Interpopulation Variation among Juvenile Chinook Salmon from California and Oregon

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Foreword

Temperature is a critical factor in salmon ecology. The salmon life cycle is complex and requires cool and cold temperatures for many of its life stages (spawning and early life stage development, juvenile development and outmigration, adult in-migration). In 2003, EPA Region 10 published temperature criteria guidance for Pacific Northwest salmonids (EPA 2003)[1] to help address these requirements. The analysis considered data from taxa in northwest states, California, and other locales. EPA 2003 underwent rigorous public and peer review and is used as the basis for many state and federal regulatory and non-regulatory decisions in California.

The Central Valley includes some of the most threatened Chinook populations in California (i.e., winter- and spring-run). Reductions and alterations in flow in the Central Valley from water development over the past several decades have led to flows that are slower and warmer and the resulting higher stream temperatures may contribute to the threatened status of Central Valley Chinook salmon populations. The study herein was conducted by UC Davis and funded by EPA. It explores whether Chinook salmon (*O. tshawytscha*) populations near the species' southernmost distribution limit (i.e., California's Central Valley) exhibit a higher thermal tolerance than more northerly populations.

Performance-based tests were used to identify temperatures associated with optimal physiologic performance, measured as critical maximum, growth, and metabolic rate. Four distinct populations of juvenile chinook salmon (two Oregon fall-run, one Central Valley fall-run, and one Central Valley winter-run) were evaluated to determine: 1) whether there is a difference in peak performance temperature among the populations and 2) whether a trade-off exists between increased thermal performance at higher temperatures and remaining capacity to acclimate to even higher temperatures. Generally, temperatures associated with peak performance differed among the four populations. Peak performance temperatures were higher in the Central Valley fall-run population than in both the two Oregon fall-run populations and in the winter-run Central Valley population, despite the two Central Valley populations being sympatric. Regarding acclimation capacity, the three fall-run populations generally showed an increase in peak performance temperature with increased acclimation temperature. However, the Central Valley fall-run population showed minimal capacity for further acclimation at the highest acclimation temperature, suggesting that it is susceptible to further increase in the temperature of its habitat. In contrast to the other three populations, the Central Valley winter-run population showed a decrease in peak performance temperature with increased acclimation temperature, implying reduced warm-temperature performance in winter-run populations.

An on-going point of discussion in evaluating thermal stress on salmon is the types of tests that are needed to determine scientifically-sound temperature thresholds, including site-specific thresholds. Performance-based studies, such as this one, typically evaluate only short-term, peak physiologic performance, in a controlled setting and free of ecological stress, and therefore may not reflect true capacity to tolerate high temperatures in a *natural setting*. In identifying temperature thresholds, including site-specific targets, it is critical to also consider how factors in the ecological setting (e.g., diet, competition, predators, disease, duration, and

[1] EPA's Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards (2003) provides an approach for states and tribes in developing temperature water quality standards for coldwater salmonids.

habitat quality) impact fish response to temperature. Other agencies also have expressed caution in using performance-based studies only. In a recent letter, NOAA commented that the Federal Energy Regulatory Commission (FERC) did not provide adequate justification for relying solely on performance information in assessing how well a temperature regime promotes population-level fitness in the natural environment.[2] CDFW, in its comment letter to FERC, indicated that the short duration of aerobic scope performance tests provides limited utility in informing chronic duration exposure experienced in the wild.[3] Further, directly equating the results of performance-based, site-specific tests to the thresholds in EPA 2003 would be inappropriate; such tests typically do not incorporate ecological factors to the extent of EPA 2003. NOAA shared this concern in a subsequent comment letter, noting that it is inappropriate to compare results from a performance-based, acute test of individuals (such as those used in FERC's analysis) to a threshold meant to protect against chronic effects to populations, as in EPA 2003, which considered exposure time (i.e., chronic vs. acute) among other population-level effects.[4]

EPA would like to acknowledge the excellent work of the research scientists at UC Davis (Fangue Laboratory and Center for Aquatic Biology and Aquaculture at UC Davis) in conducting the laboratory experiments and producing this summary report. The results of this study represent a significant contribution to our knowledge of optimal performance temperatures for Central Valley and other west coast salmon. Due to the study's consideration of multiple locations, seasons, performance traits, and acclimation temperatures, the results will help narrow the range of temperatures and conditions for subsequent studies. Future work in this field should include investigating additional populations, namely Sacramento spring-run and late fall-run, to explore the full breadth of Chinook salmon found in the Central Valley, integrating conditions encountered in the natural environment into performance-based tests, and further research on differences between hatchery and wild-reared juveniles, as domestication effects have been observed in salmonids after as little as two hatchery generations.

[2] National Oceanic and Atmospheric Administration (NOAA), February 6, 2017. Comments to FERC from National Marine Fisheries Service on the Study, "*Thermal Performance of Wild Juvenile Oncorhynchus mykiss in the Lower Tuolumne River: A Case for Local Adjustment to High River Temperature* (Farrell *et al*. 2015)

[3] California Department of Fish and Wildlife (CDFW), July 6, 2016 Comments to Rose Staple, HDR, Inc. (contractor for FERC) from National Marine Fisheries Service on the Study, "*Thermal Performance of Wild Juvenile Oncorhynchus mykiss in the Lower Tuolumne River: A Case for Local Adjustment to High River Temperature* (Farrell *et al*. 2015

[4] National Oceanic and Atmospheric Administration (NOAA), April 11, 2019. The U.S. Department of Commerce's, NOAA Fisheries, West Coast Region's Comments on the Federal Energy Regulatory Commission's Draft Environmental Impact Statement for the Don Pedro and La Grange Hydroelectric Projects (P-2299-082 and P-14581-002)

Introduction

As ectotherms, fish are strongly influenced by temperature, which affects both intrinsic physiological and extrinsic ecological performance. The role of temperature manifests across spatial scales from setting the rate of enzymatic reactions within the cell to producing weather and climatic patterns. Predicted increases in global temperature will undoubtedly alter the performance of fish, leading to challenges managing and conserving at-risk species.

Pacific salmonids (*Oncorhynchus spp.*) in the Central Valley of California are under increasing environmental strain. Rising river temperatures due to climate change and extended drought conditions are threatening some populations with extinction (Crossin et al. 2008; Yates et al. 2008; Moyle et al. 2017). Furthermore, extreme drought conditions witnessed in the past decade are anticipated to continue, if not increase in magnitude, in the future (Brown et al. 2013; Tansey et al. 2014). The construction of dams for water storage and hydropower have greatly reduced the amount of viable habitat for salmon by up to 80% (Quiñones et al. 2015). Additionally, a growing human population will increase the demand for water both agriculturally and municipally, further reducing the water available for salmonids. In order to combat the decline in salmonid populations, the state of California has incorporated a variety of management strategies (e.g. conservation hatcheries, regulated release of cold water from dams) to aid in the conservation and support of these commercially, ecologically, and culturally important species.

Much work has been done determining the thermal performance of salmonids in the Pacific Northwest (Richter and Kolmes 2005). EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards (U.S. Environmental Protection Agency 2003, hereon referred to as EPA 2003) provides recommended temperature thresholds to protect salmonids. The EPA 2003 guidance has been applied in California for various regulatory and other purposes. Still, the suitability of the thresholds in EPA 2003 for California populations is of interest, and recent research on Pacific salmonids has demonstrated interpopulation variation in thermal performance among geographically proximal populations (Eliason et al. 2011; Stitt et al. 2014; Chen et al. 2015; Verhille et al. 2016; Anttila et al. 2019). Differences among populations have been shown for multiple traits: cardiovascular physiology (Anttila et al. 2019), thermal physiology (Chen et al. 2013, 2015), morphology (Doctor et al. 2015; Bowen and Marchetti 2016), etc. For instance, previous work on sockeye salmon (*O. nerka)* has demonstrated population specific thermal performance corresponding to the thermal regime of native river systems (Eliason et al. 2011). Left out of this literature so far is an exploration of inter-population variation among Chinook salmon (*O. tshawytscha*) populations near the species' southernmost distribution limit. Chinook salmon populations in California's Central Valley represent the southernmost populations and include some of the most threatened populations/runs (i.e., winter- and spring-run).

Additionally, research demonstrated a trade-off between improved thermal tolerance and a reduced capacity to acclimate exhibited by southern populations. Stillman (2003) reported on the effects of acclimation on thermal limits of cardiac function in four congeneric (*Petrolisthes*) species of marine porcelain crab from different thermal habitats. He observed that the species that have evolved the greatest tolerance to high temperatures have done so at the expense of acclimation capacity and it is these species that will be the most susceptible to the smallest increases in micro- habitat temperatures. For Chinook salmon in California, a reduced capacity

to acclimate to future environmental change would be cause for management concern in a time of rapid environmental and anthropogenic change.

Central Valley salmonids have been observed to demonstrate thermal performance at high temperatures (> 23°C). Verhille et al. (2016) found that steelhead trout (*O. mykiss*) from the Tuolumne River maintained aerobic performance at warm temperatures and exhibited a thermal tolerance greater than northern conspecific and congeneric populations. The authors attributed the performance of the Tuolumne population as reflective of the warm temperatures experienced by a population near its southern limit. Poletto et al. (2017) conducted aerobic scope trials on juvenile Chinook salmon from the Mokelumne River hatchery (San Joaquin County, California) and found an unusual, temperature-independent metabolic response as well as sustained metabolic performance at warm temperatures (>23°C). Such a response had not been observed in salmon juveniles elsewhere. These results are consistent with interpopulation variation in thermal physiology suited for the environmental conditions experienced by Mokelumne River salmon.

The difference in thermal tolerance between the California salmonid populations and those from further north highlight the potential for interpopulation variation in thermal physiology and open the door to tailoring salmonid management to best suit the traits of specific populations. The research reported herein, aims to assess the breadth of population variation in physiological traits and acclimation capacity through comparisons of the specific thermal tolerances and performance of several Chinook salmon populations, two from California (Coleman hatchery strain and Livingston Stone hatchery strain, Shasta County CA) and two populations from Oregon (Trask hatchery strain, Tillamook County OR and Elk River hatchery, Curry County OR). Furthermore, we compare our results with those of Poletto et al. (2017) research on the Mokelumne hatchery population. This research will contribute to our understanding of thermal physiology for Chinook salmon in the San Joaquin-Sacramento River basin (CA Central Valley). It is predicted that California salmon will exhibit greater thermal performance at warmer temperatures than more northern populations.

Experimental Approach

We reared four populations of Chinook salmon (Coleman, Elk River, Trask, and Livingston Stone winter-run) under identical rearing conditions at three acclimation temperatures (11, 16, and 20°C). The three fall-run Chinook salmon populations were selected to span a latitudinal gradient with the Coleman population being the southernmost, then the Elk River population and finally the Trask population as the northernmost (Figure 1). The critically endangered winter-run population was selected to explore variation among seasonal runs of Central Valley Chinook salmon. Acclimation temperatures were selected to reflect commonly occurring environmental water temperatures of cold (11°C), medium (16°C) and warm (20°C) temperatures experienced by Chinook salmon within the Central Valley. We assessed thermal performance using standardized methods in fish thermal physiology that included the measurement of aerobic scope (see review in Clark et al. 2013 and methodology in Verhille et al. 2016 and Poletto et al. 2017), critical thermal maxima (see methodology in Becker and Genoway 1979 and Fangue and Bennett 2003), and temperature-dependent growth (see methodology of Poletto et al. 2018). Using these physiological metrics, we were able to evaluate how populations performed when reared under identical conditions, as well as how performance within and

between populations changed when acclimated to 11°C vs. 16°C vs. 20°C. With this design we sought biogeographical patterns in absolute thermal capacity as well as acclimation capacity.

Overall Research Questions:

Q1: Do Central Valley vs. more northern populations demonstrate differences in thermal performance?

> Hypothesis: Salmon from lower latitudes are exposed to warmer temperatures and therefore would exhibit more warm adapted phenotypes than population from more northern latitudes.
> Prediction: Chinook salmon juveniles from the Central Valley will demonstrate a greater thermal tolerance, metabolic performance and growth across temperatures. This would be demonstrated by increased acute thermal tolerance, greater metabolic performance and increased growth at warm temperatures when compared to populations from northern areas.

Q2: What is the variation in acclimation capacity among Chinook salmon populations?

> Hypothesis 1: A trade-off exists between thermal tolerance and acclimation capacity; as populations increase optimal performance temperature, they decrease capacity to acclimate.
> Prediction: Populations from the Central Valley of California will exhibit reduced acclimation capacity as compared to populations from more northern latitudes.
> Hypothesis 2: No trade-off exists between thermal tolerance and acclimation capacity; as populations increase optimal performance temperature, they increase capacity to acclimate.
> Prediction: Populations from the Central Valley will exhibit increased (or at least equivalent) acclimation capacity when compared to populations from more northern latitudes.

Q3: Do fall- versus winter-run fish demonstrate differences in thermal performance?

> Hypothesis: Winter-run populations, historically resident to high-elevation cold water streams, will exhibit less tolerance to warmer temperatures than fall-run populations.
> Prediction: Winter-run salmon will exhibit lower acute thermal tolerances, cold-shifted metabolic performance and reduced growth rates at when acclimated to warm temperatures (16 or 20°C).

Specific Experimental Objectives:

Obj. 1: Construct temperature-dependent aerobic scope relationships for four populations (Coleman, Elk River, Trask and Livingston Stone) across three acclimation temperatures (11, 16 and 20°C).
Obj. 2: Determine acute thermal tolerance for each population at each acclimation temperature.
Obj. 3: Quantify temperature-dependent growth rate.

Methods

Fish Populations and Experimental Design

This research was conducted upon four anadromous hatchery-spawned populations of Chinook salmon (Coleman, Elk River, Trask, and Livingston Stone winter-run) from California and Oregon. Three populations exhibit the fall-run life history strategy, with the remaining exhibiting the winter-run life history strategy. Fall-run populations came from the Coleman National Fish Hatchery in Shasta County, CA, the Elk River Salmon Hatchery in Curry County, OR and the Trask Fish Hatchery in Tillamook County, OR. The winter-run population came from the captive brood-stock population reared and spawned at the Livingston Stone National Fish Hatchery in Shasta County, CA (Figure 1). To investigate differences in acclimation response between populations, each population was acclimated to three environmentally relevant water temperatures (11, 16 and 20°C). Temperatures were selected to span the range of temperatures a juvenile salmon would likely encounter within the Sacramento-San Joaquin watershed.

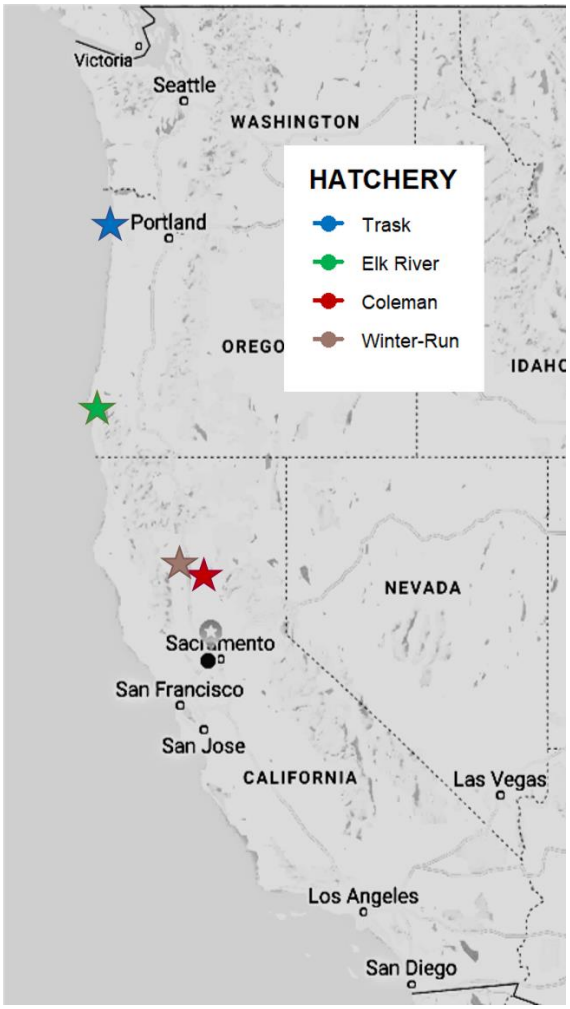

Figure 1: *Map of Chinook salmon source hatcheries used in the study. The Trask population was from the Trask Hatchery on the Trask River in Tillamook County, OR. The Elk River population was from the Elk River Hatchery on the Elk River in Curry County, OR. The Coleman Population was from the Coleman National Fish Hatchery on Battle Creek in Shasta County, CA. The winter-run population was spawned at the Livingston Stone National Fish Hatchery on the Sacramento River in Shasta County, CA, and collected from the Coleman National Fish Hatchery.*

Fish Transport, Acclimation and Husbandry

Juvenile Chinook salmon from the Coleman Hatchery were collected as eggs and hatched at the Center for Aquatic Biology and Aquaculture (CABA) at University of California, Davis. Fish from the remaining three populations were acquired as juvenile fry. Coleman eggs were collected on 11/16/2016. Juveniles from the Elk River, Trask and Livingston Stone (winter-run) Hatcheries were collected on 5/3/2017, 5/12/2017 and 2/5/2018, respectively. Fish from the Elk River and Trask hatcheries were netted from rearing raceways at those facilities. Winter-run fish were spawned and hatched at the Livingston Stone hatchery but were transported to the Coleman Hatchery facility (ca. 55 km) prior to collection by the authors. Juvenile Chinook salmon were transported to CABA via transport tank. Fish were transported in fresh well water collected at their hatchery of origin and aerated with 100% oxygen as needed to maintain oxygen concentration above 80%. Before being placed in acclimation treatments, fish were held at CABA in 1.5 m diameter, outdoor, flow-through tanks at 11°C. Fish were fed ad libitum a pelleted salmonid diet (mixture of 1 mm Skretting commercial trout feed and 1/64" Rangen semi-moist feed) daily during daylight hours.

Fish were stocked (densities in Table 1) in flow-through 1 m diameter (200 L) tanks with water fed by a dedicated well. Tanks were transitioned to target temperatures (11, 16, 20°C) at a rate of 1.5°C per day. Water temperatures were produced by mixing ambient (18°C) and cold (11°C) water and by using 800-watt titanium heaters (Model TH-0800, Finnex, USA) and temperature controllers (Model 72, YSI, Ohio) for the 20°C tanks. For the 2018 experiments on winter-run salmon, warm water treatments were produced by mixing ambient and warm (27°C) water to produce 20°C. Dissolved oxygen was maintained through constant aeration in each tank. Water temperatures were measured daily via glass thermometer (Fisher Brand™) to a 0.1°C resolution. Mean water temperatures for each acclimation group are listed in Table 1. Each treatment group (acclimation x population) was held in two replicate tanks. Fish were acclimated to treatment conditions for at least three weeks prior to beginning metabolic and critical thermal maximum experiments. Fish were fed 4.0% body mass/per fish/per day with adjustment every two weeks to account for growth. Mortality during the rearing period across all treatments were negligible. Mortalities were incidental and most commonly believed to be due to cessation of feeding or developmental deformities. There was a disease outbreak among the winter-run fish reared at 20°C; this is discussed below in the results section.

Table 1: *Starting metrics for measured populations. Starting Mass (grams) is given as the mean and standard deviation. Temperatures and starting densities are given for the two replicate tanks. Temperature (°C) readings were taken daily and are provided as mean and standard deviation. Tank replicate densities are provided as both number of fish stocked (n) and fish per L. Tanks had a water volume of 200 L.*

Hatchery	Acclimation Temperature	Starting Mass (g)	Tank 1 °C	Tank 2 °C	Tank 1 Density		Tank 2 Density	
					n	(fish/L)	n	(fish/L)
Coleman	11°C	5.65±1.27	11.2±0.3	11.2±0.3	55	0.275	60	0.3
	16°C		16.1±0.5	15.9±0.4	75	0.375	75	0.375
	20°C		19.7±0.5	19.8±0.5	70	0.35	75	0.375
Elk River	11°C	1.87±0.47	11.2±0.4	11.2±0.5	100	0.5	105	0.525
	16°C		15.9±0.4	15.9±0.4	100	0.5	105	0.525
	20°C		19.9±0.3	19.9±0.3	105	0.525	105	0.525
Trask	11°C	0.98±0.21	11.0±0.4	11.0±0.4	93	0.465	93	0.465
	16°C		15.9±0.3	15.9±0.3	93	0.465	93	0.465
	20°C		20.0±0.3	19.9±0.3	93	0.465	93	0.465
Winter-Run	11°C	2.26±0.35	11.1±0.3	11.1±0.3	78	0.39	83	0.415
	16°C		16.0±0.6	16.1±0.4	47	0.235	47	0.235
	20°C		20.0±0.4	20.0±0.4	47	0.235	47	0.235

Aerobic Scope (Metabolic Trait) Measurements

The aerobic scope (AS) metric quantifies the energetic budget for aerobic metabolism by finding the difference between how much oxygen is consumed by an organism at maximum aerobic exertion (its maximum metabolic rate; MMR) and how much oxygen is routinely needed by that organism to exist (its resting metabolic rate; RMR). This is termed the aerobic scope (*AS = MMR - RMR*) and defines the ectotherm's capacity to perform the activities essential to complete its life history (e.g. swimming, digesting a meal, migrating, smoltification) beyond baseline physiological maintenance. By defining the AS at several temperatures, a reaction-norm of metabolic performance across temperatures can be developed. This reaction norm can be used to identify temperatures at which aerobic metabolic capacity is optimal (T_{opt}). Factorial aerobic scope (FAS) is an additional metric of metabolic capacity and is the product of dividing the MMR by the RMR. This produces a quotient representing the proportion of maximum metabolic capacity consumed by routine metabolic demands. Typically, AS (absolute) is considered more informative, and comparisons of AS between groups are more intuitive than comparisons of FAS (Clark et al. 2013). Aside from identifying an energetic thermal optimum, aerobic scope measures are hypothesized to predict upper and lower thermal boundaries. The oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis theorizes that an ectotherm's thermal limits are defined by its capacity to fulfill the metabolic oxygen demand of its tissues (Pörtner 2001, 2002; Pörtner et al. 2017). The aerobic scope metric will be used to assess whether the OCLTT hypothesis applies to the thermal physiology of juvenile Chinook salmon.

Aerobic scope measurements were taken from 8-26°C, at 2°C increments. An individual fish would have its RMR and MMR measured at only one swim temperature. At each swim temperature, at least four fish from each treatment group were tested. If there were mortalities or experimental errors, additional fish would be trialed until at least 4 successful swims were accomplished. To prevent excess mortalities, a temperature was removed from testing if the first

two fish succumbed during the overnight RMR. In all treatments and for all populations, a swimming temperature of 26°C was found to be too stressful and yielded 100% mortality among the tested fish. The upper tested temperature was then reduced (e.g. 25 to 24 to 23°C) until fish could successfully complete the aerobic scope trial. Length, weight and Fulton's condition factor (Ricker 1975) for fish used in metabolic trials can be found in Table 2.

Resting Metabolic Rate (RMR)

Prior to metabolic trials, fish were netted from their rearing tanks and transferred into flow-through holding tanks (full volume turned over every hour) and fasted. Fish from the 20°C and 16°C groups were fasted for 24 hours and 11°C fish for 48 hours to accommodate the slower metabolism of fish at 11°C. Ensuring all tested fish are in a post-absorptive state prior to RMR testing is crucial to ensure RMR is not artificially elevated by the processing of the previous meal (Chabot et al. 2016). Holding tanks were kept at the acclimation temperature and continuously aerated. After the fasting period, fish were transferred into one of four 5-L swim tunnel respirometers (Loligo #SW10050) between 13:00 and 17:00. Fish were then given a 30-minute acclimation period with the water temperature being held at their acclimation temperature. After the acclimation period, the water temperature was adjusted to the testing temperature at 2°C per hour with a dedicated system heat pump (Aqualogic DHSP-7). Each system of two tunnels could be set to its own independent temperature. After the tunnels achieved testing temperature, fish were provided another 30-minute acclimation period before starting RMR measurements. RMR measurements were taken using AutoResp™ software throughout the night until approximately 08:00 the following morning. Measurement periods were at least 900 seconds (15 minutes) in length, with some variation depending on test temperature. Higher swim temperatures yielded shorter measurement periods to prevent the dissolved oxygen level in the chamber from falling too low (< 80%) and risk inducing hypoxic stress and associated metabolic response (Clark et al. 2013). Water was recirculated slowly throughout the swim tunnel to ensure adequate water mixing but did not induce fish movement. RMR trials were recorded via overhead cameras, and fish which exhibited activity throughout the RMR periods were discarded. Over the course of a night, a fish may undergo 25-45 automated measurement periods depending on when the trial started, ended and the duration of an individual measurement period. From each measurement period, a metabolic rate is determined. The lowest three of these metabolic rates are averaged to produce a single RMR value for an individual fish (Verhille et al. 2016; Poletto et al. 2017). Swim tunnels were bleached and cleaned weekly to suppress any bacterial growth within the respirometers.

Maximum Metabolic Rate (MMR)

Immediately following the RMR, MMR trials began in the morning (~08:00). MMR trials progressed by serially increasing the current in the swim tunnel every 20 minutes via a digital variable frequency drive motor. Swim speeds started at 33 cm/s and increased by roughly 10% with each step (i.e., 3 cm/s if the previous step ranged between 30-39 cm/s, 4 cm/s if between 40-49 cm/s, to a maximum of 6 cm/s). Immediately preceding each increase in velocity, the tunnel was flushed with freshwater air-equilibrated to reset the dissolved oxygen concentration. Fish continued in the swim tunnel until they were exhausted. Exhaustion was determined as two 3-second impingements against the rear screen of the swim tunnel within one

velocity step. Upon the first impingement, a rest period was given in which water velocity was decreased to 18 cm/s for 1 minute and then gradually increased to the testing velocity over a period of 2 minutes. A fish was considered exhausted if it impinged twice during the same velocity step. At this point, the time and velocity of failure was noted and the current was stopped. Following exhaustion, fish were removed from the swim tunnel and placed in a 24-hour recovery tank at their acclimation temperature. The MMR was defined as the highest metabolic rate sustained over a period of 5 minutes or greater.

After the 24-hour recovery, fish were euthanized with buffered MS-222, mass, fork and total length were measured (standard length was added in 2018), and a DNA fin clip was taken. Data from fish that died or did not fully recover (i.e., swimming normally, maintaining equilibrium) within the 24-hour window were discarded (n = 92). Fish that die in recovery absorb water post-mortality, which artificially increases the fish's mass and prevents accurate calculation of mass-specific metabolic rate. Data from fish which do not fully recover are discarded, as inability to recover may indicate that the fish was not physiologically capable of the trial or the trial was conducted improperly and therefore data obtained may reflect unusual behavior or physiology. The primary cause of mortality during swim trials was exposure to high water temperatures (> 23°C). The mortality of fish under such conditions can provide some insight into upper thermal tolerance and differences between treatment groups.

Critical Thermal Maximum Experiments

Fish (n=20) from each treatment group underwent critical thermal maxima trials (CTM). Fish of appropriate size (approximately 23 g in weight and a fork length of 12 cm) were arbitrarily netted from their acclimation tanks and placed into fasting tanks held at their acclimation temperature. To ensure all fish were in a postprandial energetic state, fish were fasted prior to experiments. Fish acclimated to 20°C and 16°C were fasted for 24 hours; fish acclimated to 11°C were fasted for 48 hours to accommodate their slower metabolism. After the fasting period, fish were placed into an individual 3000 mL glass beaker at their acclimation temperature and surrounded by a thermally matching water bath. Fish were given 30 minutes to recover from the handling stress and to acclimate to their new surroundings. After the acclimation period, three immersion water heaters (Process Technology s4229/PII 4000W) were turned on to increase the temperature of the water bath. The water bath and beakers were calibrated to warm at a rate of 0.3°C/min (Becker and Genoway 1979; Fangue and Bennett 2003). The temperature of each beaker was recorded every 5 minutes via thermocouple or glass fractional thermometer and fish were monitored continuously. When fish became unresponsive and unable to maintain their equilibrium, they were removed from the beaker and placed into a recovery bucket with water at their acclimation temperature. Immediately, the temperature of the beaker would be measured and recorded as the CTM. Fish were observed for 24 hours to ensure survival. Data from fish which did not survive the CTM trial or recovery (n=14 of replicate 249 CTMs) were discarded as mortality indicates an erroneous CTM measurement.

Growth Rate Measurements

During acclimation and rearing, fish were measured every two weeks. Fish (n=15) were arbitrarily collected from each tank (30 per treatment) and placed into a bucket containing tank

water. It is possible that netting of fish imposed a size-based selection bias upon fish captured for growth measurements. All fish were netted and sampled by the same researcher; therefore, any sampling bias would be applied similarly throughout the experiment. Fish were aerated during the measurement process. Fish were individually removed from the bucket, and excess water was removed and placed onto a balance to measure mass. Fish were then taken and placed onto a measuring board to quantify fork and total length (standard length was added in 2018) and placed into a second aerated bucket before being returned to their original tank. During this process, fish were not air exposed for more than 20-30 seconds. Growth rate measurements were collected on a treatment group until fish began entering experiments. Fish were size selected for metabolic and thermal tolerance experiments, which biased the remaining pool of rearing fish.

To compare growth rates between treatment groups, respective datasets are constrained to control for differences in acquisition date and rearing time. The population reared for the shortest time prior to experiments was the Coleman population; therefore, the starting and ending dates for growth rate comparisons were bounded for other populations to capture the same range of fish mass (7.55 ± 2.01 g to 13.79 ± 4.25 g). The short duration of rearing for the Coleman population was due to acquiring the fish at a larger size than other populations.

Analysis

Analysis of metabolic rates, CTM and growth were all performed using R Studio (version 1.1.463) with significance at $\alpha \leq 0.05$. Raw data produced from AutoResp™ during swim trials were transformed into metabolic rates using R Studio. Metabolic traits (RMR, MMR, AS and FAS) were analyzed separately using linear models, as were CTM and growth rate data. For metabolic data, the response variable for linear regressions were trait values (e.g. RMR, MMR AS and FAS) for individual fish. CTM analysis was similar with the response variable being the CTM for each individual fish. Growth rates were measured in grams per day and calculated with linear regression of measured fish mass over time. Fulton's condition factor (Ricker 1975) was calculated using the following equation:

$$K = 100\frac{Mass\ (g)}{Length(cm)^3}$$

Temperature coefficients (Q_{10}) quantify the rate of change in a metabolic process for each increase in 10°C and are a commonly used metric to gauge the temperature dependence of a process. The Q_{10} for each treatments RMR was calculated using the following equation:

$$Q_{10} = \left(\frac{RMR_2}{RMR_1}\right)^{10°C/(T_2-T_1)}$$

RMR_1 is the RMR at a test temperature of 8°C and T_1 is correspondingly 8°C.
RMR_2 is the RMR at a test temperature of 24°C and T_2 is correspondingly 24°C.

We chose to calculate Q_{10} using a temperature range of 8 to 24°C. 24°C was chosen as an upper bound as it was the highest temperature at which all treatment combinations were successfully tested.

Table 2: *Metabolic experiment fish morphometrics. Experimental test mass, lengths and condition factor of fish used in the metabolic experiments and sample size (n). All values are given as means ± the standard deviations. Condition factor is calculated as Fulton's condition factor.*

Hatchery	Acclimation Temperature	Mass (g)	Fork Length (mm)	Total Length (mm)	Condition Factor	n =
Coleman	11°C	22.1 ± 4.0	125 ± 6	136 ± 6	1.13 ± 0.07	33
Coleman	16°C	23.8 ± 3.3	127 ± 5	138 ± 6	1.16 ± 0.05	43
Coleman	20°C	24.7 ± 4.0	126 ± 6	137 ± 7	1.21 ± 0.06	45
Elk River	11°C	26.7 ± 3.7	131 ± 5	142 ± 6	1.19 ± 0.05	39
Elk River	16°C	23.8 ± 2.9	125 ± 5	136 ± 6	1.20 ± 0.07	40
Elk River	20°C	25.3 ± 3.0	125 ± 5	135 ± 5	1.29 ± 0.10	44
Trask	11°C	23.8 ± 3.1	129 ± 5	140 ± 5	1.10 ± 0.05	42
Trask	16°C	26.4 ± 3.4	130 ± 5	140 ± 6	1.20 ± 0.07	41
Trask	20°C	23.5 ± 4.0	125 ± 6	134 ± 6	1.19 ± 0.08	44
Winter-Run	11°C	21.6 ± 2.2	122 ± 4	133 ± 4	1.19 ± 0.11	39
Winter-Run	16°C	21.4 ± 2.5	122 ± 4	133 ± 5	1.17 ± 0.06	43
Winter-Run	20°C	21.1 ± 4.9	120 ± 8	130 ± 9	1.21 ± 0.11	41

Results

Metabolic Traits

Resting Metabolic Rate (RMR)

Resting metabolic rate (RMR) for all treatment groups was modeled in R using a linear model with the equation:

$$RMR \sim poly(\text{`}Swim\ Temperature\text{`}, 2) * Hatchery * \text{`}Acclimation\ Temperature\text{`} + Mass + \text{`}Tunnel\ ID\text{`}$$

This equation was one of many tested and was chosen for having the lowest AIC (Akaike Information Criterion). The final model was fitted with a statistically significant ($p = 2.2x10\text{-}16$) relationship (Figure 2).

RMR of juvenile Chinook salmon from all treatment groups increased with swimming temperature from 8 to 25°C. RMR was significantly influenced by swimming temperature ($df = 2$, $F = 2397.64$, $p < 0.0001$), hatchery of origin ($df = 3$, $F = 13.46$, $p < 0.0001$), and acclimation temperature ($df = 1$, $F = 63.96$, $p < 0.0001$). Mass was found to have a significant effect ($df = 1$, $F = 5.09$, $p = 0.02451$) on RMR despite RMR being mass corrected. This may be due to metabolic scaling between smaller and larger fish. Tunnel ID (i.e., the swim tunnel in which the fish swam) was not found to have a significant effect on RMR ($df = 4$, $F = 1.69$, $p = 0.15226$). There was a significant three-way interaction among swimming temperature, hatchery and acclimation temperature ($df = 6$, $F = 4.62$, $p < 0.00014$), as well as significant two-way interactions between swimming temperature and acclimation temperature ($df = 2$, $F = 28.31$, $p < 0.0001$) and hatchery and acclimation temperature ($df = 3$, $F = 12.82$, $p < 0.0001$). The interaction between hatchery and swimming temperature was non-significant ($df = 6$, $F = 0.91$, $p = 0.4891$). The significant interactions imply that RMR responds to acclimation temperature

differentially among populations. For simplicity of interpretation, descriptive equations presented below will be in the form of y = ax2 + bx + c.

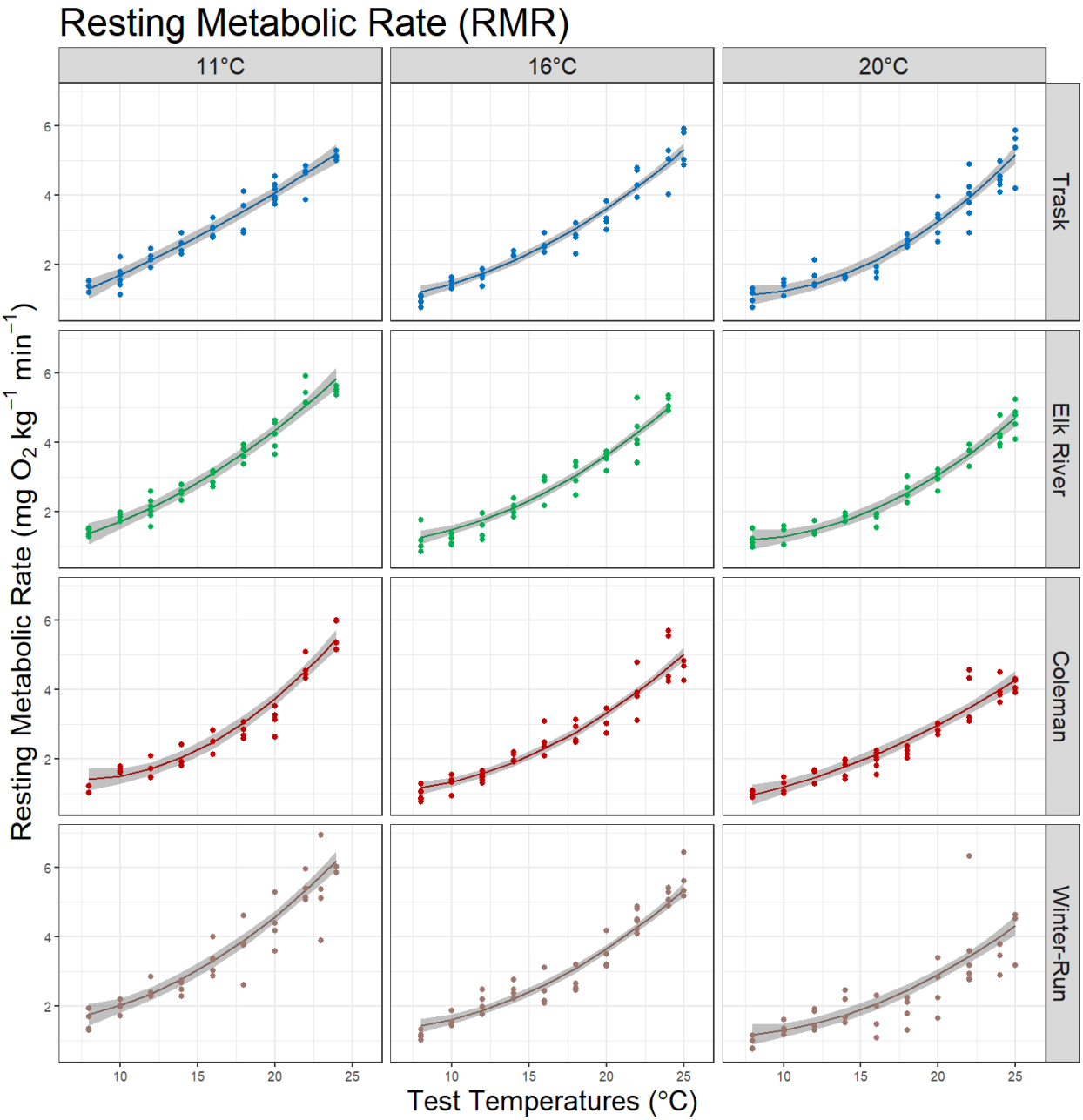

Figure 2: *Resting Metabolic Rate for all four populations and three acclimation groups (11, 16, and 20°C). Each data point represents the average of the lowest three measured metabolic rates of an individual fish during an overnight experiment. Lines are the modeled relationship outlined above. Shaded areas are 95% confidence intervals.*

Coleman Population

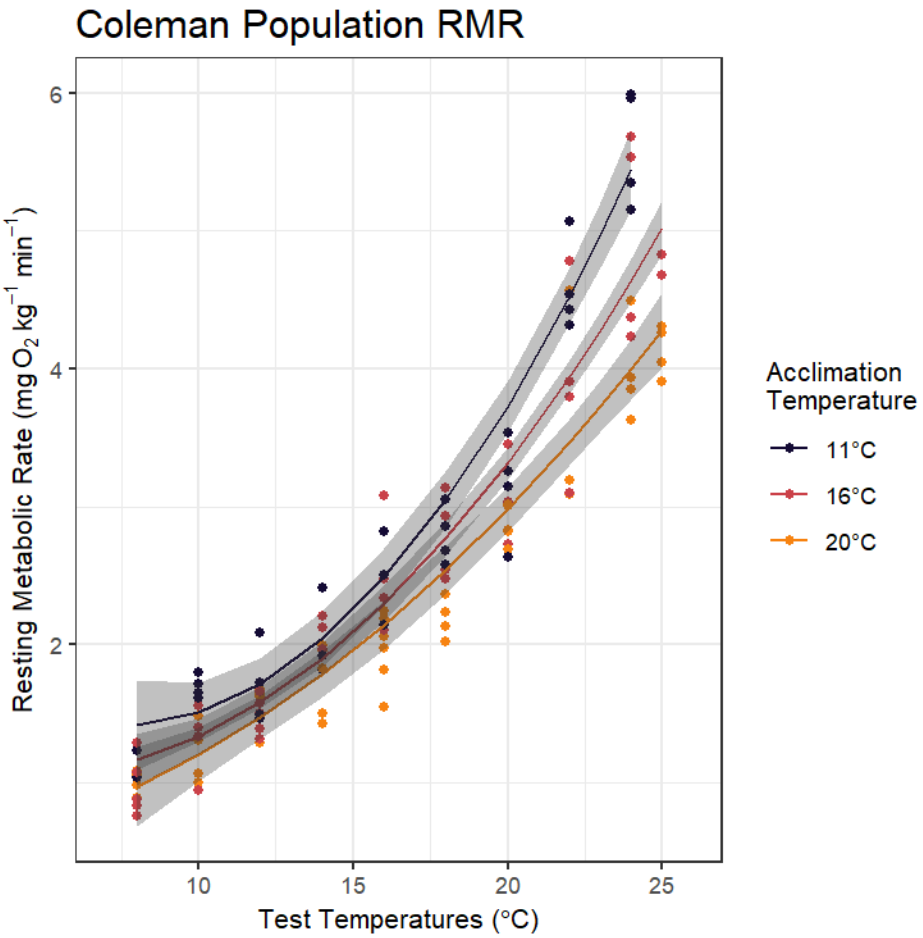

Figure 3: *Resting metabolic rates (RMR) for Coleman fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the RMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The RMR of Coleman fish acclimated to 11°C increased over the range of temperatures tested (8 to 24°C, Figure 3) and was fit with the following equation. Unlike fish acclimated to 16 or 20°C, no fish in the 11°C acclimation group survived trials conducted at 25°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.01657x^2 + 0.63217x + 3.04016$$

where x = temperature (°C).

The RMR was 1.42 ± 0.17 mg O2 kg-1 min-1 at 8°C and 5.45 ± 0.15 mg O2 kg-1 min-1 at 24°C. Over the test range (8 to 24°C), the RMR increased 3.85-fold, a lesser increase than observed in the 16 and 20°C acclimation groups. This difference is driven by the RMR at the higher test temperatures, as the RMR values at 10°C and below were similar for all three acclimation groups. The Q10 over the test range (8 to 24°C) was 2.32.

16°C Acclimation Group. The RMR of Coleman fish acclimated to 16°C increased over the range of temperatures tested (8 to 25°C, Figure 3) and was fit with the following equation. While data were obtained from this group at 25°C, below we are reporting metabolic rates obtained only to 24°C for comparison with fish acclimated to 11°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.0095x^2 + 0.08704x + 1.25752$$

where x = temperature (°C).

The RMR was 1.17 ± 0.10 mg O_2 kg^{-1} min^{-1} at 8°C and 4.64 ± 0.08 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.97-fold, a level of increase in between those observed in the 11 and 20°C acclimation groups. This difference is driven by the RMR at the higher test temperatures, as the RMR values at 10°C and below were similar for all three acclimation groups. The Q_{10} over the test range (8 to 24°C) was 2.37.

20°C Acclimation Group. The RMR of Coleman fish acclimated to 20°C increased over the range of temperatures tested (8 to 25°C, Figure 3) and was fit with the following equation. While data were obtained from this group at 25°C, below we are reporting metabolic rates obtained only to 24°C for comparison with fish acclimated to 11°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00537x^2 + 0.01746x + 0.48968$$

where x = temperature (°C).

The RMR was 0.97 ± 0.15 mg O_2 kg^{-1} min^{-1} at 8°C and 4.00 ± 0.11 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 4.11-fold, a greater increase than observed in the 11 and 16°C acclimation groups. This difference is driven by the RMR values at the higher test temperatures, as the RMR values observed at 10°C and below were similar for all three acclimation groups. The Q_{10} over the test range (8 to 24°C) was 2.42.

Elk River Population

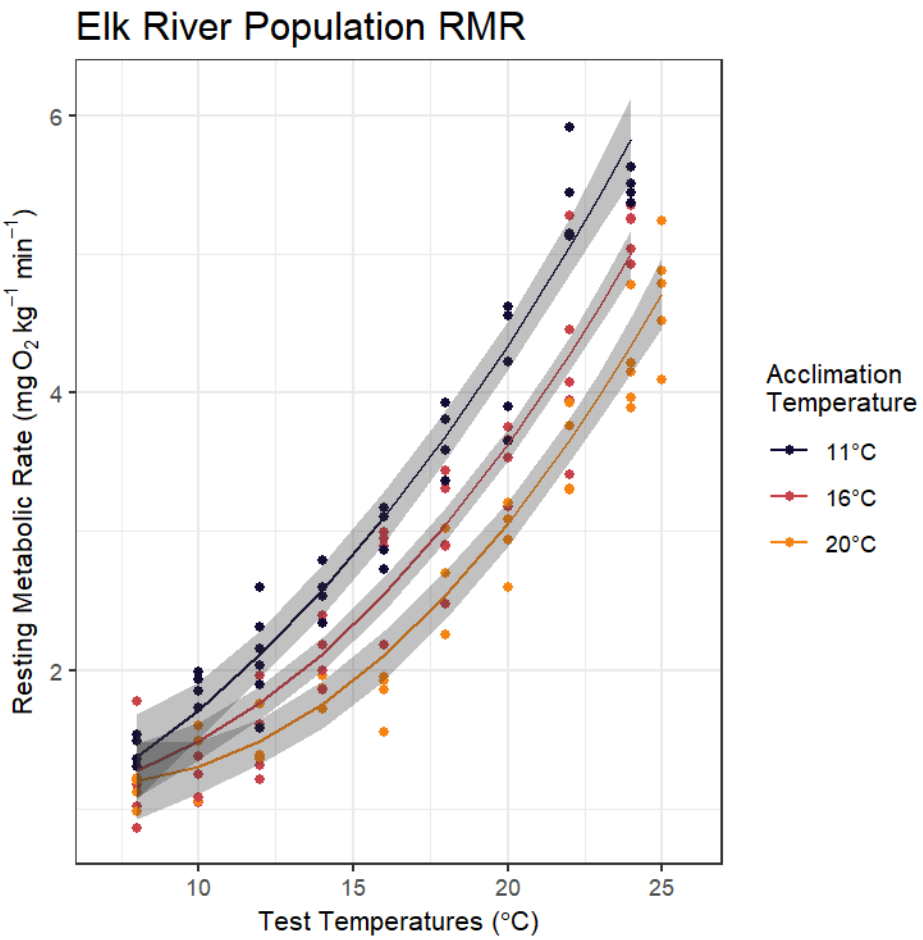

Figure 4: *Resting metabolic rates (RMR) for Elk River fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the RMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The RMR of Elk River fish acclimated to 11°C increased over the range of temperatures tested (8 to 24°C, Figure 4) and was fit with the following equation. Unlike fish acclimated to 16 or 20°C, no fish in the 11°C acclimation group survived trials conducted at 25°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00784x^2 + 0.0279x + 0.65009$$

where x = temperature (°C).

The RMR was 1.37 ± 0.16 mg O_2 kg^{-1} min^{-1} at 8°C and was 5.83 ± 0.15 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 4.24-fold, a higher increase than observed in the 16 and 20°C acclimation groups. This difference is driven by the RMR values at the higher test temperatures, as the RMR values at 8°C were similar for all three acclimation groups. The Q_{10} over the test range (8 to 24°C) was 2.47.

16°C Acclimation Group. The RMR of Elk River fish acclimated to 16°C increased over the range of test temperatures (8 to 24°C, Figure 4) and was fit with the following equation. Unlike fish acclimated to 20°C, no fish survived trials conducted at 25°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00927x^2 - 0.06352x + 1.19179$$

where x = temperature (°C).

The RMR was 1.28 ± 0.10 mg O_2 kg^{-1} min^{-1} at 8°C and 5.00 ± 0.09 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.92-fold, a level of increase between those observed for fish acclimated to 11 and 20°C. The Q_{10} over the test range (8 to 24°C) was 2.35.

20°C Acclimation Group. The RMR of Elk River fish acclimated to 20°C increased over the range of test temperatures (8 to 25°C, Figure 4) and was fit with the following equation. While data were obtained from this group at 25°C, below we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11 and 16°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.01041x^2 - 0.13666x + 1.62516$$

where x = temperature (°C).

The RMR was 1.20 ± 0.14 mg O_2 kg^{-1} min^{-1} at 8°C and was 4.34 ± 0.10 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.62-fold, a lower increase than observed for fish acclimated to 11 and 16°C. This difference is driven by the RMR values at the higher test temperatures. The Q_{10} over the test range (8 to 24°C) was 2.24.

Trask Population

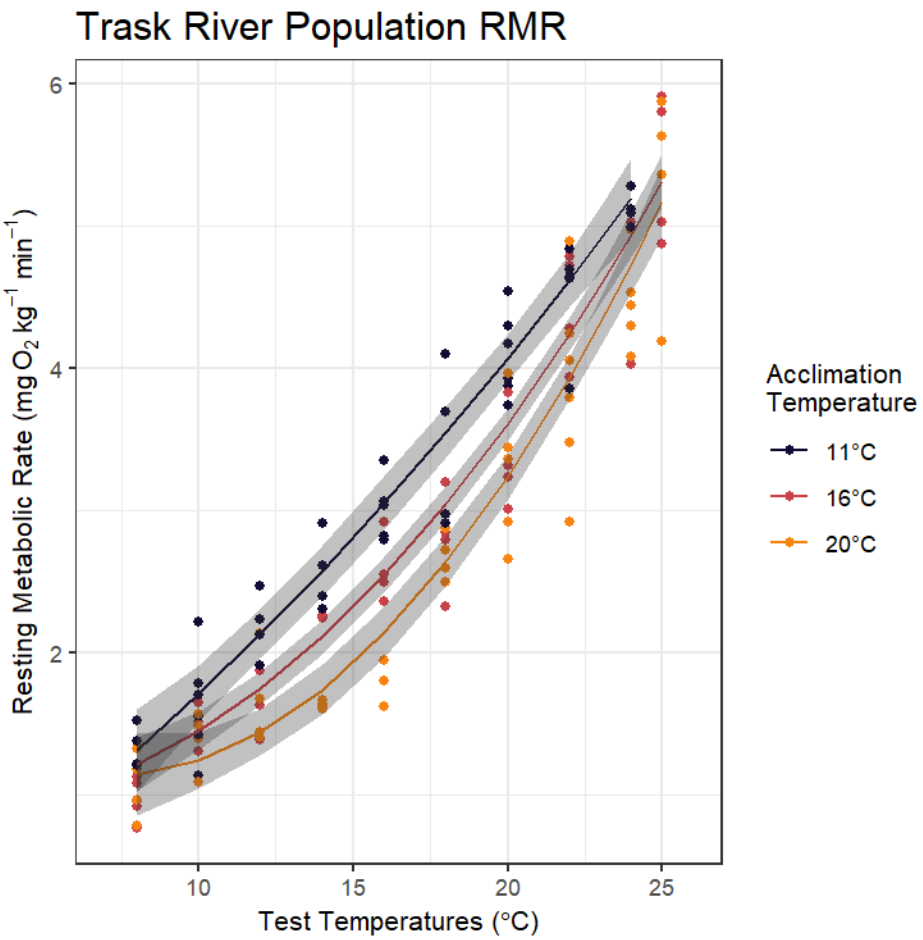

Figure 5: Resting metabolic rates (RMR) for Trask fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the RMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.

11°C Acclimation Group. The RMR of Trask fish acclimated to 11°C increased over the range of temperatures tested (8 to 24°C, Figure 5) and was fit with the following equation. Unlike the Trask populations acclimated to 16 or 20°C, no fish survived trials at 25°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00316x^2 + 0.14172x - 0.02634$$

where x = temperature (°C).

The RMR was 1.31 ± 0.15 mg O_2 kg^{-1} min^{-1} at 8°C and 5.20 ± 0.14 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 4.07-fold, a level of increase between, but similar to, those observed for fish acclimated to 16 and 20°C. The similarity reflects similar RMR values at 8 and 24°C, although the RMRs in between differed. The Q_{10} over the test range (8 to 24°C) was 2.40.

16°C Acclimation Group. The RMR of Trask fish acclimated to 16°C increased over the range of temperatures tested (8 to 25°C, Figure 5) and was fit with the following equation. While data were obtained from this group at 25°C, below we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00832x^2 - 0.03338x + 0.94926$$

where x = temperature (°C).

The RMR was 1.21 ± 0.10 mg O_2 kg^{-1} min^{-1} at 8°C and 4.94 ± 0.08 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.97-fold, a level of increase lower than, but similar to, those of the 11 and 20°C acclimated groups. The similarity reflects similar RMR values at 8 and 24°C, although the RMRs in between differed. The Q_{10} over the test range (8 to 24°C) was 2.37.

20°C Acclimation Group. The RMR of Trask fish acclimated to 20°C increased over the range of temperatures tested (8 to 25°C, Figure 5) and was fit with the following equation. While data were obtained from these fish at 25°C, below we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.01244x^2 - 0.17345x + 1.62516$$

where x = temperature (°C).

The RMR was 1.14 ± 0.15 mg O_2 kg^{-1} min^{-1} at 8°C and 4.73 ± 0.10 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 4.16-fold, a level of increase higher than, but similar to, those of the 11 and 16°C acclimated groups. The similarity reflects similar RMR values at 8 and 24°C, although the RMRs in between differed. The Q_{10} over the test range (8 to 24°C) was 2.24.

Livingston Stone (Winter-Run) Population

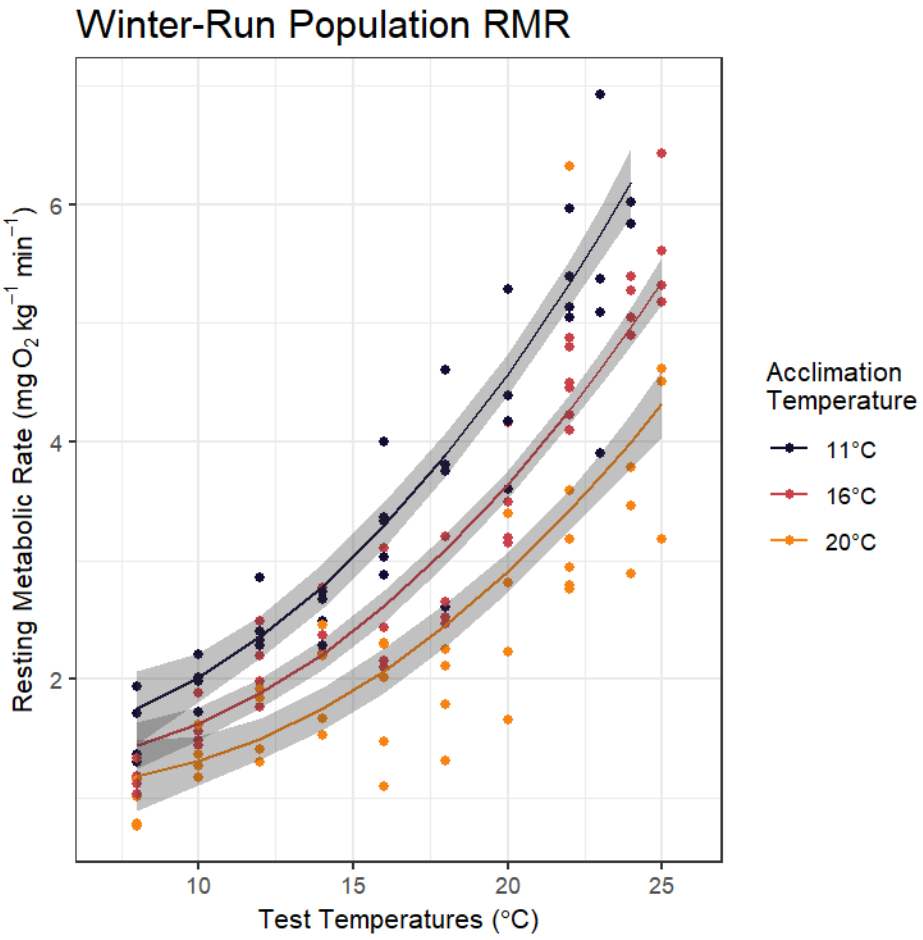

Figure 6: *Resting metabolic rates (RMR) for winter-run juvenile Chinook salmon from the Livingston Stone National Fish Hatchery brood stock, acclimated to 11, 16 and 20°C. Each point represents the RMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The RMR of Livingston Stone fish acclimated to 11°C increased over the range of temperatures tested (8 to 24°C, Figure 6) and was fit with the following equation. Unlike Livingston Stone fish acclimated to 16 or 20°C, no fish survived trials at 25°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00924x^2 - 0.07493x + 1.44794$$

where x = temperature (°C).

The RMR was 1.44 ± 0.10 mg O_2 kg^{-1} min^{-1} at 8°C and 4.97 ± 0.08 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.52-fold, a higher increase than observed in the 16 and 20°C acclimated groups. The Q_{10} over the test range (8 to 24°C) was 2.20.

16°C Acclimation Group. The RMR of Livingston Stone fish acclimated to 16°C increased over the range of temperatures tested (8 to 25°C, Figure 6) and was fit with the following equation. While data were obtained from these fish at 25°C, below we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$\mathrm{L}RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00924x^2 - 0.07493x + 1.44794$$

where x = temperature (°C).

The RMR was 1.44 ± 0.10 mg O_2 kg^{-1} min^{-1} at 8°C and 4.97 ± 0.08 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.45-fold, a level of increase in between those of the 11 and 20°C acclimated groups. The Q_{10} over the test range (8 to 24°C) was 2.17.

20°C Acclimation Group. The RMR of Livingston Stone fish acclimated to 20°C increased over the range of temperatures tested (8 to 25°C, Figure 6) and was fit with the following equation. While data were obtained from this group at 25°C, below we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$RMR\ (mgO_2kg^{-1}min^{-1}) = 0.00818x^2 - 0.0573x + 1.3481$$

where x = temperature (°C).

The RMR was 1.19 ± 0.15 mg O_2 kg^{-1} min^{-1} at 8°C and 4.01 ± 0.12 mg O_2 kg^{-1} min^{-1} at 24°C. Over the test range (8 to 24°C), the RMR increased 3.38-fold, a value lower than observed for the 11 and 16°C acclimated groups. The Q_{10} over the test range (8 to 24°C) was 2.14.

RMR Summary

Across all populations, acclimation to warmer temperatures reduced the RMR of fish. RMR's between the three acclimation temperatures were typically similar at test temperatures of 8-10°C and diverged as temperature increased. In the Coleman population, this point of conversion was shifted and was within the 12-14°C range of test temperatures. The Q_{10} of RMR values for all treatment groups was between 2.1 and 2.5, which is consistent with Q_{10} values typical for fishes (1.5 to 3 is the expected range). The winter-run population had the lowest Q_{10} values regardless of acclimation temperature. RMR summary values are located in Table 3.

Table 3: *Resting metabolic values (RMR) and Q10 values calculated across swimming/test temperatures of 8-24C) for treatment groups. RMR values are given as predicted means and standard errors.*

Hatchery	Acclimation Temperature	Q10 (8 -24°C)	RMR at 8°C	RMR at 24°C
Coleman	11°C	2.32	1.42 ± 0.17	5.45 ± 0.15
Coleman	16°C	2.37	1.17 ± 0.10	4.64 ± 0.08
Coleman	20°C	2.42	0.97 ± 0.15	4.00 ± 0.11
Elk River	11°C	2.47	1.37 ± 0.16	5.83 ± 0.15
Elk River	16°C	2.35	1.28 ± 0.10	5.00 ± 0.09
Elk River	20°C	2.24	1.20 ± 0.14	4.34 ± 0.10
Trask	11°C	2.37	1.31 ± 0.15	5.20 ± 0.14
Trask	16°C	2.40	1.21 ± 0.10	4.94 ± 0.08
Trask	20°C	2.44	1.14 ± 0.15	4.73 ± 0.10
Winter-Run	11°C	2.20	1.76 ± 0.16	6.19 ± 0.15
Winter-Run	16°C	2.17	1.44 ± 0.10	4.97 ± 0.08
Winter-Run	20°C	2.14	1.19 ± 0.15	4.01 ± 0.12

Maximum Metabolic Rate (MMR)

Maximum metabolic rate (MMR) for all treatment groups was modeled using a linear model in R with the equation:

$$MMR \sim poly(\text{`}Swim\ Temperature\text{`}, 2) * Hatchery * \text{`}Acclimation\ Temperature\text{`} + Mass + \text{`}Tunnel\ ID\text{`}$$

This equation was one of many tested and was chosen for having the lowest AIC (Akaike Information Criterion). The final model was fitted with a statistically significant ($p = 2.2x10^{-16}$) relationship (Figure 7). MMR is determined by finding the greatest rate of oxygen consumption during the exhaustive swimming trial. A single MMR is determined for each individual fish. MMR of juvenile Chinook salmon was observed to fit a curvilinear (quadratic) relationship with all treatment groups increasing in MMR with swimming temperature from 8 to 25°C; however, some treatment groups (e.g. winter-run) demonstrated reduced MMR at 25°C. MMR was significantly influenced by swimming temperature ($df = 2$, $F = 292.87$, $p < 0.0001$), hatchery of origin ($df = 3$, $F = 49.9641$, $p < 0.0001$), and acclimation temperature ($df = 1$, $F = 57.74$, $p < 0.0001$). Mass was found to have a significant effect ($df = 1$, $F = 5.27$, $p = 0.02213$) on MMR despite MMR being mass corrected. This may be due to metabolic scaling between smaller and larger fish. Tunnel ID, (i.e., the specific swim tunnel the fish swam in) also revealed a significant effect on MMR ($df = 4$, $F = 3.26$, $p = 0.01183$), which is possible due to small differences in the flow patterns produced by each tunnel. The only significant interaction was between hatchery and acclimation temperature ($df = 3$, $F = 10.98$, $p < 0.0001$). Significant interactions imply different responses to acclimation temperature between hatcheries. For simplicity of interpretation, equations will be in the form of $y = ax^2 + bx + c$.

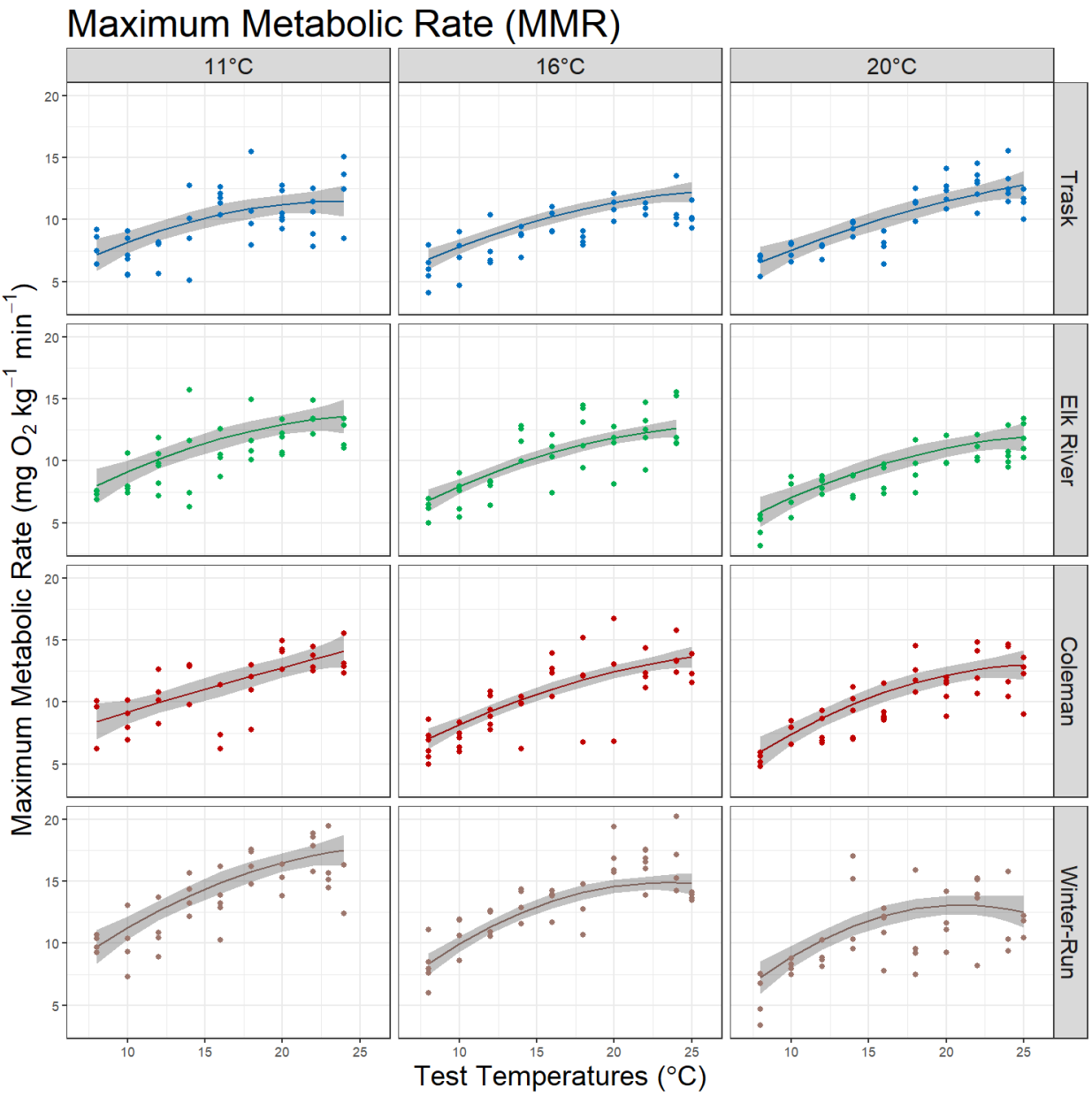

Figure 7: *Maximum Metabolic Rate for all four populations and three acclimation groups. Each data point represents the most rapid metabolic rate captured during swimming experiments. Lines are the modeled relationship as per the equation outlined above. Shaded areas are 95% confidence intervals.*

Coleman Population

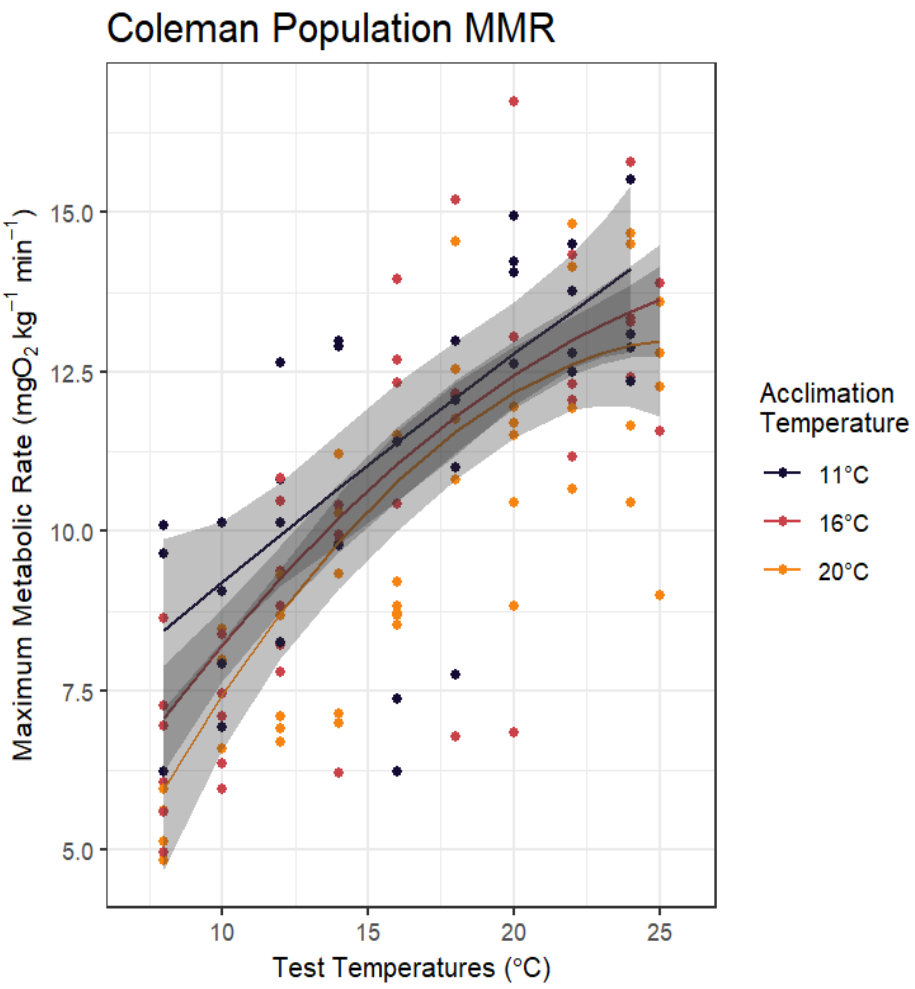

Figure 8: *Maximum metabolic rates (MMR) for Coleman fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The MMR of Coleman fish acclimated to 11°C generally increased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 8) and was fit with the following equation.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.00178x^2 + 0.41148x + 5.26648$$

where x = temperature (°C).

The MMR was 8.44 ± 0.74 mg O_2 kg^{-1} min^{-1} at 8°C and 14.11 ± 0.67 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.67-fold increase over the test range (8 to 24°C).

16°C Acclimation Group. The MMR of Coleman fish acclimated to 16°C generally increased over the range of temperatures tested (8 to 25°C, Figure 8) and was fit with the following equation. While data were obtained from fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.01249x^2 + 0.79849x + 1.47752$$

where x = temperature (°C).

The MMR was 7.07 ± 0.42 mg O_2 kg^{-1} min^{-1} at 8°C and 13.44 ± 0.37 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.90-fold increase over the test range (8 to 24°C).

20°C Acclimation Group. The MMR of Coleman fish acclimated to 20°C generally increased over the range of temperatures tested (8 to 25°C, Figure 8) and was fit with the following equation. While data were obtained from fish tested at 25°C, we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.02106x^2 + 1.1081x - 1.55366$$

where x = temperature (°C).

The MMR was 7.07 ± 0.42 mg O_2 kg^{-1} min^{-1} at 8°C and 13.44 ± 0.37 mg O_2 kg^{-1} min^{-1} at 24°C, a 2.17-fold increase over the test range (8 to 24°C).

Elk River Population

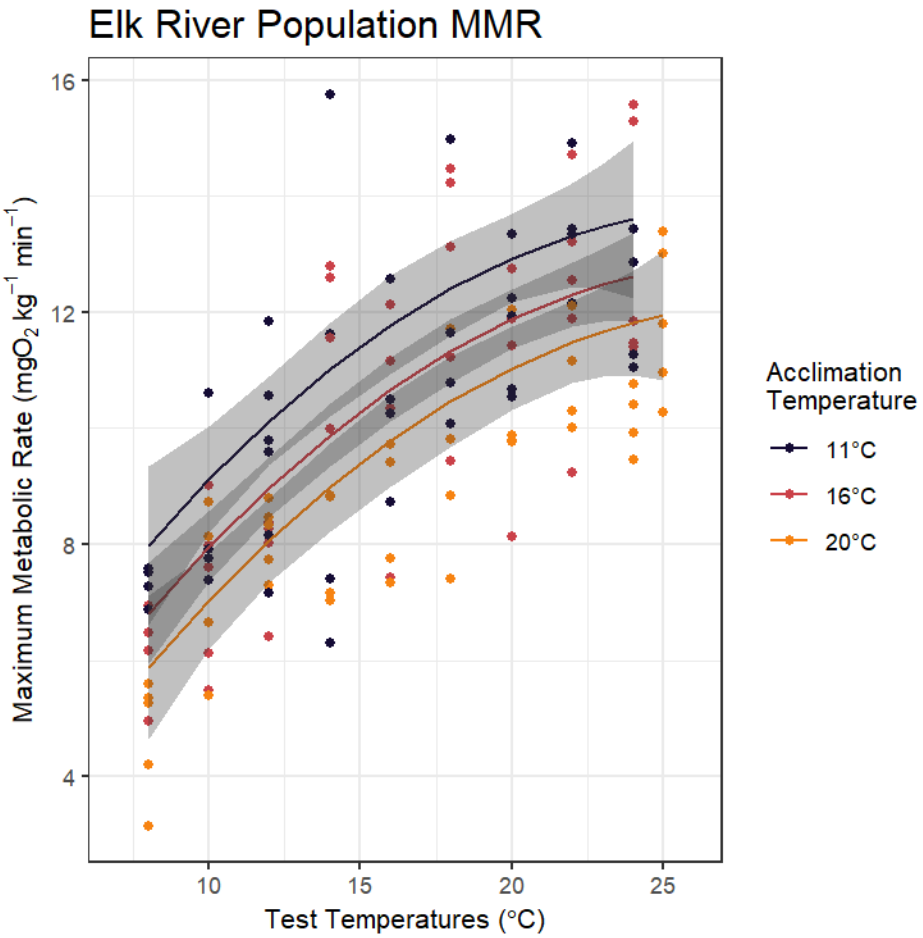

Figure 9: *Maximum metabolic rates (MMR) for Elk River fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The MMR of Elk River fish acclimated to 11°C generally increased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 9) and was fit with the following equation.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.01544x^2 + 0.84491x + 2.20175$$

where x = temperature (°C).

The MMR was 7.98 ± 0.70 mg O_2 kg^{-1} min^{-1} at 8°C and 13.60 ± 0.69 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.70-fold increase over the test range (8 to 24°C).

16°C Acclimation Group. The MMR of Elk River fish acclimated to 16°C generally increased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C, Figure 9) and was fit with the following equation.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.01496x^2 + 0.84057x + 1.04914$$

where x = temperature (°C).

The MMR was 6.82 ± 0.44 mg O_2 kg^{-1} min^{-1} at 8°C and 12.61 ± 0.38 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.85-fold increase over the test range (8 to 24°C).

20°C Acclimation Group. The MMR of Elk River fish acclimated to 20°C generally increased over the range of temperatures tested (8 to 25°C, Figure 9) and was fit with the following equation. While data were obtained from fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11 and 16°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.01457x^2 + 0.8371x + 0.11986$$

where x = temperature (°C).

The MMR was 5.88 ± 0.63 mg O_2 kg^{-1} min^{-1} at 8°C and 11.82 ± 0.46 mg O_2 kg^{-1} min^{-1} at 24°C, a 2.01-fold increase over the test range (8 to 24°C).

Trask Population

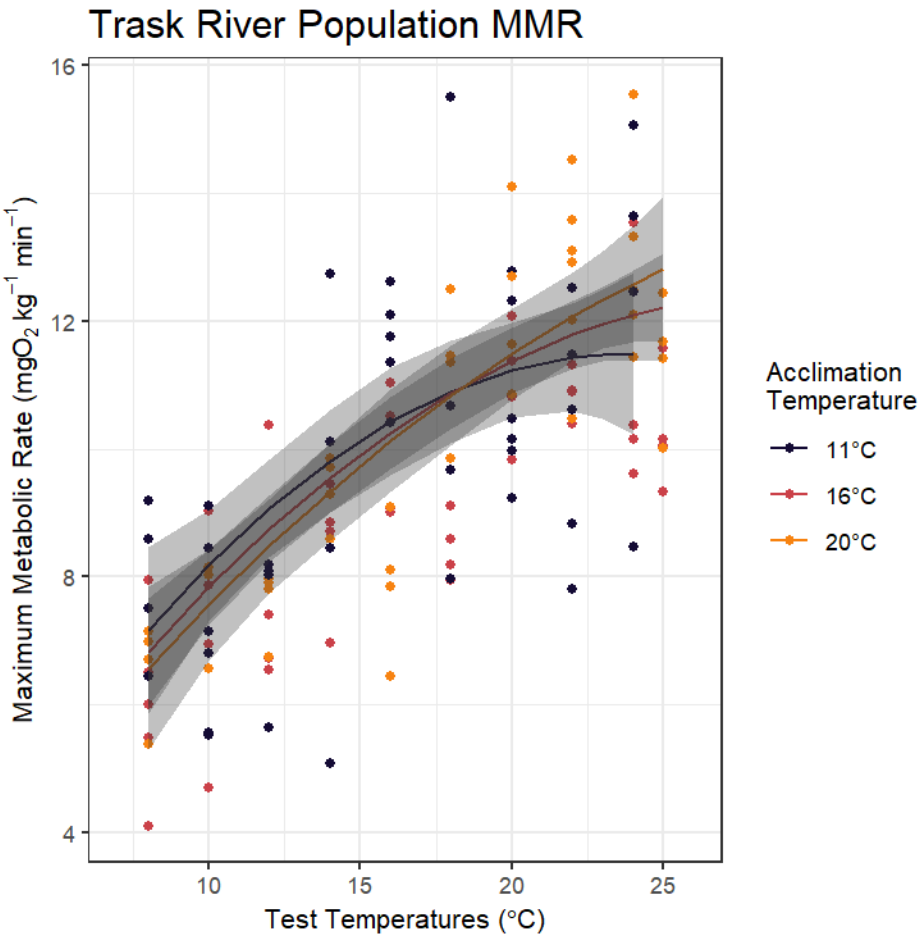

Figure 10: *Maximum metabolic rates (MMR) for Elk River fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The MMR of Trask fish acclimated to 11°C generally increased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 10) and was fit with the following equation.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.0172x^2 + 0.82146x + 1.68631$$

where x = temperature (°C).

The MMR was 7.16 ± 0.66 mg O_2 kg^{-1} min^{-1} at 8°C and 11.49 ± 0.64 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.60-fold increase over the 16°C test range (8 to 24°C).

16°C Acclimation Group. The MMR of Trask fish acclimated to 16°C generally increased over the range of temperatures tested (8 to 25°C, Figure 10) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.0124x^2 + 0.7262x + 1.81362$$

where x = temperature (°C).

The MMR was 6.83 ± 0.43 mg O_2 kg^{-1} min^{-1} at 8°C and 12.10 ± 0.36 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.77-fold increase over the test range (8 to 24°C).

20°C Acclimation Group. The MMR of Trask fish acclimated to 20°C generally increased over the range of temperatures tested (8 to 25°C, Figure 10) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison with fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.00856x^2 + 0.65x + 1.91546$$

where x = temperature (°C).

The MMR was 6.57 ± 0.65 mg O_2 kg^{-1} min^{-1} at 8°C and 12.58 ± 0.47 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.60-fold increase over the 16°C test range (8 to 24°C).

Livingston Stone (Winter-Run) Population

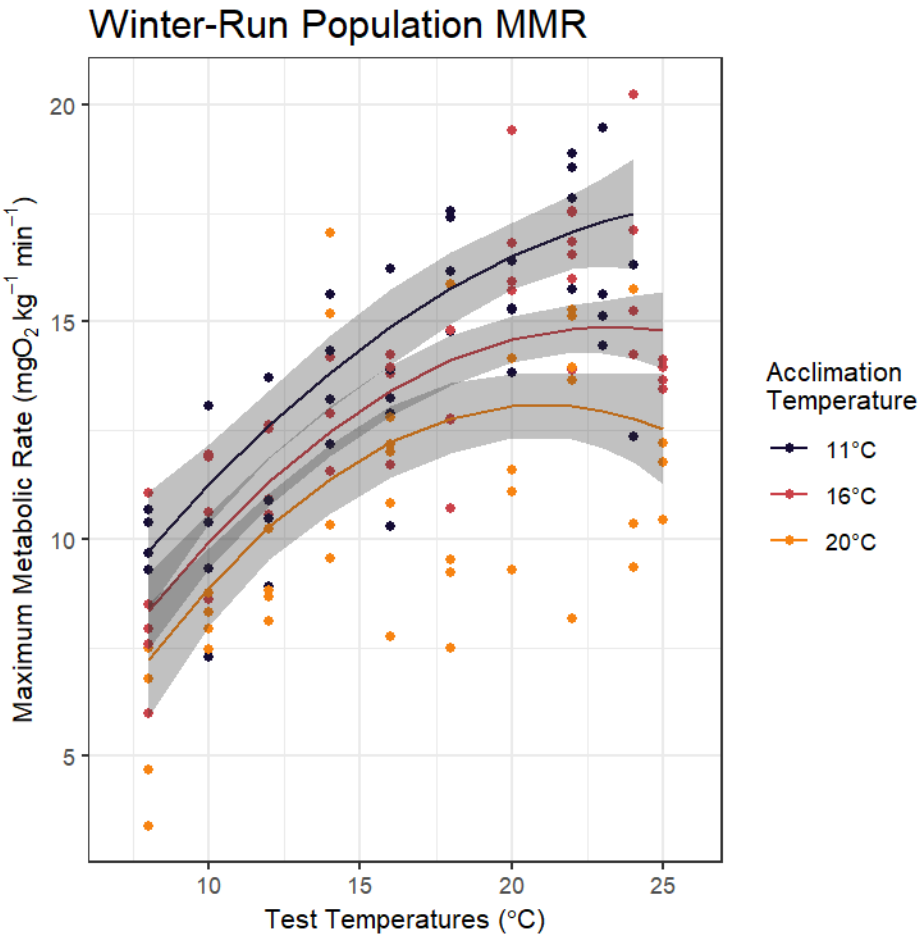

Figure 11: *Maximum metabolic rates (MMR) for winter-run Livingston Stone National Fish hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The MMR of Livingston Stone fish acclimated to 11°C generally increased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 11) and was fit with the following equation.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.02001x^2 + 1.1256x + 2.00857$$

where x = temperature (°C).

The MMR was 9.73 ± 0.70 mg O_2 kg^{-1} min^{-1} at 8°C and 17.50 ± 0.65 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.80-fold increase over the test range (8 to 24°C).

16°C Acclimation Group. The MMR of Livingston Stone fish acclimated to 16°C generally increased over the range of temperatures tested (8 to 25°C, Figure 11) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.02826x^2 + 1.31319x - 0.36085$$

where x = temperature (°C).

The MMR was 8.34 ± 0.45 mg O_2 kg^{-1} min^{-1} at 8°C and 14.88 ± 0.37 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.78-fold increase over the test range (8 to 24°C).

20°C Acclimation Group. The MMR of Livingston Stone fish acclimated to 20°C generally increased over the range of temperatures tested (8 to 25°C, Figure 11) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only up to 24°C for comparison fish acclimated to 11°C.

$$MMR\ (mgO_2kg^{-1}min^{-1}) = -0.03487x^2 + 1.46325x - 2.25638$$

where x = temperature (°C).

The MMR was 7.22 ± 0.67 mg O_2 kg^{-1} min^{-1} at 8°C and 12.78 ± 0.52 mg O_2 kg^{-1} min^{-1} at 24°C, a 1.77-fold increase over the test range (8 to 24°C).

MMR Summary

Across nearly all populations (exception for Trask Hatchery acclimated to 11°C) acclimation to warmer temperatures reduced the MMR of fish across the range of test temperature. This acclimation-related reduction in MMR was greatest when fish were trialed at warm test temperatures. In many instances, MMR did decline at the extreme warm temperatures (23-25°C), however this decline is captured as a plateauing of the MMR as test temperature increases. Winter-run fish acclimated to 16 and 20°C do not show this relationship; instead, modeled MMR declined at warm temperatures. Modeled MMR values at 8°C and 24°C for each treatment group are located in Table 4.

***Table 4**: Maximum metabolic rate (MMR) values. Values given as predicted means with standard error.*

Hatchery	Acclimation Temp	MMR at 8°C	MMR at 24°C
Coleman	11°C	8.44 ± 0.74	14.11 ± 0.67
Coleman	16°C	7.07 ± 0.42	13.44 ± 0.37
Coleman	20°C	5.96 ± 0.65	12.91 ± 0.49
Elk River	11°C	7.98 ± 0.70	13.60 ± 0.69
Elk River	16°C	6.82 ± 0.44	12.61 ± 0.38
Elk River	20°C	5.88 ± 0.63	11.82 ± 0.46
Trask	11°C	7.16 ± 0.66	11.49 ± 0.64
Trask	16°C	6.83 ± 0.43	12.10 ± 0.36
Trask	20°C	6.57 ± 0.65	12.58 ± 0.47
Winter-Run	11°C	9.73 ± 0.70	17.50 ± 0.65
Winter-Run	16°C	8.34 ± 0.45	14.88 ± 0.37
Winter-Run	20°C	7.22 ± 0.67	12.78 ± 0.52

Aerobic Scope (AS)

Aerobic (AS) is the difference between RMR and MMR found by the equation:

$$AS = MMR - RMR$$

Aerobic scope for all treatment groups was modeled using a linear model in R (Figure 12) with the equation:

$$AS \sim poly(\text{`}Swim\ Temperature\text{`}, 2) * Hatchery * \text{`}Acclimation\ Temperature\text{`} + Mass + \text{`}Tunnel\ ID\text{`}$$

This equation was one of many tested and was chosen for having the lowest AIC. The final model was fitted with a statistically significant ($p = 2.2x10^{-16}$) relationship (Figure 12).

AS of juvenile Chinook salmon was observed to fit a curvilinear (quadratic) relationship with AS first increasing with swimming temperature before reaching a thermal optimum (T_{opt}) and then decreasing. AS was significantly influenced by swimming temperature ($df = 2$, $F = 69.12$, $p < 0.0001$), hatchery of origin ($df = 3$, $F = 50.34$, $p < 0.0001$), and acclimation temperature ($df = 1$, $F = 10.96$, $p < 0.001$). Mass was found to have a significant effect ($df = 1$, $F = 8.52$, $p = 0.0037$) on AS despite AS being mass corrected. This may be due to metabolic scaling between smaller and larger fish. Tunnel ID, (i.e., the specific swim tunnel the fish swam in) also revealed a significant effect on AS ($df = 4$, $F = 3.27$ $p = 0.01156$). This is possible due to small differences in the flow patterns produced by each tunnel or a carry-over effect from MMR measurements. The only significant interaction was between hatchery and acclimation temperature ($df = 3$, $F = 7.18$, $p < 0.0001$). The significant interactions imply different responses to acclimation temperature between hatcheries. For simplicity of interpretation equations presented below will be in the form of $y = ax^2 + bx + c$.

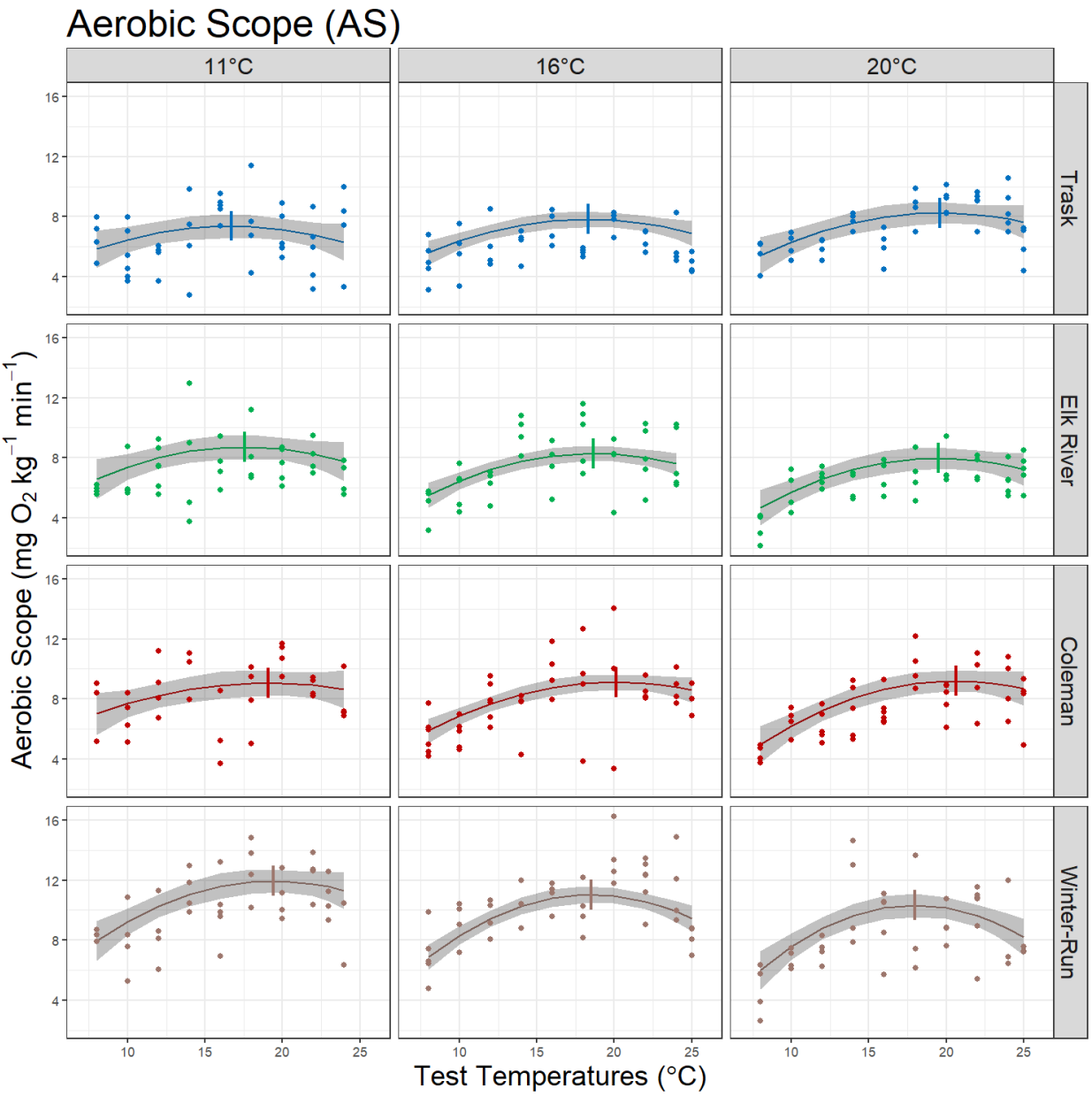

Figure 12: *Aerobic Scope for all four populations and three acclimation groups. Each data point represents the difference between RMR and MMR for one fish. Lines are the modeled relationship as per the equation outlined above. Shaded areas are 95% confidence intervals. Vertical bars represent the peak of each respective curve and are interpreted as the Topt.*

Coleman Population

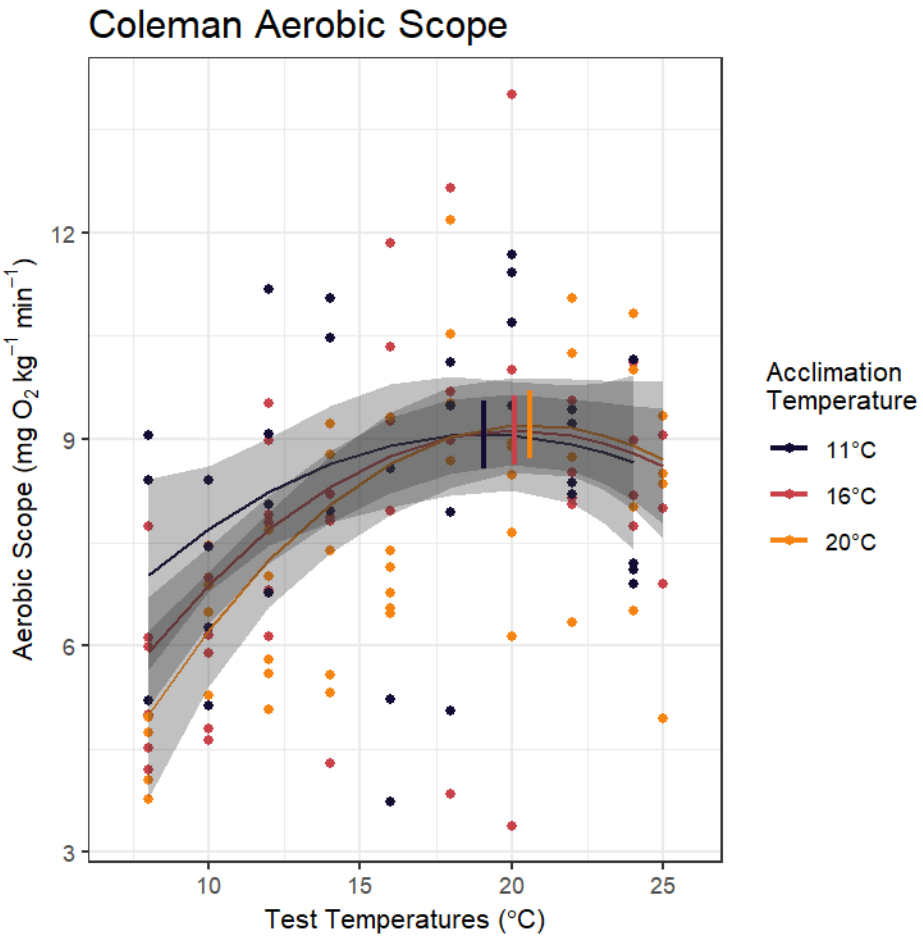

Figure 13: *Aerobic Scope (AS) for the Coleman Hatchery fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the AS for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval. The vertical bars identify the Topt for each treatment group, which is defined as the peak of the quadratic relationship.*

11°C Acclimation Group. The AS of the Coleman fish acclimated to 11°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 24°C, due to mortality at 25°C; Figure 13) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.01657x^2 + 0.63217x - 3.04016$$

where x = temperature (°C).

The T_{opt} for this treatment group was 19.1°C, which was lower than the T_{opt} for Coleman fish acclimated to 16°C and 20°C.

16°C Acclimation Group. The AS of Coleman fish acclimated to 16°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 13) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02208x^2 + 0.88745x + 0.2194$$

where x = temperature (°C).

The T_{opt} for this treatment group was 20.1°C, which was in between the T_{opt} for Coleman fish acclimated to 11°C and 20°C.

20°C Acclimation Group. The AS of Coleman fish acclimated to 20°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 13) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02648x^2 + 1.09168x - 2.0372$$

where x = temperature (°C).

The T_{opt} for this treatment group was 20.6°C, which was higher than the T_{opt} for Coleman fish acclimated to 11°C and 16°C.

Elk River Population

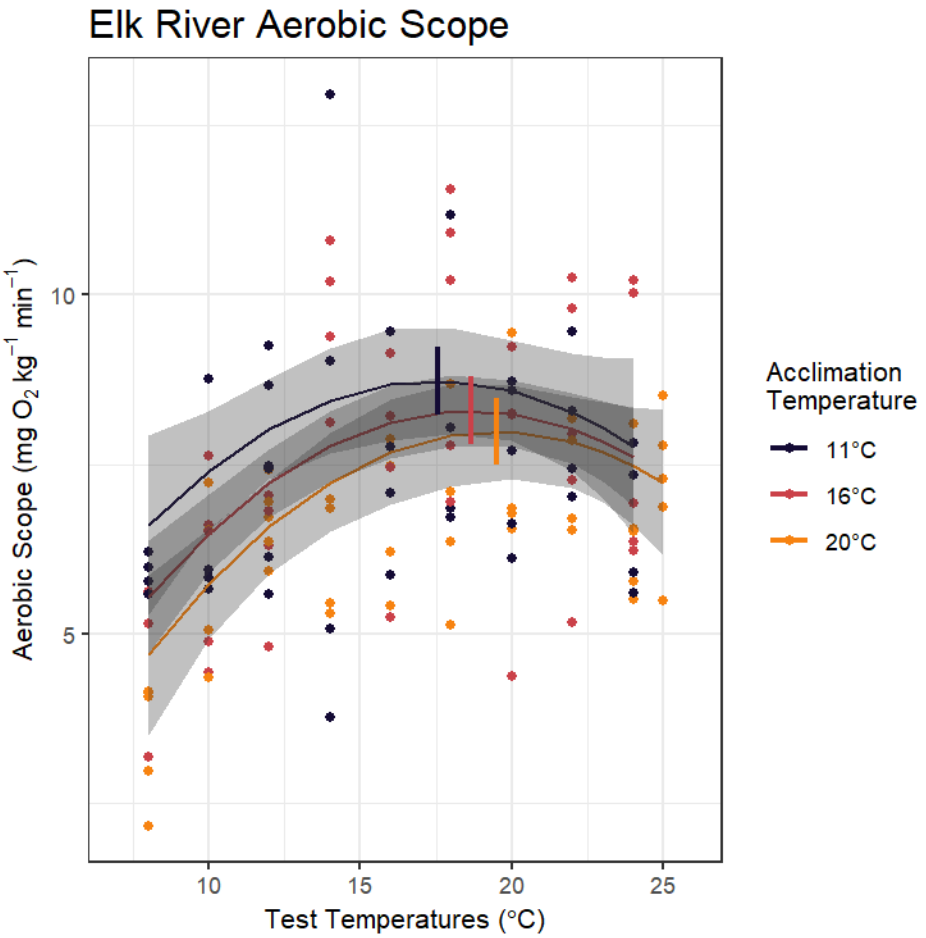

Figure 14: *Aerobic Scope (AS) for the Elk River fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the AS for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval. The vertical bars identify the Topt for each treatment group, which is defined as the peak of the quadratic relationship.*

11°C Acclimation Group. The AS of Elk River fish acclimated to 11°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 24°C, due to mortality at 25°C, Figure 14) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02326x^2 + 0.81656x + 1.56749$$

where x = temperature (°C).

The T_{opt} for this treatment group was 17.6°C, which was lower than the T_{opt} for Elk River fish acclimated to 16°C and 20°C.

16°C Acclimation Group. The AS of Elk River fish acclimated to 16°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 24°C, due to mortality at 25°C, Figure 14) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02421x^2 + 0.9037x - 0.13614$$

where x = temperature (°C).

The T_{opt} for this treatment group was 18.7°C, which was in between the T_{opt} for Elk River fish acclimated to 11°C and 20°C.

20°C Acclimation Group. The AS of Elk River fish acclimated to 20°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 14) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02497x^2 + 0.97342x - 1.49905$$

where x = temperature (°C).

The T_{opt} for this treatment group was 19.5°C, which was higher than the T_{opt} for Elk River fish acclimated to 11°C and 16°C.

Trask Population

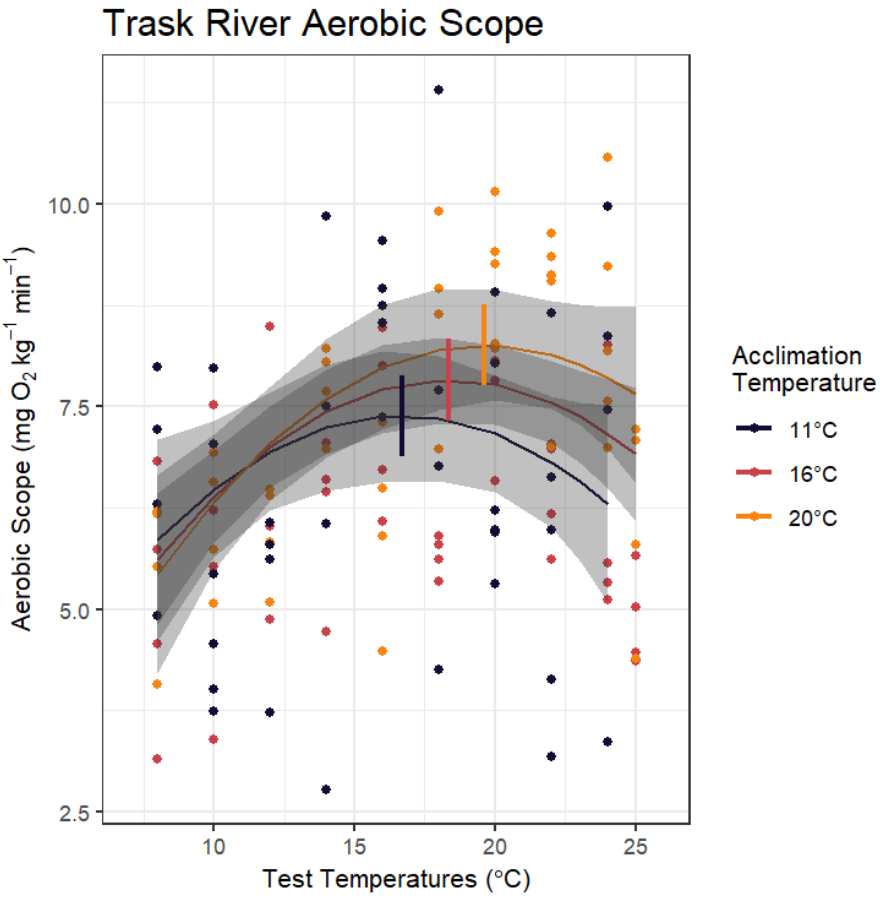

Figure 15: *Aerobic Scope (AS) for Trask River fall-run hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the AS for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval. The vertical bars identify the Topt for each treatment group, which is defined as the peak of the quadratic relationship.*

11°C Acclimation Group. The AS of Trask fish acclimated to 11°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 24°C, due to mortality at 25°C, Figure 15) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02036x^2 + 0.67966x + 1.71671$$

where x = temperature (°C).

The T_{opt} for this treatment group was 16.7°C, which was lower than the T_{opt} for Trask Hatchery fish acclimated to 16°C and 20°C.

16°C Acclimation Group. The AS of Trask fish acclimated to 16°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 15) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.02072x^2 + 0.75948x + 0.86842$$

where x = temperature (°C).

The T_{opt} for this treatment group was 18.3°C, which was in between the T_{opt} for Trask Hatchery fish acclimated to 11°C and 20°C.

20°C Acclimation Group. The AS of Trask fish acclimated to 20°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 15) and was fit with the following equation

.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.00856x^2 + 0.65x + 1.91546$$

where x = temperature (°C).

The T_{opt} for this treatment group was 19.6°C, which was higher than the T_{opt} for Trask Hatchery fish acclimated to t 11 or 16°C.

Livingston Stone (Winter-Run) Population

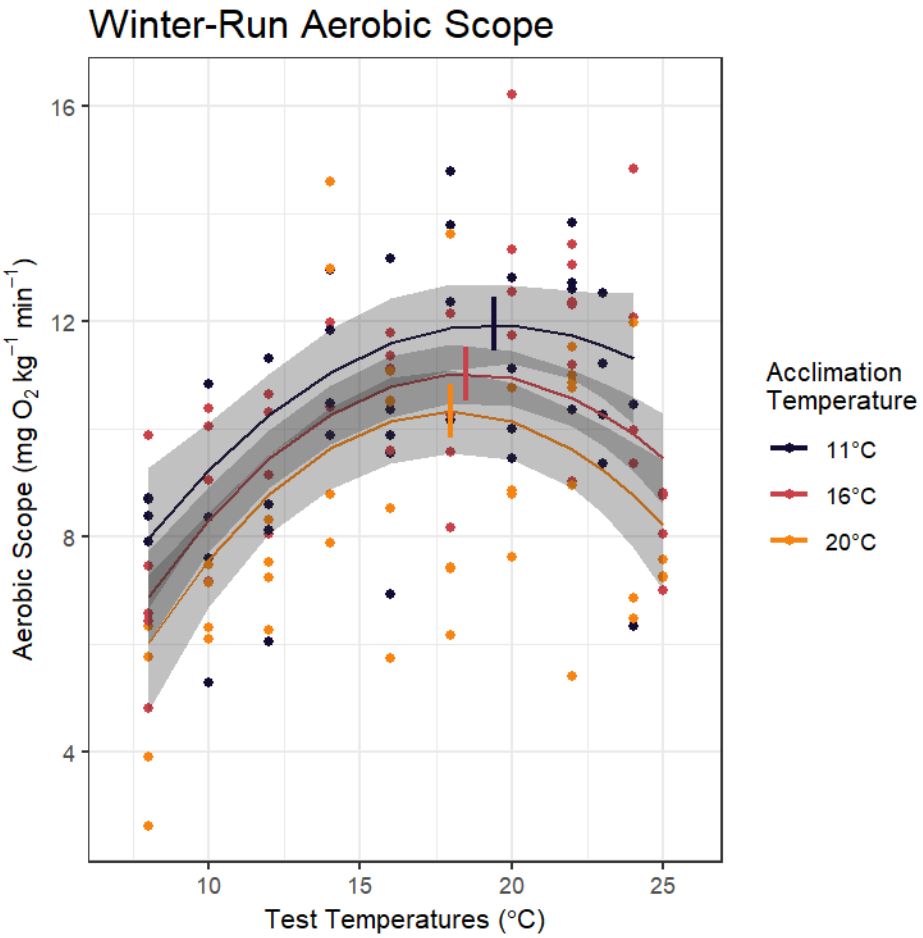

Figure 16: *Aerobic Scope (AS) for winter-run Livingston Stone National Fish hatchery juvenile Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the AS for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval. The vertical bars identify the Topt for each treatment group, which is defined as the peak of the quadratic relationship.*

11°C Acclimation Group. The AS of Livingston Stone fish acclimated to 11°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 24°C, due to mortality at 25°C; Figure 16) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.03058x^2 + 1.18716x + 0.43786$$

where x = temperature (°C).

The T_{opt} for this treatment group was 19.4°C, which was higher than the T_{opt} for Livingston Stone fish acclimated to 16°C and 20°C.

16°C Acclimation Group. The AS of Livingston Stone fish acclimated to 16°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 16) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.0375x^2 + 1.38788x - 1.80337$$

where x = temperature (°C).

The T_{opt} for this treatment group was 18.5°C, which was in between the T_{opt} for Livingston Stone fish reared at 11°C and 20°C.

20°C Acclimation Group. The AS of Livingston Stone fish acclimated to 20°C followed a typical thermal performance curve quadratic relationship across tested temperatures (8 to 25°C, Figure 16) and was fit with the following equation.

$$AS\ (mgO_2kg^{-1}min^{-1}) = -0.04304x^2 + 1.54845x - 3.59635$$

where x = temperature (°C).

The T_{opt} for this treatment group was 18.0°C, which was lower than the T_{opt} for Livingston Stone fish acclimated to 11°C and 16°C.

Aerobic Scope Summary

Across all fall-run populations, acclimation to warmer temperatures yielded an increased T_{opt}. For instance, the Coleman population fish acclimated to 11°C had a T_{opt} of 19.1°C. When this population was acclimated to 20°C the T_{opt} was 20.6°C. This pattern was not shared by the winter-run population. In the winter-run population as acclimation temperature increased, T_{opt} decreased. Winter-run fish acclimated to 11°C had a T_{opt} of 19.4°C. The T_{opt} value decreased to 18.0°C among winter-run fish acclimated to 20°C.

Of the four populations, controlling for acclimation temperature, the Coleman population exhibited the highest T_{opt} at each acclimation temperature. The Elk River population, which is geographically between the Coleman and Trask populations, exhibited T_{opt} values between those of Coleman and Trask populations (when acclimated to 11 and 16°C). At 20°C the Elk River and Trask populations had very similar T_{opt} values (19.5 and 19.6°C respectively). The Trask populations exhibited the lowest T_{opt} values when acclimated to 11 and 16°C.

We calculated the proportion of the maximum aerobic scope that was exhibited by each treatment group when swam at 24°C. 24°C was chosen as it was an extreme warm temperature that was experienced by all treatment groups. The Coleman population (southernmost) maintained the highest aerobic scope (~96% of maximum) at 24°C regardless of acclimation temperature. Among fall-run populations, acclimation to warmer temperatures increased the percentage of maximum aerobic scope available at 24°C. This relationship was reversed in winter-run Chinook salmon, where acclimation to warmer temperatures decreased the aerobic capacity available at 24°C, implying reduced warm-temperature performance in the winter-run

population. T_{opt}, and metabolic proportion at 24°C for each treatment group are listed in Table 5. On the whole, the studied fish maintained a remarkably high metabolic performance for such an extreme temperature. This implies that OCLTT hypothesis may not apply to sub-adult Chinook salmon and therefore metabolic data may not serve as a predictive metric for determining upper lethal limits. Fish were capable of maintaining ~ 90% of peak AS at 24°C but few individuals were able to survive at 25°C, therefore this metabolic performance should not be interpreted as reflecting ecological suitability of 24°C for rearing juvenile Chinook salmon.

Table 5: *Thermal Optimum (Topt) for each population and acclimation temperature. Topt calculated as the peak of the aerobic scope curve. AS at Topt is the aerobic scope at Topt in mg O2/g/hr. AS at 24°C is the aerobic scope at 24°C; this value was calculated using the individual population equations presented above. % AS at 24°C is the percentage of the Topt aerobic scope value that exists at 24.*

Hatchery	Acclimation Temp	T_{opt} (°C)	AS at T_{opt}	AS at 24°C	% AS at 24°C
Coleman	11°C	19.1	9.07	8.67	95.5%
Coleman	16°C	20.1	9.14	8.80	96.3%
Coleman	20°C	20.6	9.21	8.91	96.8%
Elk River	11°C	17.6	8.73	7.77	89.0%
Elk River	16°C	18.7	8.30	7.61	91.7%
Elk River	20°C	19.5	7.99	7.48	93.6%
Trask	11°C	16.7	7.39	6.30	85.3%
Trask	16°C	18.3	7.83	7.16	91.5%
Trask	20°C	19.6	8.26	7.85	95.1%
Winter-Run	11°C	19.4	11.96	11.31	94.6%
Winter-Run	16°C	18.5	11.04	9.90	89.7%
Winter-Run	20°C	18.0	10.33	8.78	85.0%

Factorial Aerobic Scope (FAS)

Factorial Aerobic Scope (FAS) is an additional metric of aerobic capacity (Clark et al. 2013). It is derived by dividing the maximum metabolic rate by the resting metabolic rate and is a unit-less quotient representing the proportion of MMR consumed by baseline energetic demands.

$$FAS = \frac{MMR}{RMR}$$

FAS for all treatment groups was modeled using a linear model in R with the equation:

$$FAS \sim poly(\text{`}Swim\ Temperature\text{`}, 3) * Hatchery * \text{`}Acclimation\ Temperature\text{`} + Mass + \text{`}Tunnel\ ID\text{`}$$

This equation was one of many tested and was chosen for having the lowest AIC. The final model was fitted with a statistically significant ($p = 2.2x10^{-16}$) relationship (Figure 17). FAS of juvenile Chinook salmon was observed to fit a curvilinear (cubic) relationship. FAS was significantly influenced by swimming temperature ($df = 3$, $F = 227.97$, $p < 0.0001$), hatchery of origin ($df = 3$, $F = 32.00$, $p < 0.0001$), and acclimation temperature ($df = 1$, $F = 40.47$, $p < 0.0001$). Mass was found to have a significant effect ($df = 1$, $F = 18.30$, $p = 0.0001$) on FAS

despite MMR and RMR being mass corrected. This may be due to metabolic scaling between smaller and larger fish. Tunnel ID, (i.e., the specific swim tunnel the fish swam in) also revealed a significant effect on FAS (df = 4, F = 3.24 p = 0.01217). This is possible due to small differences in the flow patterns produced by each tunnel and a carry-over effect from MMR measurements. There were significant interactions between hatchery and acclimation temperature (df = 3, F = 3.13, p < 0.0253), hatchery and swimming temperature (df = 9, F = 2.77, p = 0.0036), and acclimation temperature and swimming temperature (df =3, F = 5.99, p = 0.0005). The significant interactions imply different responses to acclimation temperature between hatcheries. Equations presented below will be in the form of $y = ax^3 + bx^2 + cx + d$.

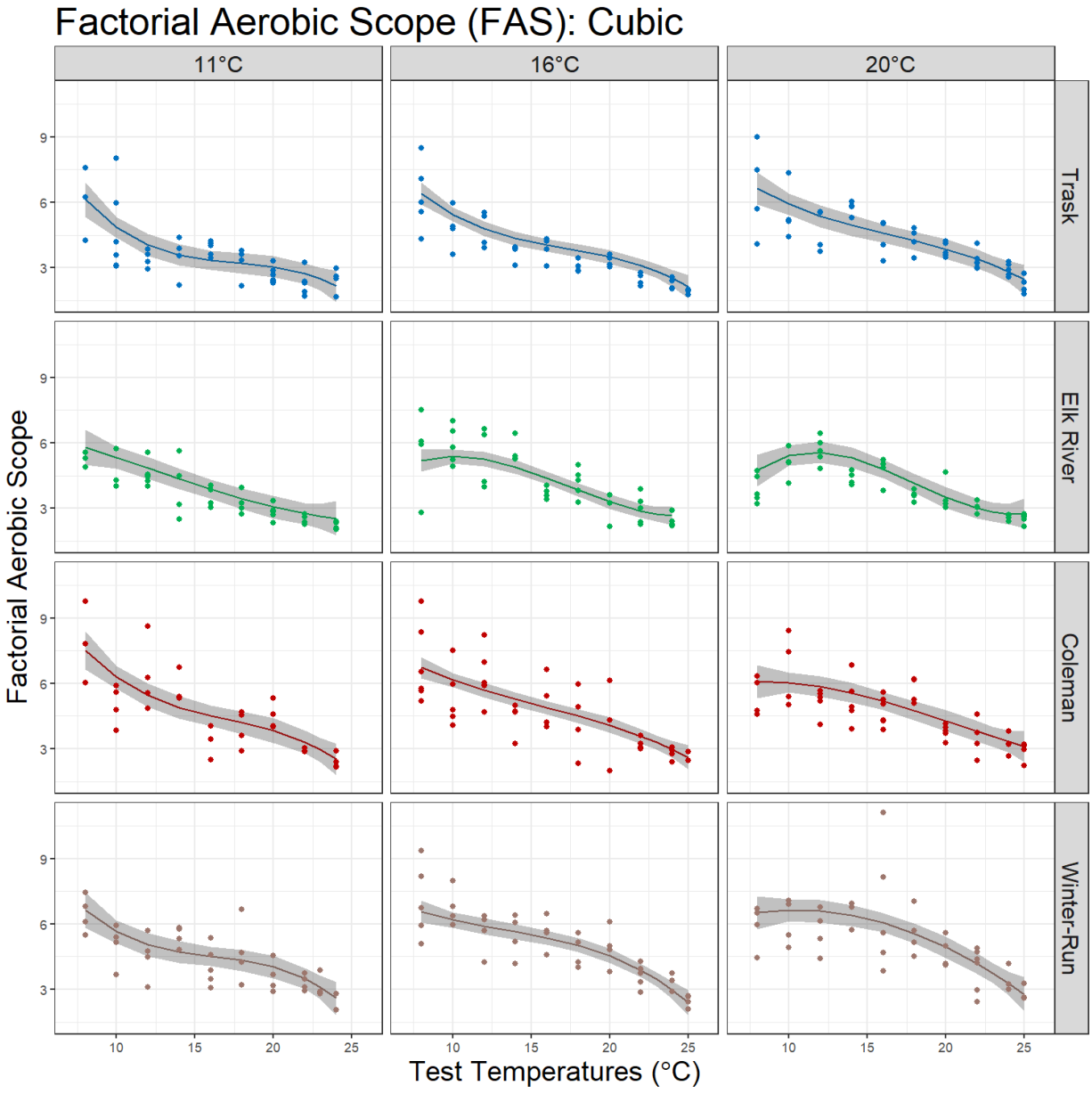

Figure 17: *Factorial Aerobic Scope (FAS) for all four populations and three acclimation groups. Each data point represents the ratio of the RMR and MMR for one fish. Lines are the modeled relationship as per the equation outlined above. Shaded areas are 95% confidence intervals.*

Coleman Population

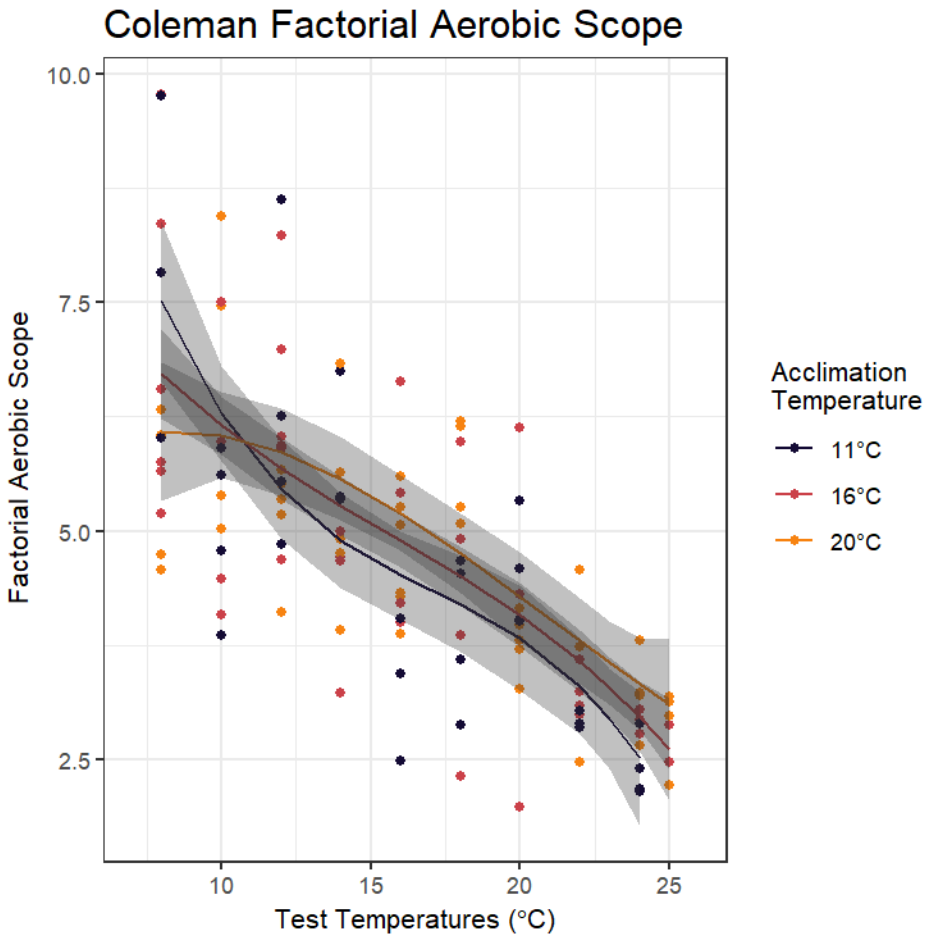

Figure 18: *Factorial Aerobic Scope for Coleman hatchery juvenile fall-run Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the FAS ratio of RMR and MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The FAS of Coleman fish acclimated to 11°C decreased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 18) and was fit with the following equation.

$$FAS = -0.00228x^3 + 0.11739x^2 - 2.16786x + 18.51101$$

where x = temperature (°C).

The FAS at 8°C was 7.51 ± 0.45 and at 24°C was 2.52 ± 0.38. The FAS at 8°C is higher than observed in Coleman fish acclimated to 16 or 20°C. At 24°C, the FAS is lower than observed in Coleman fish acclimated to 16 or 20°C.

16°C Acclimation Group. The FAS of Coleman fish acclimated to 16°C decreased over the range of temperatures tested (8 to 25°C, Figure 18) and was fit with the following equation.

$$FAS = -0.00072x^3 + 0.03375x^2 - 0.71561x + 10.65446$$

where x = temperature (°C).

The FAS at 8°C was 6.72 ± 0.25 and at 24°C was 2.97 ± 0.20. The FAS at 8°C and at 24°C is between those of Coleman fish acclimated to 11 or 20°C.

20°C Acclimation Group. The FAS of Coleman fish acclimated to 20°C decreased over the range of temperatures tested (8 to 25°C, Figure 18) and was fit with the following equation.

$$FAS = 0.00053x^3 - 0.03316x^2 + 0.44618x + 4.36923$$

where x = temperature (°C).

The FAS at 8°C was 6.09 ± 0.38 and at 24°C was 3.33 ± 0.26. The FAS at 8°C is lower than those of Coleman fish acclimated to 11 or 16°C while at 24°C is higher than those of fish acclimated to 11 or 16°C.

Elk River Population

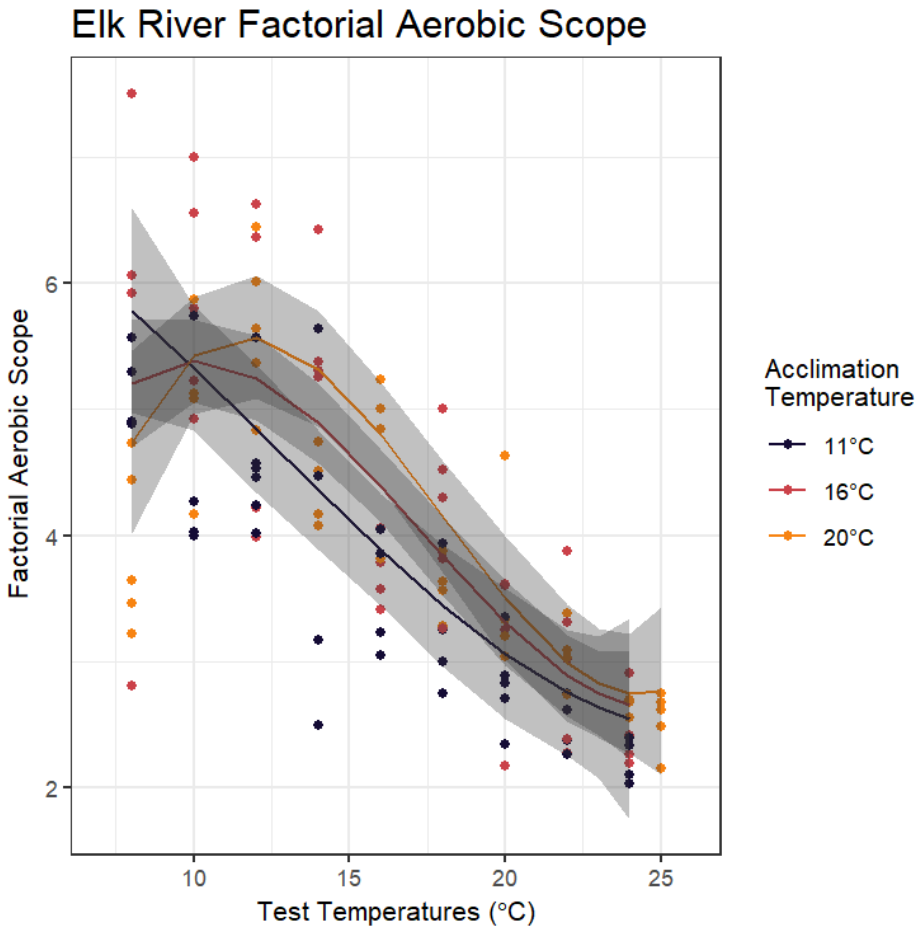

Figure 19: *Factorial Aerobic Scope for Elk River hatchery juvenile fall-run Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the FAS ratio of RMR and MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The FAS of Elk River fish acclimated to 11°C decreased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 19) and was fit with the following equation.

$$FAS = 0.00043x^3 - 0.01635x^2 - 0.03880x + 6.92132$$

where x = temperature (°C).

The FAS at 8°C was 5.79 ± 0.42 and at 24°C was 2.54 ± 0.40. The FAS at 8°C is higher than the FAS of fish acclimated to 16 or 20°C while at 24°C is lower than the FAS fish acclimated to 16 or 20°C.

16°C Acclimation Group. The FAS of Elk River fish acclimated to 16°C decreased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C; Figure 19) and was fit with the following equation.

$$FAS = 0.00175x^3 - 0.09101x^2 + 1.30071x - 0.26936$$

where x = temperature (°C).

The FAS at 8°C was 5.21 ± 0.26 and at 24°C was 2.66 ± 0.22. The FAS at 8°C and at 24°C is between the FAS of fish acclimated to 11 or 20°C.

20°C Acclimation Group. The FAS of Elk River fish acclimated to 20°C decreased over the range of temperatures tested (8 to 25°C, Figure 19) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11 and 16°C.

$$FAS = 0.0028x^3 - 0.15074x^2 + 2.37231x - 6.02191$$

where x = temperature (°C).

The FAS at 8°C was 4.74 ± 0.37 while at 24°C was 2.75 ± 0.24. The FAS at 8°C is lower than the FAS of fish acclimated to 11 or 16°C and at 24°C is higher than the FAS of fish acclimated to 11 or 16°C.

Trask Population

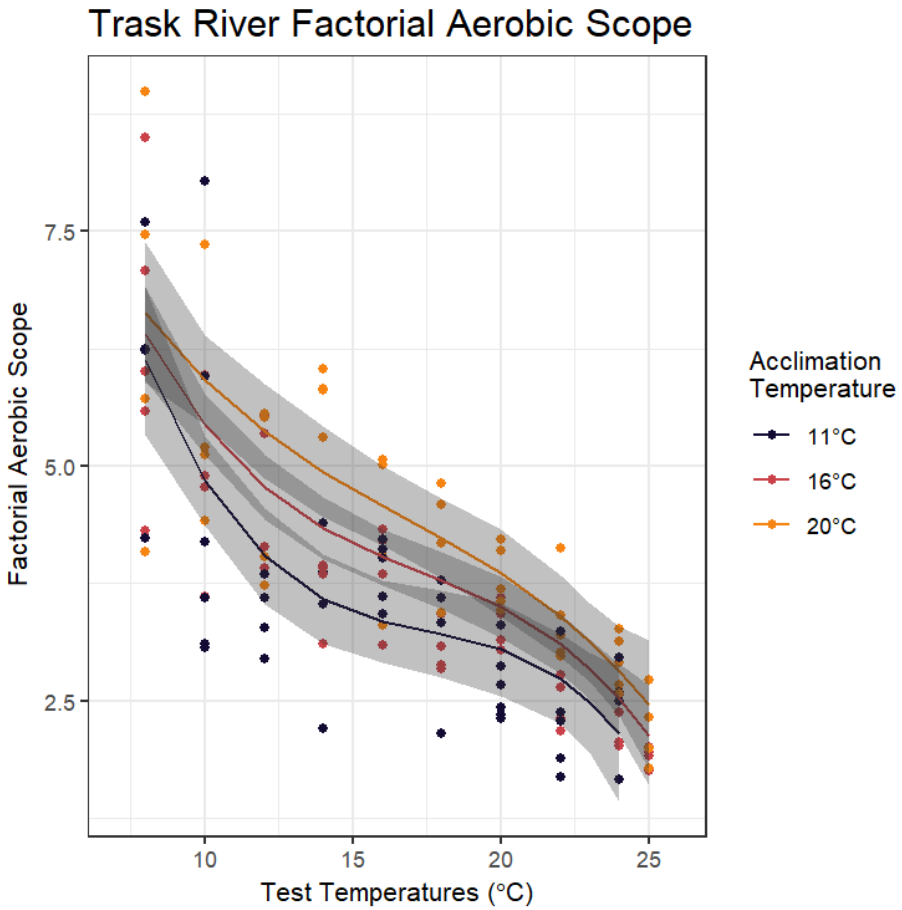

Figure 20: *Factorial Aerobic Scope for Trask River hatchery juvenile fall-run Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the FAS ratio of RMR and MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The FAS of Trask fish acclimated to 11°C decreased over the range of temperatures tested (8 to 24°C, due to mortality at 25°C, Figure 20) and was fit with the following equation.

$$FAS = -0.00258x^3 + 0.13635x^2 - 2.46188x + 18.41422$$

where x = temperature (°C).

The FAS at 8°C was 6.12 ± 0.40 and at 24°C was 2.15 ± 0.37. The FAS at 8°C is higher than those of fish acclimated to 16 or 20°C and at 24°C is lower than those of fish acclimated to 16 or 20°C.

16°C Acclimation Group. The FAS of Trask fish acclimated to 16°C decreased over the range of temperatures tested (8 to 25°C, Figure 20) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11°C.

$$FAS = -0.00172x^3 + 0.08953x^2 - 1.67322x + 14.94549$$

where x = temperature (°C).

The FAS at 8°C was 6.41 ± 0.25 while at 24°C was 2.52 ± 0.19. The FAS at 8°C and at 24°C is between those of fish acclimated to 11 and 20°C.

20°C Acclimation Group. The FAS of Trask fish acclimated to 20°C decreased over the range of temperatures tested (8 to 25°C, Figure 20) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11°C.

$$FAS = -0.00104x^3 + 0.05207x^2 - 1.04229x + 12.17051$$

where x = temperature (°C).

The FAS at 8°C was 6.63 ± 0.38 and at 24°C was 2.81 ± 0.25. The FAS at 8°C is lower than those of fish acclimated to 11 or 16°C and at 24°C is higher than those of fish acclimated to 11 or 16°C.

Livingston Stone (Winter-Run)

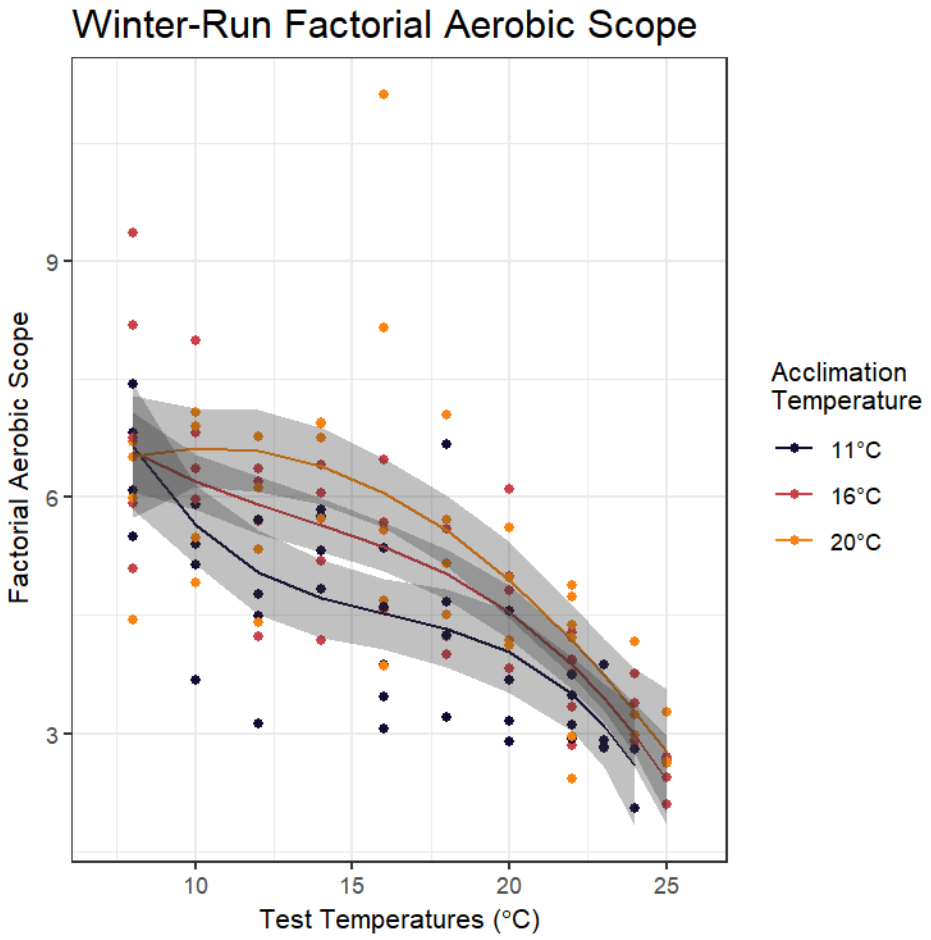

Figure 21: *Factorial Aerobic Scope for Livingston Stone hatchery juvenile winter-run Chinook salmon acclimated to 11, 16 and 20°C. Each point represents the FAS ratio of RMR and MMR for one individual fish, and the solid lines represents the best fit line for the data; equations for best-fit curve are given in the text. The shaded area surrounded each line represents the 95% confidence interval.*

11°C Acclimation Group. The FAS of Livingston Stone fish acclimated to 11°C decreased over the range of temperatures (8 to 24°C, due to mortality at 25°C; Figure 21) and was fit with the following equation.

$$FAS = -0.00264x^3 + 0.12823x^2 - 2.1602x + 17.06234$$

where x = temperature (°C).

The FAS at 8°C was 6.64 ± 0.41 and at 24°C was 2.59 ± 0.39. The FAS at 8°C is nearly identical to the FAS of Livingston Stone fish acclimated to 16 or 20°C and at 24°C is lower than the FAS of fish acclimated to 16 or 20°C.

16°C Acclimation Group. The FAS of Livingston Stone fish acclimated to 16°C decreased over the range of temperatures tested (8 to 25°C, Figure 21) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11°C.

$$FAS = -0.00115x^3 + 0.04574x^2 - 0.73315x + 10.09689$$

where x = temperature (°C).

The FAS at 8°C was 6.57 ± 0.26 and at 24°C was 2.97 ± 0.20. The FAS at 8°C is nearly identical to those of Livingston Stone fish acclimated to 11 or 20°C and at 24°C is between those of fish acclimated to 11 or 20°C.

20°C Acclimation Group. The FAS of Livingston Stone fish acclimated to 20°C decreased over the range of temperatures tested (8 to 25°C, Figure 21) and was fit with the following equation. While data were obtained from these fish at 25°C, we are reporting metabolic rates only to 24°C for comparison with fish acclimated to 11°C.

$$FAS = 0.00004x^3 - 0.02026x^2 + 0.40849x + 4.52453$$

where x = temperature (°C).

The FAS at 8°C was 6.52 ± 0.39 and at 24°C was 3.27 ± 0.28. The FAS at 8°C is nearly identical to those of Livingston Stone fish acclimated to 11 or 16°C and at 24°C is higher than those of fish acclimated to 11 or 16°C.

Factorial Aerobic Scope Summary

In all populations FAS generally decreased with increasing temperature (Table 6). This is primarily driven by the increase in RMR that occurs as swimming temperatures increase. Across all populations, acclimation to warmer temperatures increased the value of FAS across most test temperatures. Exceptions to this pattern occurred at low test temperatures (8 or 10°C) and were driven by low MMR values for populations acclimated to 20°C.

Table 6: *Reported Factorial Aerobic Scope (FAS) Values. Values are given as predicted means with standard error.*

Hatchery	Acclimation Temp	FAS at 8°C	FAS at 24°C
Coleman	11°C	7.51 ± 0.45	2.52 ± 0.38
Coleman	16°C	6.72 ± 0.25	2.97 ± 0.20
Coleman	20°C	6.09 ± 0.38	3.33 ± 0.26
Elk River	11°C	5.79 ± 0.42	2.54 ± 0.40
Elk River	16°C	5.21 ± 0.26	2.66 ± 0.22
Elk River	20°C	4.74 ± 0.37	2.75 ± 0.24
Trask	11°C	6.12 ± 0.40	2.15 ± 0.37
Trask	16°C	6.41 ± 0.25	2.52 ± 0.19
Trask	20°C	6.63 ± 0.38	2.81 ± 0.25
Winter-Run	11°C	6.64 ± 0.41	2.59 ± 0.39
Winter-Run	16°C	6.57 ± 0.26	2.97 ± 0.20
Winter-Run	20°C	6.52 ± 0.39	3.27 ± 0.28

Critical Thermal Maximum (CTM)

Differences in critical thermal maximum (CTM) among treatment groups was analyzed using a linear model that included interacting effects for hatchery of origin and acclimation temperature and fish mass. Final model with the lowest AIC was selected and had a p value < 0.0001.

$$CTM \sim Hatchery * `Acclimation\ Temperature` * Mass$$

Hatchery of origin was found to have a significant effect (df = 3, F = 8.4749, p < 0.0001) as was acclimation temperature (df = 1, F = 283.57, p < 0.0001). There was a significant interaction of hatchery and acclimation temperature (df = 3, F =7.87, p < 0.0001) as well as between hatchery and mass (df = 3, F = 3.36, p = 0.0196). The two interactions indicate that the CTM of different populations does not respond similarly to acclimation temperature. This is most visible in the Elk River populations (Figure 22).

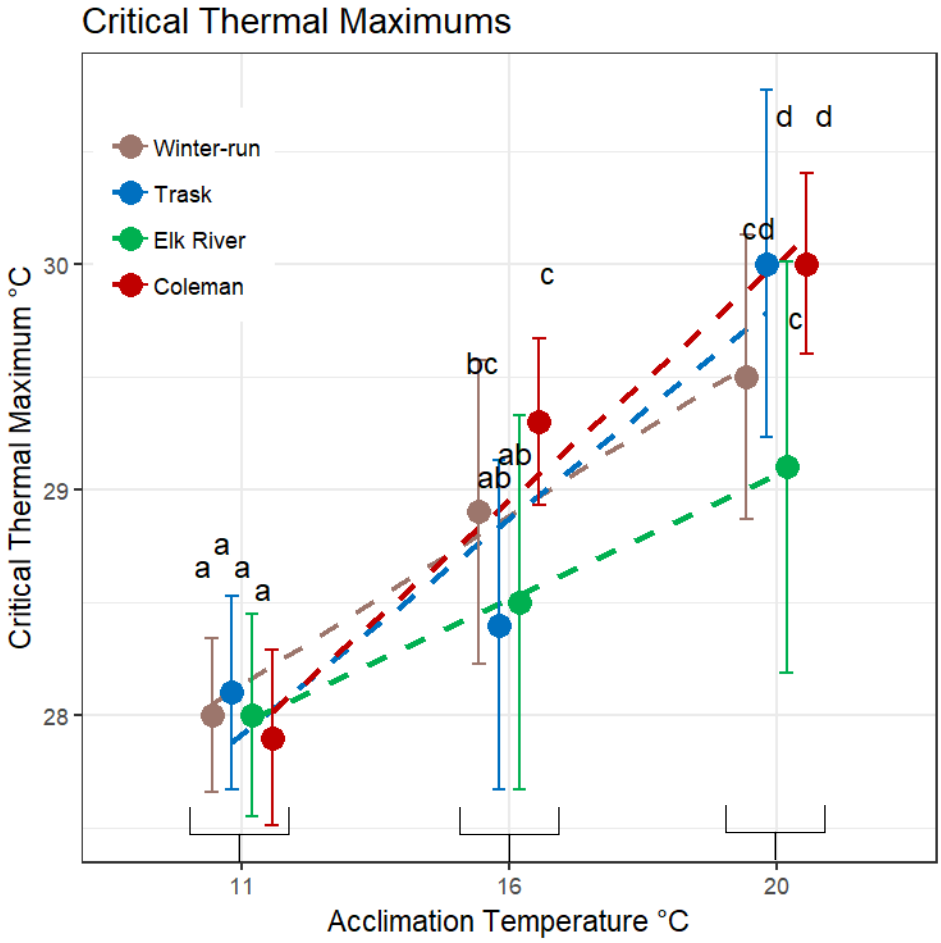

Figure 22: *Critical Thermal Maximums (CTMs) for the four populations and three acclimation temperatures. Dots represent the mean value for each treatment with error bars representing the standard deviation. Lines represented the modeled relationship between acclimation temperature and CTM for each population. Different letters indicated significant differences among groups (p < 0.05). Data are 'jittered' for each acclimation temperature so that means and error bars can be seen without overlap.*

Coleman Population

Juveniles from the Coleman population when acclimated to 11°C had an average CTM of 27.9°C ± 0.39. This increased if the fish were acclimated to 16°C to 29.3 °C ± 0.37. Acclimation to 20°C further increased the CTM to 30.0°C ± 0.40. Collectively a 9°C increase in acclimation temperature yielded an approximate 2°C increase in upper thermal tolerance.

Elk River Population

Juveniles from the Elk River hatchery population when acclimated to 11°C had an average CTM of 28.0°C ± 0.45. This increased if the fish were acclimated to 16°C to 28.5°C ± 0.83. Acclimation to 20°C further increased the CTM to 29.1°C ± 0.91. Collectively a 9°C increase in acclimation temperature yielded an approximate 1°C increase in upper thermal tolerance.

Trask Population

Juveniles from the Trask hatchery population when acclimated to 11°C had an average CTM of 28.1°C ± 0.43. This increased if the fish were acclimated to 16°C to 28.4°C ± 0.73. Acclimation to 20°C further increased the CTM to 30.0°C ± 0.77. Collectively a 9°C increase in acclimation temperature yielded an approximate 2°C increase in upper thermal tolerance.

Livingston Stone Population (Winter-Run) Population

Juveniles from the Livingston Stone population when acclimated to 11°C had an average CTM of 28.0°C ± 0.34. This increased if the fish were acclimated to 16°C to 28.9°C ± 0.67. Acclimation to 20°C further increased the CTM to 29.5°C ± 0.63. Collectively a 9°C increase in acclimation temperature yielded an approximate 2°C increase in upper thermal tolerance.

Critical Thermal Maximum (CTM) Summary

All populations demonstrated an increase in upper thermal tolerance with acclimation temperature (Table 7). However, the acquisition of thermal tolerance in response to elevated acclimation temperatures was not equivalent among all populations. Notably the Elk River population gained approximately half the thermal tolerance of the other populations when acclimated to 11 compared to 20°C. The winter-run fish, despite observed differences in growth rate and metabolic performance compared to other Chinook populations, did not appear different from the Coleman or Trask populations in upper thermal tolerance. Finally, when acclimated to 11°C, all populations had the same CTM. This may represent some form of shared physiological baseline for this species. Comparisons with additional populations as well as to fish acclimated to colder temperatures would aid in investigating this phenomenon.

Table 7: *Critical Thermal Maximum (CTM) experiment results with fish mass, lengths and Fulton's condition factor. Values are reported as the means and standard deviation.*

Hatchery	Acclimation Temp	CTM (°C)	Mass (g)	Fork Length (mm)	Total Length (mm)	Condition Factor
Coleman	11°C	27.9 ± 0.39	17.21 ± 5.15	114.55 ± 10.68	125.36 ± 12.07	1.11 ± 0.07
Coleman	16°C	29.3 ± 0.37	22.93 ± 3.37	124.25 ± 6.58	136.20 ± 6.92	1.19 ± 0.06
Coleman	20°C	30.0 ± 0.40	23.26 ± 3.76	123.20 ± 6.54	133.30 ± 7.87	1.23 ± 0.07
Elk River	11°C	28.0 ± 0.45	26.44 ± 3.10	130.43 ± 4.48	142.52 ± 4.49	1.19 ± 0.05
Elk River	16°C	28.5 ± 0.83	24.91 ± 2.97	126.95 ± 4.91	138.25 ± 5.34	1.21 ± 0.09
Elk River	20°C	29.1 ± 0.91	26.90 ± 3.07	127.11 ± 4.28	136.58 ± 4.15	1.31 ± 0.07
Trask	11°C	28.1 ± 0.43	25.69 ± 2.96	131.84 ± 4.75	143.20 ± 5.22	1.12 ± 0.05
Trask	16°C	28.4 ± 0.73	27.56 ± 4.24	131.50 ± 4.80	142.75 ± 5.15	1.20 ± 0.06
Trask	20°C	30.0 ± 0.77	26.07 ± 2.80	127.89 ± 3.97	138.17 ± 4.19	1.24 ± 0.09
Winter-Run	11°C	28.0 ± 0.34	21.67 ± 2.45	123.86 ± 5.19	136.27 ± 5.92	1.14 ± 0.11
Winter-Run	16°C	28.9 ± 0.67	21.09 ± 3.30	122.15 ± 6.06	133.30 ± 6.38	1.15 ± 0.11
Winter-Run	20°C	29.5 ± 0.63	18.54 ± 1.90	114.44 ± 5.10	125.44 ± 4.95	1.24 ± 0.07

Growth Rate

There was some variation among populations that prevented direct growth rate comparisons. Populations were acquired from hatcheries at different sizes and on different dates pursuant to the availability of fish at the hatchery. Furthermore, measurements for mass and length continued for varying lengths of time dependent on when fish grew to sizes needed for aerobic scope and CTM experiments. To control for this variation, the measurement window had to be standardized in order to compare growth rates between populations and acclimation treatments:

Size Window Determination: The population reared for the shortest time prior to experiments was the Coleman population, and therefore growth datasets for other populations were constrained to capture the same window of fish mass (e.g. mean starting size 7.55 ± 2.01g; mean ending size 13.79 ± 4.25g). The short duration of rearing for the Coleman population was due to acquiring the fish at a larger size than the other populations.

Time Frame Standardization: Growth data were standardized so that the first measurement occurred when mean fish mass was within the defined size window (see above). All time frames occurred throughout the spring and summer of 2017 and 2018. Over the course of the study, fish were exposed to natural light conditions and therefore experienced a dynamic photoperiod. Chinook salmon have not been found to adjust their growth rate in response to photoperiod (Clarke et al. 1981), therefore we do not believe differences in photoperiod account for differences in observed growth rate.

Fish were stocked in different densities due to varying numbers provided by the different hatcheries and limitations in acquiring federally endangered winter-run Chinook salmon. Different densities at time of stocking could alter growth rates. However, research on the effects of stocking density on the growth rates of Chinook salmon are ambiguous. Olson and Paiya (2013) reared Chinook salmon juveniles in hatchery raceways at densities of 0.27 fish/L, 0.42 fish/L and 0.55 fish/L. They found no effect of rearing density on the mass gain of the studied salmon. Also, these densities encapsulate the rearing densities of fish in our trial (Table 1).

However, similar research by Ewing et al. (1998) found that rearing density did yield an inverse relationship with growth rate. At present we cannot account for the effect of stocking density on population differences in growth rate as it is confounded with hatchery of origin. However, we do find that tanks stocked with the fewest fish (winter-run at 16°C or 20°C and Coleman at 11°C) exhibited some of the slowest growth rates, which runs counter to the anticipated effect of stocking density on growth.

Growth rates were analyzed using a linear model. Mass of individual fish were modeled against the interacting terms of hatchery, acclimation temperature, and time. Time is measured in days with 0 representing the start of the growth rate time frame (see above). Final model fit with a p value < 0.0001.

$$Mass(g) \sim Hatchery * Acclimation\ Temperature * Time$$

Time was found to have a significant effect (df = 1, F = 633.48, $p < 0.0001$), as did hatchery (df = 3, F = 8.08, $p < 0.0001$) and acclimation temperature (df = 1, F = 42.20, $p < 0.0001$). There were significant interactions between hatchery and acclimation temperature (df = 3, F=24.65, $p < 0.0001$), between hatchery and time (df = 3, F = 22.37, $p < 0.0001$), but not between acclimation temperature and time (df = 1, F = 1.78, p = 0.182). The three-way interaction between hatchery, acclimation temperature, and time was also significant (df = 3, F = 7.17, $p < 0.0001$). Due to the significant interactions, significance in growth rates between treatment groups were determined using a Tukey's post-hoc test (Figures 23 and 24, and Table 8).

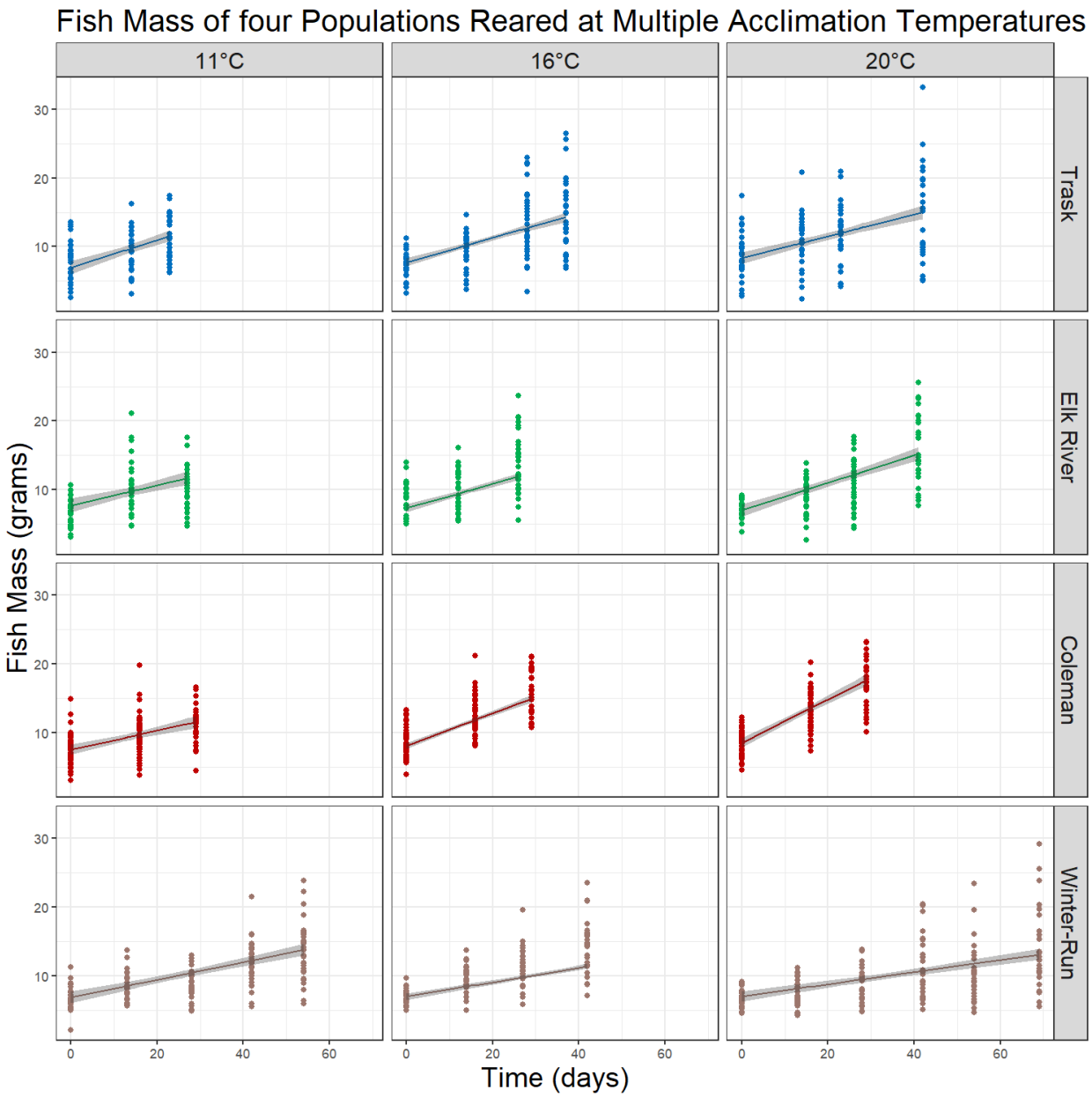

Figure 23: *Fish Mass over time. Line reflects the modeled relationship, with shaded area indicating the 95% confidence interval of the model, not the mean of the sampled data. Facets going left-to-right reflect acclimation temperatures while vertical facets indicate population of origin.*

Coleman Population

The growth rate for the Coleman population acclimated to 11°C is 0.133 ± 0.02 g^1 day^{-1}. This is the slowest growth rate for this population as compared to the 16 and 20°C acclimation groups. The growth rate increased to 0.251 ± 0.02 g^1 day^{-1} when fish were acclimated to 16°C**.** The growth rate further increased to 0.308 ± 0.02 g^1 day^{-1} when fish were acclimated to 20°C. This was the fasted growth rate observed of any treatment group by a considerable margin.

Elk River Population

The growth rate for the Elk River population acclimated to 11°C is 0.123 ± 0.03 g^1 day^{-1}. This is the slowest growth rate for this population as compared to the 16 and 20°C acclimation groups. The growth rate increased to 0.213 ± 0.03 g^1 day^{-1} when fish were acclimated to 16°C**.** The growth rate did not increase further when fish were acclimated to 20°C, where fish grew at 0.209 ± 0.02 g^1 day^{-1}.

Trask Population

The growth rate for the Trask River population acclimated to 11°C is 0.145 ± 0.04 g^1 day^{-1}. The growth rate increased to 0.220 ± 0.02 g^1 day^{-1} when fish were acclimated to 16°C**.** The growth rate did not increase further and instead declined to 0.138 ± 0.02 g^1 day^{-1} when fish were acclimated to 20°C. This rate is lower than the growth rate when fish were reared at 11°C.

Livingston Stone Population (Winter-Run) Population

The growth rate for the Livingston Stone population (winter-run) reared at 11°C is 0.123 ± 0.01 g^1 day^{-1}. The growth rate increased to 0.159 ± 0.02 g^1 day^{-1} when fish were acclimated to 16°C**.** The growth rate did not increase further and instead declined to 0.090 ± 0.01 g^1 day^{-1} when fish were acclimated to 20°C. This rate is lower than the growth rate when fish were acclimated to 11°C. Later in the season, fish in this treatment group suffered an outbreak of *Ichthyophthirius multifiliis*, which further indicates that winter-run do not perform optimally when reared at 20°C. The disease outbreak (mid-October) and subsequent mortality occurred over 100 days after cessation of growth measurements. It is likely that 20°C is a stressful acclimation temperature for rearing winter-run juveniles and that this stress is the proximate cause of both the poor growth and eventual disease outbreak.

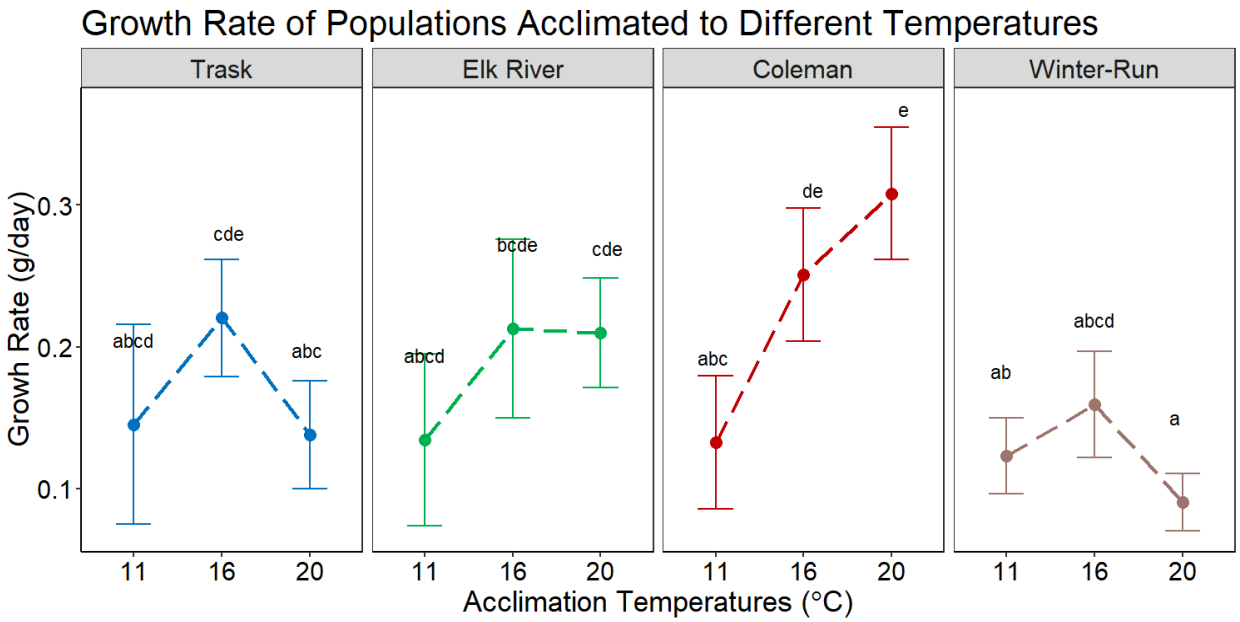

Figure 24: *Growth rate for each treatment group. Growth rate was determined as the slope of the modeled linear relationship. Error bars represent the 95% confidence interval of that slope value. Letters indicate significance (p = 0.05) and are calculated across all treatment groups.*

Table 8: *Growth Rate starting and ending values. Mass is presented in grams as the mean and standard deviation. Duration is in days and represents the time from the first sampled measurement to the last. Growth rate is grams per day with the standard error. DPH is Days Post Hatch. Sig. letters; shared letters indicate growth rate between treatment groups are not significantly different at a p = 0.05 level.*

Acclimation Temperature	Hatchery	Starting Date	DPH at Start	Starting Mass	End Date	DPH at End	End Mass	Duration	Growth Rate ± S.E.	Sig.
11°C	Coleman	4/17/2017	160	7.45 ± 2.10	5/16/2017	189	11.41 ± 2.69	29	0.133 ± 0.02	abc
16°C	Coleman	4/17/2017	160	8.41 ± 2.05	5/16/2017	189	15.69 ± 3.24	29	0.251 ± 0.02	de
20°C	Coleman	4/17/2017	160	8.34 ± 1.63	5/16/2017	189	17.29 ± 3.56	29	0.308 ± 0.02	e
11°C	Elk River	7/25/2017	192	6.81 ± 1.93	8/21/2017	219	10.39 ± 3.19	27	0.134 ± 0.03	abcd
16°C	Elk River	7/13/2017	180	8.30 ± 2.48	8/8/2017	206	13.79 ± 4.36	26	0.213 ± 0.03	bcde
20°C	Elk River	6/28/2017	165	6.99 ± 1.36	8/8/2017	206	15.71 ± 4.96	41	0.210 ± 0.02	cde
11°C	Trask	8/8/2017	237	7.80 ± 3.00	8/31/2017	260	11.22 ± 3.16	23	0.145 ± 0.04	abcd
16°C	Trask	7/25/2017	223	7.11 ± 1.95	8/31/2017	260	14.77 ± 5.32	37	0.220 ± 0.02	cde
20°C	Trask	8/8/2017	237	8.62 ± 3.34	9/19/2017	279	14.54 ± 6.51	42	0.138 ± 0.02	abc
11°C	Winter-Run	4/19/2018	177	6.90 ± 1.76	6/12/2018	231	13.60 ± 4.28	54	0.123 ± 0.01	ab
16°C	Winter-Run	4/5/2018	163	6.94 ± 1.10	5/17/2018	205	13.75 ± 3.88	42	0.159 ± 0.02	abcd
20°C	Winter-Run	4/19/2018	177	6.89 ± 1.40	6/27/2018	246	13.31 ± 5.88	69	0.090 ± 0.01	a

Growth Rate Summary

The Coleman population grew fastest at 20°C, with growth rate declining with decreasing acclimation temperature. This relationship was not shared with more northern populations. The Elk River population, which is geographically between the Coleman and Trask hatcheries, grew equally well at 16 and 20°C, but its growth rate was lowest at 11°C. Fish from the Trask

hatchery performed best at 16°C and had lower growth rates at 11 and 20°C. These results are consistent with the hypothesis that populations from lower latitudes (i.e. Central Valley) will exhibit better performance at warm temperatures than populations from higher latitudes (i.e. Pacific Northwest), however more populations are necessary to evaluate this hypothesis fully. The winter-run population (Livingston Stone) grew the slowest of any population at all acclimation temperatures and exhibited the slowest growth rates when acclimated to 20°C (0.09 ± 0.01 g^1 day^{-1}), as compared in particular to the Coleman population, which grew fastest (0.308 ± 0.02 g^1 day^{-1}) under the same conditions.

All fish acclimated at 11°C had similar growth rates (approximately 0.130 g^1 day^{-1}). This may represent some form of shared physiological baseline for this species. Comparisons with additional populations as well as growth rates measured from fish acclimated to colder temperatures would aid in investigating this phenomenon.

Mortality

Mortality due to metabolic experiments was minimal at all but the highest test temperatures. Mortality was 100% among fish tested at 26°C. Depending on the population and acclimation temperature, there were some mortality and loss of equilibrium at 25 and 24°C. These results are shown in Table 9. Fish reared at and acclimated to 11°C from all populations had greater mortality at extreme temperatures (> 22°C) than fish reared at 16 or 20°C. Elk River fish reared at 20°C experienced post-experiment loss of equilibrium at multiple swim temperatures and not just at extreme values.

Mortality during the acclimation and rearing period was also negligible with exception of the winter-run population reared at 20°C. In October of 2018, there was a disease outbreak of common *Ichthyophthirius multifiliis* and a corresponding mortality event of the winter-run fish. The mortality event occurred after 220 days of rearing at 20°C, over 100 days after growth data for this population were collected. The slow growth (see growth rate results) of the winter-run population acclimated to 20°C may have presaged an eventual collapse, but we consider this a consequence of rearing at 20°C and reflection of the physiological stress of this rearing condition. Inspection of the mortalities revealed empty digestive tracks indicating a cessation of feeding. This energy deficit could have led to a compromised immune system and subsequent infection.

Table 9: *Mortality Table for Metabolic Swim Trials. Each trial represents an individual fish. For each swimming temperature, a set of numbers in the format (X:Y:Z) is reported. X = the number of mortalities during the RMR period. Y = Number of mortalities or fish that lost equilibrium during the MMR or post-test recovery. Z = number of fish which survived the trial. NA means population wasn't tested at this temperature. This table does not report fish whose data were discarded for activity during the RMR, mechanical failure of the tunnels, or computer error in data collection.*

	Hatchery	Coleman			Elk River			Trask			Winter-run		
	Acc. Temp	*11°C*	*16°C*	*20°C*	*11°C*	*16°C*	*20°C*	*11°C*	*16°C*	*20°C*	*11°C*	*16°C*	*20°C*
Swimming Temperature	8°C	0:0:4	0:0:6	0:0:4	0:0:4	0:0:4	0:3:7	0:0:4	0:1:5	0:0:6	0:0:4	0:0:8	0:0:4
	10°C	0:0:5	0:0:6	0:0:4	0:0:4	0:0:8	0:1:7	0:0:6	0:0:4	0:0:4	0:0:4	0:0:6	0:0:4
	12°C	0:0:8	0:0:6	0:0:6	0:0:6	0:0:4	0:0:6	0:0:4	0:0:4	0:0:6	0:0:4	0:0:4	0:0:6
	14°C	0:0:4	0:0:4	0:0:6	0:0:4	0:0:4	0:1:5	0:0:6	0:0:4	0:0:6	0:0:4	0:0:4	0:0:4
	16°C	0:0:6	0:0:4	0:0:6	0:0:6	0:0:4	0:0:6	0:0:6	0:0:4	0:0:4	0:0:6	0:0:4	0:0:6
	18°C	0:0:4	0:0:4	0:0:6	0:0:4	0:0:6	0:1:4	0:0:6	0:0:4	0:0:4	0:0:4	0:0:4	0:0:6
	20°C	0:0:4	0:0:4	0:0:5	0:0:6	0:0:4	0:4:4	0:0:6	0:0:4	0:1:5	0:0:4	0:0:5	0:0:4
	22°C	0:0:4	0:0:4	0:0:4	0:0:4	0:0:6	0:0:4	0:1:5	0:0:4	0:0:6	0:0:4	0:0:6	0:0:6
	23°C	NA	NA	NA	NA	NA	NA	NA	NA	NA	1:1:4	NA	NA
	24°C	4:4:2	0:0:4	0:0:4	2:2:4	0:2:5	0:2:5	0:2:4	0:0:4	1:2:5	2:2:2	0:0:4	1:1:4
	25°C	2:2:0	0:1:3	0:0:4	2:0:0	2:0:0	0:3:5	2:0:0	0:4:4	1:1:4	2:0:0	0:2:4	0:0:5
	26°C	2:0:0	2:0:0	2:2:0	NA	NA	2:0:0	NA	NA	2:0:0	NA	2:0:0	2:0:0
	28°C	NA	NA	2:0:0	NA	NA	NA	NA	NA	NA	NA	NA	NA

Discussion

In this section, we evaluate how the study results address our research questions from the Introduction. Those questions are:

Question 1: Do California Central Valley versus more northern populations demonstrate differences in thermal performance?
Question 2: What is the variation in acclimation capacity among Chinook salmon populations?
Question 3: Do fall- versus winter-run fish demonstrate differences in thermal performance?

Question 1: Do California Central Valley versus more norther populations demonstrate differences in thermal performance?

Generally, the results of this study indicate that these populations do differ in thermal response. For instance, population of origin was found to yield a significant effect upon metabolic traits, critical thermal maxima and growth rates. Furthermore, the data (e.g. growth rate, T_{opt}) suggest that the Central Valley population (Coleman), when compared to the two Oregon populations, exhibits superior metabolic performance at warm (> 20°C) environmental temperatures as well as improved growth rate when acclimated to 20°C. This result is consistent with results found among other species of salmonids (Eliason et al. 2011; Stitt et al. 2014; Verhille et al. 2016; Poletto et al. 2017). Additionally, the Coleman (fall-run) population and the Livingston Stone (winter-run) population, despite being nearly sympatric, demonstrated considerable differences in their thermal physiologies. In particular, the Livingston Stone population expressed poor growth and reduced aerobic capacity when acclimated at 20°C.

Question 2: What is the variation in acclimation capacity among Chinook salmon populations?

Our second research question investigated whether populations demonstrated variation in their acclimation capacity across multiple traits. Populations were acclimated to three temperatures (11, 16, and 20°C) to capture the scope of thermal physiology of fish rearing throughout the Central Valley. The capacity to acclimate is important as it may predict a population's ability to cope with future climate warming (Stillman 2003). Acclimation temperature was found to be a significant factor in all the performance traits studied. Furthermore, the interaction of acclimation temperature and hatchery was also found to be significant indicating that populations are acclimating differently to the same suite of acclimation temperatures. However, the acclimation patterns among populations varied slightly depending on the physiological metric.

Aerobic scope results are consistent with the latitudinal trade-off discussed by Stillman (2003) in that the Coleman population exhibited an increase in thermal performance accompanied by a reduced capacity to acclimate. Comparing T_{opt} of aerobic scopes, the acclimation capacity between 11°C and 20°C varies between populations. The Coleman population (southernmost) T_{opt} increases from 19.1 to 20.6°C (Δ 1.5°C), while the Trask population (northernmost) T_{opt} increases from 16.7 to 19.6°C (Δ 2.9°C). These variations in acclimation capacity highlight that different populations may have different capacities to respond to environmental change, an important factor in optimizing conservation resources.

Critical thermal maximum (CTM) values also show a variation in acclimation capacity, however these differences do not reflect a latitudinal trade-off. The Trask hatchery population and the Coleman Hatchery population increased their CTM by 1.9°C and 2.1°C between fish reared at 11 and 20°C. The Elk River population, which geographically lies in between, exhibited an increase of 1.1°C across the same acclimation range. These results highlight that aerobic scope, CTM and growth rate do not inherently respond the same way to acclimation temperature. For instance, the Trask hatchery population demonstrated low growth rates (0.138 $g^1day^{-1} \pm 0.02$) when reared at 20°C, while the Coleman population grew optimally (0.308 $g^1day^{-1} \pm 0.02$) at 20°C, yet both treatment groups elicited a CTM of 30.0°C. Discontinuity among thermal performance traits mandates that research into the thermal performance of salmonids should focus on several metrics (e.g. aerobic scope, CTM, growth) as opposed to just one. Thermal capacity and performance are the manifestation of several physiological traits (e.g., stress response, metabolic capacity) as well as thermal history (i.e., acclimation temperature), therefore effectively quantifying it requires observing multiple metrics.

Question 3: Do fall- versus winter-run fish demonstrate differences in thermal performance?

Our third research question investigated whether thermal performance differed between the Livingston Stone (winter-run) and nearby Coleman (fall-run) populations. Winter-run salmon historically spawned at high elevation where river temperatures were colder than those inhabited by fall-run populations. Our results indicate pronounced differences in thermal performance between these populations. The growth rate of the Livingston Stone fish acclimated at 20°C was 0.09 ± 0.01 grams per day was the lowest of any treatment group. Oppositely, the Coleman fish grew at 0.308 ± 0.02 grams per day under the same conditions, which was the highest growth

rate of any population studied during this experiment. Differences in metabolic performance were consistent with the growth rate results. The T_{opt} of the Coleman population increased with acclimation temperature (20.6°C acclimated to 20°C), the highest of any treatment group, and the T_{opt} of the Livingston Stone population decreased across the same acclimation temperatures (18.0°C acclimated at 20°C). It should be noted that, in a recent population viability assessment by NOAA (Johnson and Lindley 2016), poor temperature and environmental conditions during the 2014 and 2015 drought years were considered a primary cause for poor development of embryos (5.9% in 2014). Our physiological data indicate that warming water temperature during droughts may be particularly detrimental to winter-run juveniles as well.

Comparison with Previous Research

The EPA previously funded a similar study, also with UC Davis (Poletto et al. 2017), on juvenile fall-run Chinook salmon from the Mokelumne hatchery, CA. Fish were acclimated to two temperatures (15 and 19°C) and tested at temperatures ranging from 12-25°C. A direct comparison of metabolic rate values from the Mokelumne population and the Coleman population demonstrates similar metabolic capacity (e.g. MMR of 5-15 mg O_2 $kg^{-1}min^{-1}$ among both populations). However, holistically the results of Poletto et al. (2017) and the present study reveal different patterns of temperature-dependent metabolic performance between populations. Poletto et al. (Mokelumne population) found that acclimation temperature had no significant effect on the AS or MMR. In contrast, our study (Coleman population) found that acclimation temperature did have a significant effect on the maximum metabolic rate ($df = 1$, $F = 11.79$, $p = 0.0008$) and the aerobic scope ($df = 1$, $F = 3.92$, $p = 0.05$) of the Coleman population. However, it should be noted that the Coleman population's metabolic capacity to acclimate was less than the other fall-run populations. It should also be noted that the difference in acclimation response between the two studies may be driven by our inclusion of 11°C as an acclimation temperature, which was not a treatment in Poletto et al. Also, Poletto et al. reported the unusual non-effect of swimming temperature on aerobic scope ($df = 14$, $F = 0.27$, $p = 0.99$). However, within the Coleman population, swimming temperature did have a significant effect on aerobic capacity ($df = 2$, $F = 20.59$, $p < 0.0001$). These differences highlight that even within the Central Valley there is potential for population variation in thermal performance and response to environmental temperature.

Regarding consistency with the OCLTT hypothesis, which predicts thermal limits based on oxygen transport capacity, results of the two studies are similar. Poletto et al. found a temperature-independent aerobic scope across the range of test temperatures (12-25°C). Over this temperature range, regardless of acclimation temperature, aerobic scope did not rise, plateau, or decrease as would be expected by the OCLTT hypothesis. These results suggest that the physiology of juvenile salmonids does not fit the OCLTT hypothesis; this is corroborated by the present study. While the juvenile salmon we tested did show declines in aerobic capacity as temperatures neared those associated with lethality (> 24°C), all treatment groups were capable of maintaining aerobic scope above 80% of maximum at 24°C (Table 5), implying that oxygen-limitation or metabolic collapse may not be a principal factor contributing to the lethality of warm-temperatures. When interpreting the results of this study and the impressive performance at high temperatures, it should be remembered that fish were reared under laboratory conditions free of ecological stressors (e.g. predation, disease, toxins or competition for food, etc.).

Therefore, the reported performance and subsequent thermal tolerance should be considered optimized; wild fish, contending with ecological stressors, likely exhibit a reduced capacity to tolerate high temperatures (> 22°C).

Conclusions

The results of this study reveal interpopulation variation in multiple traits and acclimation capacity among several populations of hatchery reared Chinook salmon. This can be seen among the three sampled fall-run populations, as well as between the Sacramento River fall- and winter-run salmon. Understanding these differences in thermal performance will help inform management decisions in protecting salmon populations. Differences between Sacramento river fall-run juveniles from Coleman Hatchery and the winter-run juveniles from the Livingston Stone hatchery highlight that even populations that share a watershed can exhibit considerable differences in thermal physiology. For example, acclimating Coleman fish at 20°C yielded the highest growth rate of any population in the present study; however, acclimating the winter-run population under the same conditions yielded the lowest growth rate. Furthermore, the variation between the Mokelumne and Coleman fall-run hatchery strains is unexpected given the amount of genetic homogenization found among Central Valley fall-run Chinook salmon (Williamson and May 2005). The observed physiological variation without underlying genetic variation between Mokelumne hatchery and Coleman hatchery fall-run juveniles poses questions regarding the role of epigenetics and maternal effects (Shama et al. 2014) upon the thermal physiology of Chinook salmon. For example, different thermal conditions experienced by returning adults of different populations may influence the physiology of their progeny and thereby produce interpopulation variation without underlying genetic variation. Maternal or epigenetic effects on the thermal physiology of salmonids is a knowledge gap in salmonid research.

It is important to note that the data derived in this study were based on fish reared under optimal conditions (e.g., satiation rations, clean water, no predators) and at stable temperatures. It is likely that environmental factors in the wild would modify the absolute values of these performance metrics and potentially the trends observed. It is possible that ecological conditions (predators, disease, hydrological dynamics, etc.) may alter the thermal performance of wild fish. It is unknown whether the influence of these ecological dynamics may serve to homogenize, or amplify, the observed interpopulation variation. Understanding the effects of environmental stressors (e.g., reduced feed or disease) on metrics such as aerobic scope would further our understanding of how at-risk populations in the wild (winter-run) will respond to future climate warming. Determining the role of ecological and environmental factors in modifying thermal performance of wild juvenile salmon would greatly improve our ability to predict and manage populations exhibiting different thermal physiologies.

This study exclusively used hatchery produced fish. Future work in this field should focus on understanding any differences that exist between hatchery and wild reared juveniles as domestication effects have been observed in salmonids after as little as two hatchery generations (Araki et al. 2007, 2008). Future work could investigate additional populations, specifically Sacramento spring-run and late fall-run populations, to explore the full breadth of Chinook salmon found in the Central Valley.

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