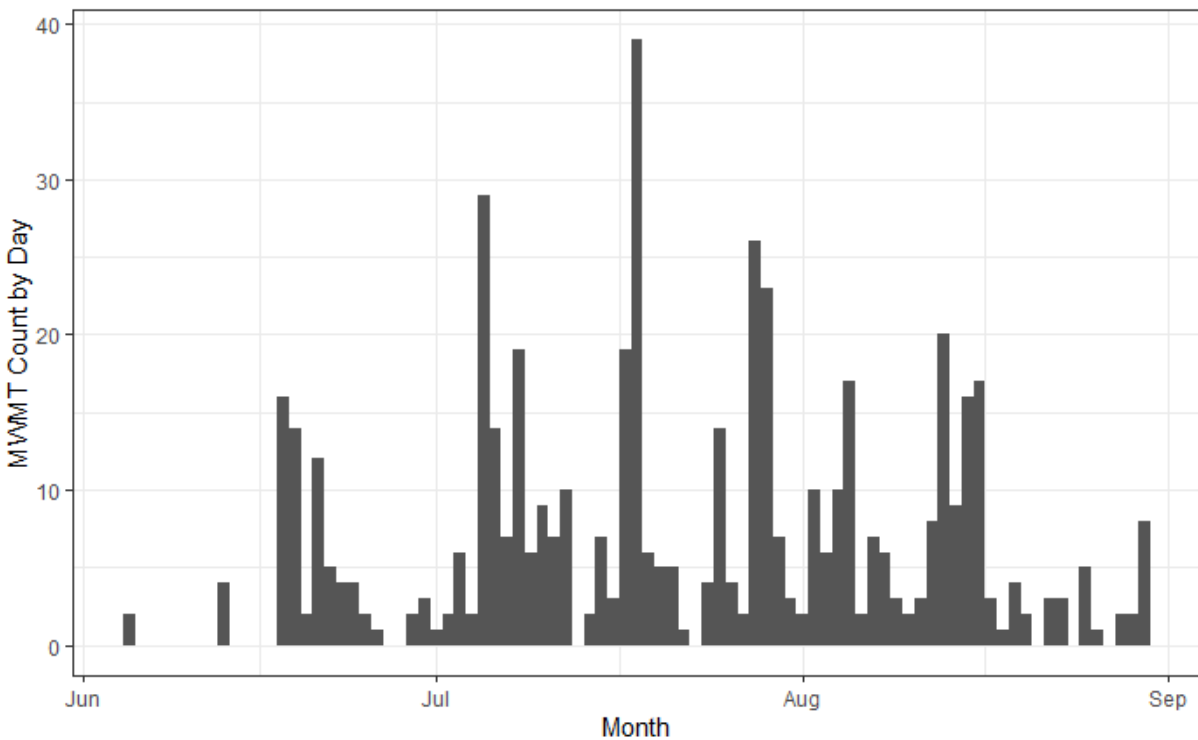


Figure 6. Distribution of the timing of annual maximum weekly mean temperatures across all site-year combinations.

Comparing Bristol Bay Thermal Regimes to Other Salmon-Producing Regions in Alaska

Overall, the Bristol Bay streams and rivers included in this study are warmer than monitored streams and rivers in the Copper River watershed and Prince William Sound, but are comparable to those in Cook Inlet and Kodiak (Figure 7), although Cook Inlet streams tend to experience more days over 18 degrees Celsius. Based on ordination (Figure 8), Bristol Bay streams had comparable thermal diversity to Cook Inlet and Kodiak, with the Copper River and Prince William Sound encompassing more of a range of the thermal metrics.

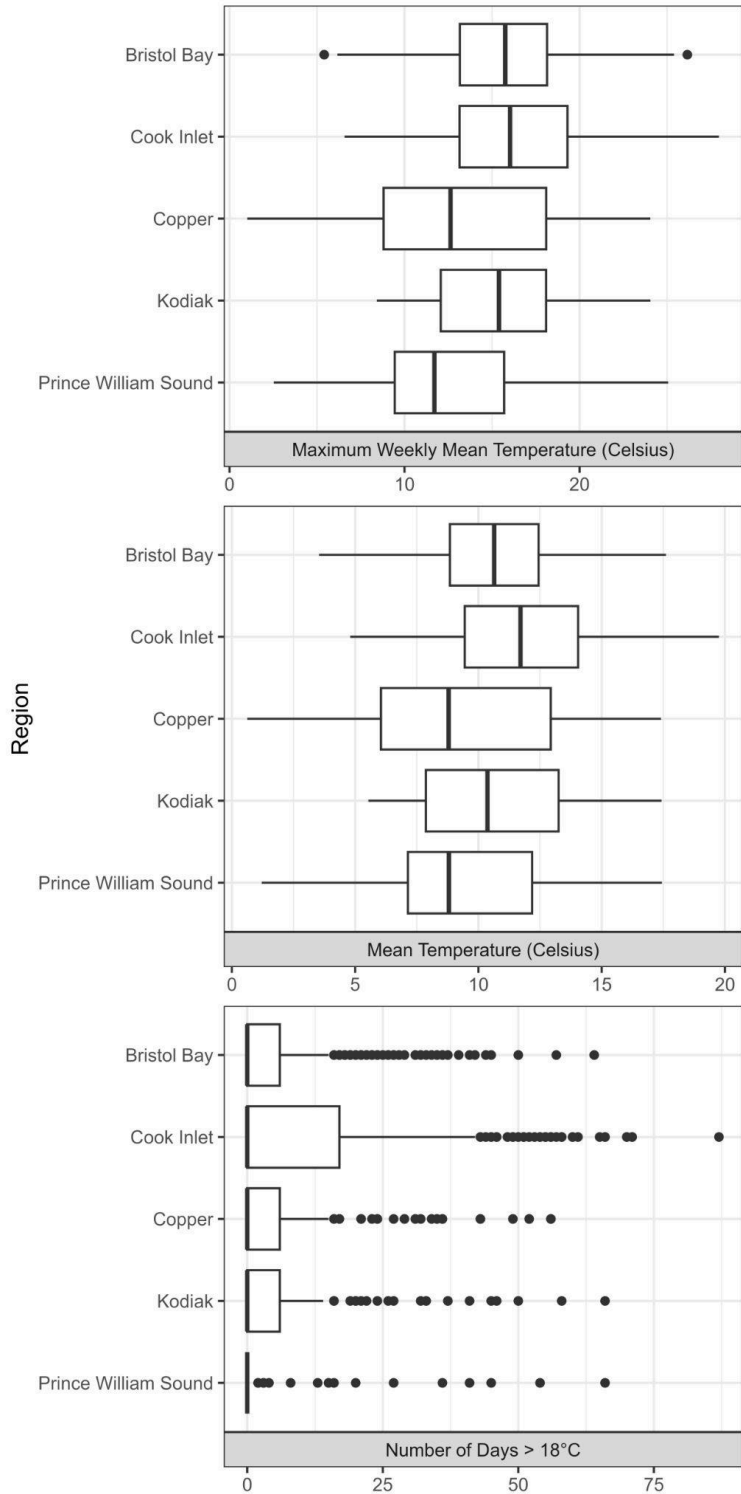


Figure 7. Distributions by region in southern Alaska of temperature metrics most relevant for juvenile salmon growth potential. Maximum weekly mean temperature shown at top, mean temperature in the middle, and number of days above 18 degrees Celsius at bottom.

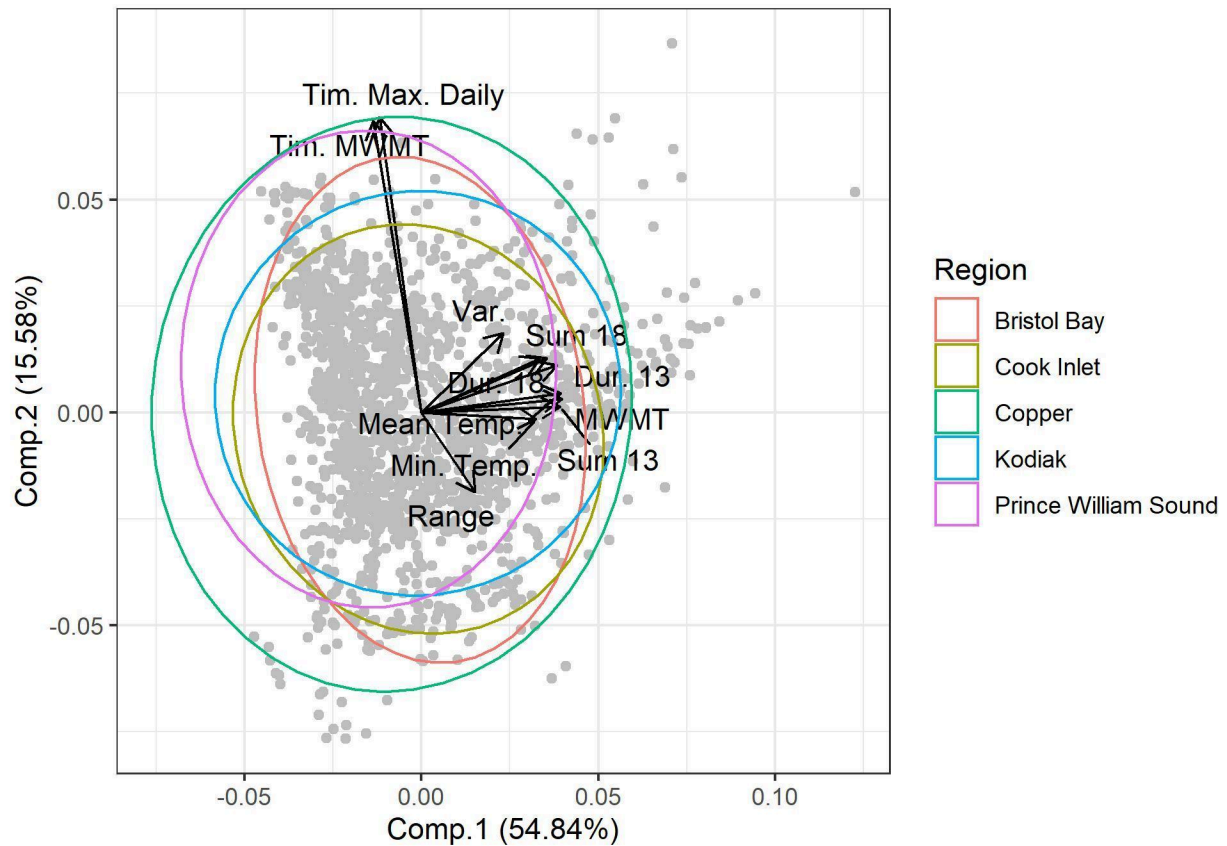


Figure 8. Ordination of 11 temperature metrics by region in southern Alaska. The included temperature metrics are maximum weekly mean temperature, mean temperature, timing of maximum daily temperature, timing of maximum weekly mean temperature, number of days above 13 degrees Celsius, number of days above 18 degrees Celsius, duration of longest warm event above 13 degrees Celsius, duration of longest warm event above 18 degrees Celsius, minimum temperature maximum daily range, and the variance of daily maximum temperatures.

Temporal Trends at Long Term Temperature Monitoring Sites

Overall, there were not strong and consistent trends over time at the long-term monitoring sites with only a few exceptions (Figure 9). The timing of maximum weekly temperature did not change significantly at any of the sites. In contrast, maximum weekly mean temperature and mean summer temperature showed significant trends over time at a few sites (Figure 9, Table 2). MWMT increased over the monitoring period in the Kaktuli River near Iliamna (monitored by the USGS - Gage 15302200). At four sites, summer mean temperatures increased over the monitoring period, with a decline at one site (Gechiak River), with data unavailable after 2014.

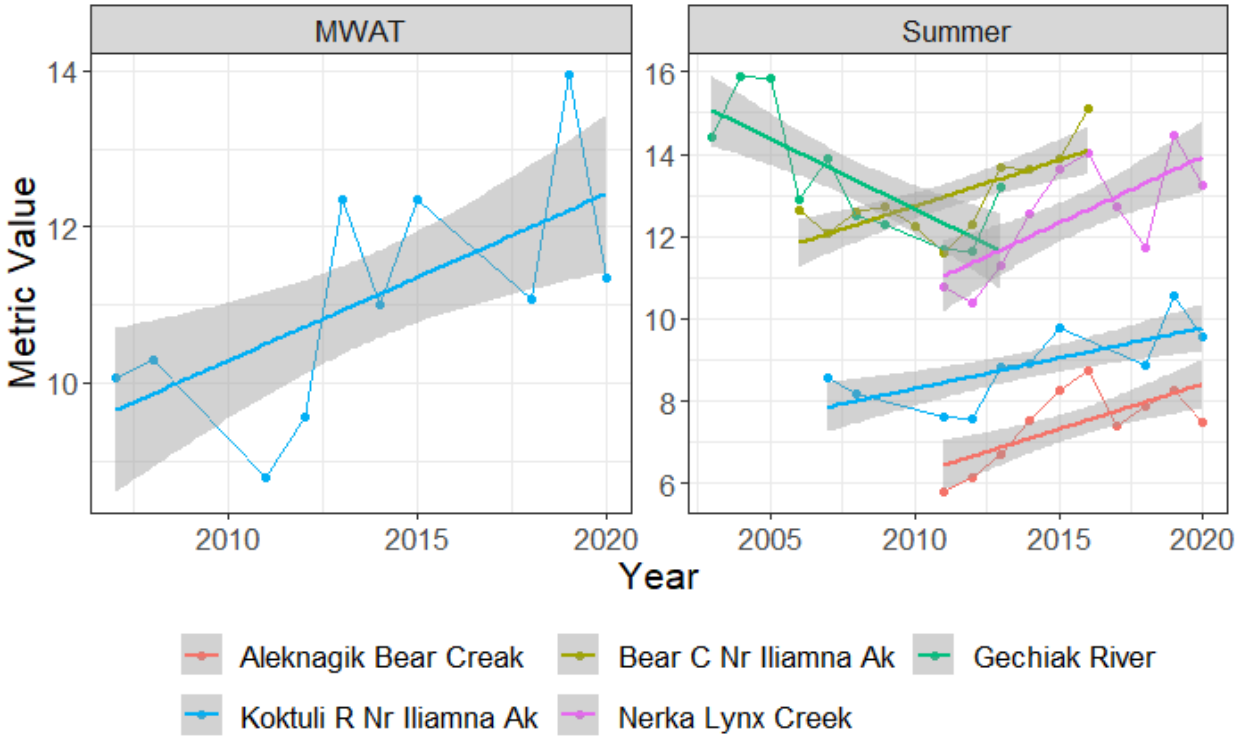


Figure 9. Significant trends over time in maximum weekly mean temperature (left), and mean summer temperature (right), with lines and points colored by site name.

Table 2. Mann-Kendall trend test statistics, p-values, and Sen's slope estimates for sites with significant temporal trends.

Site Name	Data Provider	Thermal Regime Indicator	Mann-Kend all Trend Test Statistic	p-value	Sen's slope estimate
Koktuli River near Iliamna	USGS (Gage 15302200)	MWMT	1.968	0.049	0.365
		Mean Temp.	2.147	0.032	0.225
Gechiak Creek near Togiak River	USFWS Togiak National Wildlife Refuge	Mean Temp.	-2.504	0.012	-0.353
Bear Creek near Aleknagik Lake	University of Washington Alaska Salmon Program	Mean Temp.	1.968	0.049	0.269
Lynx Creek near Nerka Lake	University of Washington Alaska Salmon Program	Mean Temp.	2.147	0.032	0.353

Bear Creek near Iliamna	USGS (Gage 15300100)	Mean Temp.	2.024	0.043	0.213
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Juvenile Salmon Growth Potential Modeling

The summer (June-August) stream temperatures used for juvenile salmon growth potential modeling exhibited considerable contrast among hydrologic units, sampling sites, and years. Across all years included in the study, mean daily temperatures were lowest in the Wood River drainage, highest in the Lower Nushagak River hydrologic unit, and intermediate in the other drainages within the Bristol Bay region (Figure 10). However, some of these apparent differences may have been an artifact of differing periods of data availability across these regions. To examine spatial differences in thermal regimes during a consistent time period, we compared summer temperatures during relatively cool 2018 and historically warm 2019, two years with high data availability throughout the region (Figure 11). During 2018, the Lower Nushagak hydrologic unit exhibited the warmest temperatures on average, whereas the Wood River hydrologic unit exhibited the coolest temperatures on average. During 2019, temperatures were substantially warmer across the entire region, with the Togiak and Lower Nushagak hydrologic units exhibiting the highest temperatures on average, and the Wood River drainage exhibiting the coolest temperatures on average.

Simulated growth potential was strongly influenced by feeding rate, across all sites and years (Figure 12). In the low feeding rate simulations, growth potential was low across all thermal regimes, averaging 0.85 g (range: 0.27-1.04 g). In the moderate feeding rate simulations growth potential was higher (mean = 2.15 g) and more variable among thermal regimes (range: 0.46-2.69 g). In the high feeding rate simulations, growth potential was highest (mean = 4.42 g) and most variable across thermal regimes (range: 0.64-5.67 g).

Across all sites, growth potential was slightly lower in warm 2019 than in cool 2018, regardless of the feeding scenario (Figure 13). In the low feeding rate simulations, growth potential averaged 0.77 g in 2019 (range: 0.27-1.01 g) vs. 0.91 g in 2018 (range: 0.48-1.03 g). In the moderate feeding rate simulations, growth potential averaged 2.06 g in 2019 (range: 0.85-2.60 g) vs. 2.27 g in 2018 (range: 0.86-2.65 g). In the high feeding rate simulations, growth potential averaged 4.39 g in 2019 (range: 1.37-5.42 g) vs. 4.62 g in 2018 (range: 1.40-5.63 g).

The relative change in growth potential from 2018 to 2019 varied considerably across individual sites, with some sites gaining and other sites losing growth potential under the historically warm thermal regimes measured in 2019 (Figure 14). Most sites exhibited reduced growth potential in warm 2019 relative to cool 2018, but some sites showed the opposite pattern, and these results differed among feeding rate scenarios. At low feeding rates, 22 of 33 sites exhibited reduced growth potential in 2019, with a mean change of -14% (range: -70% to +39%) vs. 2018. At moderate feeding rates, 18 of 33 sites exhibited reduced growth potential in 2019, with a mean change of -5.5% (range: -65% to +66%). At high feeding rates, 18 of 33 sites exhibited reduced growth potential in 2019; however, the mean percent change was positive at 0.81% (range: -61% to + 86%). Most hydrologic units included sites with both negative and positive changes in

growth potential in 2019 relative to 2018. The hydrologic units with the warmest average temperatures in 2019 (Togiak and Lower Nushagak River) exhibited reduced growth potential at all monitored sites in that year, whereas the generally cooler Wood River drainage exhibited mostly increased growth potential in 2019. Sites with relatively high growth potential were distributed across the Bristol Bay region in both years (Figure 15).

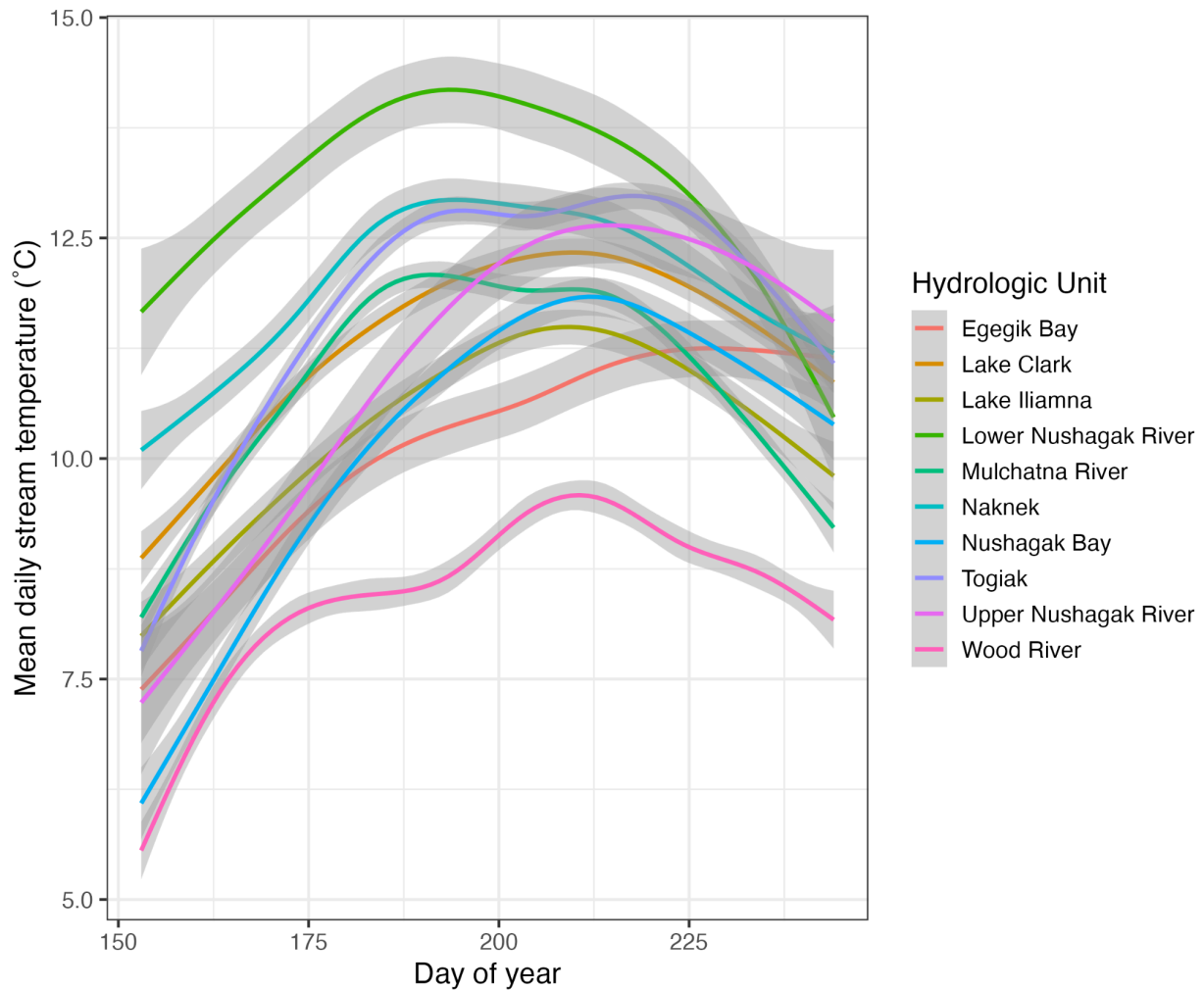


Figure 10. Mean daily stream temperatures during summer (June–August), across all site-years included in growth potential simulations, grouped by Hydrologic Unit (HUC 8). Simulations were run for each site year for which temperature measurements were available for the period June 1–August 31.

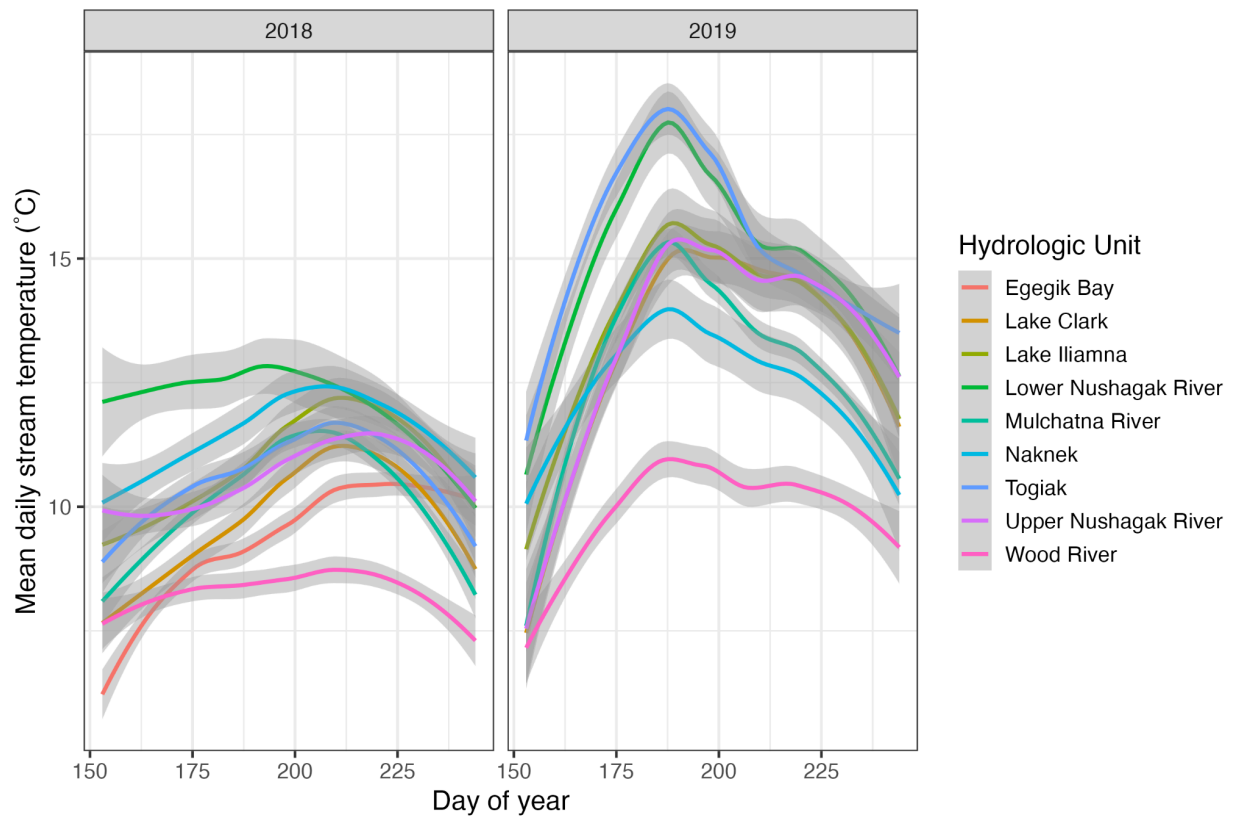


Figure 11. Mean daily stream temperatures during the summers (June–August) of 2018 (a relatively cool year) and 2019 (a warm year), across all sites included in growth potential simulations, grouped by Hydrologic Unit (HUC 8). Simulations were run for each site-year for which temperature measurements were available for the period June 1–August 31. Colored curves represent mean values on each day and gray bands represent 95% confidence regions.

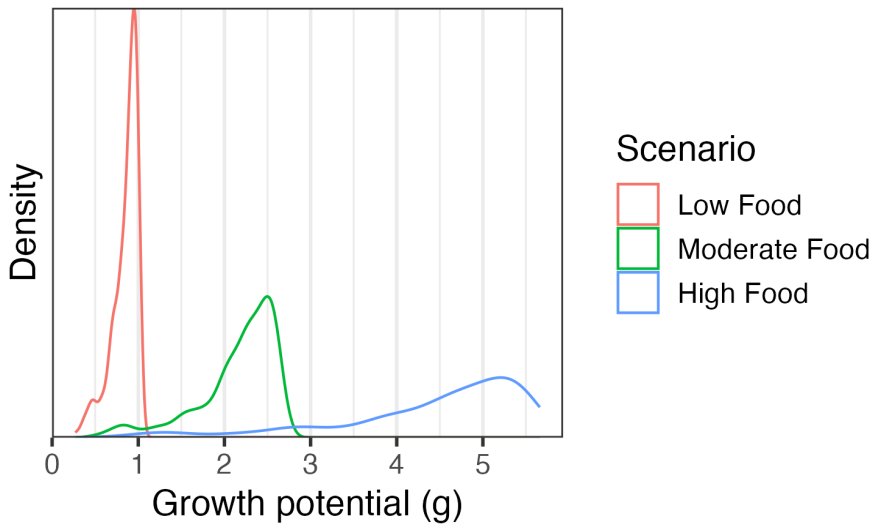


Figure 12. Density plot of simulated growth potential (g wet weight on August 31) of age-0 Chinook and coho salmon across all sites and all years with available temperature data. Growth potential was simulated from June 1 to August 31 using a bioenergetics model. Simulations assumed salmon consumed a diet of invertebrates at low (0.3), moderate (0.45), and high (0.6) feeding rates, expressed as the proportion of theoretical maximum consumption rate pC_{max} .

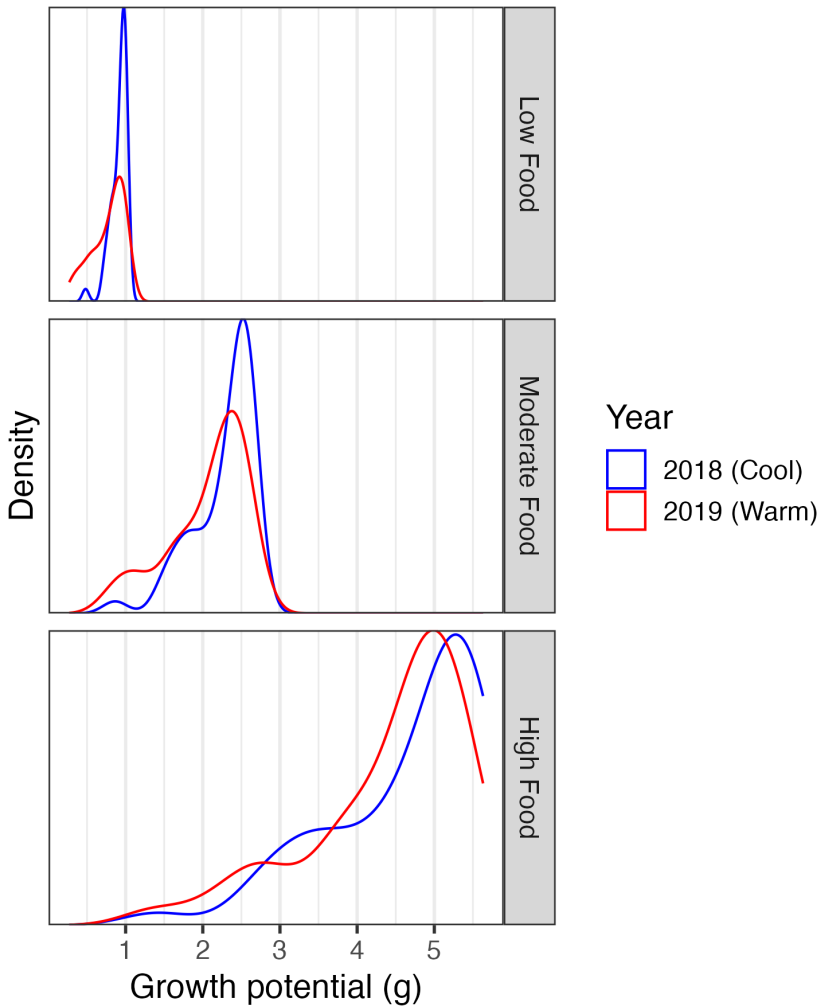


Figure 13. Simulated growth potential (g wet weight on August 31) of age-0 Chinook and coho salmon in relatively cool 2018 and warm 2019, across all sites. Growth potential was simulated from June 1 to August 31 at all sites with available temperature data in these years. Simulations assumed salmon consumed a diet of invertebrates at low (0.3), moderate (0.45), and high (0.6) feeding rates, expressed as the proportion of theoretical maximum consumption rate pC_{max} .

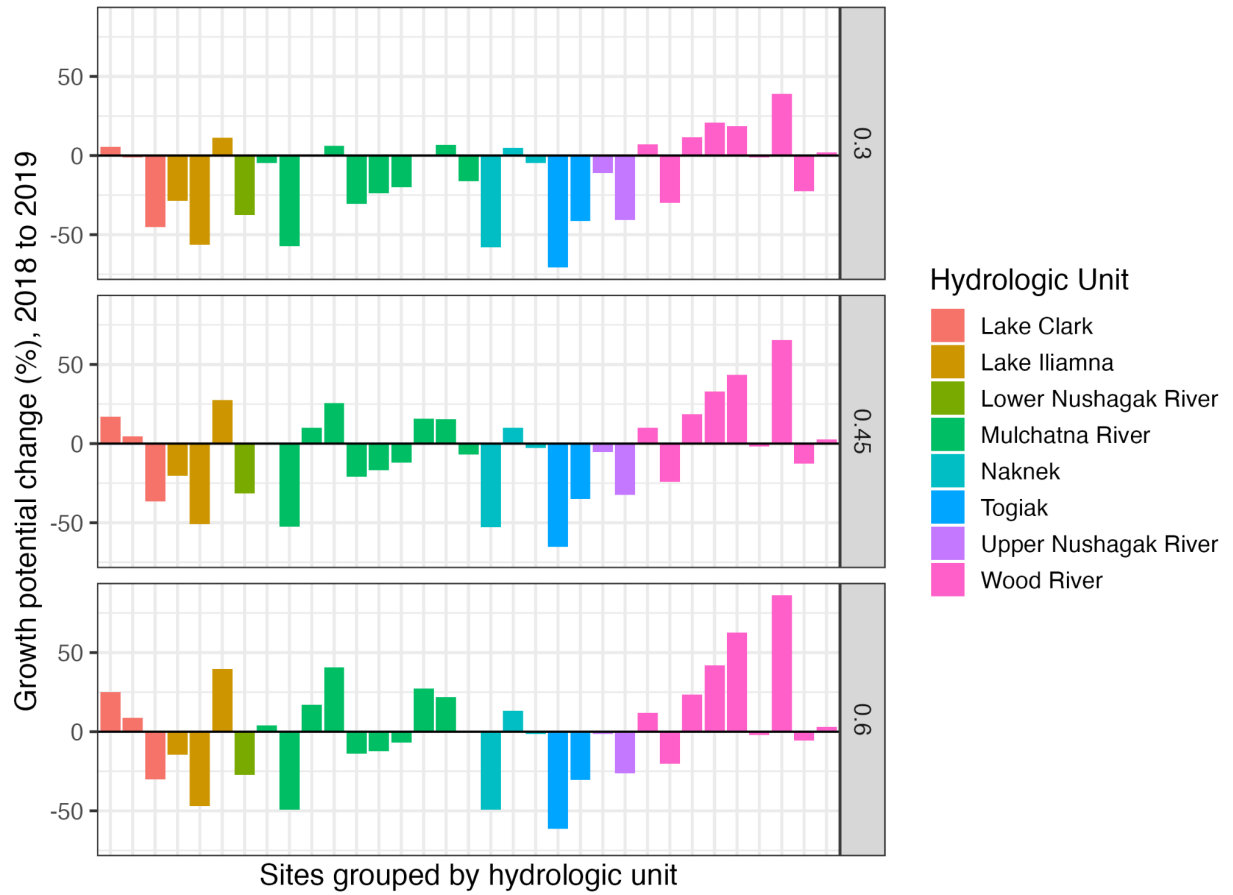


Figure 14. Percent change in growth potential of age-0 Chinook and coho salmon between 2018 and 2019, across 33 sites with available temperature data, grouped by hydrologic unit. Simulations assumed salmon consumed a diet of invertebrates at low (0.3), moderate (0.45), and high feeding rates (0.6), expressed as the proportion of theoretical maximum consumption rate pC_{max} .

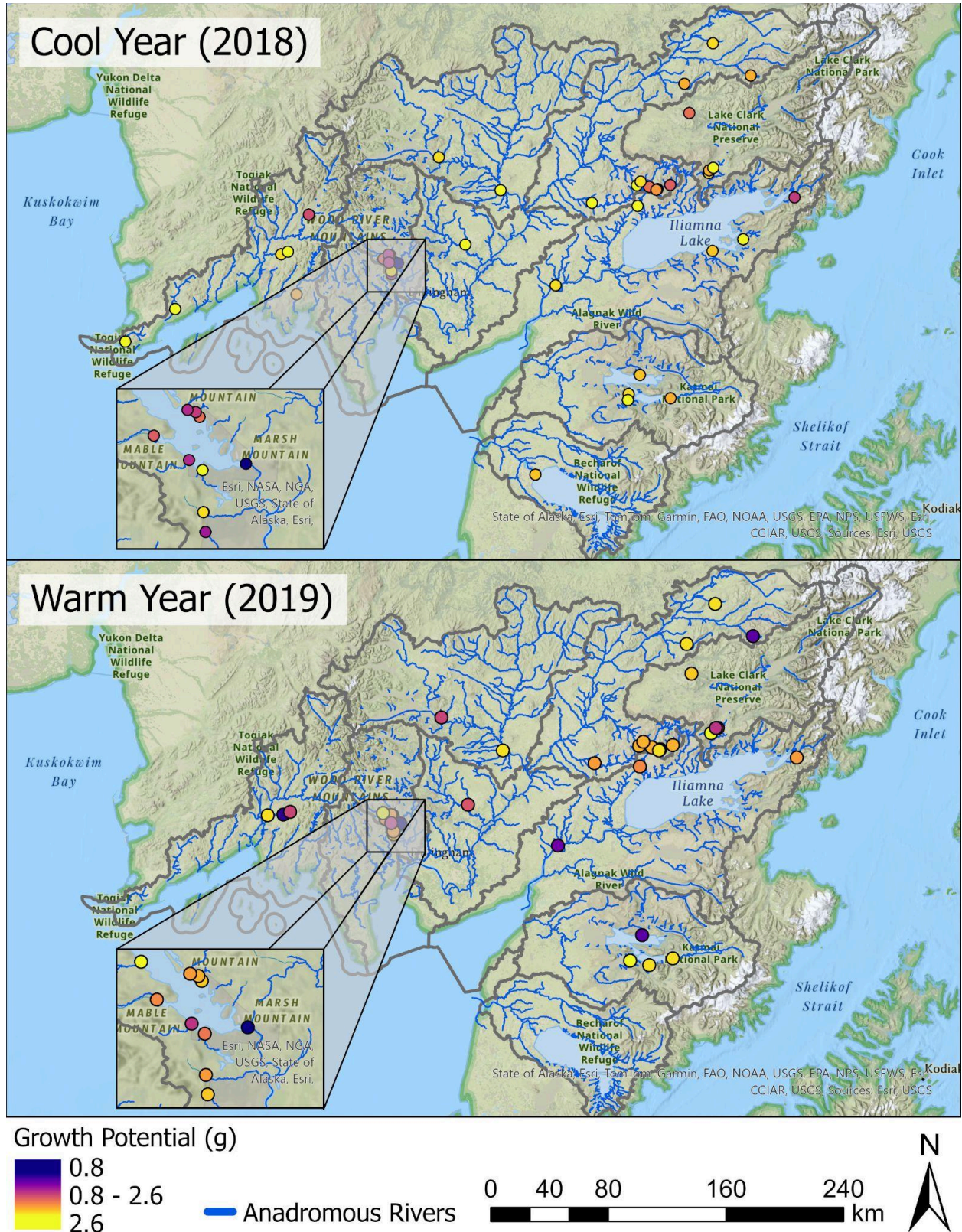


Figure 15. Simulated growth potential (g wet weight on August 31) of age-0 Chinook and coho salmon across Bristol Bay sites during two years with contrasting thermal regimes. Growth

potential simulations assumed salmon fed on invertebrates at a moderate feeding rate of 0.45 as a proportion of their theoretical maximum consumption rate (ρC_{max}). Growth potential was simulated from June 1 to August 31 at all sites with available temperature data. Map inset shows detail in the Wood River drainage, where the density of monitoring sites was especially high.

Discussion

Thermal Regimes

Thermal diversity exists both across and within major watersheds in Bristol Bay, based on multiple thermal metrics. Notably, the Wood River watershed was the coolest, on average during the study period, while the Upper Nushagak was the warmest. On the whole, thermal regimes varied more within major Bristol Bay watersheds than across them (Figure 5), which is consistent with variability within other major salmon-producing regions in Alaska (Shaftel et al. 2020). That high variability within watersheds may allow highly mobile juvenile salmon to behaviorally use that thermal diversity to their advantage, for example by seeking warm temperatures to optimize growth and finding cool refugia when needed. One watershed in particular (Egegik Bay) only had one temperature monitoring site, so caution is warranted in assuming that these thermal regime patterns hold across all sites within these Bristol Bay watersheds. More thermal monitoring may be needed in this area and other data-poor regions across Bristol Bay to identify other thermally sensitive watersheds for salmon spawning and rearing.

In comparison to other salmon-producing regions in southcentral Alaska (Cook Inlet, Copper River, Kodiak, Prince William Sound), the sites monitored in Bristol Bay were warmer than those in Copper River and Prince William Sound, and comparable to those in Cook Inlet and Kodiak. Notably though, many of these temperature monitoring networks explicitly avoid glacial streams, since they focus primarily on watersheds anticipated to warm immediately under climate change scenarios. The challenge of not having randomly selected sites across all regions, though, is difficult to avoid, given that temperature monitoring often occurs strategically and in a targeted fashion at sites of particular interest to organizations.

Surprisingly, trends in thermal metrics were not strong and consistent at the long-term monitoring sites. Only five sites experienced significant trends in mean summer temperatures, and only one site experienced a significant increase in maximum weekly temperatures over the study period. Given interannual variability in large-scale climate influences across the Arctic (Jeong et al. 2022), very long periods of time spent monitoring aquatic systems will likely be needed to detect trends. The combination of temporal and spatial variability in thermal regimes will have implications for coho and Chinook salmon spawning and rearing across the region.

Juvenile Growth Potential

The juvenile salmon growth potential analysis provided a way to interpret the large dataset of stream temperatures synthesized in this study through the lens of stream salmonid growth rates. This analysis condensed the time series of stream temperature for each site year with available data into an easily interpretable and ecologically relevant metric of body mass on August 31. As

is common in bioenergetics analyses, the simulation results are best interpreted via relative comparisons of growth potential among sites and years, rather than as precise estimates of juvenile salmon growth at any particular place and time. These simulations were based on several important assumptions, and it is important to consider their limitations when interpreting the results. First, growth rates are highly dependent on food quality and feeding rates, as well as temperature, as illustrated in Figures 13 and 14. We used a prey energy density value based on diet analysis of juvenile coho salmon in the Wood River drainage (Armstrong et al. 2010). This estimate was slightly lower than similar estimates based on diet analyses from the Yukon River (Falke et al. 2019) and Kenai River (Meyer et al. 2023) basins, and thus, our estimates of growth potential may have been biased slightly low; however, we do not expect this difference to meaningfully influence our interpretation of the results. We simulated growth potential across three feeding rate scenarios that encompassed most of the variation reported in recent studies of juvenile Chinook and coho salmon in Alaska; however, this approach assumed that juvenile salmon are able to increase their feeding rates in proportion to their metabolic demands as temperatures increase. This is a critical assumption that warrants further examination (Railsback 2022). An analysis of empirical juvenile salmon body size observations across different thermal regimes would help to determine whether this assumption is reasonable. Further, while bioenergetics models have been widely applied to Alaskan salmon populations (e.g., Beauchamp 2009, Armstrong et al. 2010, Falke et al. 2019, Meyer et al. 2023), it remains unclear how well the thermal performance curves included in published bioenergetics models fit Alaskan salmon populations, and how much local adaptation in thermal performance exists among regions and populations. Measuring thermal performance of Alaska salmon and comparing performance among species, regions, and populations with laboratory experiments would be highly valuable objectives for future research.

The simulation results illustrated how the considerable thermal diversity among rivers and streams in the Bristol Bay region provides a wide range of thermal regimes in both warm and cool years, and juvenile salmon are likely to achieve positive growth rates in some habitats in even the coolest and warmest years. Even in the warmest year on record, 2019, simulated growth potential increased in a substantial number of monitored sites, even as overall growth potential declined on average. Further quantifying and conserving this thermal diversity may enhance the resilience of Bristol Bay stream salmonid populations to climate change. This could include identifying and conserving cold-water refugia in relatively warm drainage basins and maintaining the ecosystem processes that create thermal heterogeneity in free-flowing river basins. Additionally, maintaining the connectivity of aquatic stream networks could play a key role in allowing salmonids to move freely within river networks and behaviorally utilize thermal diversity as refugia or to optimize growth potential.

Finally, this growth potential analysis suggests that the thermal regimes of Bristol Bay streams and rivers may be approaching the peak of the thermal performance curves for juvenile Chinook and coho salmon, and further climate warming is unlikely to enhance juvenile growth rates overall. Instead, if temperatures exceed those observed in 2019, overall growth rates are expected to decrease. Relatively cool regions within Bristol Bay, such as the Wood River basin, are more likely to see enhanced juvenile growth during warm years, whereas warmer regions

like the Togiak and Lower Nushagak drainages are most likely to see reduced juvenile growth. We caution that this conclusion is based solely on the thermal regimes that were measured and included in this synthesis, and it is unclear how representative the monitored sites were of their respective drainage basins as a whole. This conclusion represents a hypothesis that can be tested and refined by analyzing empirical measurements of juvenile salmon body size under contrasting thermal regimes and conducting physiological experiments to better characterize the thermal performance and local adaptation of Alaska salmon populations.

References

- Armstrong, J. B., D. E. Schindler, K. L. Omori, C. P. Ruff, and T. P. Quinn. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology* 91:1445–1454.
- Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *Am. Fish. Soc. Symp.* 70:53–72.
- von Biela, V. R., C. J. Sergeant, M. P. Carey, Z. Liller, C. Russell, S. Quinn-Davidson, P. S. Rand, P. A. H. Westley, and C. E. Zimmerman. 2022. Premature Mortality Observations among Alaska’s Pacific Salmon During Record Heat and Drought in 2019. *Fisheries* 47:157–168.
- Bowen, L., V. R. von Biela, S. D. McCormick, A. M. Regish, S. C. Waters, B. Durbin-Johnson, M. Britton, M. L. Settles, D. S. Donnelly, S. M. Laske, M. P. Carey, R. J. Brown, and C. E. Zimmerman. 2020. Transcriptomic response to elevated water temperatures in adult migrating Yukon River Chinook salmon (*Oncorhynchus tshawytscha*). *Conservation Physiology* 8:coaa084.
- Brett, J. R., J. E. Shelbourn, and C. T. Shoop. 2011. Growth Rate and Body Composition of Fingerling Sockeye Salmon, *Oncorhynchus nerka*, in relation to Temperature and Ration Size. *Journal of the Fisheries Board of Canada*.
- Cline, T. J., J. Ohlberger, and D. E. Schindler. 2019. Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution* 3:935–942.
- Deslauriers, D., S. R. Chipps, J. E. Breck, J. A. Rice, and C. P. Madenjian. 2017. Fish Bioenergetics 4.0: An R-Based Modeling Application. *Fisheries* 42:586–596.
- Falke, J. A., B. M. Huntsman, and E. R. Schoen. 2019. Climatic variation drives growth potential of juvenile Chinook Salmon along a subarctic boreal riverscape. Pages 57–82 *in* R. M. Hughes, D. M. Infante, L. Wang, K. Chen, and B. de F. Terra, editors. *Advances in understanding landscape influences on freshwater habitats and biological assemblages*. American Fisheries Society, Symposium 90, Bethesda, Maryland.
- Jeong, H., H.-S. Park, M. F. Stuecker, and S.-W. Yeh. 2022. Distinct impacts of major El Niño events on Arctic temperatures due to differences in eastern tropical Pacific sea surface temperatures. *Science Advances* 8:eabl8278.
- Jones, L. A., C. C. Muhlfeld, and L. A. Marshall. 2017. Projected warming portends seasonal shifts of stream temperatures in the Crown of the Continent Ecosystem, USA and Canada. *Climatic Change* 144:641–655.
- Jones, M., T. Sands, S. Morstad, P. Salomone, G. Buck, F. West, C. Brazil, and T. Krieg. 2013. 2012 Bristol Bay area annual management report. Fishery Management Report, Alaska Department of Fish and Game, Anchorage, Alaska.
- Knapp, G., M. Guettabi, and O. S. Goldsmith. 2013. The Economic Importance of the Bristol Bay Salmon Industry. Report, Institute of Social and Economic Research, University of Alaska Anchorage.
- Larson, E., R. Shaftel, L. Jones, D. Merrigan, M. Sloat, T. Cline, D. Schindler, and L. Adelfio. 2024a. Assessing Thermal Sensitivities of Salmon Habitats in the Bristol Bay, Kodiak

- Island, Cook Inlet, Copper River, and Prince William Sound Watersheds - Stream Thermal Sensitivities | Alaska Conservation Science Catalog. AKSSF Completion Report, University of Alaska Anchorage Alaska Center for Conservation Science, Anchorage, Alaska.
- Larson, E., R. Shaftel, L. Jones, D. Merrigan, M. Sloat, T. Cline, D. Schindler, and L. Adelfio. 2024b, July 23. Stream Thermal Sensitivities in Southern Alaska. Zenodo.
- Mauger, S., R. Shaftel, E. J. Trammell, M. Geist, and D. Bogan. 2015. Stream temperature data collection standards for Alaska: Minimum standards to generate data useful for regional-scale analyses. *Journal of Hydrology: Regional Studies* 4:431–438.
- Mauger, S., and T. Troll. 2014. IMPLEMENTATION PLAN: BRISTOL BAY REGIONAL WATER TEMPERATURE MONITORING NETWORK. Page 24. Cook Inletkeeper, Homer, AK, and Bristol Bay Heritage Land Trust, Dillingham, AK.
- Meyer, B. E., M. S. Wipfli, E. R. Schoen, D. J. Rinella, and J. A. Falke. 2023. 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. *Transactions of the American Fisheries Society* 152:169–186.
- Pohlert, T. 2023, October 10. trend: Non-Parametric Trend Tests and Change-Point Detection.
- Railsback, S. F. 2022. What We Don't Know About the Effects of Temperature on Salmonid Growth. *Transactions of the American Fisheries Society* 151:3–12.
- Rich, H. B., T. P. Quinn, M. D. Scheuerell, and D. E. Schindler. 2009. Climate and intraspecific competition control the growth and life history of juvenile sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 66:238–246.
- Schindler, D. E., D. E. Rogers, M. D. Scheuerell, and C. A. Abrey. 2005. EFFECTS OF CHANGING CLIMATE ON ZOOPLANKTON AND JUVENILE SOCKEYE SALMON GROWTH IN SOUTHWESTERN ALASKA. *Ecology* 86:198–209.
- Shaftel, R., S. Mauger, J. Falke, D. Rinella, J. Davis, and L. Jones. 2020. Thermal Diversity of Salmon Streams in the Matanuska-Susitna Basin, Alaska. *JAWRA Journal of the American Water Resources Association* 56:630–646.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. *Can. J. Fish. Aquat. Sci.* 48:909–922.