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Variation in Thermal Physiology Among Chinook Salmon Populations

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Variation in Thermal Physiology Among Chinook Salmon Populations

By

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Abstract

Understanding the variations that exist between organisms, populations, and species can provide valuable insight into the evolutionary and environmental drivers relevant to organism fitness. Developing this understanding is critical in an era of rapid environmental change, where effective conservation and management efforts must predict the response of organisms to future, novel environmental conditions.

Pacific salmonids are widely considered at-risk from anthropogenic and climatic changes. Additionally, Pacific salmonids exhibit a semelparous anadromous life-history strategy which limits gene-flow and promotes the formation of distinct populations. My first chapter reviews the literature on the thermal physiology of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California, which are the southernmost native populations in the world. I found very little prior research studying interpopulation in thermal physiology among Chinook salmon, despite a vast literature demonstrating the capacity for interaction between thermal physiology and a salmonid's local environment. I propose a place-based management paradigm which combines both and organisms fundamental and ecological thermal physiology.

My second and third chapters employed a common-garden experimental design and several physiological metrics to assess the thermal physiology and acclimation capacity of eight hatchery populations of Chinook salmon from the west coast of North America. All eight populations were reared at the same suite of acclimation temperatures (11, 16 and 20°C) and assessed using five physiological metrics, (growth rate, critical thermal maximum, routine and maximum metabolic rate and aerobic scope).

The second chapter aimed to determine whether the thermal physiology and acclimation capacity of three seasonal runs of Chinook salmon in the Sacramento River watershed (CA)

differed. I identified quantifiable population differences in CTM, growth, and metabolism among the studied populations and found compelling evidence that the critically endangered Sacramento River winter-run exhibits growth and metabolic capacities indicative of mal-adaptive physiological plasticity to warm temperatures.

The final chapter studied six populations of fall-run Chinook salmon and assessed statistical associations between the five physiological traits and 15 environmental predictors to test hypotheses of local adaptation and countergradient variation. My results support local adaptation, wherein populations from warmer habitats exhibit higher critical thermal maxima and faster growth when acclimated to warm temperatures. Among metabolic traits I also found positive associations between migration distance and metabolic capability, indicating that populations with longer migrations may have higher metabolic capacity.

Collectively, my research demonstrates that populations of Chinook salmon differ in their thermal physiology and that these differences can be associated with aspects of their environment consistent with hypotheses of local adaptation. With this understanding, one-size-fits-all management frameworks are poised to underserve unique or unusual populations. Instead, place-based population-specific strategies would best serve at-risk populations like the Sacramento River winter-run Chinook salmon.

Introduction

Variation is a fundamental aspect of biology; Genes vary, individual organisms vary, species vary. This variation is the grist for the mill of natural selection. Therefore, understanding the variations that exist between organisms, populations and species can provide valuable insight into the evolutionary and environmental drivers relevant to organism fitness. Developing this understanding is critical in an era of rapid environmental change, wherein effective conservation and management efforts must predict the response of organisms to novel environmental conditions such as temperature.

Environmental temperature has profound influence over the physiology, ecology, and behavior of ectothermic organisms (Angilletta *et al.*, 2002; Huey & Stevenson, 1979). In response to a warming environment individual organisms can respond to changes in the thermal landscape through behavioral thermoregulation and physiological acclimatization (Crozier & Hutchings, 2014). Extended exposure to warming may induce individual responses that increase fitness (Sandblom *et al.*, 2016; Stillman, 2003) and, given variation and time, species may evolve to tolerate novel thermal conditions (Chen *et al.*, 2015; Hoffmann & Weeks, 2007). Identifying species-specific responses to changes in the thermal landscape and the temporal scale upon which they act, can allow prediction of species' responses to climate change (Jeffree & Jeffree, 1996; Schulte *et al.*, 2011; Scott & Poynter, 1991). However, individual populations may possess unique traits that do not suit species-wide assumptions, challenging conservation actions.

Pacific salmonids (*Oncorhynchus* spp.) are a commercially and culturally important clade of climate-vulnerable fish which require a population-specific approach for effective conservation. The specificity at which anadromous adults migrate to their natal streams reduces

gene flow among populations (Quinn, 2018), allowing for the evolution of population-specific traits that maximize fitness to unique spawning, rearing, and migratory environments. Genetic analysis of steelhead trout (*O. mykiss*) found habitat characteristics such as migration distance, as well as slope and aspects of river temperature, to be associated with genetic markers of population differentiation (Micheletti et al. 2018). Work on Fraser River adult sockeye salmon (*O. nerka*) revealed that intraspecific variation in cardiac and metabolic physiology was associated with river temperatures and migration route difficulty (Eliason *et al.*, 2011). Complementary work on embryos and juveniles from the same Fraser River populations identified signals of local adaptation in thermal tolerance and cardiac capacity (Chen *et al.*, 2013). Finally, work on two populations of redband trout (*O. mykiss gairdneri*) identified adaptive, population-specific traits in temperature-dependent cardiac performance and respiration (Chen *et al.*, 2018; Garvin *et al.*, 2015). Interpopulation variation in thermal physiology across salmonids may produce population-specific responses to environmental change, challenging broadly applied management frameworks.

Modern anthropogenic actions have exposed populations to a variety of environmental challenges leading to population declines and extirpations (Moyle *et al.*, 2017; Waples *et al.*, 2008). Drivers of species decline include habitat degradation, overexploitation, and flow modification (Dudgeon *et al.*, 2006; Reid *et al.*, 2019). For instance, construction of hydropower dams reduces and homogenizes spawning and rearing habitat (McClure *et al.*, 2008), depriving returning adult migrants access to cold-headwaters and constraining rearing juveniles to low-elevation, channelized habitat. Reduction of water flow through agricultural diversion or climatic drought exacerbates temperature stress (Chang & Bonnette, 2016) and can lead to population reduction or extirpation (Yoshiyama *et al.*, 2001). Pacific salmonids are the focus of immense

conservation efforts attempting to protect diverse populations in the face of rapid environmental change and intense human-use. Management of salmonids is often focused on water temperature, seeking to ensure waters remain cool to facilitate migration and reduce mortality. For example, in the Pacific Northwest, management adopts a one-size-fits-all approach, prescribing specific temperature threshold criteria for multiple salmonid populations or species (U.S. Environmental Protection Agency, 2003). The *EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards* specifies thermal thresholds for different salmonid life-stages (egg incubation, juveniles, returning adults, etc.). However, these criteria were developed by synthesizing data from multiple, often geographically disparate populations and species. By design this one-size-fits-all framework does not account for differences in thermal physiology *between* populations (Gayeski *et al.,* 2018). Recent evidence suggests that individual populations often differ in thermal physiology due to local and regional environmental variation (Chen *et al.*, 2013; Eliason *et al.*, 2011; Fangue *et al.*, 2006; Stitt *et al.*, 2014). This is particularly relevant for management of salmonids populations on the southern-edge of their species range which may be confronting the limits of their thermal capacity.

Chinook salmon (*O. tshawytscha*) are the largest of the Pacific salmonids and span a large latitudinal range from high-latitude Northern rivers to the San Joaquin River in California's Central Valley. Throughout this range, Chinook salmon are commonly delineated into evolutionary significant units (ESUs), grouped by shared genetics, regional associations and life-history strategies (Waples, 1995). The greatest concentration of at-risk salmonids is in California where 23 of 31 (74%) of native salmonid ESUs are likely to be extinct within the next century (Moyle *et al.*, 2017), including all four of populations of Central Valley Chinook salmon. Furthermore, in the Pacific Northwest, an estimated 40% (159 of 396) of historical Chinook

salmon populations have been lost since Euro-American contact (Gustafson *et al.*, 2007). Protecting the remaining populations and their intrinsic diversity is essential to building Chinook salmon resistance against environmental change.

In California, Chinook salmon exhibit four runs or migratory life-history strategies, named for the season of adult return to freshwater (fall-, late fall-, spring- and winter-run). Historically, these runs allowed Chinook salmon to maximize use of the accessible riparian habitat, which differed considerably in their thermal regimes. For instance, adult winter-run Chinook salmon would return in the winter months when California's Mediterranean climate delivered increased levels of precipitation, allowing adults to reach higher and further rivers that were impassible during the dry summer months. These fish would then spawn in early summer, their thermally sensitive embryos protected by the perpetually cold, spring-fed rivers of the Southern Cascades. Later arriving fall-run populations would be unable to reach the same habitats and spawn in the warmer, low elevation rivers of the California Central Valley. The rearing embryos would be sustained by cool autumnal waters and typically outmigrate before the subsequent summer.

Historical run-habitat associations have been disrupted due to anthropogenic modification of the Central Valley (CA) hydrologic system (Thompson *et al.*, 2012; Waples *et al.*, 2008), leading to differential impacts across populations. The construction of the Central Valley rim dams catastrophically reduced habitat access for the early-migrating runs. It is estimated that spring-run Chinook have lost over 80% of their historical spawning habitat, and that winter-run populations have suffered a complete loss of habitat and are reliant upon conservation actions at the Livingston-Stone National Fish hatchery (Quiñones *et al.*, 2015; Yoshiyama *et al.*, 2001). This loss of habitat has placed these early-migrating populations in a thermal mismatch. Without

access to high elevations, returning adults and rearing embryos are forced to spawn or develop at low elevations in the Central Valley where water temperatures can exceed 20°C during the hottest summer months. Inability of current management frameworks to protect against summer thermal extremes led to the near-extinction of the Sacramento winter-run in 2014 and 2015 (Durand *et al.*, 2020). Global climate change is expected to exacerbate the thermal-threat for salmonids (Diffenbaugh *et al.*, 2015; Moyle *et al.*, 2017; Null *et al.*, 2013). Preservation of the remaining salmonid population in California and throughout the western United States requires population-specific understanding their fundamental and ecological thermal physiology.

My dissertation investigates interpopulation variation in thermal physiology among several populations of Chinook salmon in California and across the Pacific Northwest. I find evidence for population-specific thermal performance which is consistent with hypotheses of local adaptation in thermal physiology among Chinook salmon populations. These results indicate that more precise, population-specific management tools tailored to the physiology and ecology of individual populations may be necessary to preserve Chinook salmon into a warming future.

Chapter 1 is a review of the literature on the thermal performance of Central Valley Chinook salmon runs. I identify sizeable knowledge gaps in our understanding of Chinook salmon thermal performance and posit a framework for interpreting interpopulation variation in thermal performance as the interplay between an organisms fundamental and ecological thermal physiologies. Additionally, I offer a roadmap to develop population-specific management criteria.

Chapter 2 investigates the interpopulation differences in thermal physiology which exist among three seasonal runs of Sacramento River Basin Chinook salmon. I compared five metrics

of thermal performance and tested the hypothesis that local adaptation among life-history strategies would yield distinct thermal physiology among populations. My results demonstrate that the critically endangered winter-run Chinook salmon exhibits a thermal physiology suited to cold-water.

Chapter 3 explores population differences in thermal physiology among six populations of fall-run Chinook salmon and tests hypotheses of local adaptation and countergradient variation in regards to 15 local environmental parameters. I hypothesized that Chinook salmon populations may be locally adapted environmental characteristics (migratory challenge, maximum river temperature, latitude etc.). My results were consistent with a hypothesis of local adaptation. For instance, longer migrations were associated with greater aerobic capacity and warmer river temperatures were associated with higher critical thermal maxima. I did not find strong support for latitudinal effects over the range of studied populations, with populations response more closely linked to local environmental parameters.

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Chapter 1

One size does not fit all: variation in thermal eco-physiology among Pacific salmonids

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Abstract

Pacific salmonids, cold-water fishes native to the northern hemisphere, span a massive geographic range (~33° latitude) and are exposed to a wide variety of environmental conditions regionally and temporally. California is home to the greatest concentration of at-risk anadromous salmonids and warming river temperatures pose both current and future threats to numerous populations. Thermal standards for management of California populations are currently based on guidelines for multiple salmonid species and from populations across the Pacific Coast. However, a growing body of literature suggests that salmonid populations exhibit population-specific thermal requirements. Furthermore, in California, salmonid populations regularly encounter temperatures that exceed current thermal standards based upon performance of outside populations. This review focuses on Chinook salmon (*Oncorhynchus tshawytscha*), providing evidence for interpopulation variation in thermal performance across life stages, and explores the drivers of variation. To describe the formation of interpopulation variation, we define *fundamental* and *ecological* thermal physiologies. Fundamental thermal physiology is the composite of intrinsic physiological traits and abiotic factors that define a species' thermal window. Ecological and environmental interactions constrain this fundamental thermal physiology, yielding an ecological thermal physiology. Thermal physiology, viewed through this lens, provides researchers and managers avenues for salmonid research and conservation at the population scale. A more nuanced approach to west-coast salmonid conservation will be required to protect the most at-risk and vulnerable populations. Successful salmonid management must incorporate population-specific traits and present and future watershed conditions.

Introduction

Pacific salmonids (*Oncorhynchus* spp.) are native to northern latitudes and are broadly considered cold-water species. Increasing water temperatures are among a host of factors that have led to declining regional populations (Crossin et al. 2008; Moyle et al. 2017). Salmonids are strongly influenced by temperature via intrinsic physiology (e.g., metabolism) and extrinsic ecological interactions (e.g., predation, competition). Predicted increases in global temperature will undoubtedly alter these dynamics, leading to challenges in species management and conservation under a rapidly changing environment. Incorporating physiological thermal performance criteria into species management, especially in aquatic ecosystems, is widespread (U.S. Fish and Wildlife Service 1990, 1995, 2002a, b, c, 2015; U.S. Environmental Protection Agency 2003; National Marine Fisheries Service 2014). For instance, in the Pacific Northwest, the *EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards* (Region 10 Guidance) specifies thermal thresholds for different salmonid life-stages (egg incubation, juveniles, returning adults, etc.). Current management guidelines were developed by synthesizing data from multiple, often geographically disparate populations and species; by design this one-size-fits-all framework does not account for differences in thermal physiology *between* populations (U.S. Environmental Protection Agency 2003; U.S. Fish and Wildlife Service 2015; Gayeski et al. 2018). Recent evidence suggests that individual populations often differ in thermal physiology due to local and regional environmental variation (Fangue et al. 2006; Eliason et al. 2011; Chen et al. 2013; Stitt et al. 2014). This is particularly relevant for management of southern-edge populations, (e.g., California and Oregon populations) which are confronting the limits of their thermal capacity.

The greatest concentration of at-risk Pacific salmonid populations is in California. Moyle et al. (2017) identified 21 anadromous salmonid evolutionary significant units (ESU) in California, of which 14 are federally listed, and 11 are expected to be extinct within 50 years if present trends continue. Interactions between climate (e.g., increasing water temperature, drought severity, reduced snowpack) and anthropogenic effects (e.g., invasive species, pollutants, fisheries, hatcheries) have been identified as key factors driving many of these populations to the brink of extinction (Moyle et al. 2013, 2017; Katz et al. 2013). Air temperatures in California are expected to increase between 1.7 °C and 5.8 °C over the next century, causing increases in stream temperatures of 1.4 °C to 4.6 °C (Cayan et al. 2008; Null et al. 2013). River warming will be exacerbated during periods of low flow (Chang and Bonnette 2016), which are anticipated to increase in frequency and duration due to climate change impacts on snowmelt (Hamlet et al. 2005) and droughts (Diffenbaugh et al. 2015). Across California's diverse landscape, these threats manifest themselves in different combinations and intensities posing a challenge to salmonid conservation and resource management. California is the southernmost range extent for six anadromous salmonid species including endangered endemic populations of Chinook salmon (*O. tshawytscha*) and steelhead trout (*O. mykiss*). Additionally, these populations are facing increasing urbanization and habitat modification leading to population declines. Broadly, conserving populations on the receding range edge is challenged by unusual and diverse phenotypes, not necessarily represented by the species as a whole (Hampe and Petit 2005). Ultimately, population-specific thermal guidelines may offer populations in California, and more broadly those across the Pacific Northwest, resiliency in a rapidly shifting climate.

Preserving salmonid populations has long been a stated goal of state and federal fisheries management agencies. However, existing temperature standards may be poorly suited for conserving salmonids in an era of climate change. The current, Region 10 Guidance provides thermal management criteria derived from thermal performance studies of more northern salmonid populations (U.S. Environmental Protection Agency 2003). However, ample evidence exists indicating that thermal performance among salmonid populations varies both interspecifically (Cech and Myrick 1999; Myrick and Cech 2001; Richter and Kolmes 2005; Verhille et al. 2016) and intraspecifically (Sauter et al. 2001; Stitt et al. 2014). For example, physiological performance traits of adult (Eliason et al. 2011) and alevin (Chen et al. 2013) sockeye salmon (*O. nerka*) from the Fraser River in British Columbia, demonstrated interpopulation variation among locally-relevant traits (e.g., migration difficulty, water temperature), supporting hypotheses of local adaptation to natal watersheds and migratory routes. Across their geographic range, anadromous Pacific salmonids may encounter annual temperature extremes ranging from 0 °C to 18 °C in large, boreal rivers (Yang et al. 2014) and 7 °C to 25 °C in the Sacramento River (CA) watershed (Lowney 2000; Wagner et al. 2011) with variability occurring both temporally and spatially across habitats. Understanding the drivers of local thermal adaptation among salmonids and developing a mechanistic framework to predict population response to warming temperatures offers a solution to conserving salmonids in response to climate change.

We summarize the literature relevant to describing intraspecific variation of salmonid thermal performance and discuss these data in the context of design and application of temperature management criteria. More specifically, we synthesize research focused on the thermal performance, and variation therein, of Chinook salmon. Chinook salmon were chosen

because they are relatively well-studied, wide-ranging, and include several at-risk populations currently confronting thermal stress, specifically in California (Yoshiyama et al. 2001, Moyle et al. 2017). This review then expands to explore the sources and drivers of intraspecific variation within Pacific salmonids. These drivers are organized by their influence on fundamental or ecological thermal physiology. We define *fundamental thermal physiology* as the collection of intrinsic physiological traits that delineate a species' thermal capacity (Fry 1947; Pörtner and Farrell 2008). A species' *ecological thermal physiology* is defined by the circumscription of the fundamental thermal physiology by environmental forces (Brett 1971) (Figure 1.1). We argue that understanding the diversity of fundamental and ecological thermal physiologies and how they produce population-specific thermal performance is essential to developing management strategies for protecting Chinook salmon in California and salmonids more broadly. Finally, we also propose conservation strategies and research priorities that are fundamental to the conservation of salmonids in California and throughout the Pacific Northwest.

Chinook Salmon: Life Stages, Development, and Thermal Limits

Myrick and Cech (2001, 2004) reviewed the literature for California Central Valley anadromous salmonids and presented knowledge gaps in our understanding of how temperature influences these species, seasonal runs, and populations. Subsequent reviews reported differences in thermal capacity among anadromous salmonid species, but did not highlight the capacity for intraspecific variation (e.g., Carter 2005; Richter and Kolmes 2005), nor the potential mechanisms contributing to such variation. Research since Myrick and Cech (2001, 2004) has exposed intraspecific variation in thermal performance within several salmonid species (e.g., Eliason et al. 2011, Chen et al. 2013, Stitt et al. 2014). Below, we review the literature on Chinook salmon regarding intraspecific variation in thermal performance across life

stages. Chinook salmon exhibit several conserved life-history phenologies described as seasonal runs within which may exist one (e.g., winter-run), a few (e.g., spring-run), or many (e.g., fall-run) distinct populations. Literature on Chinook salmon is vast but controlled comparisons between populations are limited. Therefore, to facilitate comparisons across studies, this review focuses on available physiological trait datasets (e.g., growth rate, acute thermal tolerance) that are commonly quantified across populations using similar experimental conditions (e.g., ad libitum rations, stable temperatures).

Embryos and Alevins

Chinook salmon embryos are laid in gravel redds where eggs incubate until hatching as alevin or yolk-sac fry. Myrick and Cech (2001) reviewed multiple studies and determined that Central Valley Chinook salmon embryos successfully developed at temperatures ranging from 1.7 °C to 16.7 °C, with mortality increasing dramatically toward thermal extremes. The upper thermal limits for prolonged embryo rearing of Central Valley fall-run Chinook salmon embryos are between 13.3 °C - 13.9 °C for California winter-run Chinook salmon (USFWS 1999; Myrick and Cech 2001). Heming (1982) found that a fall-run Chinook salmon population from British Columbia had declining egg survivorship when reared at 12.0 °C. However, Jensen and Groot (1991) found that temperatures below 14.0 °C did not increase mortality of embryos from the Big Qualicum River (Canada). Upper thermal tolerance in Chinook salmon embryos among populations is relatively conserved, ranging from 12 °C - 14 °C. However, populations do appear to vary in their ontological response to temperature. Steel et al. (2012) reared Yakima River (WA) Chinook salmon eggs from eight families under eight variable thermal regimes designed to capture different absolute temperatures and amounts of thermal variability. They found that both thermal regime and family were significant factors in the ontogeny and phenology of Chinook

salmon. Their work highlights two valuable results. First, that the commonly used management metric of 'degree days' to predict salmon development is insufficient under a changing landscape, and second, that variation in thermal physiological response was influenced by genetic traits.

Geist et al. (2006) found that a population of Snake River Chinook salmon alevins from Washington survived rearing temperatures between 13.0 °C and 16.5 °C equally well, with survival declining precipitously at 17.0 °C. The authors suggest that this impressive tolerance may represent local adaption to historically warm river temperatures. Research by Garling and Masterson (1985) on Chinook salmon alevins from the Great Lakes (USA) showed reduced survival (74% vs. 98%) when alevins were reared at warmer temperatures (15.1 °C vs 11.4 °C). Fuhrman et al. (2018) compared emergence phenology and development among four hatchery populations of spring-run Chinook salmon across four thermal regimes. They observed significant variability in emergence traits (e.g., emergence date, size-at-emergence, etc.) that was population-specific, likely reflecting local adaptations with important fitness consequences. Overall, research on embryonic and larval stages indicates that critical temperature thresholds are somewhat conserved across populations. However, interpopulation variation in ontogeny and phenology does appear to be temperature-dependent, reflecting local adaptation. These sub-lethal effects may have important consequences for how a population's fundamental thermal physiology interacts with local environmental factors.

Juveniles

Once alevin absorb their yolk-sac and begin exogenous feeding they are considered juveniles. To compare populations of juvenile Chinook salmon we selected growth as a holistic physiological metric which integrates many physiological processes and stressors (Arendt 1997).

Growth rate is temperature-dependent and widely assessed using agreed methodology, furthermore it is relevant to assessing ecological fitness and wildlife management. There have been several laboratory-based growth studies using juveniles from California Central Valley fall-run Chinook salmon populations. Optimal growth for juveniles from the Nimbus Hatchery (CA), fed at satiation rations under laboratory conditions, occurred at 19 °C (Cech and Myrick 1999) and growth was optimized between 17-20 ºC for juveniles from the Coleman National Fish Hatchery (CA) (Marine and Cech 2004). This range of temperatures is broadly consistent with temperatures reported by Brett et al. (1982), who found that Chinook salmon juveniles from the Big Qualicum River (BC) hatchery and wild juveniles from the Nechako River (BC) grew optimally at 20.5 and 18.9 °C, respectively. More recently, Zillig et al. (2020) examined the thermal physiology of several populations of laboratory acclimated Chinook salmon from throughout the Pacific Northwest, revealing different responses to acclimation temperatures (11 °C, 16 °C or 20 °C) among populations. Growth rates among all populations were similar (~.15g/day) when fish were reared at 11 °C. Conversely, when different populations were reared at 20 °C, growth rates varied broadly between populations (e.g., Coleman hatchery fall-run population (CA), ~.3g/day; Trask hatchery fall-run population, OR; ~.15g/day). However, the capacity for laboratory conditions to influence thermal physiological performance cannot be ignored. Rich (1987) reared Nimbus Hatchery (CA) fall-run Chinook salmon using diverted river water and found that growth rates declined when fish were reared at temperatures exceeding 15.3 °C, a decrease of 3.7 °C as reported by Cech and Myrick (1999). This apparent discrepancy in growth rate could be attributed to the effects of disease or to differences in water chemistry between laboratory and field experiments (Myrick and Cech 2001) and highlights the importance of accounting for ecological factors when identifying management temperature targets.

Optimizing growth rate is a common target for management and conservation and the studies summarized above indicate that populations of Chinook from across the West Coast may exhibit different temperature-dependent growth relationships. Understanding the drivers of these differences and managing for this variation is important in protecting at-risk populations.

There is a general lack of research comparing smoltification (i.e., the process of transitioning to saltwater and the transition from juvenile to sub-adult) physiology among Chinook salmon populations. However, it is well documented that this process is partially temperature sensitive (Folmar and Dickhoff 1980; Marine and Cech 2004). Sauter et al. (2001) compared the thermal preference of two seasonal Chinook salmon runs, spring- and fall-run, from Washington and found a significant change in thermal preference between runs during smoltification. Fall-run smolts shifted their thermal preference (from 17.7 °C to 11.2 °C) as they achieved maximal saltwater tolerance. Conversely, spring-run Chinook salmon smolts preferred 16.6 °C, with no observed change in thermal preference associated with smoltification. The authors interpreted differences between spring- and fall-run Chinook salmon to reflect differences in naturally occurring environmental conditions experienced by Chinook salmon during smoltification. Understanding how temperature influences smoltification phenology, and whether different populations or life-history strategies exhibit different temperature-dependent smoltification phenology is an important knowledge gap for future research.

Adults

Thermal physiology studies on adult Chinook salmon are relatively limited, especially when comparing populations. However, the temperature at which adult salmon are impeded during migration can serve as a coarse, comparable indicator of adult thermal performance. After examining several Chinook salmon populations from the Pacific Northwest, McCullough (1999)

concluded that adults sought thermal refuge and migration ceased when water temperature reached 21 °C. Similarly, fall- and spring-run populations from the Columbia River (WA) limited upstream migration when temperatures reached 20 °C (Goniea et al. 2006; Mann and Snow 2018). Keefer et al. (2018) individually tagged, spring-, summer- and fall-run Chinook salmon migrating through the Columbia and Snake Rivers (WA). Migrating summer- and fall-run salmon experienced temperatures near upper thermal limits (20-22 °C) and would briefly (hours to days) halt migration and use thermal refuges when available. In California, Klamath River spring-run Chinook salmon halted migration when temperatures surpassed 23 °C (Strange 2012) and Hallock et al. (1970) reported that water temperature exceeding 19 °C inhibited migration of Chinook salmon in the San Joaquin River; however, in 2004, adults were observed migrating upstream in the San Joaquin River at temperatures exceeding 21 °C (Williams 2006). Attributing migration phenology to interpopulation variation is difficult because delays in migratory behavior may reflect intrinsic thermal physiological traits, ocean and river environmental factors (Keefer et al. 2008), state-dependent energetic limitations (Plumb 2018), or a combination of these variables. Therefore, understanding both the fundamental and ecological thermal physiology of returning adult Chinook salmon should help managers disentangle the drivers of adult migration behavior.

Extensive research on adult sockeye salmon from the Fraser River (BC), has documented thermal intraspecific variation between populations relevant to their migratory performance (Eliason et al. 2011; Anttila et al. 2019). This work, discussed in greater detail below, demonstrates local adaptation of nine populations to population-specific migration routes and spawning reaches. Given that Chinook salmon and sockeye salmon are congeners, share similar

life history traits, and are sympatric throughout much of their ranges, the ability of adult Chinook salmon to show locally adapted thermal performance traits is not surprising.

Summary

Considering the traits reviewed here, Chinook salmon do exhibit interpopulation variation in thermal physiology. This variation appears greatest during the juvenile lifestage, with embryos and adults demonstrating less plasticity. However, this may be a result of study bias because juvenile salmon are easier to study in both the lab and field than ocean dwelling adults. Similarly, juveniles exhibit more measurable and comparable traits than developing embryos. There remain large knowledge gaps in the thermal physiology of spring-run Chinook salmon and late fall-run Chinook salmon. While current management guidance criteria (Table 1.1) are broadly protective, they may not protect unique at-risk populations (e.g., Sacramento River Winter-run Chinook salmon [CA]), or account for ecological differences (e.g., predators) between populations. Management goals should seek population specific thermal criteria, built upon an understanding of both a population's fundamental thermal physiology and its ecological thermal physiology.

Fundamental Thermal Physiology

An organism's thermal physiology is dictated by the interaction of environmental conditions, behavioral responses, and intrinsic physiological traits (Hochachka and Somero 2002). A large body of research has developed over the past two decades identifying sources of variation among fundamental thermal traits of salmonids. Some of the causes of variation are associated with genotypic differences between populations or species (Nichols et al. 2016; Chen et al. 2018b), while others are a result of phenotypic plasticity applied across diverse and dynamic environmental conditions (Narum et al. 2018). Below, we review the mechanisms by

which variation in fundamental thermal physiology among populations is produced and maintained. We show that management actions can be tailored by understanding and incorporating these mechanisms to predict population-specific thermal performance under future conditions.

Acclimation and Adaptation

The strategies by which organisms adjust to fluctuations in their thermal environment fall into two broad categories: 1) acclimation or physiological change over days to weeks, and 2) adaptation or genetic change across generations (Hochachka and Somero 1968; Hazel and Prosser 1974; Schulte et al. 2011; Schulte 2015). Management frameworks, however, often recommend static thermal thresholds to manage river temperatures (U.S. Environmental Protection Agency 2003). Ultimately, salmon thermal performance is dynamic, enabling responses to environmental conditions on short time-scales via acclimation and across generations via adaptation. The juxtaposition of static management strategies against biological dynamism may introduce and obscure pitfalls to effective management and conservation. Therefore, considering the role of acclimation and adaptation in interpreting thermal performance is fundamental in determining management strategies.

It is well documented that salmonids acclimate to local water temperatures. Acclimation to warmer water temperature has been shown to increase acute upper thermal tolerance in *O. mykiss* (Myrick & Cech 2000b, Myrick & Cech 2005), sockeye salmon (Chen et al. 2013) and Chinook salmon (Brett 1952, Zillig et al. 2020). Furthermore, comparisons among Chinook salmon from Northern California, the Oregon coast and Columbia River Basin demonstrated differences in acclimation capacity among populations (Zillig et al. 2020). Across these populations, Zillig et al. (2020) assessed acute thermal tolerance and growth rate of fish reared at

three temperatures (11 °C, 16 °C and 20 °C). Acute thermal tolerance increased with acclimation temperature among all populations, but to differing extents, highlighting variation among populations in their acclimation capacity. Furthermore, growth rates also changed with acclimation temperature. Fall-run populations from California exhibited the greatest growth rate when reared at 20 °C, while the sympatric and critically endangered Sacramento River winter-run population grew at the slowest rate when acclimated to the same temperature. Differing capacity to acclimate to environmental change will alter how salmonids cope with changes across the thermal landscape. Populations with a limited thermal tolerance and reduced acclimation capacity will likely have the greatest difficulty adjusting to novel thermal environments under climate change and are therefore at the greatest risk of population decline and extinction.

Adaptation (i.e., changes in the fundamental thermal physiology) through mutation, genetic drift, and natural selection tunes organismal traits to increase biological fitness in response to environmental conditions (Narum et al. 2013). While operating across generations, adaptation can be important on management timescales and a critical part of effective conservation (Ashley et al. 2003). Muñoz et al. (2015) demonstrated that physiological adaptation to warmer temperatures was possible in Chinook salmon, provided adequate genetic variation existed. Given that the quantity of genetic diversity may vary between populations, it may be assumed that adaptation capacity varies intraspecifically as well. Therefore, defining acclimation and adaptation capacity is important to predicting population-specific responses to environmental change.

Watershed Variation

Interpopulation variation is generated through a combination of environmental heterogeneity and salmonid life-history strategies that reduce gene flow (Hilborn et al. 2003). Pacific salmonids, and specifically Chinook salmon, span a broad latitudinal range, across which streams vary widely in environmental characteristics and habitat types. Life history plasticity enables salmon to adapt to most accessible river systems, while spawning site fidelity and adult homing behavior reduce regional gene-flow and permit genetic drift between geographically proximate populations (Taylor 1991; Dittman and Quinn 1995; Hilborn et al. 2003). Therefore, local watershed characteristics can strongly influence the thermal physiology of populations.

Eliason et al. (2011) demonstrated that multiple physiological traits (e.g., heart mass, aerobic scope, heart rate) correlated strongly with environmental conditions of migratory routes and spawning locations in Fraser River (BC) sockeye salmon. Researchers captured returning adults, genotyped them to identify different source populations, and collected data on a suite of physiological traits. They found that populations that migrated further and traversed challenging river features exhibited increased heart mass. Additionally, individuals belonging to populations native to warmer habitats exhibited improved aerobic scope and cardiac performance at warm temperatures when compared with populations associated with historically cooler thermal regimes. In an extension of this work, Chen et al. (2013) found that Fraser River sockeye salmon embryos and alevins exhibited population variation and local adaptation in upper thermal tolerance. Within the Central Valley of California, Tuolumne River steelhead trout juveniles exhibited `warm-adapted` phenotypes (Verhille et al. 2016) and Mokelumne River Chinook salmon juveniles revealed unusual temperature-independent metabolic performance (Poletto et al. 2017). The authors of both studies suggest that these results are evidence of local adaptation to elevated temperature regimes at the southern range boundary. Evidence of salmonid

adaptation to local environmental conditions has also been observed in brook trout (Stitt et al. 2014), red band trout (Chen et al. 2018a, b), sockeye salmon (Anttila et al. 2019) and rainbow trout (Chen et al. 2015).

The capacity for anadromous salmonids to adapt to local watershed conditions is fundamental to advocating for population-specific management (Gayeski et al. 2018). Watersheds exhibit variation across numerous environmental gradients that influence the experienced temperatures of salmonids. For instance, Lisi et al. (2013) demonstrated that environmental characteristics such as watershed steepness, size, and the presence of lakes, accounted for variability in spawn timing of Alaska sockeye salmon, primarily through moderation of river temperature. Others have shown that water source (Nichols et al. 2014), discharge volume (Eliason et al. 2011; Anttila et al. 2019), riparian habitat (Moore et al. 2005), dissolved nutrients (Selbie et al. 2009; Ranalli and Macalady 2010), and turbidity (Thomas 1975) can co-vary with temperature and differentially between and within watersheds. Micheletti et al. (2018) explored relationships between environmental variables of migration routes and adaptive genetic variation among Columbia River steelhead. They found migration distance, migration slope, water temperature and precipitation correlated with changes in allelic frequencies among populations, further indicating that populations will genetically respond to local environmental conditions. Similarly, Spence and Dick (2014) modeled the role of photoperiod, temperature, flow and lunar phase in predicting coho salmon (*O. kisutch*) smolt out-migration across four geographically distant populations. Their results indicated that different combinations of environmental variables are capable of predicting the outmigration of different coho salmon populations. Environmental factors, even regional or watershed-specific, represent useful predictors in determining the fundamental thermal physiology of local salmonid populations.

Metrics such as water temperature, flow regime, and migration distance are easily quantifiable and should be incorporated into conservation management actions (Figure 1.2). Defining these population-specific watershed characteristics is useful when interpreting potential differences in fundamental thermal physiology (Figure 1.1) between populations.

Ecological Thermal Physiology

Variation in fundamental physiology is a result of acclimation and adaptation applied to spatially and temporally heterogeneous environments, leading to differences in thermal physiology between populations. A population's fundamental thermal physiology is then modified by secondary interactions to produce an *ecological thermal physiology* which further constrains, and potentially diversifies, a population's thermal performance (Figure 1.1). Here, we review some of the ecological factors that influence ecological thermal physiology.

Bioenergetics: Growth, Metabolism and Asynchrony

Environmental temperature bounds the growth and survival of ectothermic organisms like most fishes, but some species have shown a capacity to compensate for increases in water temperature when food resources are abundant. Bioenergetic theory stipulates that ectotherm growth is a function of energy consumed versus energy expended or lost (Railsback and Rose 1999). Energy loss is generally dictated by metabolic activity which increases positively with temperature. As temperature increases, so do metabolic outputs such as egestion, excretion, and costs associated with digestion (Railsback and Rose 1999). Under such circumstances in the wild, salmonids must either seek out thermal refuges to reduce energy expenditure or compensate with increased food consumption (Lusardi et al. 2020). Otherwise, an energy deficit will occur, leading to reduced growth rates with potential consequences for fitness (see Beakes et al. 2010).

Most stream ecosystems are naturally oligotrophic (Allan and Castillo 2007), suggesting that behavioral thermoregulation and movement to thermal refuges is an effective strategy to deal with rising stream temperature (see Welsh et al. 2001). However, in productive ecosystems (e.g., spring-fed rivers, tailwaters below dams, floodplains, coastal lagoons) salmonids may be able to compensate for increases in stream temperature with increases in food consumption. The phenomenon has been shown to occur in numerous laboratory studies where salmonids are fed to satiation and exposed to warming temperatures. For instance, Foott et al. (2014) found that California juvenile coho salmon reared at 16.3 °C and 21.3 °C (mean temperatures) exhibited similar growth rates when fed to satiation. Empirical evidence for growth compensation in natural ecosystems has been less frequently observed. However, Bisson et al. (1988) found exceptionally high rates of juvenile coho salmon production in a Washington stream exhibiting daytime temperatures up to 29.5 °C and speculated that high food abundance was a causative mechanism supporting observed high rates of production. In a field experiment, Lusardi et al. (2020) reared juvenile coho salmon across a longitudinal gradient of temperature and food availability in a California spring-fed stream. The found food to be the proximate factor affecting juvenile coho salmon growth. Specifically, they found that juvenile coho salmon growth rates peaked at a maximum weekly maximum temperature of 21.1 °C and were 6-fold greater than fish reared at a maximum weekly maximum temperature of 16 ºC.

Modeling work has also supported the bioenergetic relationship between temperature and food availability in salmonids. Railsback and Rose (1999) found that food consumption was the primary determinant of *O. mykiss* growth during summer (as opposed to temperature) and Weber et al. (2014) used reach-specific food web data and bioenergetic models to accurately predict *O. mykiss* growth rates in several streams in the John Day River basin (OR). Work by McCarthy et

al. (2009) on wild populations of steelhead in Trinity River tributaries found that high water temperatures and reduced feeding rate influenced growth, sometimes causing weight loss. Their models indicated that reduced growth may occur at temperatures as low as 15 °C and that increased food availability or quality would expand the window of viable temperatures. Their conclusions were extrapolated to indicate that under future warming conditions steelhead populations in food-limited systems will decline. Dodrill et al. (2016) modeled a similar response in rainbow trout, concluding that warmer temperatures resulted in reduced growth, unless accompanied by increases in prey availability and prey size. These studies suggest that river productivity, and subsequent prey availability, will strongly influence a population's ability to survive under warming water temperatures. Food availability and productivity vary both across the landscape and through time; quantifying these environmental characteristics offers powerful predictors for understanding how the fundamental thermal physiology of salmonid populations may be energetically constrained into a population specific ecological thermal physiology (Figure 1.1).

Annual changes in water temperature, habitat, and flow regime also alter the phenology, abundance and community composition of aquatic macroinvertebrate communities (Boulton et al. 1992; Bonada et al. 2007; Lusardi et al. 2016; Lusardi et al. 2018; Peterson et al. 2017) and phenological shifts in food availability have been shown to have population-level effects on predator species such as salmonids (Møller et al. 2008; Thackery et al. 2010). In extreme cases, termed 'phenological mismatch', shifts in the timing of species interactions can lead to population declines (Møller et al. 2008). Phenological mismatch is of greatest concern for species which are specialist predators or rely upon historically reliable but ephemeral food resources (Visser et al. 1998; Green 2010; Kudo and Ida 2013). Recent work by Campbell et al.

(2019) explored temperature-dependent phenological traits among different populations of coho salmon from several southern Alaska rivers exhibiting diverse thermal profiles. All populations were physiologically tuned to local thermal conditions and exhibited synchrony in embryo hatching and development despite differences in temperature between rivers. Synchrony across such varied and population-specific thermal landscapes may unveil compensatory local adaptation to match resource timing (Campbell et al. 2019), but disturbance of historical temperature profiles may disrupt such synchrony. In summary, bioenergetic research highlights that even if fundamental salmonid thermal physiology among populations is conserved, differences between populations in food availability and quality could produce differences in population-specific ecological thermal physiology.

Biotic Interactions

Temperature also plays an important role in influencing biotic interactions (e.g., predation, competition, disease) of salmonids (Coutant 1973; Ward and Morton-Starner 2015). Biotic interactions can moderate a salmonid's fundamental thermal physiology to produce observed thermal performance (Brett 1971). Different populations of salmonids confront different suites of biotic interactions and therefore, may exhibit different ecological thermal physiologies in response to different thermal regimes. These indirect, ecological drivers of salmonid thermal performance should be considered when evaluating thermal management guidelines of at-risk populations.

Competition

Competition may be amplified by the effects of warming water temperature and negatively affect salmonids (Bear et al. 2007; Myrvold and Kennedy 2017, 2018). Loss of cold-water habitats will increase fish density and competition for space in remaining cold-water

refuges. As water temperature increases, salmonids experience increased metabolic demand (Fryer and Pilcher 1974), leading to enhanced demand for prey resources. Taken together, without corresponding increases in prey availability, habitat carrying capacity will decline. Reese and Harvey (2002) tested competitive dynamics between Sacramento pikeminnow (*Ptychocheilus grandis*) on the growth and behavior of juvenile steelhead from the Eel River (CA) in artificial streams. Elevated temperatures (20 °C - 23 °C) coupled with competition by pikeminnow reduced juvenile steelhead growth by 50% (Reese and Harvey 2002). This growth reduction was not observed when fish were reared at lower water temperatures (15 °C - 18 °C) or without competitors, indicating a synergistic effect of temperature and competition stress. Similarly, Reeves et al. (1987) found that when redside shiner (*Richardsonius balteatus*) and steelhead trout were reared together at warm temperatures (19 °C - 22 °C), growth rate of steelhead declined by 54%. However, at cooler temperatures (12 °C - 15 °C) steelhead suffered no loss in production, instead redside shiner grew at reduced rates. Wenger et al. (2011) modeled the impact of future climate scenarios on four species of western trout and found that increases in temperature enhanced competitive interactions and reduced habitat carrying capacity. Differences in competitor assemblage, and therefore ecological thermal physiology (Figure 1.1), between watersheds may lead to differential outcomes for salmonid populations managed under a shared thermal management paradigm.

Predation

Predation is considered to be a primary cause of juvenile salmonid mortality both directly and indirectly (Nehlsen et al. 1991; Lindley and Mohr 2003; Sabal et al. 2016; Erhardt et al. 2018). As ectotherms, the susceptibility of juvenile salmonids to predation is sensitive to environmental temperature. In the California Central Valley, Marine and Cech (2004) examined

the influence of temperature on predation risk; they reared juvenile Chinook salmon from the Sacramento River at three temperature regimes (13–16 °C, 17–20 °C, and 21–24 °C) and exposed them to striped bass (*Morone saxatilis).* The authors found that fish reared at 21-24 °C were preferentially consumed. Petersen and Kitchell (2001) modeled the bioenergetics of three predators of juvenile salmonids (northern pikeminnow, *Ptychocheilus oregonensis*, smallmouth bass, *Micropterus dolomieu,* and walleye, *Stizostedion vitreum*) in the Columbia River (WA), and found that predation by all three increased during climatic warm periods. This is consistent with laboratory studies by Vigg and Burley (1991) who found that the rate of prey consumption of northern pikeminnow was temperature dependent and increased exponentially across a temperature gradient (8 °C to 21.5 °C). Temperature can also augment sub-lethal effects of predation. Kuehne et al. (2012) conducted semi-natural stream experiments observing changes in direct mortality, behavior and physiological traits of salmon exposed to predation by smallmouth bass at 15 °C and 20 °C. There were no observed differences in direct predation, although salmon occupying warmer water exhibited reduced growth relative to control treatments without smallmouth bass. Sub-lethal effects of temperature on predation risk for salmonids is poorly studied and warrants further research as such effects may represent a considerable portion of thermally influenced biotic interactions.

Predator assemblages (i.e., warm-water vs. cold-water predators) and predation risks also vary among watersheds with implications for salmonid fundamental thermal physiologies (Figure 1.1). Permutations of predator assemblage and thermal physiology may produce different predatory outcomes among salmonid populations experiencing the same temperature. For instance, the California Central Valley predator assemblage is highly invaded by non-native species (e.g., striped bass, black bass [*Micropterus spp.*], sunfish [*Lepomis spp.*]) which may

present different, temperature-dependent, trophic pressures when compared to native or cold-water predator assemblages found elsewhere (e.g., pikeminnows [*Ptychocheilus spp.*], bull trout [*Salvelinus confluentus*], northern pike [*Esox lucius*]). Understanding the role of temperature in structuring trophic relationships and developing a mechanistic framework for ecological thermal physiology could improve temperature management guidelines that address the influences of temperature on salmonid predators.

Embracing Population Variation

Across the Pacific Coast, several factors have contributed to the loss of genetic and environmental variability among salmonid populations. Homogenization, both genetic and environmental, suggests that application of current, non-population-specific, thermal management frameworks may have some validity. However, the effects of homogenization on population-specific thermal performance is unknown. Furthermore, the erosion of the intrinsic diversity of salmonids is essential to population resilience via the portfolio effect (Hilborn et al. 2003; Schindler et al. 2010; Greene et al. 2010; Carlson and Satterthwaite 2011). The portfolio effect typically refers to life-history diversity but can be extended to diversity among physiological traits or even management actions (Sturrock et al. 2020). Contained within different life-history phenotypes are interpopulation differences in fundamental thermal physiology (Satterthwaite et al. 2017). A diverse portfolio of fundamental thermal physiological traits within and between populations can increase species resiliency to thermal stress and maintain variation for adaptive change. As populations become homogenized, selection pressures are reduced and locally adapted thermal traits may be lost. Furthermore, as genetic variation declines, the overall capacity of a population to physiologically adapt or acclimate to future environmental conditions becomes impaired (Carlson and Seamons 2008; McClure et al. 2008).

Ongoing homogenization of genetic diversity and habitat heterogeneity erodes the portfolio effect and reduces population resilience to change (Moore et al. 2010; Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015; Dedrick and Baskett 2018).

Hatchery supplementation of wild salmonid stocks is an observed cause of widespread genetic homogenization in salmonids (Williamson and May 2005). Hatchery production of juvenile salmon has been shown to rapidly reduce the fitness of domesticated strains as well as hybrids in the wild (Araki et al. 2007, Araki et al. 2008) through amplification of hatchery-selected traits and outbreeding depression as these mal-adapted traits become incorporated into wild populations (Hindar et al. 1991; Araki et al. 2008, Lusardi et al. 2015). Williamson and May (2005) documented genetic homogenization among five hatchery populations and eight wild populations of Chinook salmon in California's Central Valley and concluded that gene flow between wild and hatchery populations is due to the long history of hatchery production and out-of-basin release of juveniles. Similar research conducted on wild and hatchery populations of Chinook salmon elsewhere in the Pacific Northwest indicates that hatchery introgression and subsequent genetic homogenization is present but less widespread (Moore et al. 2010; Smith and Engle 2011; Matala et al. 2012, Van Doornik et al. 2013). Jasper et al. (2013) and McConnell et al. (2018) studied hatchery straying among wild and hatchery Alaskan chum salmon (*O. keta*) populations. Despite straying, populations maintained genetic and trait differences, revealing both local adaptation and local resistance to introgression among wild populations. Unfortunately, salmon populations in California have been strongly influenced by hatchery propagation for over a half-century (Sturrock et al. 2019) which may explain differences in homogenization observed between California populations and more northern populations. Despite improved understanding of the effect of hatchery fish on wild fish and the erosion of

native genome, few studies have examined the direct consequences of this on thermal performance or distinctiveness between populations.

Land use and management may also erode environmental heterogeneity, reducing the environmental selection pressures that historically produced both genotypic and phenotypic diversity. Dams have altered ecological processes, river flow and thermal regimes, and eliminated access to historical habitat, homogenizing the evolutionary experience of Chinook salmon and other anadromous fishes (e.g., Zarri et al. 2019). Numerous salmonid stocks in California can no longer access historical ranges (Lindley et al. 2006, Yoshiyama et al. 2011, Moyle et al. 2017), especially high elevation, cold-water habitats. (McClure et al. 2008). The loss of habitat diversity may increase homogenization of life-history strategies crucial to the portfolio effect. Finally, habitat loss reduces landscape carrying capacity and imposes greater sympatry amongst populations and seasonal runs, increasing risks of genetic introgression (Waples 1991; McClure et al. 2008).

Applying a uniform suite of temperature thresholds across populations, some of which are homogenized and others diverse, poses the same issues of mismatch caused by applying general thermal guidance to multiple unique populations. Successful management of salmon in a rapidly changing environment must embrace a portfolio of genetic and phenotypic diversity (Moore et al. 2010; Carlson and Satterthwaite 2011; Anderson et al. 2015; Moyle et al. 2017; Dedrick and Baskett 2018). Ultimately, maintaining remaining diversity (environmental or genetic) is fundamental to a population's adaptive capacity and resilience to global change. Population-specific temperature guidelines of salmonids could protect remaining diversity in thermal performance traits that offer resilience against future global change.

Rethinking Thermal Management

To combat the effects of warming river temperatures associated with anthropogenic and environmental change, management agencies have established thermal criteria intended to constrain river warming and protect salmonid populations throughout the Pacific Northwest. These temperature criteria allow for rapid determination of thermal risks to fish and can trigger release of cold-water reserves from reservoirs. The largest of these management frameworks is the Region 10 Guidance (U.S. Environmental Protection Agency 2003) implemented throughout the Pacific Northwest and considered for application to California. The Region 10 document was heavily researched, combining thermal performance data (e.g., mortality and growth) across populations and species designed to provide temperature guidance thresholds for the conservation of native salmonid populations and provides temperature thresholds to protect salmonids (Table 1.1). The Region 10 temperature guidelines appear to be broadly protective of California salmon. However, these thresholds do not account for interpopulation variation or the observable diversity in thermal physiology and ecological parameters known to influence population thermal performance. Furthermore, these criteria use a rolling seven-day average of daily maximums (7DADM) as a metric for river temperature. While intuitive and easily calculated, the 7DADM metric captures neither the absolute maximum nor the duration of exposure, crucial aspects to a fish's thermal experience. Successful salmonid conservation requires protecting inherent thermal diversity among populations. While broad management regulations (e.g., Region 10 Guidelines) may serve as a starting point or backstop, conserving diversity requires population-specific management strategies. Population-specific thermal regulations may be considered overly burdensome to common regulatory frameworks; however, managing at the population level amplifies diversity and leverages the portfolio effect to protect species regionally. Managing to conserve diverse thermal physiologies will increase the

resilience of populations and their ability to withstand stochastic events and adapt to environmental change.

Accounting for Thermal Eco-Physiology in Salmonids

California contains the southern range boundary for several native migratory salmonid species, including endemic and critically endangered populations (Moyle et al. 2017). In the future, these populations will confront increasingly severe and frequent drought conditions (Diffenbaugh et al. 2015). For instance, the recent prolonged and severe California drought (2012 – 2016) led to the collapse of Sacramento River winter-run Chinook salmon population. This population is reliant upon cold-water releases from Shasta Dam in the Sacramento River (ICF International et al. 2016). Despite having population-specific thermal criteria (13.3 °C 7DADM for rearing embryos, [USFWS 1999]) the extended drought conditions exhausted the cold-water pool in Shasta Reservoir and water temperatures exceeded 15.5 °C, leading to extremely low embryo and larval survival (Moyle et al. 2017, Durand et al. 2020). Continued persistence of this population is aided by a conservation hatchery and reintroductions into Battle Creek in Northern California (ICF International et al. 2016).

As addressed above, salmonid populations vary in their ecological thermal physiology, dependent upon how their fundamental thermal physiology interacts with ecological factors. A population's specific combination of factors, such as prey-availability, acclimation capacity and life-history strategy, can aid management in defining critical thermal thresholds (e.g., upper physiological limits) to prevent mortality as well as optimal temperature targets (e.g., fastest growth, smoltification success, maximum juvenile recruitment). Quantifying population-specific, ecologically linked thermal criteria is necessary to manage at-risk salmonids under warming climatic conditions, where meeting rigid temperature thresholds in California's Mediterranean

climate and highly-modified hydroscape will become increasingly difficult. More broadly, this approach can be used to assess and identify vulnerable populations throughout the Pacific Northwest.

We pose a series of research questions to improve assessment of population-specific thermal vulnerability and to offer insights actionable for management.

1. Do the seasonal runs of Chinook salmon exhibit differences in thermal physiology and performance?
2. Do temperature tolerances or acclimation capacities differ between wild and hatchery salmonid populations?
3. How does temperature influence smoltification success; does the relationship vary between populations or seasonal runs?
4. How does energetic state (e.g., satiated vs. starved) influence a fish's thermal performance?
5. How does temperature influence salmonid prey and predator species and their effects on juvenile salmon populations?
6. How do interspecific and intraspecific competition influence thermal physiology?

Optimizing the thermal landscape requires data addressing both ecological and physiological traits of different populations. We outline a research framework to assess ecological factors pertinent to fish thermal performance and to develop population-specific datasets for California salmonids (Figure 1.2). We recommend two tiers of data collection. First, a comprehensive collection of a few, rapidly sampled environmental characteristics meant to identify populations with declining environmental or ecological conditions (e.g., lack of thermal refugia, poor water quality, limited rearing habitat). For instance, populations with limited thermal refugia may have

greater difficulty responding to environmental warming. Understanding these environmental characteristics would allow for identification of at-risk populations for which more thorough thermal assessments are warranted. Once at-risk populations are identified, a second tier of data collection should focus on important physiological and ecological parameters necessary to determine both fundamental and ecological thermal physiologies of different populations. Defining these physiologies will provide managers with metrics useful for establishing thermal thresholds (e.g., growth rates [Marine and Cech 2004; Lugert et al. 2016], critical thermal maximums [Becker and Genoway 1979], temperature dependent metabolism [Farrell et al. 2008; Clark et al. 2013]). Defining fundamental and ecological thermal physiology of at-risk populations will also help identify strategies for improving population robustness and resiliency (e.g., predator removal, reduced hatchery supplementation, genetic rescue).

We recommend prioritizing research on early migrating populations (e.g., Sacramento River winter-run, Columbia River and Klamath Basin spring-run populations) or populations that exhibit an over-summering component to their freshwater life history (e.g., coho salmon) because many are at risk of extinction within 50 years (Moyle et al. 2017). Indeed, many of these populations are already listed as federally threatened or endangered. Furthermore, Chinook populations arising from the San Joaquin River watershed and steelhead trout from southern California coastal streams warrant prioritization because they represent the southernmost populations of their species. Understanding the effect of hatchery supplementation and genetic homogenization on populations which support commercial fisheries will be important in predicting the response of these economically and culturally valuable resources.

Conclusion

Pacific salmonids are a collection of wide-spread and differing populations. Across their ranges, diverse environmental factors have produced variation in both their fundamental and ecological thermal physiologies. Understanding how variation in thermal physiology yields population-specific thermal performance of populations is crucial from a management perspective. For each population, thermal performance is challenged by rapidly changing environmental conditions. The inherent complexity of interactions between changing ecosystems and organismal thermal physiology challenges the application of broad thermal management criteria. Simple static temperature criteria can be improved by incorporating local data on salmonid fundamental physiology and on ecological conditions to produce population-specific thermal management strategies.

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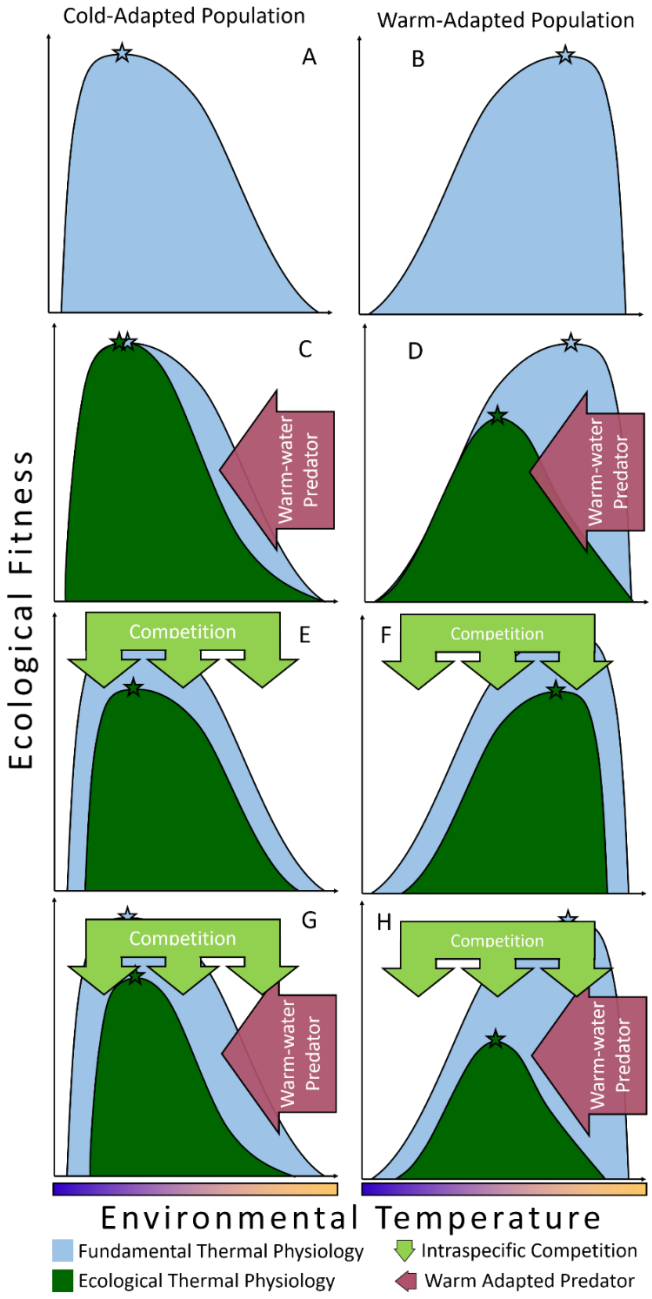

Figure 1.1: Conceptual diagram of fundamental and ecological thermal physiology. A fish's intrinsic physiological traits dictate the size and shape of the fundamental thermal capacity (blue). Ecological factors such as competition for food resources or predation by warm water predators constrain the fundamental thermal physiology to smaller ecological thermal physiology (green). Sub-figures A & B are hypothetical fundamental thermal physiologies for cold-adapted or warm-adapted populations respectively. Star icons indicate the optimal temperature for ecological fitness of a given fundamental or ecological physiology. Tracking of the thermal optimum reveals how populations with the same fundamental thermal physiology (e.g., B, D, F, H) can have variable ecological thermal physiology dependent on ecological factors. Likewise, populations encountering the same ecological factors (e.g., C vs. D or G vs. H) will elicit different ecological thermal physiology, dependent upon their underlying fundamental thermal physiology.

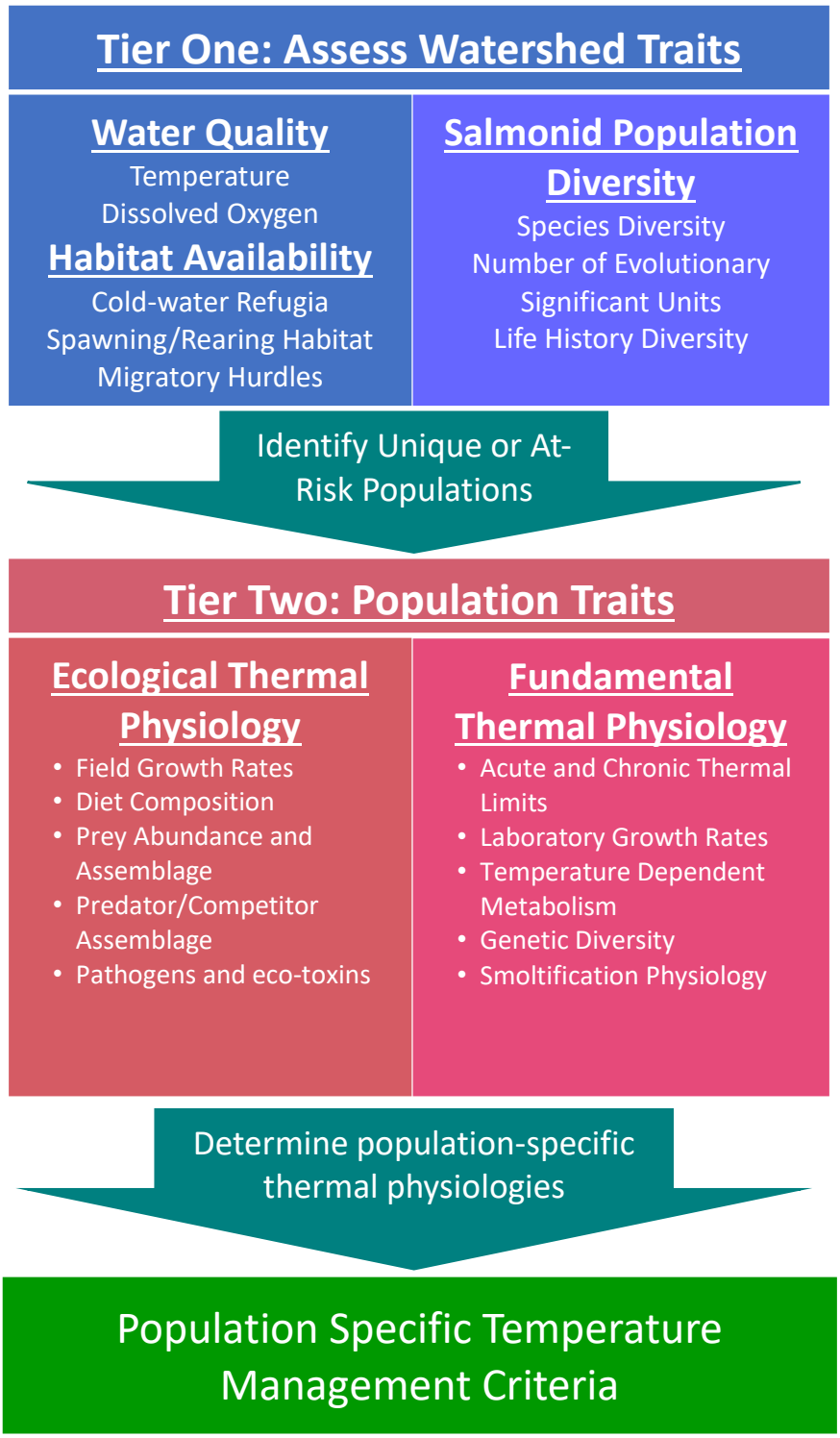

Figure 1.2: Determining Population Specific Temperature Criteria. First tier of experiments to assess and triage at-risk populations. Once threatened populations are prioritized, research focuses on quantifying population thermal performance traits and environmental risk-factors (e.g., low food abundance, lack of thermal refugia). Population-specific temperature criteria are produced that reflect the fundamental and ecological thermal physiology of the selected population and specific management goals (e.g., recruitment, growth, smoltification).

Table 1.1: EPA Region 10 Guidance Criteria for Salmon and Trout. Modified from U.S. Environmental Protection Agency (2003). 1) "7DADM" refers to the 7-day average of the daily maximums; 2) "Salmon" refers to Chinook, coho, sockeye, pink and chum salmon; 3) "Trout" refers to steelhead and coastal cutthroat trout

Salmonid Uses During the Summer Maximum Conditions	**Criteria**
Bull Trout Juvenile Rearing	12 °C (55°F) 7DADM
Salmon/Trout "Core" Juvenile Rearing (Salmon adult holding prior to spawning, and adult and sub-adult bull trout foraging and migration may also be included in this use category)	16 °C (61 °F) 7DADM
Salmon/Trout Migration plus Non-Core Juvenile Rearing	18 °C (64 °F) 7DADM
Salmon/Trout Migration	16 °C (61 °F) 7DADM
Salmonid Uses	**Criteria**
Bull Trout Spawning	9 °C (48 °F) 7DADM
Salmon/Trout Spawning, Egg Incubation, and Fry Emergence	13 °C (55 °F) 7DADM
Steelhead Smoltification	14 °C (57 °F) 7DADM

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Chapter 2

Variation in thermal physiology among seasonal runs of Chinook salmon

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Abstract

Successful conservation of species facing rapid environmental change will require an understanding of interpopulation variation and its role in both offering resiliency and challenging existing conservation frameworks. Interpopulation variation is widely observed within the Salmonidae family of teleost fishes with a variety of life-history strategies expressed both within and between populations. Chinook salmon (*Oncorhynchus tshawytscha*), particularly populations in California near their southernmost range extent, are at risk from climatic and anthropogenic changes, with some populations on the brink of extinction. We aimed to determine whether the thermal physiology and acclimation capacity of three seasonal runs of Chinook salmon in the Sacramento River watershed (CA) differed, and assess whether differences among populations reflect locally-adapted traits. Fish were reared at three temperatures (11, 16 and 20°C) and physiological trials included growth rate, critical thermal maxima (CTMax) (i.e. acute upper thermal limit) and aerobic scope (i.e. the difference between maximum and minimum metabolic rates). We identified quantifiable population differences in CTM, growth, and metabolism among the studied populations and found compelling evidence that the critically endangered Sacramento River winter-run exhibits growth and metabolic capacities indicative of mal-adaptive physiological plasticity to warm temperatures. The results of this work not only demonstrate the breadth of variation in Chinook salmon thermal physiology that exists within California and across seasonal run phenotypes, but also provides actionable physiological metrics to inform conservation plans currently being proposed to protect winter- and spring-run Chinook salmon within the Central Valley.

Introduction

Increased attention is being paid to the role interpopulation variation plays in the successful conservation and management of at-risk species (Gayeski *et al.,* 2018; Waples & Lindley, 2018; Zillig *et al.*, 2021). Unique genetic and/or phenotypic traits may offer populations increased resilience or risk when confronting environmental challenges. Identifying populations uniquely at-risk or resilient to environmental change will enable resource managers to cater to a population's specific needs (Gayeski *et al.*, 2018), facilitate evolutionary rescue (Aitken & Whitlock, 2013; Carlson *et al.*, 2014) and foresee environmental risk-factors before they pose a threat to the larger meta-population or species. Rarely are individual populations targets for management. Instead conservation and management actions often focus on entire species, sub-species or evolutionary significant units (ESUs) wherein multiple similar populations are grouped based on genetics or shared regional associations (Waples, 1995). Collective management of distinct populations may ignore unique habitat requirements or life-history strategies, and fail to provide adequate protection against environmental change (Gayeski *et al.*, 2018; Zillig *et al.*, 2021). There is a developing body of literature on the prevalence of interpopulation variation, much of it focused on salmonid fishes (i.e. Chen *et al.*, 2013; Eliason *et al.*, 2011; Gamperl *et al.*, 2002; McDermid *et al.*, 2013; Stitt *et al.*, 2014), which as a group inhabit a wide variety of environments and exhibit life-history strategies that promote interpopulation variation. Furthermore, many populations if not entire ESUs of salmonids are facing extirpation and extinction (Gustafson *et al.*, 2007; Moyle *et al.*, 2017).

Anadromous Pacific salmonids refers to eight species of the *Oncorhynchus* genus that are historically native to the northern Pacific Ocean and widespread in both freshwater and marine systems due to an anadromous life-history strategy. Populations exhibit local genetic and

phenotypic adaptations to environmental characteristics suited to their unique spawning, rearing, and migratory environments (e.g. Chen *et al.*, 2013; Eliason *et al.*, 2011). Modern anthropogenic actions have exposed many populations to a variety of environmental challenges leading to population declines and extirpation (Moyle *et al.*, 2017; Waples *et al.*, 2008). Furthermore, Pacific salmonids are a common target of recreational anglers while simultaneously supporting large international commercial marine fisheries in the Pacific Ocean. Therefore, Pacific salmonids are the focus of immense conservation efforts attempting to protect diverse populations in the face of rapid environmental change and intense human-use. These conservation efforts range from conservation hatchery programs, reintroduction efforts (USFWS, 2018), migration assistance (Lusardi & Moyle, 2017), and managed reservoir releases to control temperature and river flow (Johnson & Lindley, 2016).

Threats to Pacific salmonids are diverse and often interact with environmental temperature (Crossin *et al.*, 2008; Moyle *et al.*, 2017; Zillig *et al.*, 2021). Broadly considered cold-water fish, global climate change and local anthropogenic stressors can degrade the thermal water quality of salmonid habitats. For instance, construction of hydropower dams reduce and homogenize spawning and rearing habitat (McClure *et al.*, 2008), depriving returning adult migrants access to cold-headwaters and constraining rearing juveniles to low-elevation, channelized habitat. Reduction of water flow either through agricultural diversion or climatic drought exacerbates temperature stress (Chang & Bonnette, 2016) and can lead to population reduction or extirpation (Yoshiyama *et al.*, 2001). Therefore, management of salmonids is often focused on water temperature, seeking to ensure waters remain cool to facilitate migration and reduce mortality. In the United States, management adopts a one-size-fits-all approach prescribing specific temperature threshold criteria for multiple salmonid populations or species

(U.S. Environmental Protection Agency, 2003). This strategy has been critiqued recently (Gayeski *et al.*, 2018; Zillig *et al.*, 2021) for failing to protect interpopulation variation crucial to salmon resiliency (i.e. the portfolio effect, see Carlson & Satterthwaite, 2011; Hilborn *et al.*, 2003) and suppressing place-based conservation actions to address both physiological and ecological manifestations of thermal threat.

The greatest concentration of at-risk Pacific salmonid populations is in California, USA. Moyle et al. (2017) identified 21 anadromous salmonid ESUs in California, of which 14 are federally listed, and 11 are expected to be extinct within 50 years if present trends continue. Interactions between climate (e.g., increasing water temperature, drought severity, reduced snowpack) and anthropogenic effects (e.g., invasive species, pollutants, fisheries, hatcheries, habitat degradation) have been identified as key factors driving many of these populations to the brink of extinction (Moyle et al. 2013, 2017; Katz et al. 2013).

The most prominent salmonid in California is the Chinook salmon (*O. tshawytscha)*, which is delineated into six ESUs. Three of these ESU's are native to the Sacramento river and are defined based upon the season of adult freshwater entry: winter-, spring- or fall- and late fall-run. These different seasonal runs enable Chinook salmon utilization of the Sacramento watershed throughout the year. The winter- and spring-run populations exhibit early migration, with winter-run adults entering freshwater from December to March and spring-run migrating from February to April. Winter- and spring-run adults enter freshwater sexually immature and mature en route or at the spawning grounds. Fall- and late fall-run Chinook salmon adults enter freshwater in August through December and are sexually mature upon entering freshwater. The early migratory strategy, exhibited by winter- and spring-run Chinook salmon, historically allowed returning adults access to the highest, coldest reaches of the Central Valley rivers.

Winter-run adults would migrate to the cold spring-fed systems of the Upper Sacramento, Pit, and McCloud Rivers, as well as Battle Creek in Northern California (Yoshiyama *et al.*, 2001). Spring-run adults would migrate into the Sierra Nevada and Southern Cascade mountains where snowmelt or cold-water springs would supply high-elevation reaches with cold-water throughout the summer months (Yoshiyama *et al.*, 2001). Cold water is essential for the successful spawning of adult Chinook salmon and incubation of embryos, and early migration to high-elevation habitat enabled winter- and spring-run populations to spawn earlier (March – July; July – September, respectively) and reduce competition with the late-arriving fall- and late-fall populations.

Anthropogenic modification to the Central Valley hydrologic system via water impoundment and diversion has impacted the ecology of Chinook salmon through alteration of historical temperature and flow regimes as well as habitat loss (Thompson *et al.*, 2012; Waples *et al.*, 2008). The construction of the Central Valley rim dams catastrophically reduced habitat access for the early-migrating seasonal runs. It is estimated that spring-run Chinook have lost over 80% of their historical spawning habitat and winter-run populations have suffered a complete loss of habitat and are now maintained through the Livingston-Stone National Fish hatchery at the base of Shasta Dam (Quiñones *et al.*, 2015; Yoshiyama *et al.*, 2001). The loss of this habitat has placed these early-migrating populations in a thermal mismatch. Without access to high elevations, returning adults and rearing embryos are forced to spawn or develop at low elevations in the Central Valley where water temperatures can exceed 20°C during the hottest summer months.

Our work sought to determine whether the different runs of Chinook salmon which share the Sacramento River, but differ in seasonal migratory phenotypes, demonstrate interpopulation

variation in thermal physiological traits consistent with their life-history strategy. We conducted a suite of physiological research upon two fall-run Chinook salmon populations; the Coleman National Fish Hatchery (Battle Creek, CA) fall-run population which shares a watershed with the reintroduced winter-run population; and the Feather River Hatchery fall-run population which is both sympatric and genetically introgressed with the Feather River spring-run population (Lindley *et al.*, 2004). These two fall-runs are dominant hatchery strains produced and transplanted throughout the Sacramento river watershed, leading to genetic homogenization (Williamson & May, 2005), but it is unknown to what extent they may remain physiologically distinct. Our final two populations were the critically endangered winter-run Chinook salmon, and the Feather River spring-run, which is the only hatchery produced spring-run strain in the California Central Valley.

Winter-run Chinook salmon are the most critically endangered representative of the species and exist as a single, hatchery-reliant population. Furthermore, the gene that permits early migration has evolved only once and would be lost forever should the remaining population disappear (Prince *et al.*, 2017). Currently, management actions are seeking to establish satellite populations of winter-run salmon via the JumpStart program, initiated in 2018, whereby progeny of captive-broodstock winter-run Chinook are released in Battle Creek (USFWS, 2018). In 2020, adult fish from the initial cohort were found to be returning to Battle Creek to spawn. Satellite populations may also be established via 'trap-and-haul', wherein adult fish are trapped in freshwater and transported beyond impassible dam infrastructure (Lusardi & Moyle, 2017). Spring-run Chinook salmon from the Feather River have likewise been reintroduced into the San Joaquin River to restart the extirpated San Joaquin River spring-run, historically the most numerous and southern-most population of Chinook salmon (Yoshiyama *et al.*, 2001).

Reintroduction efforts highlight the dire state of Chinook salmon conservation in California, and may be a harbinger of requisite management strategies in a warming future (ICF International *et al.*, 2016). Success of reintroduction plans (e.g. the JumpStart program, hatchery transplants, or trap and haul) require transplanted populations to possess phenotypes adaptive to their potential future habitats. Determination of population-specific thermal physiology is a first step in categorizing at-risk populations and pairing them to suitable habitats and effective management strategies.

We reared juvenile Chinook salmon from all four populations at three acclimation temperatures (11, 16 and 20°C) which span the range of temperatures experienced by Sacramento River Chinook salmon (FitzGerald *et al.*, 2020). We measured growth rates and conducted physiological trials upon Chinook salmon smolts (85-125mm fork length), the life stage where all populations would be migrating through the Central Valley and likely exposed to the breadth of acclimation temperatures. This life history stage is a period of thermal and energetic stress as fish migrate to and physiologically prepare for the ocean, requiring passage through the relatively warm San Francisco Bay-Delta (Baker *et al.*, 1995; Wagner *et al.*, 2011). We quantified acute thermal tolerance (critical thermal maxima; CTMax), temperature-dependent growth rate, and metabolic performance (routine, maximum and aerobic scope), to assess differences in trait performance and acclimation capacity between these twelve treatment groups (4 populations x 3 acclimation temperatures). CTMax is a widely applied and standardized physiological metric of acute thermal tolerance and acclimation capacity and has been used to assess interpopulation differences in fish (Fangue *et al.*, 2006) and specifically salmonids (Chen *et al.*, 2013, 2015). Growth rate is a common, temperature dependent, holistic physiological trait which is used commonly by resource managers to assess habitat suitability for

salmonids (Marine & Cech, 2004; Myrick & Cech, 2001). Growth rate has been demonstrated to vary between populations (Unwin, 1997) with observed fitness benefits (Beakes *et al.*, 2010). Therefore, identifying intraspecific variation in growth rate may expose ecological trade-offs in proposed conservation strategies.

Aerobic scope, the difference between an organism's minimum and maximum aerobic metabolic rates, quantifies the organism's energetic capacity. In ectotherms, aerobic scope is temperature dependent, and structuring the aerobic scope as a thermal performance curve provides insight into how organisms may respond to changes in the thermal environment (Schulte, 2015). The oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis extends aerobic scope measures to define an organism's upper and lower thermal boundaries (T_{crit}) as well as the temperature(s) of optimal capacity (T_{opt}) (Pörtner *et al.*, 2017). Aerobic scope, and the OCLTT hypothesis have been used to characterize population differences (Chen *et al.*, 2015) and identify potential local adaptation in salmonids (Eliason *et al.*, 2011; Poletto *et al.*, 2017; Verhille *et al.*, 2016). In the present study, we assess aerobic scope values of all four Chinook salmon populations, acclimated at three temperatures and tested across a broad, ecologically relevant thermal window (8 – 25°C), providing a comprehensive look at how aerobic scope varies between populations and acclimation groups as well as whether the OCLTT hypothesis may apply to young salmonids.

We hypothesized that Chinook salmon runs are locally adapted and would possess thermal tolerance, growth capacity and metabolic performance suited to their life-history strategies. We predicted that early-migrating populations (spring- and winter-run) would exhibit reduced thermal performance when acclimated to warmer temperatures, indicating maladaptive plasticity and potential local adaptation to historic cold temperature regimes. Reduced

performance may be exhibited through lower CTMax values, and reduced growth or aerobic capacity when acclimated to warm temperatures (20°C). We predicted that fall-run fish, which did not historically migrate to cold, high-elevation rivers, would have reduced physiological performance when acclimated to 11°C, and reduced aerobic capacity overall, reflecting their shorter, and less energetically challenging migrations.

Methods

Data Collection

This experiment was conducted from 2017- 2019 and sampled hatchery produced Chinook salmon from the Sacramento River winter-run, Coleman Hatchery fall-run, Feather River fall-run and Feather River spring-run populations (Figure 2.1). Fish were reared under a common-garden design with each of the four populations being reared to the same set of acclimation temperatures (11, 16, and 20°C), for a total of 12 treatment groups. These temperatures were chosen to be ecologically relevant to the conditions that a juvenile Chinook salmon may encounter during its rearing and outmigration through the Central Valley, CA (FitzGerald *et al.,* 2020). Information on acquisition and rearing of each population can be found in Table 2.1. This research was approved by the Institutional Animal Care Committee of UC Davis (Protocol # 19928), and use of endangered and threatened species was authorized via California Endangered Species Act memorandum of understanding (Fangue_SRWR_CHN_123118, Zillig_CVSR_CHN_123119) and 10(a)(1)(A) permit 17299-2M.

Fish Husbandry

Fish were acquired from their respective hatcheries from November through February and trucked to the Center for Aquatic Biology and Aquaculture at the University of California,

Davis in a 765-L tank. Once received, fish were held at 11-13°C until placed within their experimental treatment (population x acclimation temperature) tanks. Acclimation temperatures were achieved by increasing tank temperature by ~1.5°C per day. Once tanks achieved their specific acclimation temperature (11, 16, or 20°C), it was maintained for the duration of the experiments (4-9 months). Each combination of acclimation temperature and population was reared in two replicate 470 L cylindrical tanks. Fish were exposed to natural photoperiods and fed *ad libitum* rations which were updated biweekly to account for fish growth. Fish were held at their acclimation temperatures for three weeks prior to any experimental data collection. Temperatures were maintained for the duration of the experiment.

Critical Thermal Maximum

CTMax values were quantified according to established methods (Becker & Genoway, 1979). The CTMax bath is a 1m x 2m x 20cm fiberglass tray. Within this tray were placed six covered 4 L Pyrex beakers. Beakers were aerated with an airstone to ensure both adequate oxygen saturation as well as circulation of water within the beaker. The volume of water in each individual beaker was calibrated to ensure even heating across all CTMax beakers (approx. 2.5 L). Two pumps (PM700, Danner USA) were used to circulate water, one pump recirculated water across three heaters (Process Technology S4229/P11), while the other distributed heated water through the CTMax bath via a distribution manifold. Water temperature within each beaker warmed at 0.33°C per minute.

Fish of appropriate size (n = 253, 12.4 cm ± .76 SD) were selected from treatment tanks and transferred to separate tanks for fasting. To ensure fish were in a similar postprandial state, fish reared at 20°C and 16°C were fasted for 24 hours and 11°C fish were fasted for 48 hours to account for their slower metabolic rate. Once fasted, fish were individually netted and transferred

into individual beakers within the CTMax heat bath. Fish were given 30 minutes to acclimate to their CTMax beaker after which the CTMax trial was started.

During the CTMax trial, beaker temperature was taken every 5 minutes using a thermocouple (Omega HH81A). Thermocouple measurements were calibrated to a Fisherbrand® NIST certified mercury thermometer following each trial. Fish were observed continually for signs of distress and loss of equilibrium. The CTMax endpoint was loss of equilibrium (Beitinger *et al.*, 2000; Fangue *et al.*, 2006), when this point was reached, fish were removed and retuned to a recovery bath at their acclimation temperature and the temperature of the CTMax beaker was recorded. Fish that did not fully recover within 24-hours were not included in analysis (6% of individuals). After 24-hr recovery fish were weighed (wet mass ± 0.01g) and measured (fork length ± 0.1 cm). After measurement fish were returned to a second aerated bucket for recovery and return to their original rearing tank. Fish were netted and measured by the same experimenter across all sampling days.

Growth

Growth data were gathered every two weeks by measuring a sample of 30 fish from each treatment (n=15 per tank, n = 1528 total measurements). Fish were not individually marked and therefore growth rate was calculated across individuals. Fish were arbitrarily netted from their treatment tank and transferred to an aerated five-gallon bucket until measured, at which point they were air exposed for ~15-20 seconds to measure mass (± 0.1 grams, Ohaus B3000D) and fork length (± 0.1 cm). After measurement fish were returned to a second aerated bucket for recovery and return to their original rearing tank. Fish were netted and measured by the same experimenter across all sampling days.

Growth measurements were conducted biweekly until CTMax and metabolic experiments began. CTMax and metabolic experiments necessarily required size-selection and therefore biased any further collection of growth data. In order to standardize growth rate comparisons between populations acquired at different times and sizes, the analyzed data were bounded between a mean mass of 7.81 ± 0.83 g and 14.42 ± 1.95 g for each treatment. Time was defined as days since the first measurement point. Population specific growth criteria are contained in Table 2.2. Growth rate was calculated as absolute growth rate (*AGR*, Equation 2.1) using data derived from the growth rate model (Table 2.2).

Equation 2.1: $$AGR = \frac{M_t - M_i}{t}$$

Where M_t is mean treatment mass at the final timepoint, M_i is the initial mean treatment mass, and t is the duration of the measurement window in days.

Metabolic Experiments

Respirometry

Fish underwent metabolic trials in one of four, 5 L automated swim tunnel respirometers (Loligo, Denmark). The four tunnels were split into two paired systems with two tunnels sharing a single sump and heat pump. Water for each swim tunnel system was pumped (PM700, Danner USA) from the designated sump into an aerated water bath surrounding each swim tunnel which overflowed down a drain and returned to the sump. Sump water was supplied with non-chlorinated fresh water from a designated well and aerated with air stones. The temperature of the sump (and therefore the swim tunnels) was maintained by circulating water through a heat pump (model DSHP-7; Aqua Logic Delta Star, USA) and pumping it back to the sump using a high-volume water pump (Sweetwater SHE 1.7 Aquatic Ecosystems, USA). In addition, each sump contained an 800 W titanium heater (TH-800; Finnex, USA) connected to a thermostatic

controller. Water temperature within the swim tunnels was maintained to a precision of ±0.5°C. Swim tunnels and associated sump systems were cleaned and sanitized with bleach weekly to reduce potential for bacterial growth.

Dissolved oxygen saturation within the swim tunnels was measured using fiber-optic dipping probes (Loligo OX11250) which continuously recorded data via AutoResp™ software (version 2.3.0). Oxygen probes were calibrated weekly using a two-point, temperature-paired calibration method. Water velocity of the swim tunnels was quantified and calibrated using a flowmeter (Hontzcsh, Germany) and regulated using a variable frequency drive controller (models 4x and 12K; SEW Eurodrive, USA). The velocity (precision <1 cm s^{-1}) for each tunnel was controlled remotely using the Autoresp™ program and a DAQ-M data acquisition device (Loligo, Denmark). Swim tunnels were surrounded by shade cloth to reduce disturbance of the fish. Fish were remotely and individually monitored using infrared cameras (QSC1352W; Q-see, China) connected to a computer monitor and DVR recorder.

Oxygen consumption rates for both routine and maximal metabolisms were captured using intermittent respirometry (Brett, 1964). A flush pump (Eheim 1048A, Germany) for each tunnel pumped aerated fresh water through the swim chamber and was automatically controlled via the AutoResp™ software and DAQ-M system. This system would seal the tunnel and enable the measurement of oxygen consumption attributable to the fish. Oxygen saturation levels were not allowed to drop below 80% and restored within three minutes once the flush pump was activated. Oxygen saturation data from AutoResp™ was transformed to oxygen concentration using the following equation:

Equation 2.2: $$[O_2] = \frac{\%O_2Sat}{100} \times \alpha(O_2) \times BP$$

Where $\%O_2Sat$ is the oxygen saturation percentage reported from AutoResp™; αO_2 is the coefficient temperature-corrected oxygen solubility ($mgO_2\ L^{-1}\ mmHg^{-1}$); and *BP* is the barometric pressure (mmHg). Oxygen concentration (milligrams of oxygen per liter) was measured every second and regressed over time, and the coefficient of this relationship (milligrams of oxygen per liter per second) was then converted to metabolic rate (milligrams of oxygen per kilogram per minute, Equation 2.3).

Equation 2.3: $$MR = R \times V \times M^{-1} \times 60$$

Where *R* is the calculated coefficient of oxygen over time; *V* is the volume of the closed respirometer; *M* is the mass of the fish in kilograms and *'60'* transforms the rate from per second to per minute. An allometric scaling exponent was not incorporated due to similarity in fish sizes and to maximize comparability with the existing dataset on metabolism from the Mokelumne Hatchery (CA) fall-run population (Poletto *et al.*, 2017).

Routine Metabolic Rate

Prior to routine metabolic rate (RMR) trials fish were fasted to ensure a post-prandial state. Fish reared at 16 or 20°C were fasted for 24 hours, while fish acclimated to 11°C were fasted for 48 hours. Fish were then transferred into a swim tunnel respirometer between 13:00 and 17:00, and provided a 30-minute acclimation period at their acclimation temperature before the temperature was adjusted at 2°C h^{-1} to the swimming temperature (8 – 26°C). Automated intermittent flow respirometry began 30 minutes after the swimming temperature was achieved and continued overnight. Measurement periods ranged from 900 to 1800 seconds in duration, flush periods were 180-300 seconds. Periods varied in length in response to fish size and swimming temperature in order to ensure oxygen saturation was kept high (>80%) during the overnight trial. A small circulation pump (DC30A-1230, Shenzhen Zhongke, China) ensured that

water was mixed without disturbing the fish. Fish activity was monitored by overhead infra-red cameras and measurement periods when the fish were active were discarded. RMR was calculated by averaging the three lowest RMR values (Poletto *et al.*, 2017).

Maximum Metabolic Rate

RMR measurements were concluded between 08:00±40 minutes and followed by a modified critical swimming velocity protocol to elicit maximal metabolic rate (MMR) (Poletto *et al.*, 2017). Tunnel speed was increased gradually from 0 to 30 cm s^{-1} over an ~2 min period and held there for 20 min. For each subsequent 20-min measurement period, tunnel velocity was increased 10% up to a maximum of 6 cm s^{-1} per step. Fish were swum until exhausted and unable to swim. Swimming metabolism was measured by sealing the tunnel for approximately 16 minutes of the 20-minute measurement period. Oxygen levels within the tunnel were not allowed to drop below 80%. When a fish became impinged upon the back screen (>2/3 of body in contact with screen) the tunnel velocity was stopped for ~1 minute and then gradually returned to the original speed. A fish was determined to be exhausted if it became impinged twice within the same velocity step. At this point the tunnel propeller was turned off and the chamber was flushed to allow for recovery. The highest metabolic rate measured over a minimum of 5 minutes during active swimming was taken as the MMR.

Post-experiment, the tunnel was returned to the acclimation temperature and fish were transferred to a recovery tank and monitored. Data from fish which did not survive the trial or recovery were not used in analysis. After a 24-hour recovery period fish were euthanized in a buffered solution of MS-222 (0.5g/L). Measurements for mass (g), fork length (cm) and total length (cm) were taken, and Fulton's condition factor was calculated.

Aerobic scope (AS) was calculated as the difference between a fish's RMR and MMR. Thermal optimums (T_{opt}) were defined as the temperature when aerobic scope was maximized, and calculated as the root-value of the derivative of the quadratic function describing the relationship between AS and test temperature. In seeking evidence of metabolic collapse at near-critical temperatures, some metabolic trials were conducted at temperatures exceeding the tolerance of the fish. These mortality events represent potential lethal upper limits for sub-acute thermal persistence (Table 2.4 and Supplemental Table 2.1).

Statistical Analyses

For each physiological trait, models with the lowest widely applicable information criteria (WAIC) score were selected. Models were visually checked for fit, and data visualization was conducted with packages *ggplot2* (Wickham, 2016) and *tidybayes* (Kay, 2020). All models assumed a Gaussian distribution for the mean and uninformed priors. All models included population and acclimation temperature as interacting categorical fixed predictors. Additional predictor variables and random effects were included depending on the response variable and model fit. All statistical analyses were conducted in R (version 4.0.2) using the package *brms* (Bürkner, 2017, 2018) to construct Bayesian generalized linear mixed effect models.

We implemented separate models for each physiological trait (CTM, Growth Rate, RMR, MMR, and AS) to examine the effect of acclimation temperature and population on each trait. The final CTMax model additionally included fixed effects for fish mass and age (days post hatch). Mass was modeled as a linear function of time with an additional fixed effect for the starting mass of each treatment group and a random effect for rearing tank. The final RMR model used log-transformed RMR values to fit an exponential function and included non-interacting fixed effects for swim-tunnel and fish age. The final MMR model was fit to the log-

transformation of swim-temperature with non-interacting fixed effects for swim-tunnel, Fulton's condition factor and fish age. The final AS model was defined by a second order polynomial function of swimming temperature and an additional fixed effect for Fulton's condition factor. Mass, condition factor, swimming temperature and all response variables were centered and scaled to standard deviations (Z-scores). The predictor variables for time (growth model) and fish age (days post hatch; MMR, RMR and CTMax models) were scaled as a proportion of the maximum datum observed.

Mean physiological trait values for each population and acclimation temperature treatment were calculated using the package *emmeans* (Lenth, 2020). To determine whether mean estimates of the response variable were significantly different, 14,000 samples from the modeled posterior distributions were drawn. For each draw, the difference between all pairs of treatment means was computed, generating a distribution of treatment contrasts for each pair of treatments. If 94.5% of the contrast distribution was above or below 0, treatments were considered significantly different. Full model comparisons are provided in supplementary figures (S 2.1-2.8).

Values for the T_{opt} of AS the Q_{10} coefficient of the RMR for each population were calculated via bootstrapping. 500 simulated datasets were drawn from the final model posteriors, within each simulated dataset the T_{opt} was calculated by fitting a quadratic equation and calculating the root of the second derivative. Likewise, bootstrap sampling was used to calculate Q_{10} coefficients (Equation 2.4).

Equation 2.4: $$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}}$$

Where R_1 is the RMR at 10°C, and R_2 is the RMR at 22°C with *T1* and *T2* at 10 and 22°C respectively. This bootstrapped dataset was also used to calculate Q_{10} coefficients for whole populations using the model predicted RMR values for fish acclimated to 11 and 20°C.

Results

Critical Thermal Maxima

CTMax trials demonstrated significant differences among populations in both absolute value of CTMax and response to acclimation temperature. There were no significant differences between CTMax values when populations were acclimated to 11°C. The four populations demonstrated an increase in CTMax between fish acclimated from 11 to 16°C, with the Coleman fall-run population exhibiting a greater increase than the other populations (Table 2.3). The CTMax of both Feather fall-run and spring-run did not increase further when acclimated to 20°C; in fact, the CTMax of the Feather river fall-run decreased slightly (29.03 ± 0.53°C at 16°C vs. 28.74 ± 0.81°C at 20°C). The Coleman fall-run and the winter-run population improved their thermal tolerance with acclimation to 20°C. Variation among populations' CTMax values increased with acclimation temperature, indicating greater variation in CTMax among fish reared at higher temperatures (Figure 2.2.B). There are considerably fewer CTMs for the winter-run population reared at 20°C (n = 9) due to a disease induced mortality event (see *Winter-run Mortality* below) that necessitated remaining fish be allocated to the aerobic scope trials. Individual pairwise comparisons between treatment groups can be found in supplemental figures (S 2.1-2.4). Capacity to acclimate, quantified as the difference between CTMax at 11°C and 20°C, varied among the populations (Table 2.3). The Feather River fall-run and spring-run had the smallest acclimation capacity (0.89±0.18°C and 1.30 ± 0.19°C respectively).

Growth

Fish mass increased over the trial duration in all treatments and the resulting growth rate was significantly influenced by acclimation temperature and population. Average error between the modeled growth rates and observed growth rates was -0.003 ± 0 .017 g/day. Modeled growth rates ranged from 0.094 ± 0 .011 g/d (Winter-run at 20°C) to 0.266 ± 0 .023 g/d (Coleman fall-run at 20°C). As acclimation temperature increased, the growth rate of the two fall-run populations and spring-run population increased (Figure 2.2.A). Within populations, increasing acclimation temperature from 11°C to 16°C always increased the growth rate. The winter-run population was the only population to exhibit reduced growth when acclimated to 20°C.

Metabolic Trials

Routine Metabolic Rate

Routine metabolic rate (RMR) increased exponentially with swimming temperature across all populations and acclimation temperatures. Increasing acclimation temperature reduced RMR across all populations (Figure 2.3). This effect was greatest at the warmest swimming temperatures. Winter and spring-run Chinook salmon populations exhibited larger proportional reductions in RMR when acclimated to 16 and 20°C. Both fall-run populations shared similar proportional reductions in RMR (Table 2.4). Q_{10} coefficients quantify the temperature sensitivity of a biological rate with a value of 1 indicating thermal independence and values above 1 indicating increasing temperature dependence. Among acclimation groups Q_{10} coefficients varied between 2.1 and 2.8 (Table 2.4). The Q_{10} coefficient for populations acclimated to 16 °C were typically the greatest while the Q_{10} coefficients of populations acclimated to 20°C were typically the lowest. Q_{10} coefficients calculated for fully-acclimated fish were considerably lower (below 2.0), indicating that full acclimation reduces the

temperature sensitivity of the RMR. Furthermore, the acclimated Q_{10} coefficients for early-migrating populations were lower than the two fall-run populations (Table 2.4).

Maximum Metabolic Rate

Maximum metabolic rate was best fit as a function of the log (base 2) of the test temperature. This relationship prescribes an increasing, monotonic relationship between MMR and swimming temperature. Acclimation to warmer temperatures typically depressed MMR regardless of population (Figure 2.3). MMR was typically highest across swimming temperatures in fish acclimated to 11°C, and was slightly reduced in fish acclimated to 16°C. When acclimated to 20°C the two Feather river populations had the greatest reductions in MMR capacity, with the fall-run maintaining 69.16% of their 11°C acclimated capacity, and the spring-run maintaining 71.34%. The winter-run population, acclimated to 20°C, maintained 80.73% of the MMR capacity of 11°C acclimated fish. Furthermore, in these three populations the effect of acclimation temperature on MMR was negatively associated with swimming temperature with the greatest reductions in MMR capacity occurring at the highest swimming temperatures. The Coleman fall-run population showed a muted response to acclimation temperature, maintaining 94.18 and 89.68 % of their 11°C MMR capacity when acclimated to 16°C and 20°C respectively, and no further influence of swimming temperature.

Aerobic Scope

The aerobic scope of all treatments increased with swimming temperature, reached a maximum, and in some treatments declined as the swimming temperatures exceeded T_{opt} (Figure 2.3). Across all four populations, acclimation to higher temperatures (16 or 20°C) reduced overall aerobic capacity (Table 2.4). The strength of acclimation response varied between populations: The Coleman fall-run population demonstrated the lowest response to acclimation

temperature, while the Feather fall-run and Feather spring-run populations maintained 73.08 ± 7.31% and 78.19 ± 11.44% of their 11°C AS when acclimated to 20°C (Table 2.4). This decline in metabolic capacity generally increased with swimming temperature.

T_{opt} was sensitive to acclimation temperature. Coleman fall-run and Feather spring-run Chinook salmon populations exhibited increasing T_{opt} and decreasing aerobic capacity as acclimation temperatures increased. Winter-run was unusual, demonstrating a decrease in the temperature of the thermal optimum (19.2 °C to 18.6 °C) when the acclimation temperature was increased from 11 °C to 20 °C. Feather fall-run (acclimated to 16°C) and Feather spring-run (acclimated to 20°C) exhibited unusually high T_{opt} values, highlighting a challenge in fitting a quadratic model to potentially monotonic data.

Winter-run Mortality

On October 17th 2018, a single tank of winter-run Chinook salmon rearing at 20°C suffered an outbreak of *Columnaris*, resulting in the mortality of the entire tank (n=7). Necropsy of the salmon indicated empty stomachs. The mortality of this population is hypothesized to be a result of thermal stress after being reared at 20°C for a long period (202 days). The impact of this disease did not influence growth data as collection of growth data preceded disease onset by 107 days. CTMax data for the 20°C acclimation group was limited to 9 fish tested 41 days prior to the mortality event. Three fish from the infected tank were used in metabolic trials in the three weeks prior to the mortality event. It is possible that these fish were battling an infection at the time of their trials, however their metabolic rates did not exhibit unusual values. To compensate for lost fish, 6 winter-run salmon previously tested were re-acclimated to 20°C to replace the lost fish. These recovered fish were re-acclimated for at least 40 days and then re-tested. As fish were

not individually marked, it is not possible to determine the prior acclimation temperature or trial date for these recovered fish.

Discussion

We compared seasonal runs of Chinook salmon from the Sacramento River in California to assess whether differences in migration phenology may be associated with population-specific traits in thermal physiology. We compared four Chinook salmon populations (two fall-run, one spring-run and one winter-run) from the Sacramento River watershed (Figure 2.1). Comparative physiology in growth rate, CTMax and metabolic performance (RMR, MMR, and AS) measured across three acclimation temperatures (11, 16 and 20 °C) indicate pronounced differences in thermal physiology among these populations.

In agreement with other metabolic research on Central Valley salmonids (Poletto *et al.*, 2017; Verhille *et al.*, 2016) our work affirms that juvenile Central Valley Chinook salmon are capable of maintaining near-optimal aerobic capacity (90% of max AS) at 23°C, above which temperatures become increasingly lethal. These results agree with the hypothesis that juvenile organisms may be more eurythermal than adults or embryos (Pörtner & Farrell, 2008). However, our results cast doubt on the OCLTT hypothesis (Pörtner *et al.*, 2017), which predicts that thermal limits are bounded by oxygen acquisition and delivery. The best fitting model for MMR as found to be monotonic across all swimming temperatures indicating that any declines in MMR at high-temperatures, if present, were slight (Figure 2.3). Aerobic scope values declined as temperatures increased beyond the thermal optimum. However, even at temperatures approaching lethality (23-25 °C), overall aerobic capacity remained above 90% for all treatment groups except winter-run fish acclimated to 20°C. These results demonstrate that juvenile Chinook salmon are capable of peak oxygen absorption at temperatures approaching lethality.

Across all populations acclimation to 20°C reduced overall metabolic performance across the range of swimming temperatures, but varied in severity. The Coleman fall-run had the smallest acclimation effect, maintaining 89.68 ± 4.86% of their 11°C MMR and 88.24 ± 11.58% of their 11°C acclimated AS capacity when acclimated to 20°C. The other populations had greater reductions in MMR and AS capacity when acclimated to 20°C (Table 2.4). RMR rates also decreased with acclimation temperature, potentially due to thermal metabolic compensation (Evans, 1990; Franklin *et al.*, 2007; Guderley, 1990; Johnston & Dunn, 1987; Somero, 1969). When viewed as a reaction to high temperature acclimation, a reduction in RMR would maintain aerobic capacity in light of a commensurate reduction in MMR, but with possible trade-offs (i.e., somatic growth, development or immune function). Effective metabolic compensation is evident in the Coleman fall-run population and in the Mokelumne Hatchery fall-run population studied by Poletto et al. (2017), wherein aerobic scope performance between groups acclimated to 15 and 19 °C was indistinguishable across the measured swimming temperatures. Feather river fall- and spring-run, and the winter-run populations all show pronounced declines in MMR and AS as acclimation temperatures increased, indicating that only partial thermal compensation was achieved. While limited compensation may be expected for winter-run and spring-run populations which historically reared in colder streams (Moyle *et al.*, 2017), the lack of metabolic compensation in Feather river fall-run diverges from the response observed among the Coleman fall-run and the Mokelumne Fall-run (Poletto *et al.*, 2017). This result highlights the challenges of prescribing single management targets across geographically proximal Chinook salmon populations (Zillig *et al.*, 2021).

It is well documented that thermal physiological traits do not necessarily shift in tandem. For instance, high CTMax does not necessarily indicate increased metabolic performance at high

temperatures. Both the Coleman fall-run and the winter-run populations, which exhibited divergent aerobic scope and growth profiles, exhibited similar CTMax values across all acclimation temperatures (Figure 2.2.B). Variation among CTMax values and fish mass increased with acclimation temperature, with the greatest intra-treatment variation occurring when fish were acclimated to 20°C. It is hypothesized that increasing temperatures can release cryptic genetic variation due to changes in the efficacy of heat shock proteins, and that release of previously constrained variation may allow for rapid local adaptation (Ghalambor *et al.*, 2007; Queitsch *et al.*, 2002; Rutherford, 2003; Rutherford & Lindquist, 1998). Managers seeking to identify at-risk populations may be able to determine a population's adaptive capacity by studying these individual stress-induced variants. Furthermore, evolutionary rescue may be facilitated by research on the genetics of this cryptic thermal variation.

Winter-run Chinook Salmon

Endangered winter-run Chinook salmon are the only population that exhibit winter-onset of adult migration (Moyle *et al.*, 2017). Early adult migration and spawning is made feasible by high-elevation cold-water springs of the southern Cascade Mountains, which provide the requisite thermal environment for developing salmon embryos (Martin *et al.*, 2017; McCullough, 1999). Access to these cold-water habitats has been eliminated, and the remaining winter-run populations are reliant on cold-water releases from Shasta Dam. We predicted that if winter-run were locally adapted to the historical environmental conditions of their native range (i.e. cold, high-elevation springs in the McCloud River, CA) they would exhibit reduced growth and aerobic capacity when acclimated to a warm temperature (20°C). The winter-run population demonstrated a significant decline in growth rate and a reduced thermal optimum when acclimated to 20°C, consistent with our hypothesis of maladaptive phenotypes and local

adaption. Comparison of CTMax data for winter-run is limited due to limited data for fish acclimated to 20°C (n=9, see Mortality). However, the available data suggest that winter-run Chinook salmon do not express unusual thermal tolerance under acute thermal stress.

Metabolic performance of winter-run Chinook salmon varied considerably from other test populations. The T_{opt} of winter-run Chinook salmon declined as acclimation temperature increased mirroring the reduced growth capacity at this temperature. The inverse relationship between acclimation temperature and aerobic capacity indicates that winter-run may struggle to acclimate to a warming environment. In California, river temperatures are expected rise with a warming atmosphere (Null *et al.*, 2013) and be exacerbated by increasing drought (Diffenbaugh *et al.*, 2015) and reduced snow pack (Hamlet *et al.*, 2005). Even if temperatures remain well below winter-run critical temperatures (28-30°C), the poor winter-run response to warm-acclimation highlights the challenge of preserving this unique population. Conservation plans seeking to reintroduce winter-run should select their habitats carefully to ensure winter-run can avoid thermal extremes.

Spring-run Chinook Salmon

Spring-run Chinook salmon are another target population for reintroduction. Spring-run Chinook salmon were once the most productive seasonal run of Chinook salmon in the Central Valley (Lindley *et al.*, 2007; Moyle *et al.*, 2017; Yoshiyama *et al.*, 1998). Access to high elevation, spring- or snowmelt-fed rivers in the Sierra Nevada and southern Cascades mountains kept over-summering adults in cold, highly oxygenated waters. Despite their historical dominance, the San Joaquin river population was extirpated in 1948 (Yoshiyama *et al.*, 1998), and the population has been reintroduced using progeny of the Feather River Hatchery spring-run population.

Genetic work on the Feather river spring-run population indicates high introgression with the sympatric Feather River fall run (Lindley *et al.*, 2004). However, differentiation remains, specifically among genes hypothesized to influence run timing (Meek *et al.*, 2020; O'Malley *et al.*, 2007, 2013). Whether genes underpinning thermal performance are introgressed or not is unknown, and our results indicate considerable similarity among the tested traits. We see similar CTMax values (Table 2.3) and growth rates (Supplementary Figure 2.6) in both Feather River populations. Whether these similarities are due to recent genetic homogenization or shared adaptation to the Feather River is unknown. Physiological work on spring-run populations from Deer and Mill Creeks, CA, which remain genetically distinct (Meek *et al.*, 2020), would allow for determination of whether the spring-run phenotype contains unique thermal traits similar to the winter-run. These comparisons could also determine whether the Feather River spring-run's thermal profile may be impacted by introgression with the Feather fall-run. From a management perspective, the results of our study indicate that juvenile Feather spring-run Chinook salmon should perform similarly to the Feather fall-run population. Due to the genetic introgression, preservation of this seasonal run likely rests on protecting migrating and over-summering spring-run adults from temperature extremes, as rearing juveniles of the fall- and spring-runs are similar in their thermal performance.

Fall-run Chinook Salmon

Our results indicated that the Coleman fall-run is the most thermally tolerant population. They possess both the highest CTMax (29.9 ± .13 °C) and greatest increase in CTM between groups acclimated to 11 or 20°C (1.9 °C). Furthermore, they exhibited the greatest capacity for growth at 20 °C. The stability in metabolic capacity across acclimation temperatures likely reflects a plastic population capable of metabolically compensating for changes in acclimation

temperature. These traits differ from the Feather fall-run population, whose traits are more similar to the sympatric Feather spring-run. Sources for this population difference could reflect hatchery practices, genetic diversity or local adaptation. Despite an unknown driver, these population specific differences are relevant to management strategies seeking to protect salmonids (Zillig *et al.*, 2021).

Hatchery Supplementation

There are specific caveats when extrapolating these results to wild fish rearing in field settings. For instance, all the populations used in this study were sourced from hatcheries. The effect of hatcheries on the thermal capacity and performance of salmonids is an important research area. Past research revealed rapid declines in reproductive capacity among hatchery produced or supplemented populations (Araki *et al.*, 2007, 2008). Possible drivers of these deleterious hatchery effects include hatchery conditions (Araki *et al.*, 2008; Satake & Araki, 2012), effective population size within the hatchery (Wang *et al.*, 2002; Waples & Teel, 1990), spawning and release management strategies (Lusardi & Moyle, 2017; Sturrock *et al.*, 2019), duration of hatchery supplementation (Sturrock *et al.*, 2019), and proportion of wild population of hatchery origin (Araki *et al.*, 2008). In the present study the selected hatchery populations differ in many aspects of hatchery production (e.g. broodstock vs. wild returners, number of spawners, release strategies), and therefore apparent differences between populations may be due to 'hatchery selection' as opposed to natural selection of native environmental characteristics.

Despite the potential impacts of hatchery production on the physiology of juvenile Chinook salmon, the contribution of these hatcheries to the wild population, especially in California, make them the dominant source of Chinook salmon moving through the system (Barnett-Johnson *et al.*, 2007; Yoshiyama *et al.*, 1998). Furthermore, the decades of hatchery

supplementation ensure that even un-supplemented wild populations have been genetically homogenized with hatchery populations (Williamson & May, 2005). Protecting remaining Chinook salmon genetic diversity is essential to population resilience (i.e. the portfolio effect, Carlson & Satterthwaite, 2011). Therefore, understanding the thermal physiology of hatchery genotypes remains pertinent to identifying unique wild populations that may offer novel variation in thermal physiology.

The winter-run population is a special case. The fish used in this experiment were sourced from the captive broodstock of adult Chinook that are reared and maintained at Livingston-Stone National Fish Hatchery. These adult fish are never exposed to wild conditions, and their progeny serve as an existential back-up in case the wild-rearing population collapses. It is unknown how the thermal physiology of the fully-captive brood-stock may differ from their wild counterparts. However, the winter-run fish used in this study had wild-rearing siblings released as part of the Jumpstart reintroduction program, the first of which successfully returned to Battle Creek as adults in the spring of 2020.

Laboratory Conditions

In addition to being hatchery-sourced, all fish used in this study were reared and tested under lab conditions which can differ from wild conditions in important ways (e.g. lack of predators, clean water, abundant food etc.). Collectively, the effect of laboratory conditions may produce physiological trait phenotypes that differ from fish exposed to wild conditions (McDonald et al., 1998; Smith & Fuiman, 2004; Sundström & Johnsson, 2001). It is unknown whether exposure to the field conditions of each population's natal environment would accentuate or mitigate observed population differences. The effect of laboratory conditions on the performance of juvenile Chinook salmon is understudied, and future projects should consider

the potential for different performance under wild rearing conditions. Reciprocal transplant experiments would address this shortcoming. Given the context of the present research, we feel that understanding the role of food limitation and energetic restriction has on the thermal performance of rearing juvenile Chinook salmon is essential for improved estimation of wild fish performance.

Conservation of At-Risk Populations

Physiological data are becoming increasingly valuable for species conservation, and can offer mechanistic understanding to a species' or population's response to environmental change (Madliger *et al.*, 2016; Patterson *et al.*, 2016). Our research suggests that some salmonid populations (i.e., winter-run) do express distinctly different physiological responses (e.g. growth and metabolism) compared to fall-run populations, and that these responses can vary among common physiological traits (CTMax vs. aerobic scope). Current management frameworks (e.g., U.S. Environmental Protection Agency, 2003) propose single temperature thresholds for defining thermally-impaired rivers and triggering management responses (e.g. increasing dam releases). These threshold criteria often apply to entire groups of species and are based upon research drawn from geographically disparate populations (Zillig *et al.*, 2021) creating management pitfalls for unique populations. A looming challenge to this management framework in a warming climate is attainability. For instance, 18°C is a recommend threshold for Chinook salmon smolts (U.S. Environmental Protection Agency, 2003). This temperature would likely protect the four populations of Chinook salmon in this study, however, increasing atmospheric temperatures (Null *et al.*, 2013) and prolonged drought conditions (Diffenbaugh *et al.*, 2015) will prevent achievement of these management targets. In 2014, persistent drought conditions depleted the cold-water pool in Shasta Reservoir, precluding attainment of temperature targets

and culminating in over 90% mortality of developing winter-run embryos (Durand *et al.*, 2020). Conservation of salmonids under future environmental scenarios will likely require trade-offs between species and populations, and knowledge of interpopulation variation in thermal physiology will be essential to effectively triage at-risk populations (Zillig *et al.*, 2021).

Further work should investigate the impact of warming on the energetic demands of wild-rearing juvenile Chinook salmon. Our RMR results indicate that juvenile fall-run Chinook salmon consume 1.7 times the oxygen when acclimated and tested at 20°C than when acclimated and tested at 11°C. RMR is shown to reflect energetic demands (Hansen *et al.*, 2020; Killen *et al.*, 2011; Millidine *et al.*, 2009) and therefore increasing temperatures will increase the demand of rearing salmonids for food resources. Hatcheries in California have produced over 2 billion fall-run Chinook salmon juveniles since 1946, recently releasing approximately 30 million fish per year (Huber & Carlson, 2015). Without corresponding increases in food abundance, a warmer environment will increase resource competition between the numerically dominant hatchery-produced salmon and their wild rearing counter-parts. Expanding floodplain habitat has been demonstrated to increase food densities and may represent an essential management tool for conserving salmon in a warmer future (Aha *et al.*, 2021; Jeffres *et al.*, 2008; Sommer *et al.*, 2001). Research investigating differential use of this habitat type and competition among populations would focus conservation efforts seeking to restore floodplain access.

Conclusions

Physiology data conducted at the organism level is providing improved insights into species response to environmental change and offering guidance for managers on conservation actions. For salmonids, which exist as a diverse metapopulation of life-history strategies, diversity in phenotypes offers resilience against environmental stochasticity. Understanding how

physiology may differ between populations can allow customized environmental regulation. Our results not only reveal variation in Chinook salmon thermal physiology among different seasonal run phenotypes in California, but also provides actionable physiological metrics to inform the conservation options currently being proposed to protect winter- and spring-run Chinook salmon within the Central Valley.

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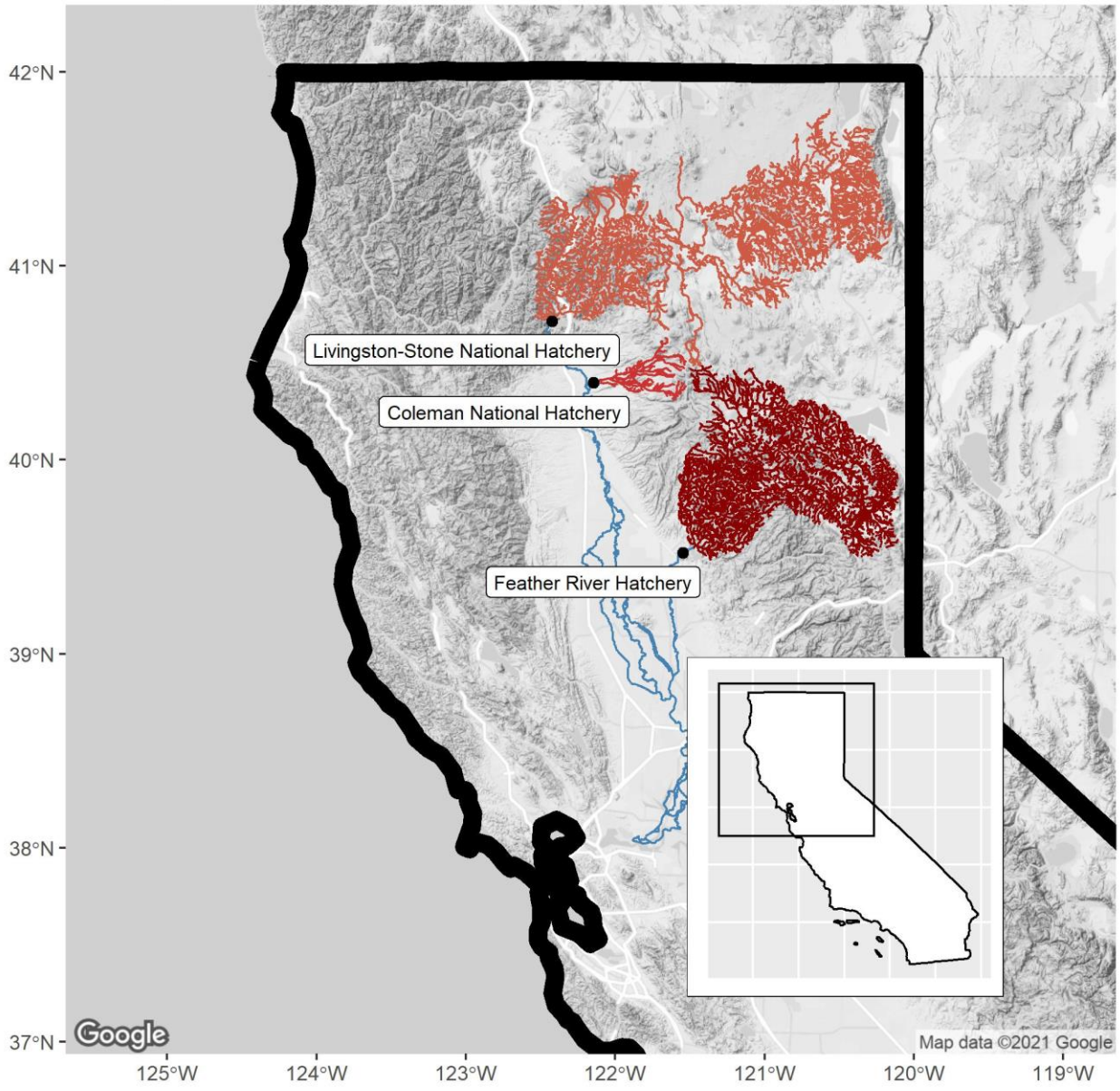

Figure 2.1: Map of the three source hatcheries. Accessible rivers and migration paths are identified in blue, inaccessible historical habitat is in red. The Feather River Hatchery produces both the feather fall-run and feather spring-run. The Livingston-stone National Hatchery produces the Sacramento River winter-run and the Coleman National Hatchery produces the fall-run.

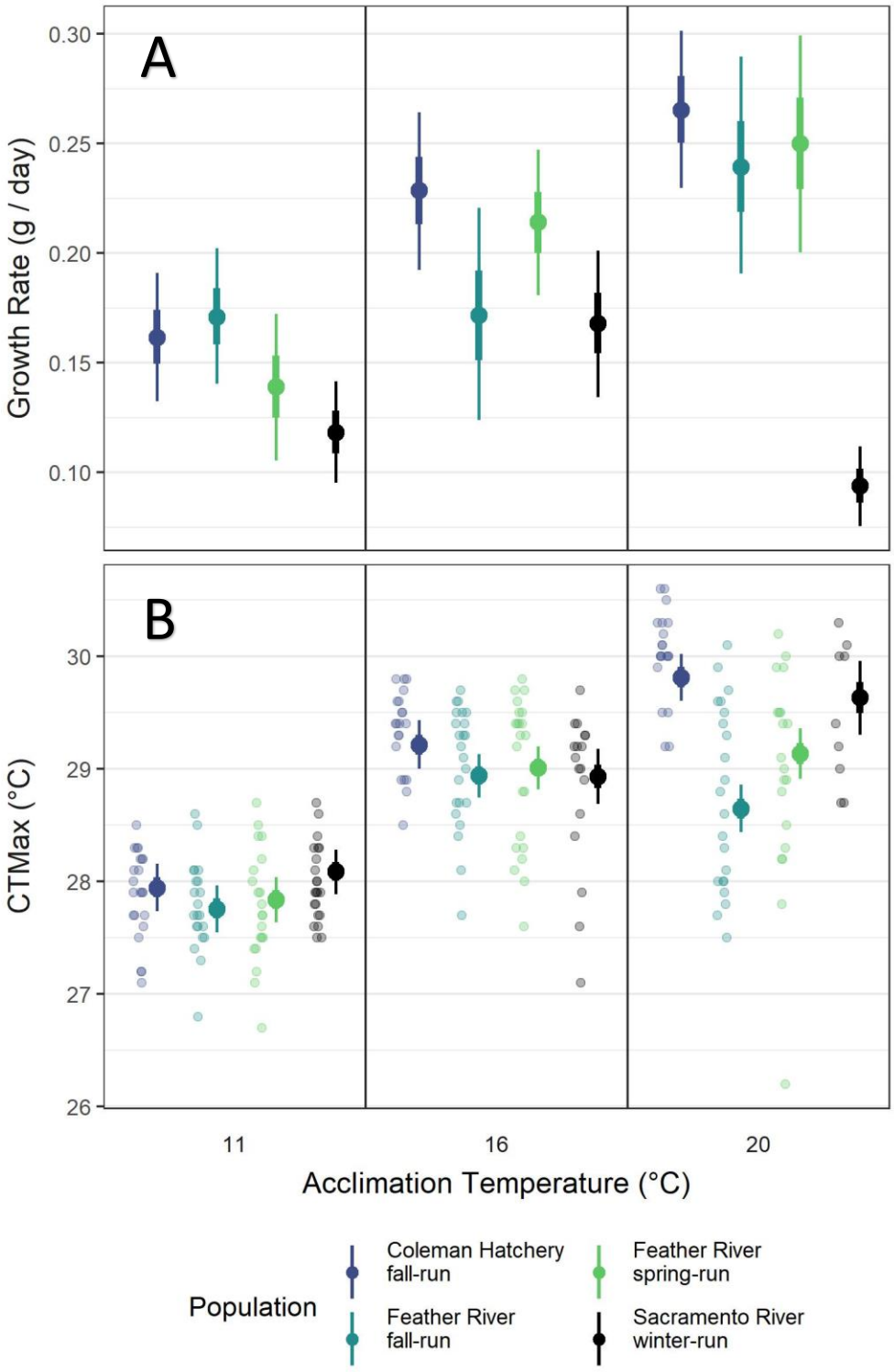

Figure 2.2: CTMax and Growth Rates of four populations of Sacramento River Chinook salmon acclimated to three temperatures. A) Modeled growth rates (g/day). B) Observed (points) and model estimate CTMax values (°C) Mean model estimate is represented by the point, while the 50% (thick) and 89% (narrow) credible intervals are represented by the whiskers.

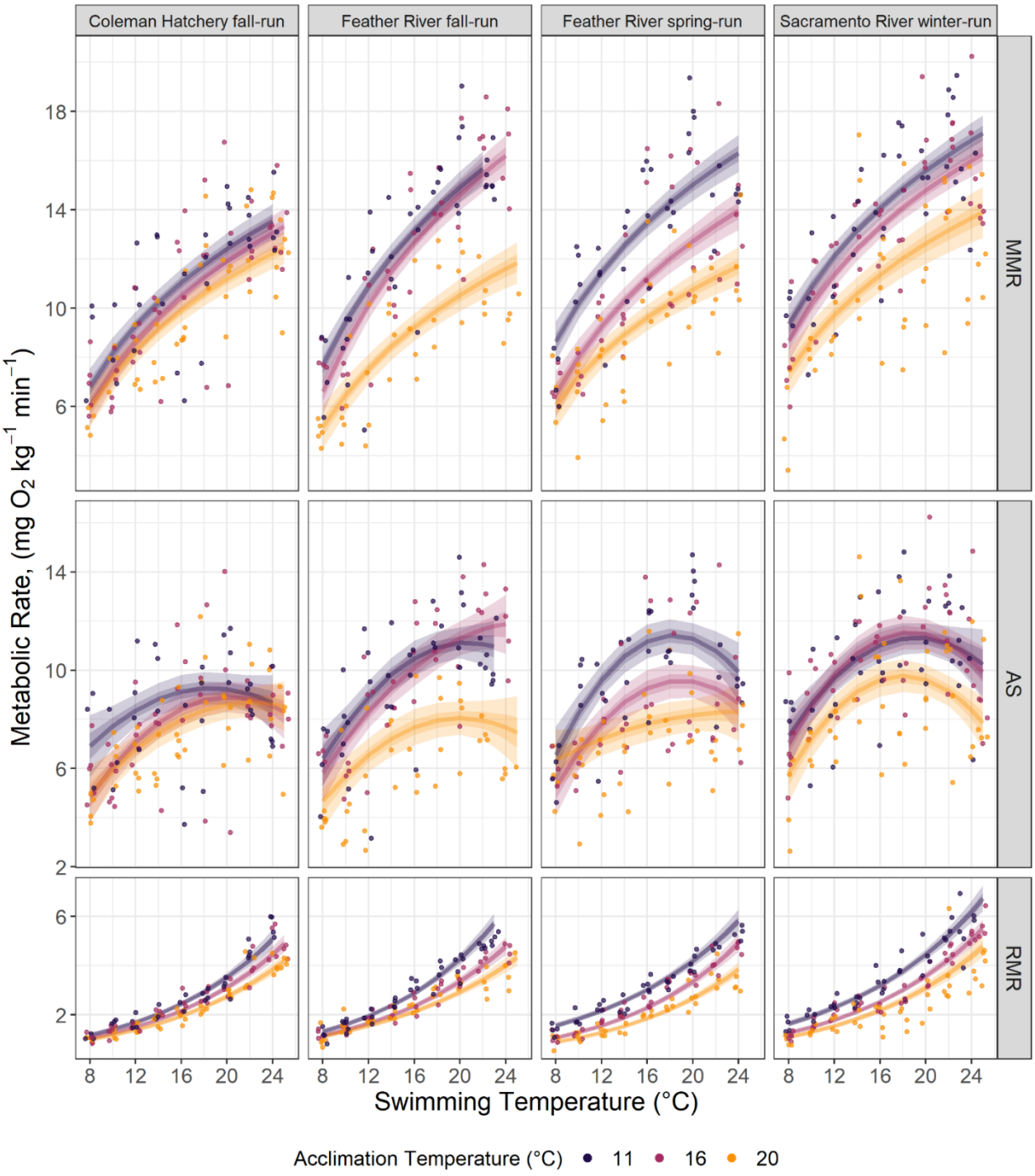

Figure 2.3: Metabolic rates for four populations (columns) of Sacramento River Chinook salmon reared at three acclimation temperatures. An individual fish was trialed at only one test temperature, and provided a routine (RMR) and maximum (MMR) metabolic rate, from which an aerobic scope (AS) could be calculated. Colors represent acclimation temperature groups. Points reference observed data while lines are the trait estimates derived from the lowest-WAIC model. Shaded regions represent the 50% (dark) and 89% (light) credible interval.

Table 2.1: Population and acclimation treatment metadata for four population of Sacramento River Chinook salmon. Year is the year experiments were conducted, run identifies which of the four seasonal runs a hatchery population belongs to. Elev. is the elevation at the hatchery in meters and 'Mig. Dist.' is the length of the river from the hatchery to tidally influenced waters. Stocking density is the number of fish per tank when experiments were started.

Population	Year	Run	Hatchery	Latitude, Longitude	Elev. (m)	Mig. Dist. (km)	Hatching Date	Acc. Temp.	Initial Stocking Density
Coleman	2017	Fall	Coleman National Fish Hatchery	40.398°N, 122.145°W	123	407	11/8/2016	11 °C	55-60
								16 °C	70-75
								20 °C	70-75
Winter-Run	2018	Winter	Livingston Stone National Fish Hatchery	40.716°N, 122.425°W	179	486	10/24/2017	11 °C	70
								16 °C	50
								20 °C	50
Feather Fall	2019	Fall	Feather River Fish Hatchery	39.519°N, 121.554°W	41	277	11/29/2018	11 °C	70
								16 °C	70
								20 °C	70
Feather Spring	2019	Spring	Feather River Fish Hatchery	39.519°N, 121.554°W	41	277	11/13/2018	11 °C	67
								16 °C	67
								20 °C	67

Table 2.2: Growth Rate Data for four population of Chinook Salmon at three acclimation temperatures. Mass, fork length and condition factor (Fulton's) are all reported as means and standard deviations from the observed data. Absolute growth rate is the modeled growth rate reported as the mean and standard deviation of 14,800 draws from the posterior distribution of lowest WAIC growth model. Other columns are the means and standard deviations of the measured values.

Hatchery and Acclimation Temperature		Initial Date	Final Date	Duration (Days)	Mass		Fork Length		Condition Factor		Absolute Growth Rate (g/day)
					Initial	Final	Initial	Final	Initial	Final	
Coleman	11 °C	4/17/2017	5/16/2017	29	7.445 ± 0.497	11.413 ± 2.694	8.33 ± 0.75	9.73 ± 0.78	1.26 ± 0.09	1.21 ± 0.06	0.162 ± 0.018
Coleman	16 °C	4/17/2017	5/16/2017	29	8.415 ± 0.090	15.688 ± 3.238	8.76 ± 0.77	10.83 ± 0.74	1.23 ± 0.11	1.22 ± 0.07	0.229 ± 0.023
Coleman	20 °C	4/17/2017	5/16/2017	29	8.340 ± 0.024	17.293 ± 3.560	8.66 ± 0.58	11.07 ± 0.74	1.27 ± 0.08	1.26 ± 0.08	0.266 ± 0.023
Feather Fall	11 °C	5/20/2019	7/1/2019	42	8.225 ± 0.279	16.014 ± 4.880	8.59 ± 0.95	10.7 ± 1.02	1.24 ± 0.08	1.26 ± 0.09	0.171 ± 0.019
Feather Fall	16 °C	5/6/2019	6/3/2019	28	8.825 ± 0.668	13.168 ± 5.895	8.51 ± 1.39	9.87 ± 1.57	1.31 ± 0.09	1.26 ± 0.10	0.172 ± 0.030
Feather Fall	20 °C	5/6/2019	6/3/2019	28	8.439 ± 0.154	14.899 ± 5.385	8.44 ± 1.11	10.31 ± 1.32	1.32 ± 0.11	1.29 ± 0.07	0.240 ± 0.031
Feather Spring	11 °C	5/6/2019	6/12/2019	37	7.837 ± 0.084	12.800 ± 3.878	8.50 ± 0.78	10.05 ± 0.89	1.25 ± 0.07	1.22 ± 0.07	0.139 ± 0.021
Feather Spring	16 °C	4/8/2019	5/20/2019	42	7.235 ± 1.001	16.319 ± 9.133	8.03 ± 1.35	10.52 ± 2.07	1.26 ± 0.10	1.25 ± 0.06	0.214 ± 0.021
Feather Spring	20 °C	4/8/2019	5/6/2019	28	7.465 ± 0.520	14.507 ± 7.886	8.14 ± 1.09	9.95 ± 1.77	1.29 ± 0.09	1.32 ± 0.10	0.250 ± 0.031
Winter-Run	11 °C	4/19/2018	6/12/2018	54	6.900 ± 0.518	13.597 ± 4.281	8.32 ± 0.64	10.26 ± 0.93	1.17 ± 0.09	1.21 ± 0.10	0.118 ± 0.014
Winter-Run	16 °C	4/5/2018	5/17/2018	42	6.940 ± 0.245	14.080 ± 3.864	8.26 ± 0.41	10.48 ± 0.86	1.22 ± 0.05	1.19 ± 0.07	0.168 ± 0.021
Winter-Run	20 °C	4/19/2018	6/27/2018	69	6.890 ± 0.085	13.312 ± 5.880	8.33 ± 0.53	10.01 ± 1.31	1.18 ± 0.07	1.25 ± 0.07	0.094 ± 0.011

Table 2.3: Treatment measurements for Critical Thermal Maximum: Modeled data is the mean and standard deviation of 14000 draws from the posterior distribution. Acclimation capacity for each hatchery was calculated as the mean difference (and standard deviation) between the 11°C and 20°C acclimation group. The remaining columns are the respective means and standard deviations from the observed data.

Hatchery and Acclimation Temperature		Data CTM (°C)	Modeled CTM (°C)	Mass (g)	Fork Length (cm)	Fulton's Condition Factor	Count	Acclimation Capacity ΔCTM
Coleman	11°C	27.89 ± 0.39	27.95 ± 0.13	17.208 ± 5.147	11.45 ± 1.07	1.11 ± 0.07	22	1.86 ± 0.18 °C
	16°C	29.34 ± 0.37	29.21 ± 0.13	22.925 ± 3.371	12.43 ± 0.66	1.19 ± 0.06	20	
	20°C	30.02 ± 0.40	29.81 ± 0.13	23.264 ± 3.764	12.32 ± 0.65	1.24 ± 0.07	20	
Feather Fall	11°C	27.78 ± 0.40	27.76 ± 0.13	25.264 ± 2.486	13.08 ± 0.44	1.13 ± 0.04	21	0.89 ± 0.18 °C
	16°C	29.03 ± 0.53	28.94 ± 0.12	22.033 ± 2.337	12.32 ± 0.36	1.18 ± 0.08	23	
	20°C	28.74 ± 0.81	28.65 ± 0.13	23.618 ± 2.979	12.19 ± 0.45	1.30 ± 0.11	22	
Feather Spring	11°C	27.77 ± 0.50	27.84 ± 0.13	23.315 ± 2.392	12.69 ± 0.42	1.14 ± 0.07	21	1.30 ± .19 °C
	16°C	28.99 ± 0.66	29.01 ± 0.12	22.334 ± 2.906	12.41 ± 0.47	1.16 ± 0.07	22	
	20°C	28.96 ± 0.93	29.14 ± 0.14	21.724 ± 4.218	11.82 ± 0.62	1.31 ± 0.15	20	
Winter-Run	11°C	27.99 ± 0.34	28.09 ± 0.12	21.675 ± 2.455	12.39 ± 0.52	1.14 ± 0.11	22	1.54 ± .24 °C
	16°C	28.84 ± 0.71	28.93 ± 0.15	20.690 ± 3.423	12.26 ± 0.63	1.11 ± 0.06	17	
	20°C	29.49 ± 0.63	29.63 ± 0.21	18.539 ± 1.904	11.44 ± 0.51	1.24 ± 0.07	9	

Table 2.4: Summary metabolic data for four populations of Sacramento River Chinook salmon: Fish swam is the number of successful swims conducted while mortality is the number of fish that did not survive the trial. Max. Temp. is the highest temperature at which fish could be successfully tested. Mass, fork length and condition factor are reported as means and std. dev. of the observed data. RMR, MMR and AS values are all derived from the respective Bayesian models. Values are reported as mean and std. dev. of the model estimates. Q_{10} coefficients of the RMR were calculated for each treatment (Q_{10}) and holistically for each population (Acc. Q_{10}). For each metabolic rate, we compared the amount of metabolic capacity relative to a hatchery's metabolic capacity when acclimated to 11°C, these are reported as the mean percentage and standard deviation.

Hatchery and Acclimation Temperature		Fish Swam (n=)	Mort. (n=)	Max. Temp. °C	Mass (g)	Fork Length (cm)	Cond. Factor	RMR			MMR	AS		
								Q_{10}	Acc. Q_{10}	% of 11 C	% of 11	Capacity at T_{OPT}	T_{OPT} (°C)	% of 11
Coleman	11°C	32	7	24	22.18 ± 4.02	12.5 ± 0.65	1.13 ± 0.071	2.50 ± 0.03	1.89 ± .03	-	-	9.28 ± 0.11	18.72 ± 0.65	-
Coleman	16°C	42	3	25	23.72 ± 3.25	12.7 ± 0.50	1.16 ± 0.048	2.46 ± 0.03		88.91 ± 4.46	94.18 ± 5.44	8.93 ± 0.09	20.32 ± 0.53	90.36 ± 11.83
Coleman	20°C	45	5	25	24.72 ± 4.01	12.6 ± 0.64	1.21 ± 0.06	2.33 ± 0.03		79.65 ± 4.92	89.68 ± 4.86	8.71 ± 0.11	22.41 ± 1.26	88.24 ± 11.58
Feather Fall	11°C	39	4	23	25.36 ± 2.57	13.0 ± 0.44	1.14 ± 0.054	2.65 ± 0.04	1.74 ± .02	-	-	11.14 ± 0.14	20.78 ± 0.89	-
Feather Fall	16°C	35	5	24	24.09 ± 2.59	12.7 ± 0.38	1.17 ± 0.067	2.42 ± 0.03		81.89 ± 5.6	94.4 ± 6.43	12.02 ± 0.41	26.17 ± 2.52	98.05 ± 9.93
Feather Fall	20°C	38	12	25	26.08 ± 4.26	12.6 ± 0.47	1.3 ± 0.118	2.20 ± 0.03		74.43 ± 7.89	69.61 ± 4.72	8.07 ± 0.12	20.1 ± 0.75	73.08 ± 7.31
Feather Spring	11°C	37	3	24	25.12 ± 3.08	13.0 ± 0.54	1.14 ± 0.081	2.27 ± 0.03	1.37 ± .02	-	-	11.41 ± 0.11	18.32 ± 0.29	-
Feather Spring	16°C	37	3	24	25.15 ± 4.63	12.9 ± 0.61	1.17 ± 0.084	2.61 ± 0.03		76.84 ± 7	82.61 ± 5.49	9.59 ± 0.11	18.98 ± 0.41	83.85 ± 8.00
Feather Spring	20°C	39	16	24	24.65 ± 4.02	12.4 ± 0.55	1.28 ± 0.092	2.50 ± 0.03		61.86 ± 4.48	71.34 ± 4.18	8.42 ± 4.81	26.27 ± 87.59	78.19 ± 11.44
Winter-Run	11°C	39	6	24	21.59 ± 2.21	12.2 ± 0.38	1.19 ± 0.109	2.29 ± 0.03	1.53 ± .02	-	-	11.34 ± 0.10	19.2 ± 0.46	-
Winter-Run	16°C	44	4	25	21.45 ± 2.51	12.2 ± 0.44	1.17 ± 0.061	2.38 ± 0.02		79.82 ± 4.29	94.52 ± 3.96	11.54 ± 0.10	18.66 ± 0.24	100.21 ± 7.80
Winter-Run	20°C	42	4	25	21.14 ± 4.81	12.0 ± 0.84	1.21 ± 0.11	2.38 ± 0.03		69.15 ± 4.19	80.73 ± 4.29	9.78 ± 0.12	18.02 ± 0.21	83.47 ± 7.81

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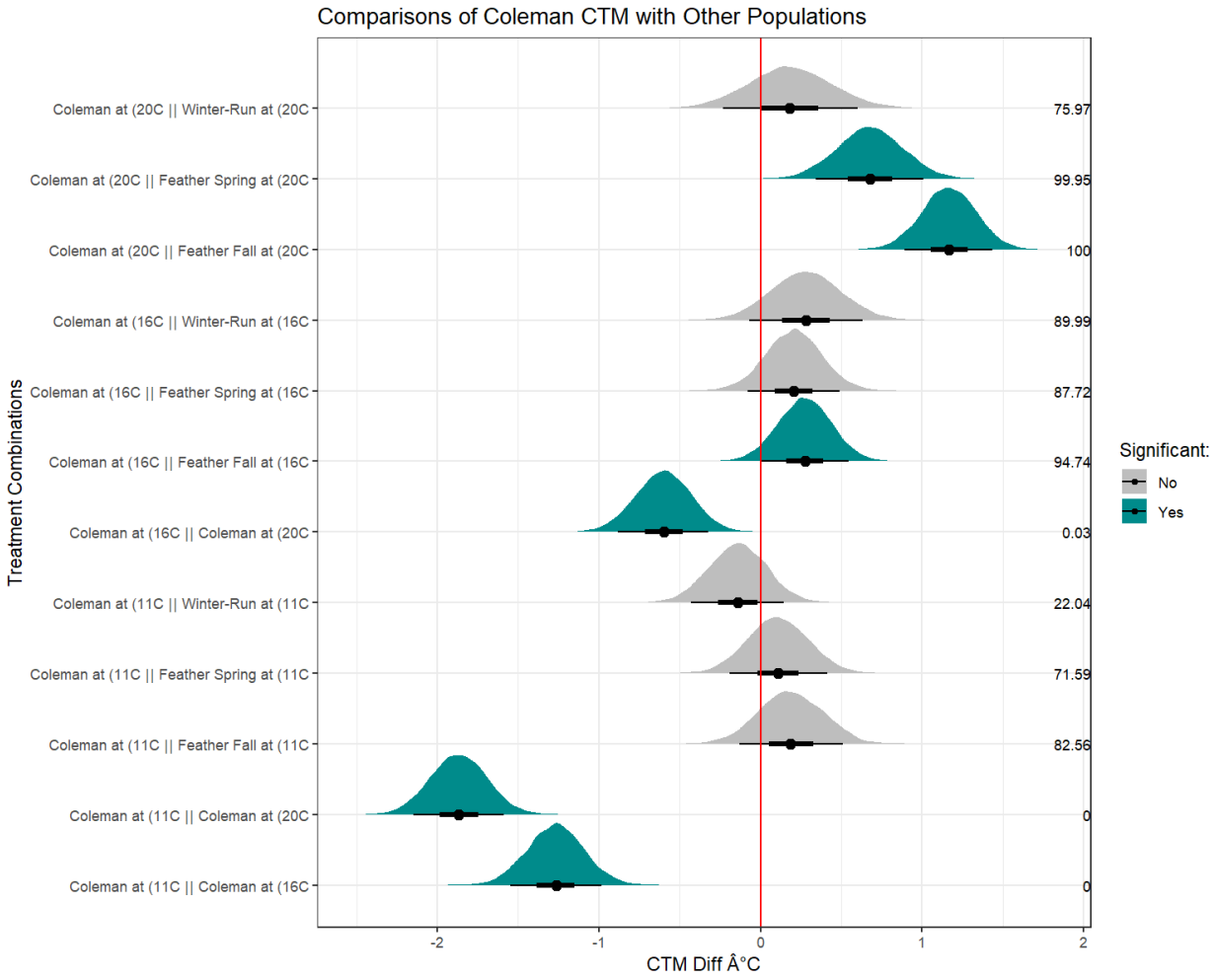
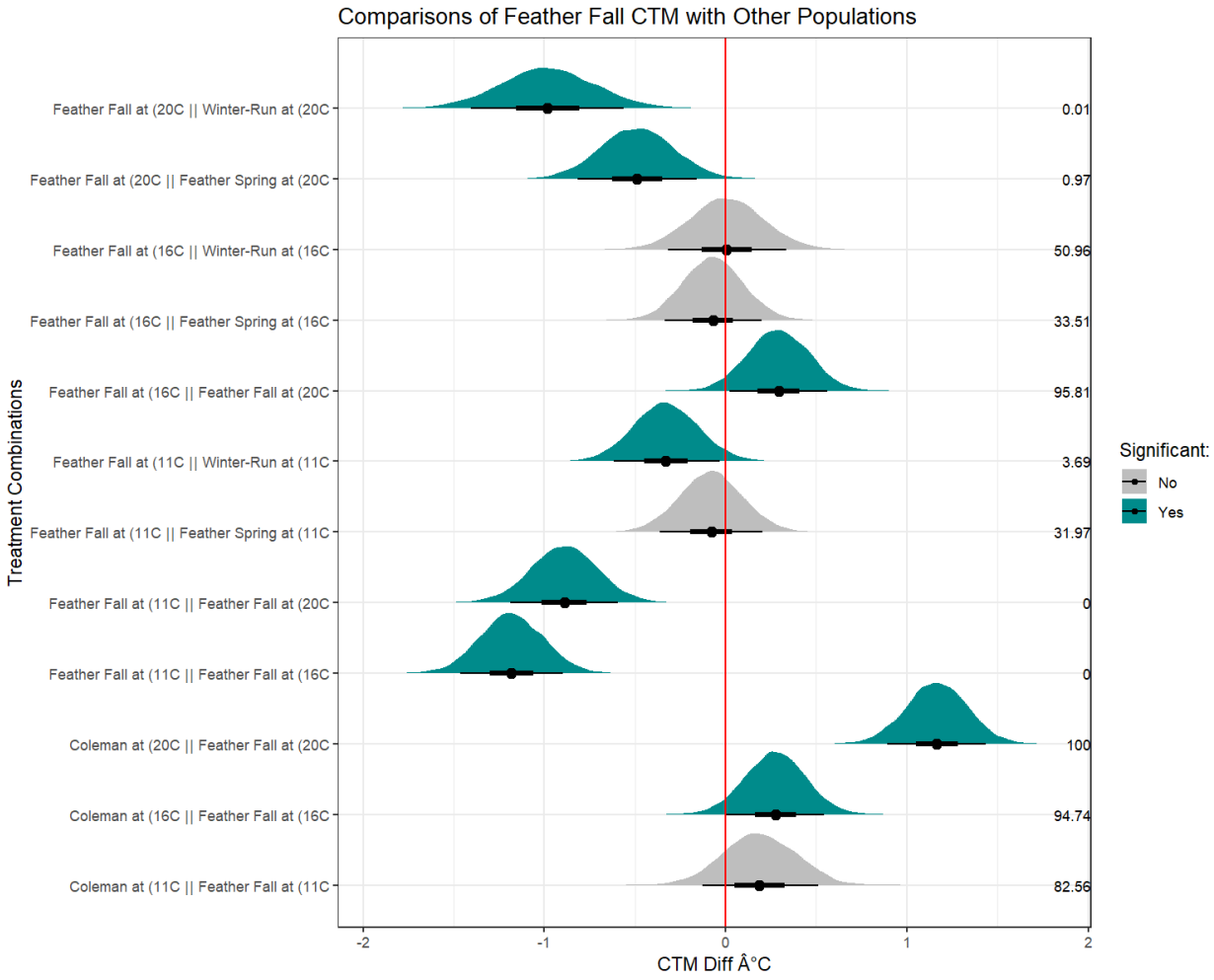
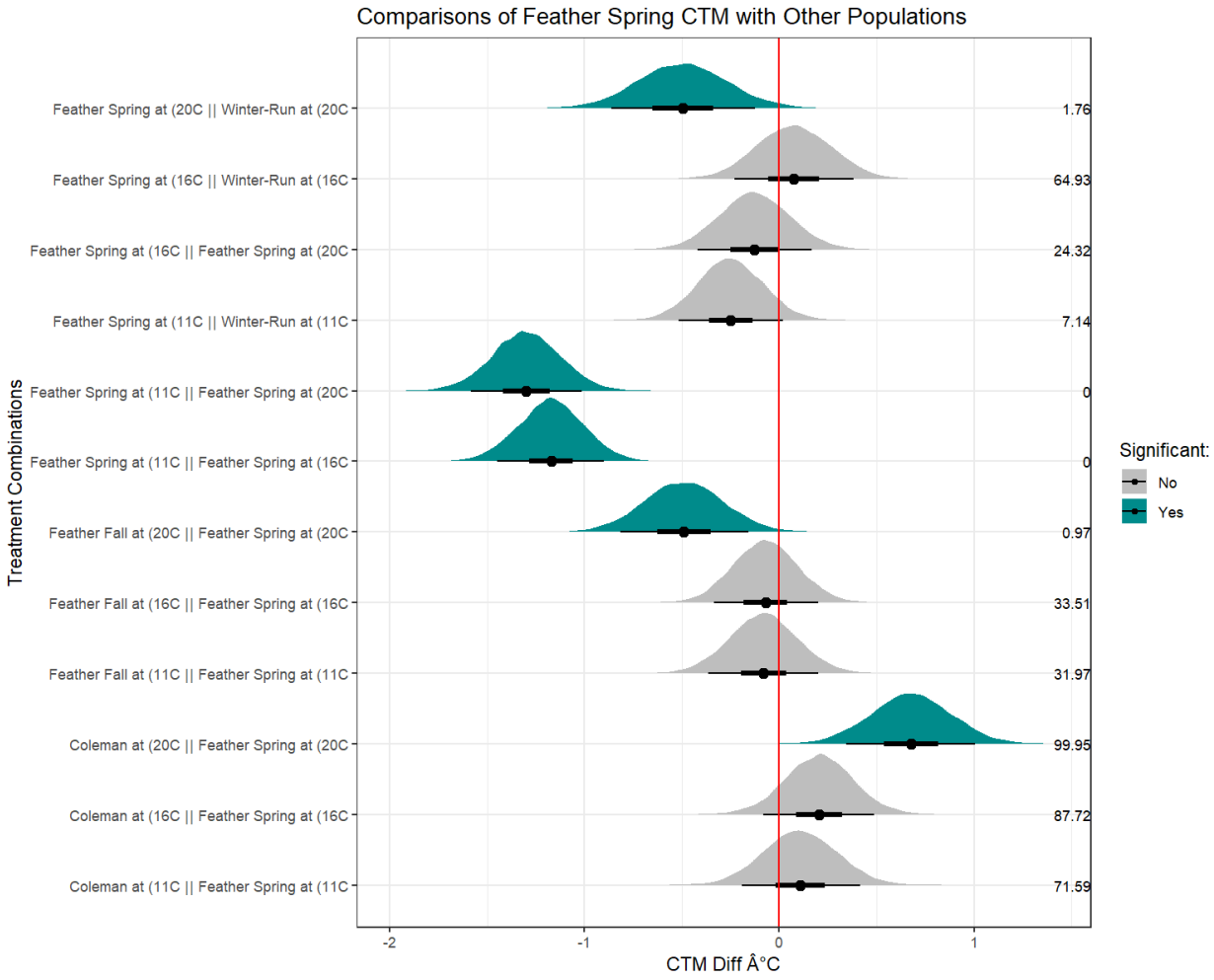


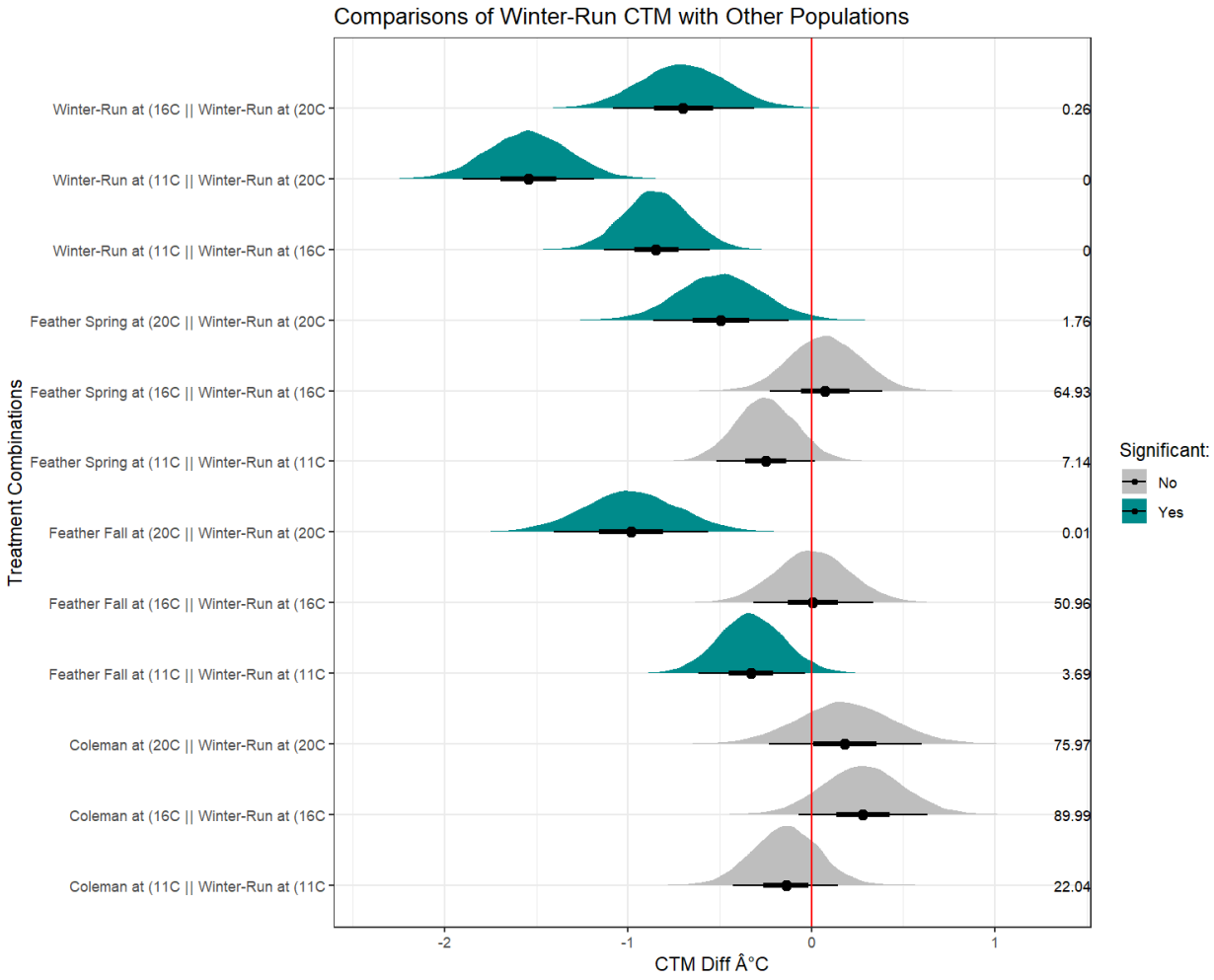
Supplemental Figure 2.1: Treatment Contrasts of CTMax values between Coleman River Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



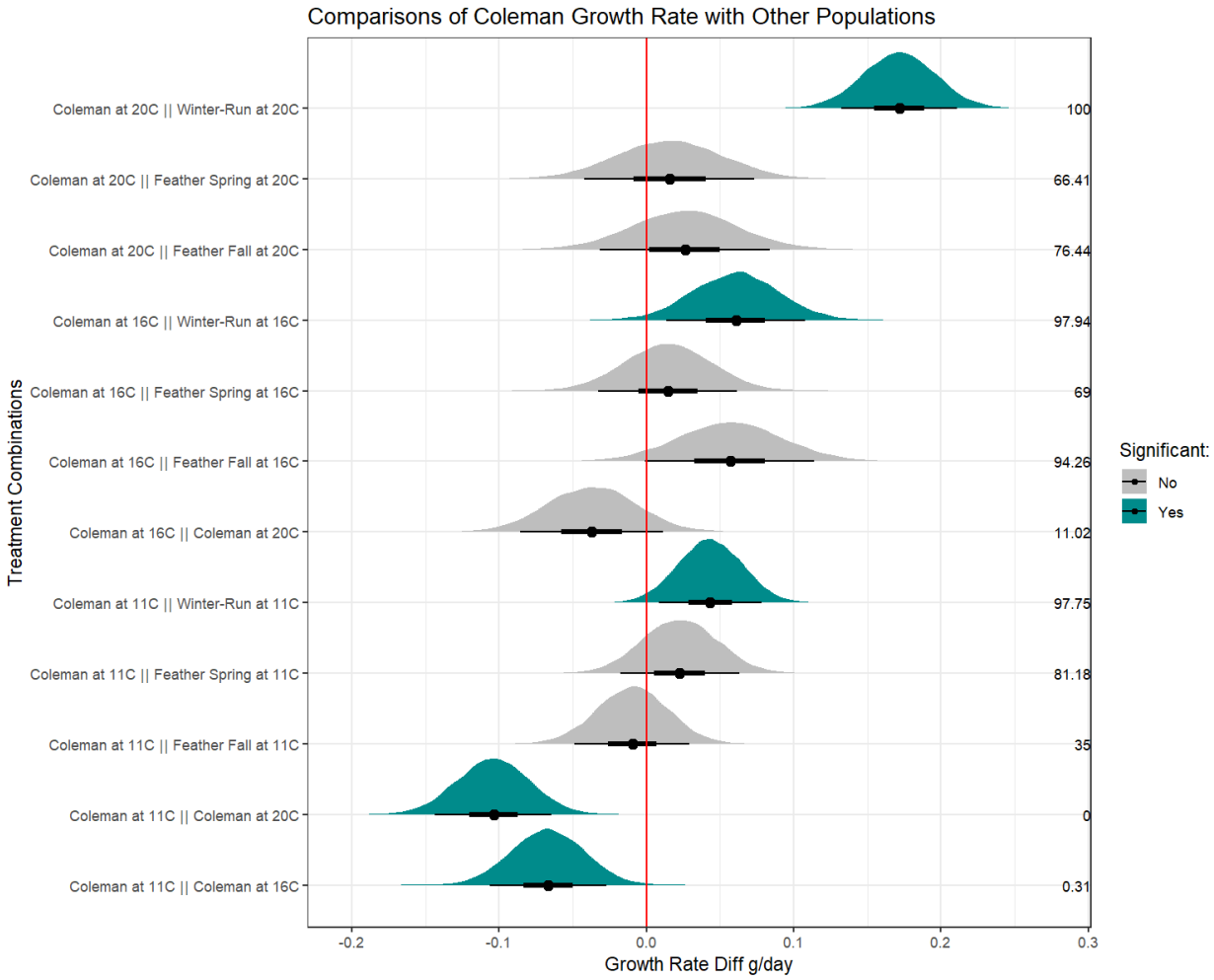
Supplemental Figure 2.2: Treatment Contrasts of CTMax values between Feather Fall-run Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



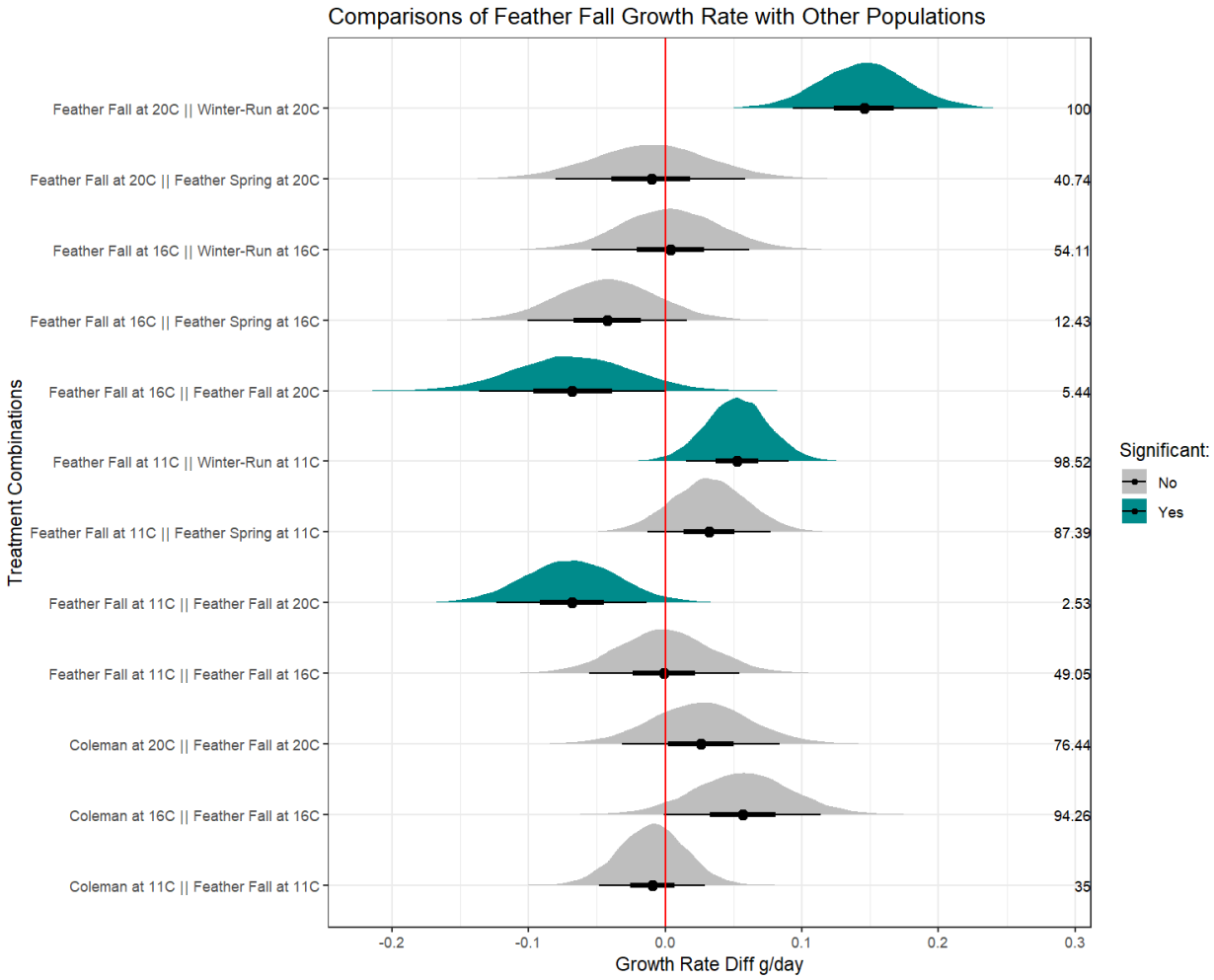
Supplemental Figure 2.3: Treatment Contrasts of CTMax values between Feather spring-run Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



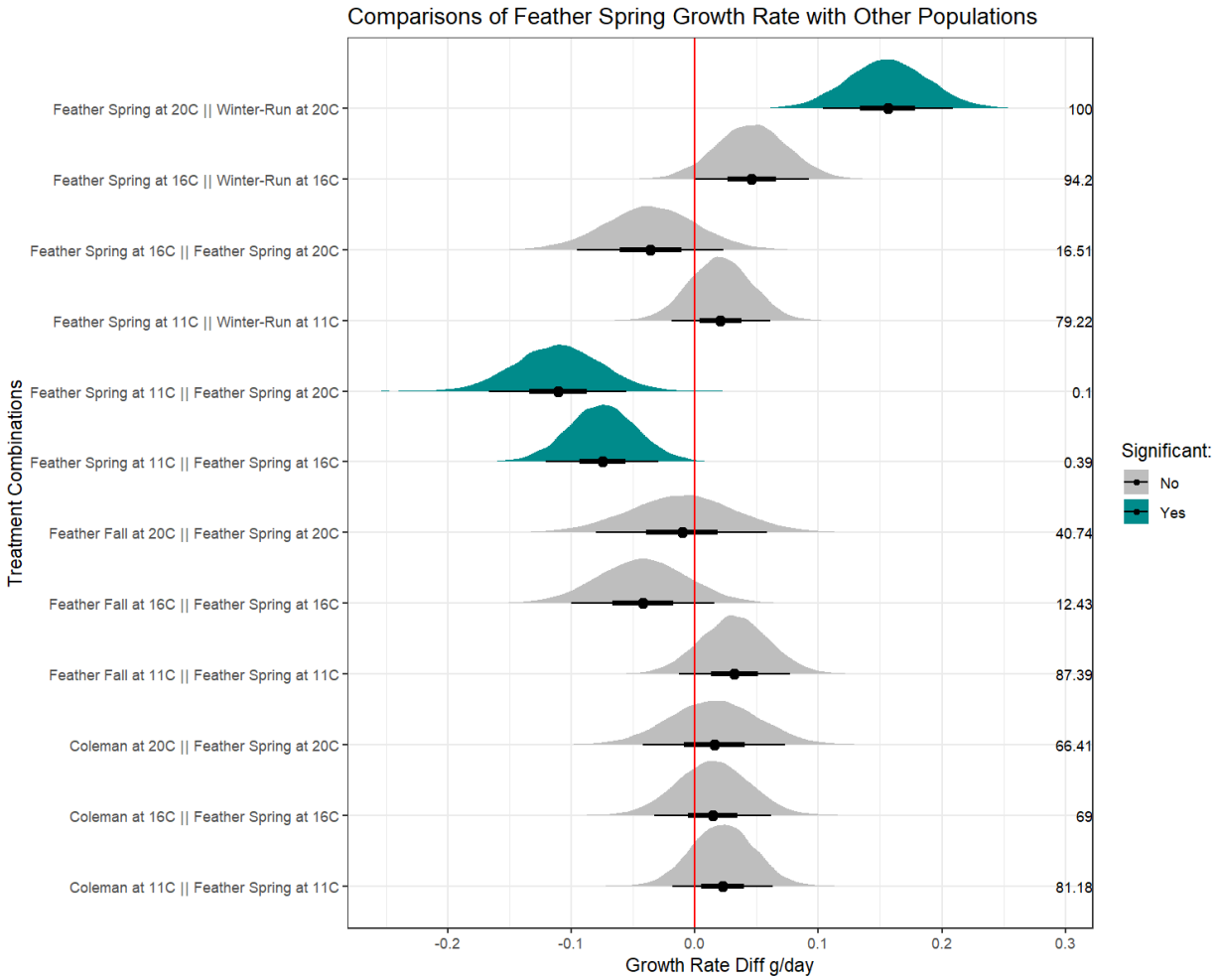
Supplemental Figure 2.4: Treatment Contrasts of CTMax values between Feather spring-run Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



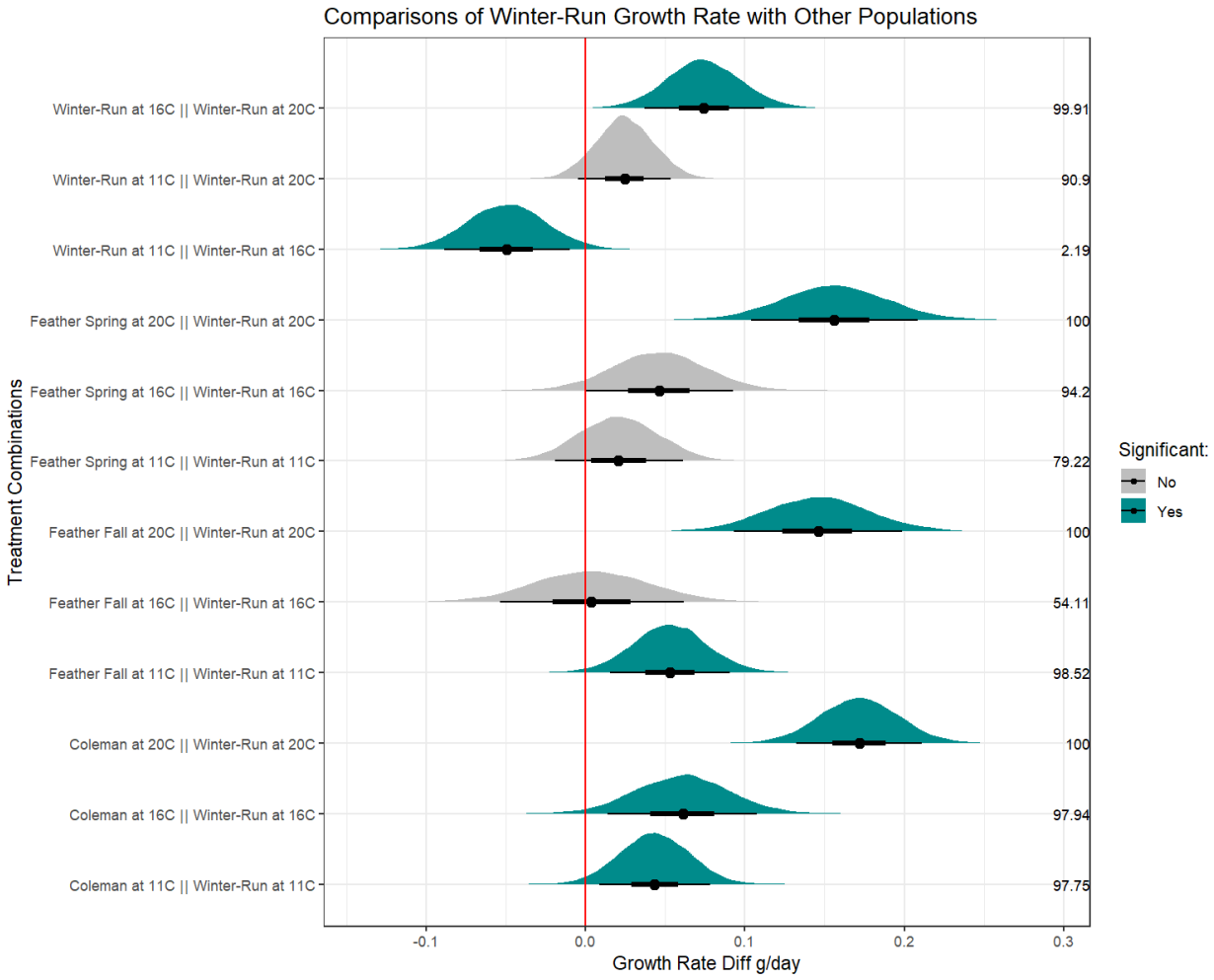
Supplemental Figure 2.5: Treatment Contrasts of Growth Rate estimates between Coleman Hatchery fall-run population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



Supplemental Figure 2.6: Treatment Contrasts of Growth Rate estimates between Feather Hatchery fall-run population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



Supplemental Figure 2.7: Treatment Contrasts of Growth Rate estimates between Feather Hatchery spring-run population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).



Supplemental Figure 2.8: Treatment Contrasts of Growth Rate estimates between winter-run population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line).

Supplemental Table 2.1: Summary table of all populations and test temperatures. Fish swam is the number of fish successful swam from each treatment group at each temperature. Mort. Is the number of mortalities at each temperature. Mass, fork length and condition factor are reported as the mean and standard deviation of the observed fish that underwent the trial.

Population	Acc. Temp. (°C)	Trial Temp. (°C)	Fish Swam (n=)	Mort. (n=)	Mass (g)	Fork Length (cm)	Condition Factor
Coleman	11	8	3	0	21.71 ± 5.202	12.4 ± 0.74	1.13 ± 0.064
Coleman	11	10	3	0	22.80 ± 4.017	12.7 ± 0.57	1.11 ± 0.048
Coleman	11	12	4	0	21.90 ± 4.850	12.3 ± 0.57	1.17 ± 0.101
Coleman	11	14	3	0	21.36 ± 1.437	12.4 ± 0.44	1.12 ± 0.043
Coleman	11	16	3	0	21.25 ± 1.241	12.3 ± 0.10	1.14 ± 0.039
Coleman	11	18	4	0	22.78 ± 2.912	12.5 ± 0.48	1.16 ± 0.060
Coleman	11	20	4	0	20.88 ± 2.799	12.4 ± 0.50	1.09 ± 0.041
Coleman	11	22	4	0	24.78 ± 8.844	12.9 ± 1.29	1.12 ± 0.059
Coleman	11	24	4	4	21.78 ± 1.919	12.5 ± 0.92	1.12 ± 0.144
Coleman	11	25	0	1	NA	NA	NA
Coleman	11	26	0	2	NA	NA	NA
Coleman	16	8	5	0	21.48 ± 3.102	12.4 ± 0.58	1.12 ± 0.025
Coleman	16	10	6	0	23.74 ± 2.249	12.8 ± 0.48	1.14 ± 0.026
Coleman	16	12	5	0	22.74 ± 2.250	12.6 ± 0.51	1.12 ± 0.030
Coleman	16	14	4	0	24.09 ± 3.640	12.7 ± 0.61	1.18 ± 0.030
Coleman	16	16	4	0	24.80 ± 3.670	12.8 ± 0.57	1.18 ± 0.032
Coleman	16	18	4	0	23.71 ± 4.613	12.6 ± 0.71	1.17 ± 0.045
Coleman	16	20	3	0	22.18 ± 0.029	12.4 ± 0.10	1.16 ± 0.029
Coleman	16	22	4	0	25.25 ± 5.335	12.8 ± 0.60	1.20 ± 0.081
Coleman	16	24	4	0	25.85 ± 4.045	12.9 ± 0.60	1.21 ± 0.023
Coleman	16	25	3	1	23.75 ± 1.001	12.6 ± 0.06	1.20 ± 0.067
Coleman	16	26	0	2	NA	NA	NA
Coleman	20	8	4	0	28.49 ± 4.864	13.3 ± 0.44	1.20 ± 0.105
Coleman	20	10	4	0	26.37 ± 8.441	12.8 ± 1.31	1.23 ± 0.026
Coleman	20	12	5	0	26.05 ± 2.488	12.7 ± 0.44	1.26 ± 0.040
Coleman	20	14	5	0	25.75 ± 4.298	12.8 ± 0.59	1.23 ± 0.049
Coleman	20	16	6	0	21.48 ± 3.107	12.2 ± 0.78	1.18 ± 0.070
Coleman	20	18	4	0	21.71 ± 3.132	12.2 ± 0.54	1.19 ± 0.020
Coleman	20	20	5	0	25.82 ± 1.213	12.8 ± 0.12	1.23 ± 0.045
Coleman	20	22	4	0	24.69 ± 1.073	12.8 ± 0.30	1.17 ± 0.080
Coleman	20	24	4	0	23.43 ± 0.898	12.5 ± 0.28	1.19 ± 0.040
Coleman	20	25	4	0	24.13 ± 3.628	12.4 ± 0.60	1.26 ± 0.046
Coleman	20	26	0	3	NA	NA	NA
Coleman	20	28	0	2	NA	NA	NA
Feather Fall	11	8	4	0	23.53 ± 2.729	12.7 ± 0.32	1.14 ± 0.047
Feather Fall	11	10	6	0	25.51 ± 2.599	13.2 ± 0.43	1.11 ± 0.028

Feather Fall	11	12	4	0	26.22 ± 2.817	13.0 ± 0.41	1.19 ± 0.067
Feather Fall	11	14	4	0	24.31 ± 3.586	13.0 ± 0.60	1.11 ± 0.025
Feather Fall	11	16	4	0	24.56 ± 1.163	12.9 ± 0.24	1.15 ± 0.073
Feather Fall	11	18	4	0	25.45 ± 1.405	12.8 ± 0.29	1.21 ± 0.019
Feather Fall	11	20	5	0	26.11 ± 2.897	13.2 ± 0.61	1.14 ± 0.040
Feather Fall	11	22	4	0	25.81 ± 2.321	13.2 ± 0.22	1.12 ± 0.073
Feather Fall	11	23	4	0	26.48 ± 3.665	13.3 ± 0.66	1.13 ± 0.043
Feather Fall	11	24	0	2	NA	NA	NA
Feather Fall	11	25	0	2	NA	NA	NA
Feather Fall	16	8	4	0	25.38 ± 3.828	12.8 ± 0.59	1.21 ± 0.035
Feather Fall	16	10	4	0	26.55 ± 3.280	12.8 ± 0.38	1.26 ± 0.057
Feather Fall	16	12	4	0	23.10 ± 2.067	12.5 ± 0.17	1.20 ± 0.07
Feather Fall	16	14	4	0	22.38 ± 2.402	12.3 ± 0.35	1.22 ± 0.079
Feather Fall	16	16	4	0	24.29 ± 2.272	12.9 ± 0.36	1.13 ± 0.044
Feather Fall	16	18	4	0	24.53 ± 3.461	12.8 ± 0.34	1.16 ± 0.067
Feather Fall	16	20	3	1	23.00 ± 1.433	12.7 ± 0.26	1.12 ± 0.044
Feather Fall	16	22	4	0	23.64 ± 1.222	12.8 ± 0.28	1.12 ± 0.033
Feather Fall	16	24	4	2	23.67 ± 1.788	12.7 ± 0.39	1.15 ± 0.042
Feather Fall	16	25	0	2	NA	NA	NA
Feather Fall	20	8	5	1	27.43 ± 8.765	12.6 ± 1.03	1.34 ± 0.12
Feather Fall	20	10	5	0	28.41 ± 3.991	12.7 ± 0.23	1.38 ± 0.153
Feather Fall	20	12	4	0	23.70 ± 3.536	12.2 ± 0.13	1.32 ± 0.186
Feather Fall	20	14	4	1	23.58 ± 1.810	12.5 ± 0.33	1.21 ± 0.078
Feather Fall	20	16	4	0	26.11 ± 2.283	12.8 ± 0.29	1.26 ± 0.112
Feather Fall	20	18	4	0	25.20 ± 1.410	12.7 ± 0.37	1.23 ± 0.095
Feather Fall	20	20	4	0	24.68 ± 3.467	12.5 ± 0.34	1.27 ± 0.081
Feather Fall	20	22	4	0	28.31 ± 4.113	12.8 ± 0.42	1.36 ± 0.103
Feather Fall	20	24	3	4	27.57 ± 2.317	12.7 ± 0.45	1.36 ± 0.034
Feather Fall	20	25	1	4	NA	NA	NA
Feather Fall	20	26	0	2	NA	NA	NA
Feather Spring	11	8	4	0	23.76 ± 2.635	12.9 ± 0.43	1.11 ± 0.064
Feather Spring	11	10	4	0	25.97 ± 3.748	13.1 ± 0.67	1.16 ± 0.140
Feather Spring	11	12	4	0	23.65 ± 1.545	12.7 ± 0.28	1.15 ± 0.051
Feather Spring	11	14	4	0	27.04 ± 4.168	13.1 ± 0.70	1.20 ± 0.057
Feather Spring	11	16	5	0	25.31 ± 1.636	13.1 ± 0.24	1.13 ± 0.024
Feather Spring	11	18	4	0	23.03 ± 4.017	12.6 ± 0.66	1.15 ± 0.030
Feather Spring	11	20	5	0	26.87 ± 3.531	13.6 ± 0.58	1.08 ± 0.122
Feather Spring	11	22	3	1	22.40 ± 0.480	12.6 ± 0.12	1.13 ± 0.050
Feather Spring	11	24	4	0	26.87 ± 1.651	13.1 ± 0.51	1.20 ± 0.085
Feather Spring	11	25	0	2	NA	NA	NA
Feather Spring	16	8	4	0	24.89 ± 3.429	12.9 ± 0.45	1.17 ± 0.063
Feather Spring	16	10	4	0	26.71 ± 7.358	13.1 ± 0.99	1.18 ± 0.058
Feather Spring	16	12	4	0	28.78 ± 4.806	13.4 ± 0.69	1.20 ± 0.036

Feather Spring	16	14	5	0	25.48 ± 6.227	12.9 ± 0.75	1.18 ± 0.091
Feather Spring	16	16	4	0	24.30 ± 4.555	12.9 ± 0.53	1.13 ± 0.113
Feather Spring	16	18	4	0	23.75 ± 3.099	12.8 ± 0.56	1.12 ± 0.039
Feather Spring	16	20	4	0	20.21 ± 1.761	12.2 ± 0.54	1.11 ± 0.063
Feather Spring	16	22	4	0	24.45 ± 2.030	12.9 ± 0.3	1.13 ± 0.038
Feather Spring	16	24	4	1	27.72 ± 3.502	12.9 ± 0.43	1.28 ± 0.127
Feather Spring	16	25	0	2	NA	NA	NA
Feather Spring	20	8	4	0	27.09 ± 3.081	12.5 ± 0.39	1.40 ± 0.107
Feather Spring	20	10	5	2	26.03 ± 7.832	12.4 ± 1.21	1.32 ± 0.042
Feather Spring	20	12	5	1	25.67 ± 5.063	12.6 ± 0.57	1.28 ± 0.099
Feather Spring	20	14	4	0	23.54 ± 2.143	12.3 ± 0.17	1.26 ± 0.083
Feather Spring	20	16	4	0	22.54 ± 3.042	12.3 ± 0.52	1.21 ± 0.051
Feather Spring	20	18	4	0	27.40 ± 2.481	12.9 ± 0.26	1.29 ± 0.080
Feather Spring	20	20	5	1	22.76 ± 2.18	12.2 ± 0.45	1.27 ± 0.084
Feather Spring	20	22	4	1	23.25 ± 1.666	12.3 ± 0.10	1.24 ± 0.113
Feather Spring	20	24	4	4	23.48 ± 3.117	12.4 ± 0.48	1.23 ± 0.089
Feather Spring	20	25	0	3	NA	NA	NA
Feather Spring	20	26	0	4	NA	NA	NA
Winter-Run	11	8	4	0	20.79 ± 3.108	11.9 ± 0.45	1.24 ± 0.086
Winter-Run	11	10	4	0	22.14 ± 1.622	12.4 ± 0.29	1.16 ± 0.071
Winter-Run	11	12	4	0	20.67 ± 1.326	12.1 ± 0.29	1.16 ± 0.138
Winter-Run	11	14	4	0	23.12 ± 3.504	12.3 ± 0.28	1.24 ± 0.138
Winter-Run	11	16	5	0	21.89 ± 1.318	12.3 ± 0.38	1.17 ± 0.073
Winter-Run	11	18	4	0	23.04 ± 2.351	12.2 ± 0.43	1.27 ± 0.097
Winter-Run	11	20	4	0	19.98 ± 1.920	12.2 ± 0.42	1.11 ± 0.103
Winter-Run	11	22	4	0	20.81 ± 2.831	12.0 ± 0.42	1.20 ± 0.115
Winter-Run	11	23	4	1	21.95 ± 1.700	12.5 ± 0.29	1.13 ± 0.127
Winter-Run	11	24	2	3	21.30 ± 1.054	12.2 ± 0.49	1.20 ± 0.205
Winter-Run	11	25	0	2	NA	NA	NA
Winter-Run	16	8	6	0	24.09 ± 1.123	12.8 ± 0.23	1.16 ± 0.020
Winter-Run	16	10	4	0	22.84 ± 1.667	12.3 ± 0.36	1.23 ± 0.069
Winter-Run	16	12	4	0	19.15 ± 2.319	11.8 ± 0.33	1.17 ± 0.082
Winter-Run	16	14	4	0	21.37 ± 2.433	12.3 ± 0.47	1.16 ± 0.052
Winter-Run	16	16	4	0	20.67 ± 1.301	12.3 ± 0.14	1.11 ± 0.035
Winter-Run	16	18	4	0	19.54 ± 1.127	12.0 ± 0.36	1.12 ± 0.041
Winter-Run	16	20	4	0	19.40 ± 1.860	12.0 ± 0.60	1.14 ± 0.064
Winter-Run	16	22	6	0	21.75 ± 3.849	12.3 ± 0.56	1.17 ± 0.075
Winter-Run	16	24	4	0	21.86 ± 2.538	12.3 ± 0.39	1.18 ± 0.039
Winter-Run	16	25	4	2	22.37 ± 0.504	12.2 ± 0.22	1.23 ± 0.050
Winter-Run	16	26	0	2	NA	NA	NA
Winter-Run	20	8	4	0	24.93 ± 3.417	12.4 ± 0.43	1.30 ± 0.096
Winter-Run	20	10	4	0	23.45 ± 4.845	12.3 ± 0.81	1.26 ± 0.044
Winter-Run	20	12	4	0	18.21 ± 3.502	11.6 ± 0.83	1.17 ± 0.057

Winter-Run	20	14	4	0	21.95 ± 3.046	12.0 ± 0.44	1.28 ± 0.055
Winter-Run	20	16	5	0	18.21 ± 4.027	11.3 ± 0.65	1.24 ± 0.070
Winter-Run	20	18	4	0	24.05 ± 7.132	12.8 ± 0.72	1.13 ± 0.181
Winter-Run	20	20	4	0	20.63 ± 2.824	11.9 ± 0.61	1.21 ± 0.049
Winter-Run	20	22	6	0	19.57 ± 6.796	11.8 ± 1.24	1.18 ± 0.169
Winter-Run	20	24	3	2	18.07 ± 4.663	11.6 ± 0.81	1.15 ± 0.068
Winter-Run	20	25	4	0	23.10 ± 1.929	12.5 ± 0.81	1.18 ± 0.134
Winter-Run	20	26	0	2	NA	NA	NA

Chapter 3

Physiological variation among Chinook salmon populations indicates local thermal adaptation

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Abstract

Interpopulation variation is a consequence of genetic variation and environment-induced plasticity spread across heterogeneous landscapes. Identifying thermal physiological trait diversity among populations is important to predicting species responses to climate change. A growing body of literature has revealed interpopulation variation among several species of Pacific salmonid, with population traits reflecting temperature regimes or migration routes specific to population, and consistent with local adaptation. In contrast, countergradient variation (trait evolution opposite of phenotypic gradient) among populations may reduce phenotypic variation along a gradient (e.g. water temperature, growing season). Interpopulation variation has been observed in critical thermal maxima, growth rate and metabolic capacity, highlighting the potential for selective pressures to influence thermal physiology. Our experiment sought to determine the extent of interpopulation variation among six populations of fall-run Chinook salmon from California, Oregon and Washington (USA). We acclimated juvenile fish to three temperatures and tested five physiological metrics (critical thermal maxima, growth rate, routine metabolic rate, maximum metabolic rate and aerobic scope). We assessed statistical associations between our five physiological traits and 15 environmental predictors to test hypotheses of local adaptation and countergradient variation. Our experimental results support local adaptation, wherein populations from warmer habitats exhibit higher critical thermal maxima and faster growth when acclimated to warm temperatures. Among metabolic traits we also find positive associations between migration distance and metabolic capability, indicating that populations with longer migrations may have higher metabolic capacity. These results are valuable for predicting the response of juvenile Chinook salmon to environmental change and for implementing more efficacious conservation strategies.

Introduction

A core pursuit in ecology is the investigation of biological variation. Manifestations of variation between or within species can provide valuable insight into how organisms optimize fitness and maintain physiological homeostasis in response to environmental pressures. Such variation among populations may highlight local adaptation of populations to unique environmental conditions (Eliason *et al.*, 2011; Fangue *et al.*, 2006; Lonsdale & Levinton, 1985; Nyboer *et al.*, 2020; Ridgway, 2001). Local adaptation among populations is a result of selective pressures applied to genetic variation across an environmentally heterogeneous landscape (Blanquart *et al.*, 2013), and in general, local adaptation leads to increased fitness for a population under environmental conditions specific to its point of origin (Blanquart *et al.*, 2013; Kawecki & Ebert, 2004). For example, populations from warm range boundaries may perform better in warm environments than populations from cold range boundaries. Alternatively, phenotypic variation among populations may operate to counter the effects of an environmental cline. So-named countergradient variation exists when the evolutionary response along an environmental gradient compensates for the phenotypic effect of that gradient, reducing the phenotypic variance among populations (Conover & Schultz, 1995; Levins, 1969). For instance, populations from high latitudes may grow faster than populations from low latitudes to compensate for a shortened growing season. This is a particular form of interpopulation variation, where observed population variation on the landscape is small or absent, but emerges when populations are reared under shared conditions. Countergradient variation has been documented in response to multiple environmental factors, including temperature, latitude, and the presence or absence of competitors (Arendt & Wilson, 1999; Conover & Present, 1990; Levins, 1969). Finally, interpopulation variation may also manifest as reversible plastic changes,

with populations acclimatizing to local conditions (Via *et al.*, 1995). While reversible plastic responses typically would not be considered evidence of local adaptation, studying populations acclimated to a shared range of environmental conditions can reveal environment-dependent variation in physiological traits, as well as the population-specific differences in their capacity to acclimate, manifested as population-specific reaction norms (Eliason *et al.*, 2011; Schulte *et al.*, 2011). Historical assumptions of physiological similarities among populations or species may not be appropriate if future environmental conditions lead to divergent outcomes due to local adaptation, countergradient variation or acclimation capacity. Identifying if phenotypic variation is present and its cause (i.e., local adaptation or countergradient variation) is necessary to accurately predict species' responses to rapid environmental change.

Environmental temperature has profound influence over the biology and ecology of ectothermic organisms as temperature defines their physiological and behavioral responses (Angilletta *et al.*, 2002; Huey & Stevenson, 1979). In response to a warming environment species individual organisms can respond to changes in the thermal landscape through behavioral thermoregulation and physiological acclimatization (Crozier & Hutchings, 2014). Extended exposure to warming may induce individual responses that increase fitness (Sandblom *et al.*, 2016; Stillman, 2003) and, given variation and time, species may evolve to tolerate novel thermal conditions (Chen *et al.*, 2015; Hoffmann & Weeks, 2007). Identifying species-specific responses to changes in the thermal landscape, and the temporal scale upon which they act, can allow prediction of species' responses to climate change (Jeffree & Jeffree, 1996; Schulte *et al.*, 2011; Scott & Poynter, 1991). However, individual populations may possess unique traits that result in unpredictable responses.

Variation in physiological plasticity among populations may highlight important physiological trade-offs relevant to predicting species' outcomes under future environmental conditions. Adaptation, acclimatization, or acclimation to thermal conditions can lead to trade-offs in physiological performance (Comte & Olden, 2017; Feder, 1978; Stillman, 2003). For example, porcelain crab (*Petrolisthes* spp.) species from lower latitudes are capable of greater thermal tolerance but possess reduced acclimation capacity (Stillman 2003). For species already existing near their thermal limits, limited acclimation capacity would prevent further physiological response to protect against environmental warming. Furthermore, along a latitudinal gradient local adaptation or countergradient variation may lead to divergent outcomes as the environment warms. Local adaptation to warm temperatures at low latitudes may provide for resilience to future warming, whereas locally adapted, high-latitude, cold-temperature physiologies may be unable to tolerate future warming. Alternatively, if populations exhibit countergradient variation, high-latitude populations may improve their performance relative to their low-latitude counterparts. The mixed responses of interpopulation variation to environmental change challenges our capability to predict species' responses and promote efficacious conservation actions (Gayeski *et al.*, 2018; Zillig *et al.*, 2021).

Pacific salmonids (*Oncorhynchus* spp.) are a commercially and culturally important clade of climate-vulnerable species which require a population-specific approach for effective conservation. The specificity at which anadromous adults migrate to their respective natal streams reduces gene flow among populations (Quinn, 2018), allowing for neutral genetic divergence as well as the evolution of population-specific traits that maximize fitness in local environmental conditions. Genetic analysis of steelhead trout, an anadromous form of *O. mykiss,* found habitat characteristics such as migration distance, as well as slope and aspects of river

temperature, were associated with genetic markers of population differentiation (Micheletti et al. 2018). Work on Fraser River adult sockeye salmon (*O. nerka*) revealed that intraspecific variation in cardiac and metabolic physiology was associated with river temperatures and migration route difficulty (Eliason *et al.*, 2011). Complementary work on embryos and juveniles from the same Fraser River populations identified signals of local adaptation in thermal tolerance and cardiac capacity (Chen *et al.*, 2013). Work on two populations of redband trout (*O. mykiss gairdneri*) identified adaptive, population-specific traits in temperature-dependent cardiac performance and respiration (Chen *et al.*, 2018; Garvin *et al.*, 2015). There is also evidence for countergradient variation among salmonids. Countergradient variation in standard metabolic rate across stream temperatures was observed among six populations of brown trout (*Salmo trutta*) fry (Álvarez *et al.*, 2006). Two studies have found evidence for countergradient variation across latitude in growth rate among populations of arctic char (*Salvelinus alpinus*) (Chavarie *et al.*, 2010; Sinnatamby *et al.*, 2015). However, research on four populations of lake trout (*S. namaycush*) found no population-level differences in CTMax or other metabolic traits, indicating that interpopulation variation among salmonids is not always observed (Kelly *et al.*, 2014).

Anthropogenic modification of freshwater ecosystems and the global impacts of climate change endanger the persistence of Pacific salmonid populations (Martins *et al.*, 2011; Moyle *et al.*, 2017; Reid *et al.*, 2019). Drivers of species decline include habitat degradation, overexploitation, and flow modification (Dudgeon *et al.*, 2006; Reid *et al.*, 2019). Salmonids are considered cold water species, and increasingly warm river temperatures, persistent droughts, non-native species, and novel pathogens further exacerbate risk to salmonids both regionally and globally (Lehman *et al.*, 2020; Mauduit *et al.*, 2022; Moyle *et al.*, 2017; Reid *et al.*, 2019). Ensuring effective conservation of remaining populations and their associated biological

diversity requires an understanding of intraspecific variation among Chinook salmon populations.

Chinook salmon are commonly delineated into evolutionary significant units (ESUs), grouped by shared genetics, regional associations and life-history strategies (Waples, 1995). The greatest concentration of at-risk salmonids is in California where 23 of 31 (74%) of native salmonid ESUs are likely to be extinct in the next century (Moyle *et al.*, 2017). Additionally, a 2007 survey of pacific salmon populations in the western contiguous United States found that 29% of populations have been lost since Euro-American contact (Gustafson *et al.*, 2007). Of the six species of anadromous pacific salmonids, Chinook salmon (*O. tshawytscha*) have lost the greatest number of populations (159 of an estimated 396, 40%).

Chinook salmon exhibit impressive diversity in life-history strategies with well-documented variation in phenology and age of both returning adults and outmigrating juveniles (Bourret *et al.*, 2016; Brannon *et al.*, 2004; FitzGerald *et al.*, 2020). Of the four seasonal migratory phenotypes of Chinook salmon, fall-run is the dominant hatchery produced strain in California, Oregon and Washington (USA), and most accessible streams harbor a wild fall-run population. All seasonal runs of Chinook salmon are semelparous, with adult fall-run fish returning to freshwater in the fall and spawning quickly upon returning to their natal reaches. Fall-run juveniles typically rear in freshwater for several months and outmigrate to the ocean during their first spring.

This study assessed patterns in interpopulation variation among six fall-run Chinook salmon populations (from five distinct ESUs) and tested hypotheses of local adaptation, countergradient variation and physiological trade-offs among physiological traits. Chinook

salmon juveniles were reared at three ecologically relevant temperatures (11, 16 and 20°C; FitzGerald *et al.*, 2020) and five physiological metrics were assessed.

Growth rate is a common, temperature dependent, holistic physiological trait which varies among populations (Bærum *et al.*, 2016; Forseth *et al.*, 2009; Sogard *et al.*, 2012) and is used by resource managers to assess habitat suitability for salmonids (Marine & Cech, 2004; Myrick & Cech, 2001). Similarly, CTMax is a widely applied and standardized physiological metric of acute thermal tolerance and acclimation capacity. Aerobic scope is the difference between an organism's minimum and maximum aerobic metabolic rates, and quantifies the organism's energetic capacity. In ectotherms, aerobic scope is temperature dependent, and evaluating aerobic scope across a temperature window provides insight into how organisms may respond to changes in the thermal environment (Schulte, 2015). Past research has used these physiological metrics to assess local adaptation and countergradient variation (Chen *et al.*, 2013, 2015; Eliason *et al.*, 2011; Fangue *et al.*, 2006, 200; Poletto *et al.*, 2017; Unwin, 1997; Verhille *et al.*, 2016).

We predicted that Chinook salmon would exhibit interpopulation variation associated with habitat characteristics (e.g. temperature, migratory distance). Additionally, we tested for relationships between physiological trait values and 15 environmental parameters including latitude, migration route length, river slope, and multiple temperature characteristics specific to the rearing ranges of each population. Should populations be locally adapted we would expect greater thermal performance (e.g. increased CTMax, greater warm-acclimated aerobic capacity, etc.) from populations from warmer habitats as observed in past research (Chen et al., 2015, 2018; Eliason et al., 2011). Interpopulation variation in growth rate has been shown to reflect local adaptation (Handelsman et al., 2013; Rikardsen & Elliott, 2000) or countergradient

variation (Conover & Present, 1990; Kokita, 2004; Sinnatamby *et al.*, 2015). If populations exhibit countergradient variation across latitude, then northern populations should exhibit accelerated growth relative to southern populations to compensate for the shortened growing season at higher latitudes. Finally, capacity to acclimate is also an inheritable trait (Schlichting & Pigliucci, 1993; Via *et al.*, 1995), and we may expect to find trade-offs in acclimation capacity and overall thermal performance (Stillman, 2003), with more warm-tolerant Chinook salmon populations exhibiting a reduced capacity to acclimate.

Methods

Fall-run Chinook salmon from six hatchery populations (Table 3.1) were reared under a common-garden design with each population held to the same set of acclimation temperatures (11, 16, and 20°C), for a total of 18 treatment groups. These temperatures were chosen to be ecologically relevant to the conditions that a juvenile Chinook salmon may encounter during its rearing and outmigration through the Central Valley, CA (FitzGerald *et al.*, 2020). We conducted this study from 2017- 2019 testing 2 or 3 populations per year. This research was approved by the Institutional Animal Care and Use Committee of UC Davis (Protocol # 19928).

Environmental Data

We tested for relationships between physiological performance and 15 environmental parameters including latitude, migration distance, river slope, and multiple temperature characteristics specific to the rearing ranges of each population (Table 3.2). Latitude often serves as a proxy for other environmental predictors (e.g. temperature, growing season length) and is used as a predictor of physiological performance and interpopulation variation among teleosts (Conover & Present, 1990; Fangue *et al.*, 2006; Stitt *et al.*, 2014). However, latitude may not capture relevant landscape drivers of physiological traits, for example migration distance.

Therefore, we also examined associations between migration distance and average slope of a migratory route. Latitude and the elevation of the source hatchery was determined through google earth. Migration distance was calculated using the R package 'dataRetrieval' which provides access to US Geological Survey hydrological data. Migration slope was calculated by dividing the elevation of a population's hatchery by its migration distance.

We used the modified NorWeST temperature model developed by FitzGerald *et al* (2020) to construct temperature profiles for each hatchery population based upon the associated wild juvenile rearing habitat (see Discussion for hatchery caveats). From this data we isolated the maximum, minimum and average temperature across a calendar year as well as temperature limited by the months of juvenile rearing specific to each population. We used observed population-specific distributions of spawning and rearing to quantify occupied reaches (FitzGerald et al., 2020). Mean monthly stream temperature (average of 2002-2011) was determined for each river kilometer within a population's occupied reach. Annual mean, maximum and minimum stream temperatures were then calculated for each population; note that temperature metrics are based on the monthly mean. Additionally, for each population we isolated the months of juvenile rearing and calculated the maximum and average stream temperatures within this timeframe. Finally, we identified the maximum temperature experienced by each population during peak emergence and the subsequent month, when fry are generally still near the spawning grounds.

Additionally, as most of our hatchery populations are limited by an adjacent dam, we modeled the same thermal characteristics on the stream reaches immediately upstream the dam or hatchery as a coarse approximation of pre-dam thermal regimes for each population. We identified historical habitat as formerly accessible reaches above existing dams where spawning

was documented (Yoshiyama *et al.*, 2001) or as physiologically bounded by slope, flow or intermittency (Agrawal *et al.*, 2005; Bjornn & Reiser, 1991; Isaak *et al.*, 2017). Once reaches were isolated, the same six thermal metrics were calculated, providing twelve total metrics of habitat temperature (Table 3.2).

Fish Husbandry

The six studied populations arise from five defined Chinook salmon ESUs (Moyle *et al.*, 2017; Waples *et al.*, 2001): The Feather and Coleman populations arise from the California Central Valley fall-run ESU; the Trinity population from the Upper Klamath-Trinity Rivers fall-run ESU; the Elk River population from the Southern Oregon and Northern California coastal ESU, the Trask population from the Oregon coastal ESU, and the Priest Rapids population from the Upper Columbia fall-run ESU.

Fish from the Priest Rapids fish hatchery were received as eyed eggs via overnight mail and upon arrival surface sterilized with iodophore. Fish from the Coleman population were acquired as eggs and did not receive iodophore treatment. All fish were reared at the Center for Aquatic Biology and Aquaculture at UC Davis (CABA). Eggs and hatched alevin were incubated at 9°C until the start of exogenous feeding. Fish from all other populations were acquired from their respective hatcheries when of transportable size (~1-2g) and trucked to the CABA in a 765-L tank. Temperature and dissolved oxygen were monitored during the transport to ensure fish did not experience stressful hypoxic or thermal conditions. Once at CABA, fry from all populations were reared at 11-13°C until distributed into their acclimation treatment tanks. Fish were fed *ad libitum* rations which were updated biweekly throughout the experiment to account for fish growth and tank density. Acclimation temperatures were achieved by increasing tank temperature by ~1.5°C per day. Once tanks achieved their specific acclimation temperature (11,

16, or 20°C), fish were acclimated for three weeks prior to any experimental data collection. Tank temperatures were maintained for the duration of the experiments (4-7 months).

Growth

Growth measurements were conducted biweekly until CTMax and metabolic experiments began. CTMax and metabolic experiments necessitated size-selection and therefore biased any further collection of growth data. Fish were measured by first taking an arbitrary sample of 30 fish from each treatment (n=15 per tank, n = 2149 total measurements). Fish were gently netted from their treatment tank and transferred to an aerated five-gallon bucket until measured, at which point they were air exposed for ~15-20 seconds to measure mass (± 0.1 grams, Ohaus B3000D) and fork length (± 0.1 cm). After measurement, fish were returned to a second aerated bucket for recovery and then returned to their original rearing tank. Fish were netted and measured by the same experimenter across all sampling days. Fish were not individually marked and therefore growth rate was calculated at the treatment level. Time was defined as days since the first measurement point. Population specific growth criteria are contained in Table 3.3. Growth rate was modeled as the linear change in mass over time.

Critical Thermal Maximum

CTMax values were quantified according to established methods, briefly described below (Becker & Genoway, 1979). We placed six 4L Pyrex beakers in a fiberglass bath tray (1m x 2m x .2m). Beakers were aerated with an air stone to ensure both adequate oxygen saturation and circulation of water within the beaker. The volume of water in each individual beaker (approx. 2.5 L) was calibrated to ensure even heating across all CTMax beakers (0.33°C/min). Two pumps (PM700, Danner USA) were used to circulate water: one pump recirculated water across three heaters (Process Technology S4229/P11), while the other distributed heated water through

the CTMax bath via a distribution manifold. Experiments began with water temperature set at the fish's acclimation temperatures (11, 16 or 20°C).

Fish of appropriate size (n = 377, 12.4 ± 0.83 cm) were arbitrarily selected from treatment tanks and transferred to separate tanks for fasting. To ensure fish were in a similar postprandial state, fish reared at 20°C and 16°C were fasted for 24 hours and 11°C fish were fasted for 48 hours to account for their slower metabolic rate. Once fasted, fish were individually netted and transferred into individual beakers within the CTMax heat bath. Fish were given 30 minutes to acclimate to their CTMax beaker after which the CTMax trial began.

During the CTMax trial, beaker temperature was taken every 5 minutes using a thermocouple (Omega HH81A). Thermocouple measurements were calibrated to a Fisherbrand® NIST certified mercury thermometer following each trial. Fish were observed continually for signs of distress and loss of equilibrium. The CTMax trial endpoint was loss of equilibrium, at which point the temperature of the CTMax beaker was recorded (Beitinger *et al.*, 2000; Fangue *et al.*, 2006). Fish were then removed and retuned to a recovery bath at their acclimation temperature. Fish that did not fully recover within 24-hours were not included in analysis (6% of individuals, n = 23). After the 24-hr recovery, fish were weighed (wet mass ± 0.01g) and (fork length ± 0.1 cm).

Metabolic Experiments

Respirometry

Fish (n = 710, 23.92 ± 4.25 g) underwent metabolic trials in one of four, 5 L automated swim tunnel respirometers (Loligo, Denmark). The four tunnels were split into two paired systems with two tunnels sharing a single sump and heat pump. Water for each swim tunnel system was pumped (PM700, Danner USA) from the designated sump into an aerated water bath

surrounding each swim tunnel which overflowed down a drain and returned to the sump. Sump water was supplied with non-chlorinated fresh water from a designated well and aerated with air stones. The temperature of the sump (and therefore the swim tunnels) was maintained by circulating water through a heat pump (model DSHP-7; Aqua Logic Delta Star, USA) and pumping it back to the sump using a high-volume water pump (Sweetwater SHE 1.7 Aquatic Ecosystems, USA). In addition, each sump contained an 800 W titanium heater (TH-800; Finnex, USA) connected to a thermostatic controller. Water temperature within the swim tunnels was maintained to a precision of ±0.5°C. Swim tunnels and associated sump systems were cleaned and sanitized with bleach weekly to reduce potential for bacterial growth.

Dissolved oxygen saturation within the swim tunnels was measured using fiber-optic dipping probes (Loligo OX11250) which continuously recorded data via AutoResp™ software (version 2.3.0). Oxygen probes were calibrated weekly using a two-point, temperature-paired calibration method. Water velocity of the swim tunnels was quantified and calibrated using a flowmeter (Hontzcsh, Germany) and regulated using a variable frequency drive controller (models 4x and 12K; SEW Eurodrive, USA). The velocity (precision <1 cm s^{-1}) for each tunnel was controlled remotely using the Autoresp™ program and a DAQ-M data acquisition device (Loligo, Denmark). Swim tunnels were surrounded by shade cloth to reduce disturbance of the fish. Fish were remotely and individually monitored using infrared cameras (QSC1352W; Q-see, China) connected to a computer monitor and DVR recorder.

Oxygen consumption rates for both routine and maximal metabolic rates were captured using intermittent respirometry (Brett, 1964). A flush pump (Eheim 1048A, Germany) for each tunnel pumped aerated fresh water through the swim chamber and was automatically controlled via the AutoResp™ software and DAQ-M system. This system would seal the tunnel and enable

the measurement of oxygen consumption attributable to the fish. Oxygen saturation levels were not allowed to drop below 80% and were restored within three minutes once the flush pump was activated. Oxygen saturation data from AutoResp™ was transformed to oxygen concentration using the following equation:

Equation 3.1: $$[O_2] = \frac{\%O_2Sat}{100} \times \alpha(O_2) \times BP$$

Where $\%O_2Sat$ is the oxygen saturation percentage reported from AutoResp™; $\alpha(O_2)$ is the coefficient temperature-corrected oxygen solubility ($mgO_2\ L^{-1}\ mmHg^{-1}$); and *BP* is the barometric pressure (mmHg). Oxygen concentration (milligrams of oxygen per liter) was measured every second and regressed over time; the coefficient of this relationship (milligrams of oxygen per liter per second) was then converted to metabolic rate (milligrams of oxygen per kilogram per minute, Equation 3.2).

Equation 3.2: $$MR = R \times V \times M^{-1} \times 60$$

Where *R* is calculated coefficient of oxygen over time; *V* is the volume of the closed respirometer; *M* is the mass of the fish in kilograms and *'60'* transforms the rate from per second to per minute. An allometric scaling exponent was not incorporated due to similarity in fish sizes and to maximize comparability with the existing dataset on metabolism from the Mokelumne Hatchery (CA) fall-run population (Poletto *et al.*, 2017).

Routine Metabolic Rate (RMR)

Prior to routine metabolic rate (RMR) trials fish were fasted to ensure a post-prandial state using the same methods as for the CTMax trials. Fish were then transferred into a swim tunnel respirometer between 13:00 and 17:00. Fish were provided a 30-minute acclimation period at their acclimation temperature before the temperature was adjusted at 2°C h^{-1} from the acclimation temperature (11, 16 or 20°C) to the swimming temperatures (8, 10, …, 22, 24, 25,

26°C). Automated intermittent flow respirometry began 30 minutes after the swimming temperature was achieved and continued overnight. Measurement periods ranged between 900 to 1800 seconds in duration, flush periods were 180-300 seconds. Measurement and flush periods varied in length to accommodate for fish mass and swimming temperature, ensuring oxygen saturation was kept high (>80%) during the overnight trial. A small circulation pump (DC30A-1230, Shenzhen Zhongke, China) ensured that water was mixed within the tunnel without disturbing the fish. Fish activity was monitored by overhead infra-red cameras and measurement periods where the fish were active were discarded. RMR was calculated by averaging the three lowest RMR values (Poletto *et al.*, 2017). RMR experiments (n = 710) were concluded between 08:00±40 minutes.

Maximum Metabolic Rate (MMR)

After RMR measurements, we implemented a modified critical swimming velocity protocol to elicit maximal metabolic rate (MMR) from each fish (Poletto *et al.*, 2017). Tunnel speed was increased gradually from 0 to 30 cm s^{-1} over an ~2 min period and held for 20 min. For each subsequent 20-min measurement period, tunnel velocity was increased 10% up to a maximum of 6 cm s^{-1} per step. Fish were swum until exhausted and unable to swim or avoid impingement. Swimming metabolism was measured by sealing the tunnel for approximately 16 minutes of the 20-minute measurement period. Oxygen levels within the tunnel were not allowed to drop below 80%. When a fish became impinged upon the back screen (>2/3 of body in contact with screen) the tunnel velocity was stopped for ~1 minute and then gradually returned to the original speed over two minutes. A fish was determined to be exhausted if it became impinged twice within the same velocity step. At this point the tunnel propeller was turned off and the chamber was flushed to allow for recovery. The highest metabolic rate measured over a

minimum of 5 minutes during active swimming activity was taken as the MMR. Aerobic scope (AS) was calculated as the difference between a fish's RMR and MMR.

Post-experiment the tunnel was returned to the acclimation temperature and fish were transferred to a recovery tank and monitored. After a 24-hour recovery period fish were euthanized in a buffered solution of MS-222 (0.5g/L). Measurements for mass (g), fork length (cm) and total length (cm) were taken, and Fulton's condition factor was calculated. In seeking evidence of metabolic collapse at near-critical temperatures, some metabolic trials were conducted at temperatures exceeding the tolerance of the fish. These mortality events represent potential lethal upper limits for sub-acute thermal persistence (Supplemental Table 3.1). Data from fish which did not survive the trial or recovery were not used in analysis.

Statistical Analyses

We developed separate generalized linear mixed models (GLMMs) for each of the five physiological traits (CTMax, Growth Rate, RMR, MMR and AS) to estimate mean treatment responses. All models assumed a Gaussian distribution for the response variable mean and uninformed priors. All models included population and acclimation temperature as interacting categorical fixed predictors. Additional predictor variables and random effects were included depending on the response variable and model fit (see below). Stepwise model selection was used to identify the model with the lowest widely applicable information criteria (WAIC) to avoid overfitting (See supplementary materials for final models). Models were visually checked for fit with the packages *ggplot2* (Wickham, 2016) and *tidybayes* (Kay, 2020). All statistical analyses were conducted in R (version 4.0.2) using the package *brms* (Bürkner, 2017, 2018) to construct Bayesian GLMMs.

Each physiological model was slightly different to maximize fit. The final CTMax model additionally included fixed effects for fish mass and age (days post hatch). The final growth rate model incorporated mass as a linear function of time with an additional fixed effect for the starting mass of each treatment group. A random effect for rearing tank was tested but was not included in the lowest WAIC model. The relationship between RMR and test temperature was fit to an exponential curve by log-transforming the RMR values. The final model included non-interacting fixed effects for swim-tunnel and fish age. The final MMR model was fit to the log-transformation of swim-temperature with a fixed effect for swim-tunnel, Fulton's condition factor, and fish age. The final AS model was defined by a second order polynomial function of swimming temperature and an additional fixed effect for Fulton's condition factor. Across models, mass, condition factor, swimming temperature and all response variables were centered and scaled to standard deviations (Z-scores). The predictor variables for time and fish age (days post hatch) were standardized to range from 0 to 1.

Using the lowest WAIC model for each physiological trait, mean values for each treatment group were calculated using the package *emmeans* (Lenth, 2020). To determine whether mean estimates of CTMax and growth rate variable were significantly different between populations, 14,000 samples from the modeled posterior distributions were drawn. For each draw, the difference between all pairs of treatment means was computed, generating a distribution of treatment contrasts for each pair of treatments. If 94.5% of the contrast distribution was above or below 0, treatments were considered significantly different (Supplemental Figures 1-12).

Acclimation capacity, the difference in mean trait estimate between 11 and 20°C acclimated fish, were quantified by repeated sampling (24,000 draws) from the respective

posterior distributions of the final CTMax and growth rate models. From each model draw the difference between the 11 and 20°C mean trait estimate was calculated for each population.

Two additional metabolic traits were estimated using model posteriors: 1) The thermal optimum (T_{opt}) is the temperature at which AS is maximized, and 2) the Q_{10} temperature coefficient of the RMR which estimates the temperature independence (Q_{10} =1) or sensitivity ($Q_{10} \neq 1$) of a biological process. Values for the T_{opt} and the Q_{10} coefficients for each treatment group were calculated using 500 simulated datasets randomly sampled from the posterior distributions of the AS and RMR models respectively. T_{opt} was calculated by fitting a quadratic equation to each AS sample and calculating the root of the first derivative. Likewise, RMR estimates calculated from each drawn dataset were used to calculate Q_{10} coefficients for each treatment group (Equation 3.3).

Equation 3.3: $$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}}$$

Where R_1 is the modeled RMR at *T1*, R_2 is the modeled RMR at *T2*, and *T1* and *T2* are 10 and 22°C respectively.

We assessed the effect of 15 environmental predictor variables (e.g. latitude, migration distance, Table 3.2) to each of the five physiological traits using GLMMs. For each physiological trait, we first developed models that included latitude with additional predictors for fish age, mass, body length etc. We identified the model that both included latitude and had the lowest WAIC score. Next, we constructed 14 additional models corresponding to the 14 remaining environmental predictors, replacing latitude with a given environmental predictor of interest. For example, the lowest WAIC model of the association between latitude and CTMax included fixed effects for latitude, acclimation temperature, fish mass and fish age, and random effects for CTM test chamber and hatchery. This model was then replicated 14 additional times,

replacing latitude with a different environmental predictor. This process was repeated for all five physiological metrics (See supplementary materials for final model structure). The resulting 75 models (15 models per five physiological traits) were then used to assess the association of environmental predictors with physiological traits for fish reared at each acclimation temperature (11, 16 or 20 °C). For the three metabolic traits (RMR, MMR and AS), we additionally included an interaction of each environmental predictor variable with the swimming temperature of the metabolic trial (8 – 25°C), as well as the fixed effect for acclimation temperature. This allowed us to assess the association between a given environmental predictor and metabolic trait across test temperatures. For each of the three metabolic traits (RMR, MMR and AS) we additionally report the effect of each predictor at three test temperatures (11, 16 and 20°C) within each acclimation group (9 associations per environmental predictor per metabolic trait) for a total of 495 associations. For each association we determined directionality of effect (positive or negative) and attributed strong significance (greater than 94.5% of the posterior distribution is above or below 0), weak significance (greater than 70% of the posterior distribution is above or below 0), or no significance.

Results

Growth Rate

Across all populations, growth rates were the slowest in fish acclimated to 11°C and typically increased with acclimation to 16°C (Figure 3.1). The three California populations, Coleman, Feather River and Trinity River, further increased growth rate when acclimated to 20°C. The Coleman population had the fastest growth rate at 0.269 ± 0.026 g day^{-1}, although this value was not statistically different from the nearby Feather River Hatchery (0.238 ± 0.037 g

day^{-1}). The Elk River, Trask River and Priest Rapids populations had non-significant declines in growth rate when acclimated to 20°C.

The slowest growth rates were observed in the Trinity hatchery population which grew significantly slower than any other comparably acclimated population. The Trinity hatchery did show an increase in growth rate with acclimation temperature, with the lowest growth rate (0.059 ± 0.032 g day^{-1}) at 11°C and the highest growth rate at 20°C (0.119 ± 0.018 g day^{-1}). Despite, overall slow growth, the acclimation capacity of the Trinity population (0.059 ± 0.036 g day^{-1}) was comparable to the other populations, 0.017 to .107 g day^{-1} (Trask and Coleman respectively, Table 3.3).

The association of 15 environmental predictors with growth rate was assessed for each acclimation temperature. Due to the slow growth of the Trinity population, we modeled growth rate both including (Supplemental Table 3.2) and excluding the data from the Trinity population (Table 3.4) as this population may be demonstrating an alternate life-history strategy (see Discussion), reducing its comparability to the other populations. We chose to consider only associations which were robust to the exclusion of the Trinity population for significance, as associations which varied between the two models are possibly confounded. Growth rate of fish acclimated to 11°C or 16 °C did not have any strongly significant associations with any environmental predictor variables, regardless of inclusion of the Trinity population growth data. However, when acclimated to 20°C, there were strong significant positive associations between the maximum and average monthly average temperatures fish experience on their core rearing grounds (CRCMax, HRCMax, CCRAve, HCRAve) as well as the annual minimum monthly average temperature (CAMin, HAMin). Migration distance was found to have weakly significant associations with growth rate; fish acclimated to 11°C exhibited a negative association which

switched to a positive association when fish were acclimated to 20°C. Fish acclimated to 16°C exhibited no association between growth rate and migration distance.

Critical Thermal Maximum (CTMax)

Acclimation temperature had a positive effect on the CTMax of all six populations; increasing acclimation temperatures from 11 to 16°C resulted in increased CTMax. Five populations increased their CTMax further with acclimation to 20°C (Figure 3.2). The highest modeled CTMax values belonged to the Coleman (30.02 ± 0.15 °C) and Trask (30.12 ± 0.18°C) hatchery populations acclimated to 20°C. The Feather River population demonstrated a non-significant decrease in CTMax between groups acclimated to 16 vs. 20°C (29.04 ± 0.14 °C vs. 28.88 ± 0.15°C, respectively). Acclimation capacity, as measured as the difference between CTMax at 11 and 20°C, varied between populations (Table 3.5). The Trinity River population had the lowest acclimation capacity (0.74 ± 0.19 °C), while the Trask River population had the greatest acclimation capacity (2.14 °C ± 0.19).

Variation in the mean population CTMax among populations and the within-treatment deviation of individual CTMax values increased with acclimation temperature (Figure 3.2). When acclimated to 11°C, mean population estimates ranged from 27.76 ± 0.13 °C (Feather River) to 28.41 ± 0.15 °C (Trinity Hatchery), an approximate 0.65 °C difference. When acclimated to 16°C, mean population estimates ranged from 28.54 ± 0.14 °C (Elk River) to 29.32 ± 0.15 °C (Coleman), an approximate 0.78°C difference. This difference increased when fish were acclimated to 20°C, with 1.24°C separating the Trask population (30.12 ± 0.18 °C) from the Feather River population (28.88 ± 0.15 °C). Within each population standard deviations of the observed CTMax values increased with acclimation temperature, with 5 of 6 populations exhibiting the greatest variation at 20°C; in contrast, Priest Rapids exhibited the greatest

variation at 16°C (28.92 ± 0.70°C) vs. 20°C (29.56 ± 0.67°C). Mass was included as a fixed effect in the treatment model for CTMax, as well as the interaction of mass and acclimation temperature. For fish acclimated to 11°C mass had no effect on the CTMax. However, for fish acclimated to 16 or 20°C, increasing fish mass was inversely correlated with CTMax value. This strength of this effect increased with acclimation temperature.

The association of 15 environmental predictors with CTMax were assessed at each acclimation temperature (Table 3.6). We found no relationships between CTMax and any of our predictor variables among fish acclimated to 11°C. Fish acclimated to 16°C had strong significant positive associations with the historical annual maximum monthly average temperature (HAMax) and migration distance (Mig.D). There were weakly-significant but positive associations with current annual maximum monthly average temperature (CAMax), and both current and historical estimates of maximum and average stream temperatures during periods of juvenile rearing (CRCMax, CCRAve, HRCMax, HCRAve and HRMax). Fish acclimated to 16°C exhibited a weakly-significant negative association with latitude. Fish acclimated to 20°C had strong significant positive associations with the historical average and maximum monthly temperatures (HCRAve, HCMax) within the core months of juvenile rearing and across the full rearing period (HCRMax). There were weakly-significant but positive associations with latitude, and HAMax and CAMax. Historical estimates of stream temperature were more likely to be significantly associated with CTMax values than current estimates.

Metabolism

Routine Metabolic Rate (RMR)

The final RMR model treated RMR as an exponential function of swimming temperature and included fixed effects for fish condition factor, fish age and specific swim tunnel. Fish age

had a significantly negative effect on RMR, with older fish having lower RMR values. Fulton's condition factor had a significantly negative association with RMR. Swim tunnel was found to have a marginal effect. The effect of three of the four tunnels was non-significant while a single tunnel measured an average of 0.15 $mgO2kg^{-1}min^{-1}$ above the rates of the other tunnels. RMR Q_{10} coefficients for each treatment group were between 2 and 3, indicating that within an acclimation group RMR is temperature dependent. In all populations, acclimating fish to warmer water temperatures reduced RMR rates across the range of swimming temperatures (Figure 3.3). Acclimation to 20°C reduced the overall RMR of a given population to between 80.00% (Coleman) and 68.88% (Elk River) of the overall RMR elicited at 11°C (Table 3.7).

Generally, the historical maximum monthly temperature (HAMax) and migration distance (Mig.D) were significantly negatively associated with RMR (Table 3.8). Both traits were significantly negatively associated with RMR across all three swimming temperatures (11,16 and 20°C) when fish were acclimated to 11 or 20°C. Fish acclimated to 16°C demonstrated no effect of HAMax at 11°C, a weakly significantly negative effect at 16°C, and a strongly significant negative effect at 20°C. Similarly, for Mig.D, fish acclimated to 16°C exhibited no effect on RMR when swum at 11°C, and weakly significantly effect when swum at 16°C or 20°C.

Maximum Metabolic Rate (MMR)

The final MMR model quantified MMR as a function of the base 2 logarithm of swimming temperature with an interaction of acclimation temperature and hatchery. In addition, swim tunnel and fish condition factor were included as fixed effects. Three of four tunnels had non-significant marginal effects, with a single tunnel found to yield significantly elevated MMR measures. This difference amounted to an average increase of 0.66 $mgO_2kg^{-1}min^{-1}$ above the

measured rates of the other tunnels. Fulton's condition factor was negatively associated with MMR, with higher condition factors leading to reduced MMR values. Acclimation to warmer temperatures reduced overall MMR capacity in all populations except the Trask population, whose MMR remained broadly constant across acclimation temperatures (Table 3.7).

The association of environmental predictors (n = 15) on MMR were assessed at three swim temperatures (11, 16 and 20°C). No environmental predictors were found to have strong significant associations at a test temperature of 11°C or among fish acclimated to 20°C (Table 3.9). Six environmental predictors had strong significant positive associations with MMR when fish were acclimated to 11 or 16°C. These associations were strongest when fish were at a test temperature of 20°C (versus 11 or 16°C). Measurements of the current temperature regime, both annually and specific to periods of core juvenile rearing, were significantly and positively associated with MMR (CAMax, CARange, CRCMax, CRMax) for fish acclimated to 11°C or 16°C (Table 3.9). Migration distance was positively associated with MMR when fish were acclimated to 11°C, and a weak, positive association was found among fish acclimated to 16°C.

Aerobic Scope (AS)

The final AS model quantified AS as a second order polynomial function of swimming temperature. The model included an interaction of acclimation temperature and hatchery, an interaction of acclimation temperature and condition factor, and a fixed effect of swim tunnel. The effect of condition factor on AS was dependent on the acclimation temperature of the fish, with no effect among fish acclimated to 11°C, but significantly negative effects when fish were acclimated to 16 or 20°C. Due to the mathematical relationship between RMR, MMR and AS, the marginal effect of swim tunnel additionally impacted AS measurements. The average

difference between the single swim tunnel with an effect on AS and the three tunnels that did not was 0.54 $mgO2kg^{-1}min^{-1}$.

The thermal optima of aerobic scope (T_{opt}) was calculated by taking the root of the 1st derivative of the polynomial function fit to the aerobic scope data. In two treatments (Feather acclimated to 16°C and Trask acclimated to 20°C) the modeled AS thermal performance did not decline as swim temperatures increased, therefore subsequent T_{opt} calculations likely over-estimate the actual value. Among the remaining treatments T_{opt} ranged between 17.45 ± 0.41 °C (Elk River acclimated to 11°C) to 22.71 ± 1.11 °C (Priest Rapids acclimated to 20°C). In five of the six populations T_{opt} increased between fish acclimated to 11°C and those acclimated to 20°C (Table 3.7). The Feather population was the only population to demonstrate a decline (-0.91°C) in T_{opt}, although this decrease was not considered significantly different than zero.

Acclimation to warmer temperatures tended to reduce AS, however the strength of this effect varied among populations. The Coleman, Elk River and Trask populations all demonstrated relatively muted responses in AS to acclimation temperature, preserving much of their 11°C AS when acclimated to 20°C. In the case of Trask, overall AS increased with acclimation to 20°C. The Feather, Priest Rapids and Trinity populations all exhibited greater declines (72.44, 79.22, and 74.32% respectively) in their overall AS when acclimated to 20°C vs. 11°C (Table 3.7).

The effect of 15 environmental predictors on aerobic scope were assessed at three swim temperatures (11, 16 and 20°C). No environmental predictors were found to have strongly significant associations among fish acclimated to 20°C or at a swimming temperature of 11°C. Five environmental predictors (CAMax, HAMax, CARange, CRCMax and Mig.D) had strongly significant positive associations with AS for fish acclimated to 11 or 16°C. Effects were most

pronounced among fish acclimated to 11 °C, and within acclimation groups the strength of the effect increased with test temperature (Table 3.10).

Discussion

Understanding the variation among populations of organisms provides insight into the drivers of that variation and how populations, and species as a whole, may respond to future climatic change. Because juvenile Chinook salmon inhabit a wide latitudinal range across a highly heterogeneous freshwater landscape (Quinn, 2018) there are ample axes for local adaptation. Our research not only quantified population-specific physiological performance and variation in five traits, but tested associations of this variation with 15 environmental predictors. Our results are consistent with hypotheses of local adaptation among the six studied populations of Chinook salmon. We did not find evidence in any of our traits of countergradient variation in the physiological traits we assessed.

Acute thermal tolerance associated with local temperature traits

Across all six populations, CTMax values increased with acclimation temperature and were consistent with previous work on salmonids (Cech & Myrick, 1999; Chen *et al.*, 2015; Myrick & Cech, 2000, 2001). Unlike research on brook trout (Stitt *et al.*, 2014), we found a weakly-significant and countervailing effect of latitude on of CTMax. These countervailing results suggest that latitude may be a poor predictor of acute thermal tolerance, especially if local watershed characteristics (e.g. snowmelt-fed vs. rain-fed systems) disrupt the latitude/temperature relationship. We found that CTMax was positively associated with HAMin, HRMax, HRCMax and HRAve, a result consistent with local adaptation. There was also a weakly negative effect of migration distance, indicating longer migrating populations have lower CTMax values similar to the results of Chen *et al.*, (2013) with juvenile sockeye salmon. Effects

of local environmental characteristics and overall interpopulation differences were greatest when fish were warm-acclimated. It may be that fish acclimated to 11°C are ecologically quite distant from stressful temperatures, but that extended exposure to 16°C or 20°C cues fish to be more physiologically prepared for thermal stress, manifesting as population-specific, locally adapted thermal tolerance traits.

Countergradient variation is not observed in growth rate

Our results are inconsistent with countergradient variation, wherein higher latitude populations are predicted to exhibit increased growth (Conover & Present, 1990; Sinnatamby *et al.*, 2015). Instead, the two southernmost populations (Coleman and Feather) exhibited the fastest growth rate at 20°C (Figure 3.1). Furthermore, growth rate was positively associated with aspects of the local thermal environment, particularly traits capturing the maximum and average temperatures of habitats during the time of core juvenile rearing (CRCMax, HRCMax, CCRAve, HCRAve) supporting a hypothesis that juvenile Chinook salmon are locally adapted to their natal reaches and consistent with research demonstrating warm-adaptation among southern salmonid populations (Chen *et al.*, 2015; Poletto *et al.*, 2017; Verhille *et al.*, 2016). However, if fish were locally adapted, we may expect to find that populations from colder habitats display relatively faster growth rates at cold temperatures than populations from warm habitats; we did not observe this result. It may be that our coldest acclimation temperature (11°C) was not cold enough to elicit population-specific variations in cold-water physiology. Investigations of variation in cold-water tolerance would be improved by comparing the present populations and those from Alaska or Russia. More northerly populations also have a shorter growing season. Therefore, countergradient variation as observed in high latitude (56-82°N) populations of brook trout

(Sinnatamby *et al.*, 2015) may be detectable if studied populations extended to this northern extreme.

The Trinity hatchery exhibited the slowest growth of any population at any acclimation temperature, possibly due to differences in life-history (Beckman *et al.*, 1998). Outmigration life-histories of the Trinity fall-run are more diverse than the other five populations examined here, exhibiting three distinct outmigration strategies (Moyle *et al.*, 2017; Sullivan, 1989). The dominant strategy is a 'rapid' outmigration strategy with fish emigrating quickly after emergence from the gravel. However, fish exhibiting a second, 'delayed' strategy will oversummer in rivers, outmigrating to the ocean in the fall. The third, and most uncommon strategy, yields fish spending an entire year in freshwater and outmigrating in the following spring. The slow growth of the Trinity fish we studied may indicate one of these delayed outmigration strategies (Beckman *et al.*, 1998). The mechanisms which produce three life-history strategies is unknown, and maybe a product of hatchery production (McDonald *et al.*, 1998) or hybridization with sympatric spring-run Chinook salmon (Kinziger *et al.*, 2008). Diversity in outmigration timing, specifically late-outmigration, have been shown to buffer populations from extreme climatic events (Cordoleani *et al.*, 2021) and future work should explore the proximate drivers of life-history diversity among Trinity River Chinook salmon and whether hatchery supplementation practices are influencing the intrapopulation variation in the Trinity watershed.

Metabolic performance is suited to local environmental conditions

Metabolic performance was also consistent with local adaptation among populations. Higher temperatures (CAMax, HAMax, CRCMax, HRCMax) were positively associated with greater aerobic capacity (Table 3.10), particularly when fish were acutely exposed to warmer swimming temperatures (20°C). These results are consistent with Eliason *et al.*, (2011) and

indicate that metabolic traits may be locally adapted, as populations from warmer waters had greater metabolic capacity under acute warm water conditions. However, these effects disappeared among fish acclimated to 20°C, reflecting the shared decline in MMR and AS across populations (Figure 3.4 and 3.5). Reduced performance under warm rearing conditions indicates that while juvenile Chinook salmon are capable of growth at 20°C and can maintain aerobic performance at temperatures exceeding 23°C, they remain cold-water fish.

We hypothesized that locally-adapted metabolic traits may reflect the aerobic burden of a migratory route. Micheletti *et al.*, (2018) identified migration distance and migration slope as environmental predictors associated with genetic indicators of local adaptation among steelhead trout (*O. mykiss*). Work by Eliason *et al.*, (2011) found that populations of adult sockeye salmon (*O. nerka*) from more challenging migratory environments had greater metabolic and cardiac scopes and larger hearts. Therefore, we predicted that populations undertaking longer and more challenging migrations may require increased aerobic capacity. We found longer migration distance was associated with lower RMR and greater MMR and AS (Tables 3.9-3.11), supporting local adaptation. However, these associations were dependent upon fish acclimation temperature and decreased with acclimation to 16 and 20°C. This result highlights the risks of future environmental warming; if adapted metabolic performance is eroded by warming temperatures then inland populations with long migrations may lack the aerobic capacity to complete their life-history strategies.

Acclimation capacity

We quantified acclimation capacity as the difference between trait means at acclimation temperatures of 11 and 20°C. Of the five physiological traits examined, growth rate and CTMax varied most among populations (Tables 3.3 and 3.4). CTMax acclimation capacity ranged

between 0.75 and 2.14°C (Trinity and Trask populations respectively). These values are similar to the 2-3°C observed increase in CTMax observed in steelhead trout (Myrick & Cech, 2005), lake trout (Kelly *et al.*, 2014; McDermid *et al.*, 2013), cutthroat trout (*O. clarkii*) (Underwood *et al.*, 2012), and brook trout (*S. fontinalis*) (Stitt *et al.*, 2014). The growth rate of fish acclimated to 11 vs. 20°C also increased between 0.017 to 0.107 g/day (Trask and Coleman population respectively). The response of CTMax and growth rate to acclimation temperature appeared to be independent among the six populations studied, with plasticity in one trait not predictive of plasticity in the other, although we are limited by the number of populations (6). Furthermore, our data do not suggest any trade-off between higher overall CTMax and greater capacity to acclimate. Instead, populations with higher CTMax also benefited from greater acclimation capacity.

RMRs across swimming temperatures declined with acclimation temperature (Figure 3.3) indicating metabolic compensation for performance at warmer temperatures. However, only in three populations (Coleman, Trask and Elk River) were warm-acclimated reductions in RMR capable of compensating for accompanying declines in MMR. When acclimated to 20°C these three populations preserved above 90% of their respective 11°C acclimated aerobic capacity (Table 3.7). In the remaining three populations (Priest Rapids, Trinity and Feather River) only partial metabolic compensation was achieved, with only 70-80% of aerobic scope preserved when acclimated to 20°C. Metabolic compensation for warming is observed across ectotherms (Evans, 1990; Guderley, 1990; Hazel & Prosser, 1974), and thought to be important in preserving performance under warmer temperatures. Limited ability for a population to metabolically compensate for increased warming may limit performance under future climate scenarios.

Historical vs. Current temperature predictions

Our environmental predictors included both below dam (current) and above dam (historical) estimates of river temperatures. Past work across taxa has indicated thermal physiology, especially heat tolerance, to be evolutionarily rigid (Araújo *et al.*, 2013; Bennett *et al.*, 2021; Hoffmann *et al.*, 2013; Sandblom *et al.*, 2016). Work by Eliason et al. (2011), demonstrated that metabolic traits could be more strongly affiliated with historical temperatures as compared to current regimes. Our comparison of current (i.e., below-dam) and historical (i.e., above-dam) estimates of river temperature permits a coarse assessment of evolutionary trait plasticity. Strongly significant associations between environmental temperature and CTMax were more likely to be historical (HAMin, HRMax, HRCMax, HRAve) consistent with a meta-analysis by Bennet et al. (2021) and hypotheses of 'concrete ceilings' (Sandblom *et al.*, 2016). However, associations with growth rate were balanced between the current and historical estimates and associations with metabolic traits were mixed; RMR was more likely to be associated with historical temperature regimes (HAMax, HARange), and MMR and AS more commonly associated with current temperatures (CAMax, CARange, CRMax, CRCMax, CRAve). Historical vs. current pairs of thermal characteristics were positively correlated (r-values 0.6 to 0.9) and while current temperature estimates were generally warmer, the ranges overlapped. We cannot conclude whether population traits are responding to recent changes in the thermal environment or reflect local adaptation to historical conditions. Furthermore, the speed of adaptation may be trait-dependent (Sandblom *et al.*, 2016).

Inter- and Intrapopulation variation increases with temperature

Inter- and intrapopulation variation in CTMax and growth rate were greatest at 20°C, a presumably more stressful condition. Stressed-induced phenotypic variation is widely observed

(Queitsch *et al.*, 2002; Rutherford & Lindquist, 1998; Waddington, 1953) and is hypothesized to be due to changes in the efficacy of heat shock proteins subsequently releasing cryptic genetic variation and ultimately phenotypic variation (Ghalambor *et al.*, 2007; Rutherford, 2000, 2003). Our results indicate that in a warmer future, populations of Chinook salmon may express divergent phenotypes which are hidden under historically natural temperature conditions (e.g. 11°C). These 'hopeful monsters' are hypothesized to offer pathways of rapid adaptation (Badyaev, 2005; Theißen, 2009). Given the rapid rate of environmental change confronting salmonids and discussions of genetic rescue (Robinson *et al.*, 2017) or population translocation (Lusardi & Moyle, 2017; Weise *et al.*, 2020), determination of population-specific thermal physiology acclimatized to future climate scenarios is necessary to identify populations most at risk or most robust (Gayeski *et al.*, 2018; Zillig *et al.*, 2021).

Hatchery Supplementation

All the populations used in this study were sourced from hatcheries and care should be taken extrapolating the results to wild rearing fish. Past research on the effects of domestication on salmonids has revealed rapid declines in reproductive capacity among hatchery produced or supplemented populations (Araki *et al.*, 2007, 2008). Possible evolutionary drivers of these deleterious hatchery effects include hatchery conditions (Araki *et al.*, 2008; Satake & Araki, 2012), effective population size within the hatchery (Wang *et al.*, 2002; Waples & Teel, 1990), spawning and release management strategies (Lusardi & Moyle, 2017; Sturrock *et al.*, 2019), duration of hatchery supplementation (Sturrock *et al.*, 2019), and proportion of wild population of hatchery origin (Araki *et al.*, 2008). In the present study the selected hatchery populations differ in many aspects of hatchery production (e.g. number of spawners, release strategies), and therefore apparent differences between populations may be due to 'hatchery selection' as

opposed to natural selection of native environmental characteristics. Likewise, hatchery-specific methods of adult recovery, spawning and incubation could produce population or cohort-specific phenotypes via maternal or developmental effects (Banet *et al.*, 2019; Falica *et al.*, 2017; Tierney *et al.*, 2009), which we were unable to control. The impact of domestication and the role of maternal effects on thermal biology is understudied.

Despite the potential impacts of hatchery production on the physiology of juvenile Chinook salmon, the contribution of these hatcheries to the wild population makes them relevant for study on population-specific thermal physiology. Protecting remaining Chinook salmon genetic diversity is essential to population resilience (i.e. the portfolio effect, Carlson & Satterthwaite, 2011). Therefore, understanding the thermal physiology of hatchery genotypes remains pertinent to identifying unique wild populations which may offer novel variation in thermal physiology.

Laboratory Conditions

In addition to being hatchery-sourced, all fish used in this study were reared and tested under lab conditions which can differ from wild conditions in important ways (e.g. lack of predators, clean water, abundant food etc.). Collectively, the effect of laboratory conditions may produce physiological trait phenotypes that differ from fish exposed to wild conditions (McDonald et al., 1998; Smith & Fuiman, 2004; Sundström & Johnsson, 2001). It is unknown whether exposure to the full complement of ecological conditions and stressors of each population's natal environment would accentuate or mitigate observed population differences. The effect of laboratory conditions on the performance of juvenile Chinook salmon is understudied, and future projects should consider the potential for different performance under wild rearing conditions. Reciprocal transplant experiments would address this shortcoming.

However, transplanting salmonids is highly-regulated therefore necessitating laboratory research to assess population variation.

Population Responses

Salmonids are broadly considered cold-water fish and increasing water temperatures, due to climate change or other anthropogenic factors, continue to have detrimental effects upon salmonid species (Moyle *et al.*, 2017). It may be predicted that southern populations are more at-risk than northern counterparts. This assumption clouds the likelihood that the response of salmonids will depend on the physiology of specific-populations paired with local conditions. For instance, the Priest Rapids population (WA) experiences greater annual maximum temperatures than the Coleman and Feather populations (CA) yet exhibits slower growth rates when acclimated to 20°C. Furthermore, our results also indicate that longer-migrating populations (e.g. Coleman, Priest Rapids) may be metabolically limited as temperatures warm and more at risk than short migrating populations (e.g. Trask, Elk River). Therefore, of the studied populations, Priest Rapids, the northernmost, may be the most thermally imperiled. Our results indicate that physiological performance cannot be estimated using geographically proximal populations and that management and conservation actions require population-specific physiological data. Finally, conservation of northern populations, such as Priest Rapids, may rely upon currently at-risk southern populations. Salmonid adaptation occurs in part via the long-distance introgression of adaptive alleles (Miller *et al.*, 2012) and therefore extant alleles from southern populations may offer future-climate resiliency. The conservation of salmonids in the face of rapid environmental change requires protection of individual populations.

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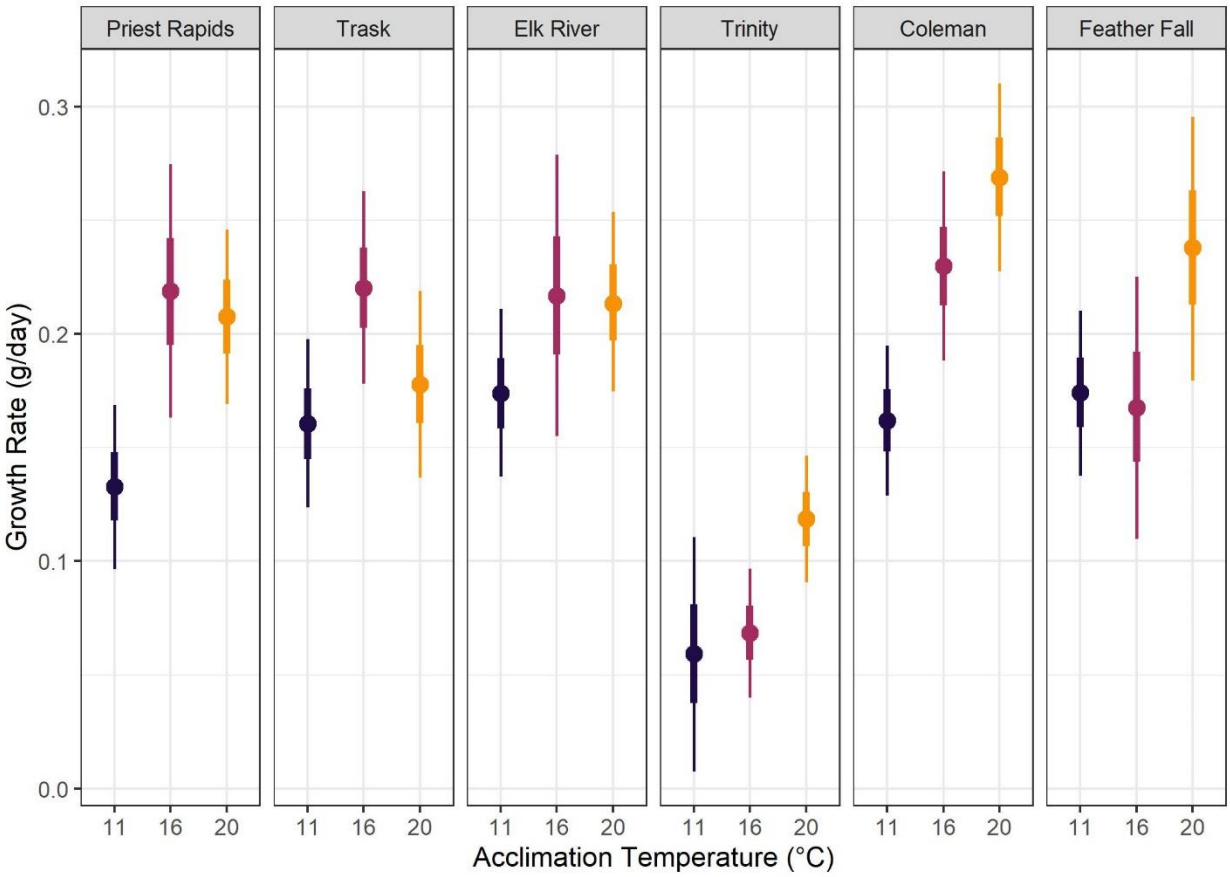

Figure 3.1: Growth Rate (grams/day) for six populations of Fall-run Chinook salmon reared at three temperatures. Data is reported as the mean, 50% and 89% credible intervals for the posterior distribution.

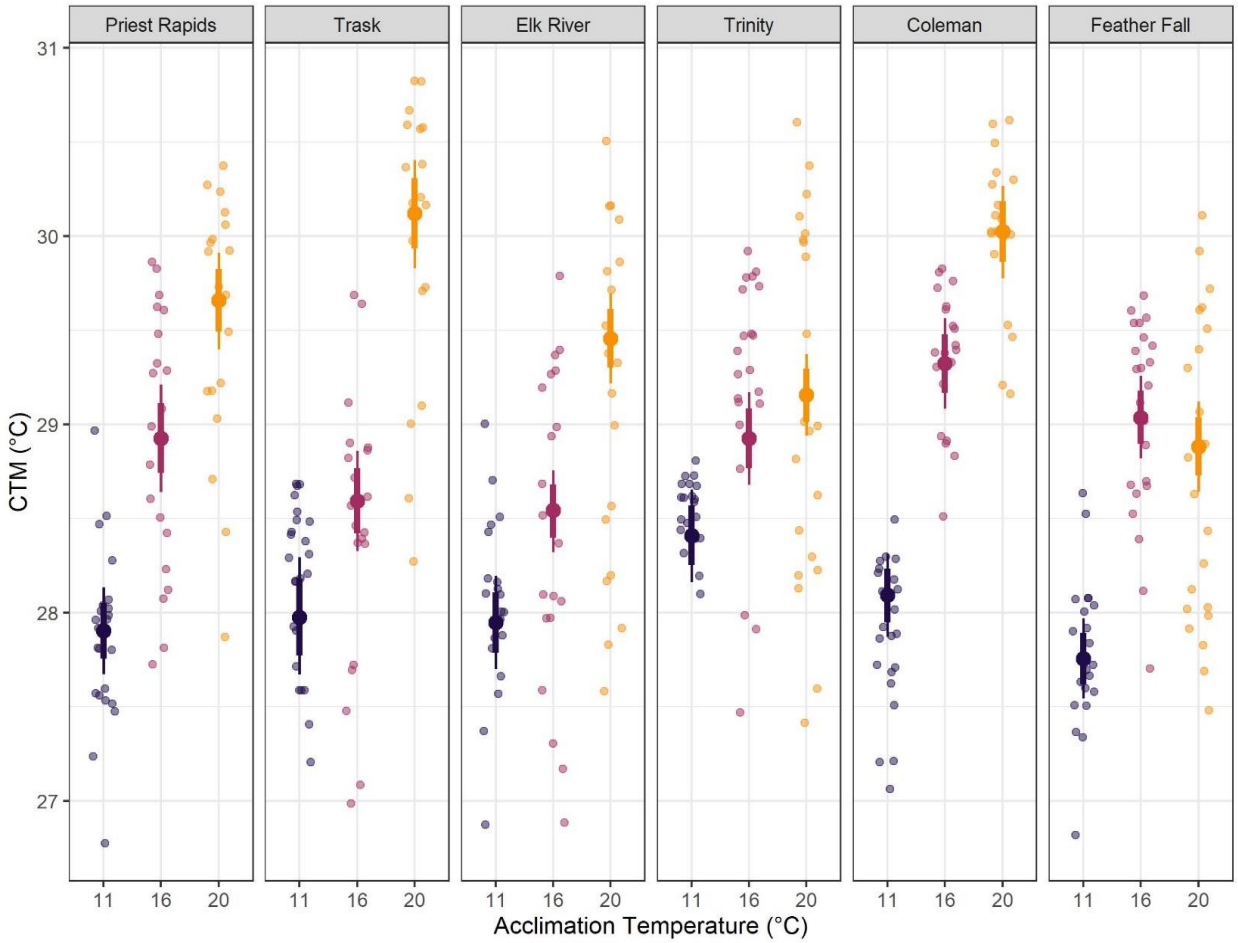

Figure 3.2: Critical Thermal Maximum (CTMax) of six populations of Fall-run juvenile Chinook Salmon. Dots represent the CTMax of individual fish while the large point interval captures the mean estimate and 70 and 89% credible intervals of the best-fitting model.

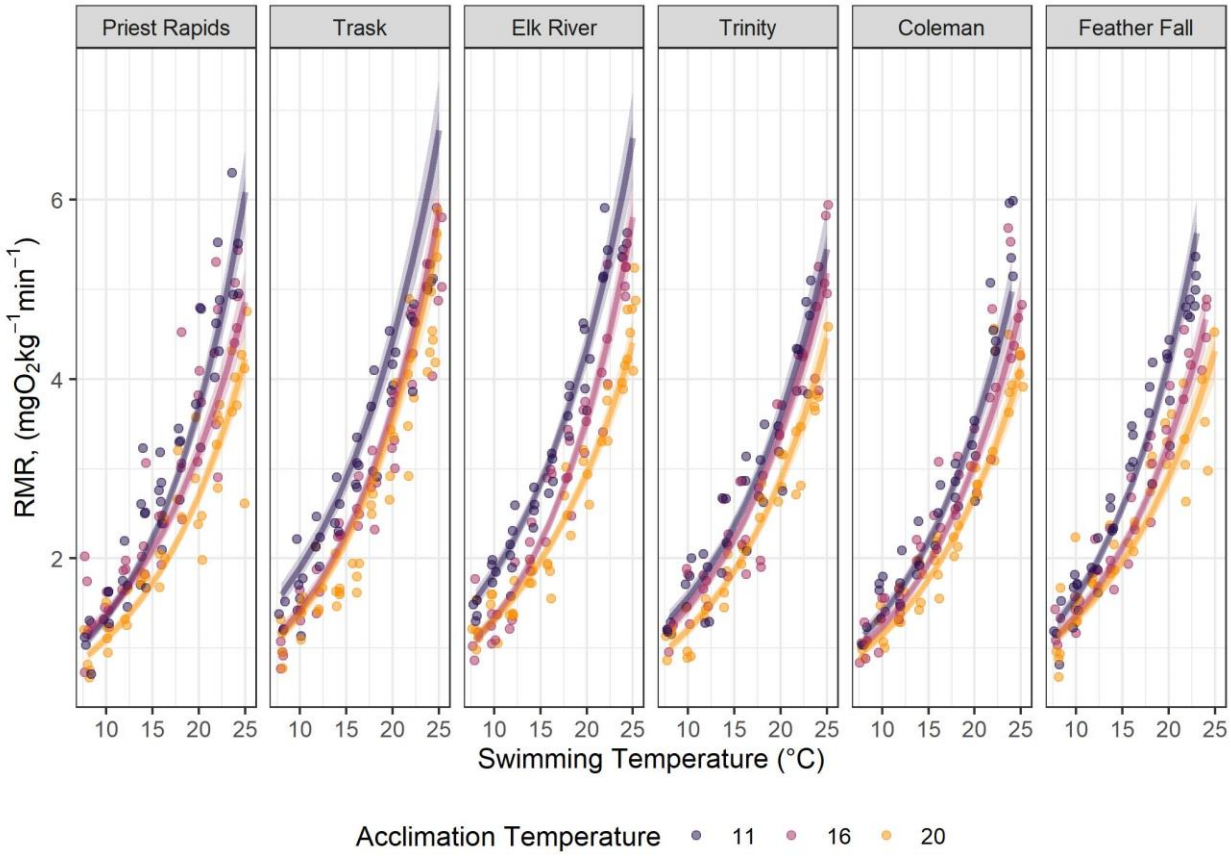

Figure 3.3: Routine Metabolic Rates (RMR) of six populations of fall-run juvenile Chinook salmon. Points represent the metabolic rates of individual fish and the lines represent the modeled estimate mean RMR. Shaded areas capture the 89% (light) and 50% (dark) credible intervals of the model. Colors represent acclimation groups (purple = 11°C, red = 16°, and yellow = 20°C).

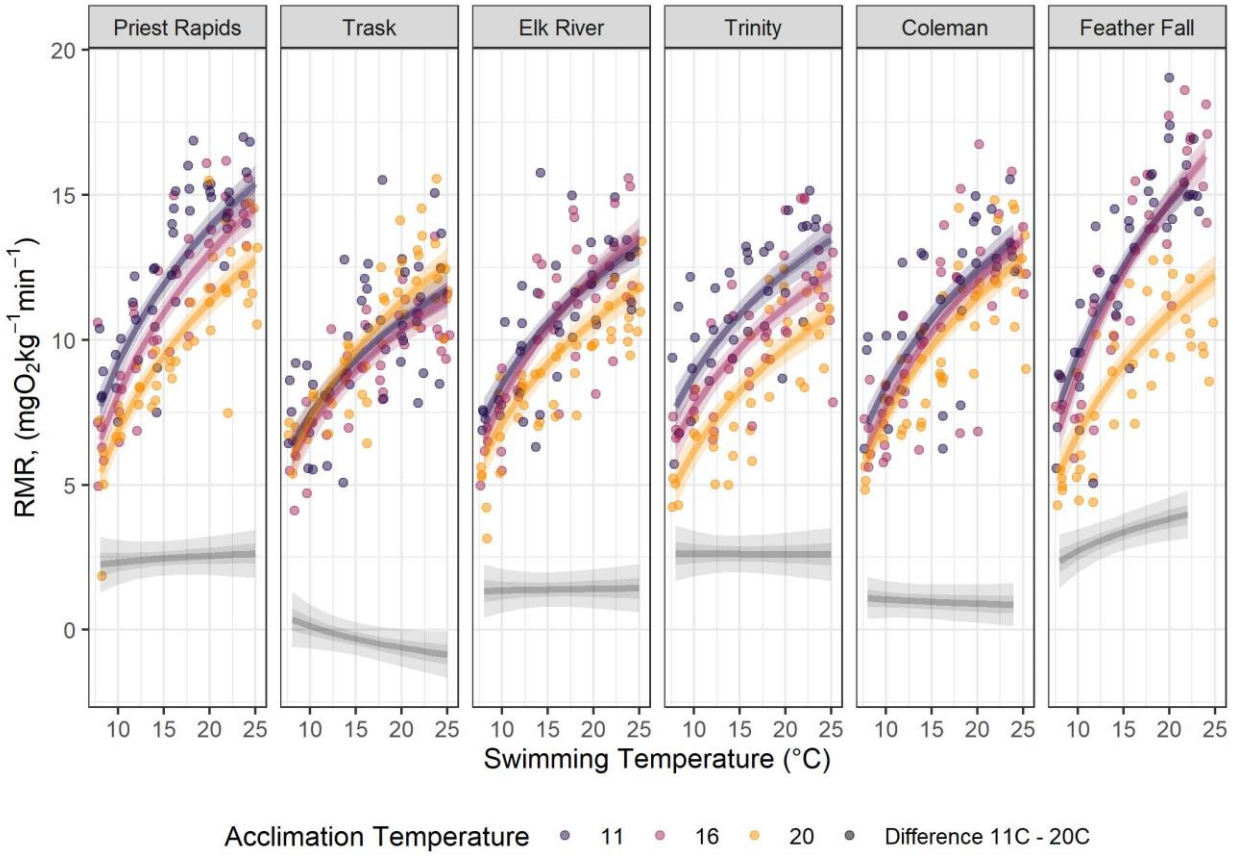

Figure 3.4: Maximum metabolic rate of six populations of juvenile Fall-run Chinook salmon. Points represent the metabolic rates of individual fish and the lines represent the modeled estimate. The gray line and shaded area is the difference between the estimates for MMR of fish acclimated to 11 and 20°C. Shaded areas capture the 89% (light) and 50%(dark) credible intervals of the model. Colors represent acclimation groups (purple = 11°C, red = 16°, and yellow = 20°C).

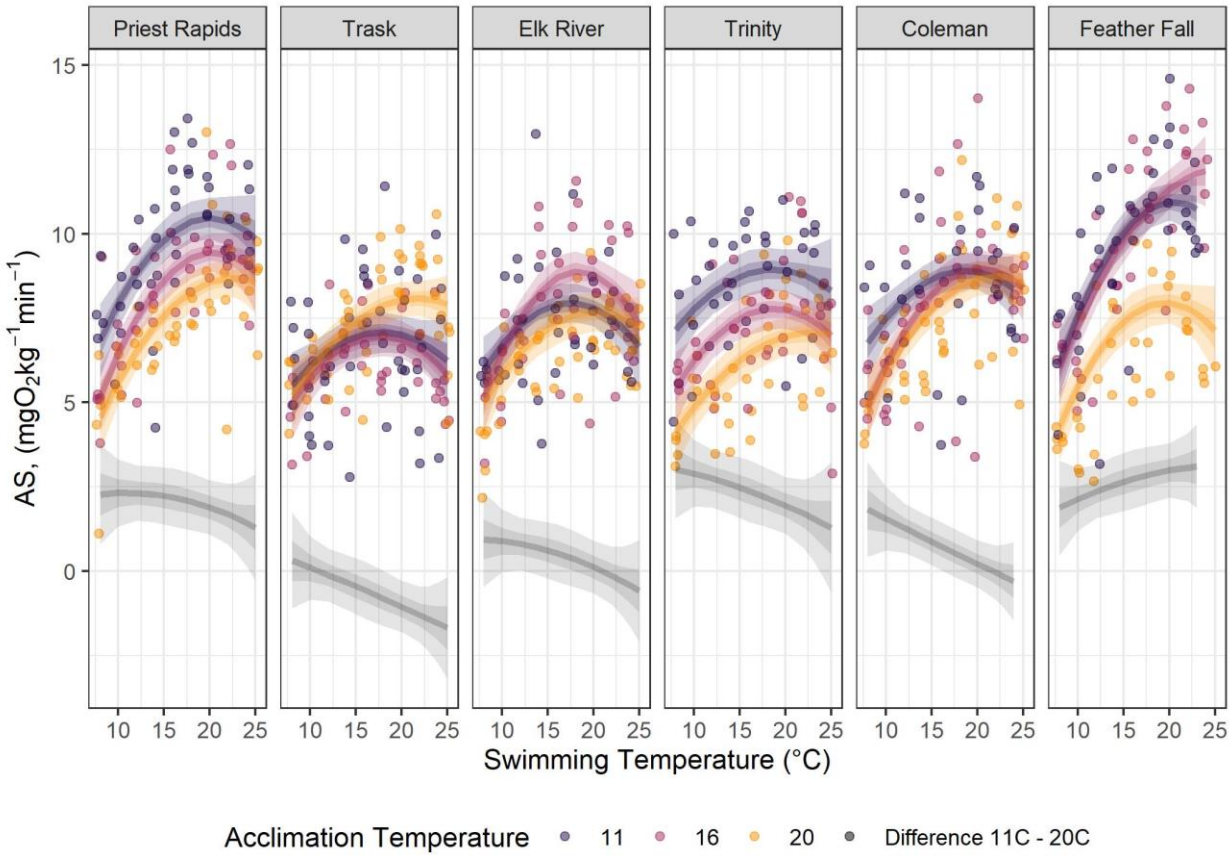

Figure 3.5: Aerobic Scope of four populations of juvenile Fall-run Chinook salmon. Points represent the calculated (AS = MMR – RMR) aerobic scope of individual fish and the lines represent the modeled estimate. The gray line and shaded area are the difference between the 11°C and 20°C treatment groups. Shaded areas capture the 89% (light) and 50% (dark) credible intervals of the model. Colors represent acclimation groups (purple = 11°C, red = 16°, and yellow = 20°C).

Table 3.1: Population and acclimation treatment metadata for six population of Sacramento River Chinook salmon.

Population	State	Year	Evolutionary Significant Unit ESU	Hatchery	Hatchery Coord.	Elev. (m)	Migration Distance (km)	Hatch Date
Coleman	CA	2017	California Central Valley Fall-run ESU	Coleman National Fish Hatchery	40.398°N, 122.145°W	123	441	11/08/2016
Elk River	OR	2017	Southern Oregon and Northern California Coastal ESU	Elk River Hatchery	42.740°N, 124.403°W	35	22	01/14/2017
Feather	CA	2019	California Central Valley Fall-run ESU	Feather River Hatchery	39.519°N, 121.554°W	41	233	11/29/2018
Priest Rapids	WA	2018	Upper Columbia Fall-run ESU	Priest Rapids Hatchery	46.630°N, 119.872°W	125	631	02/01/2018
Trask	OR	2017	Oregon Coastal ESU	Trask Hatchery	45.433°N, 123.726°W	17	28	12/14/2016
Trinity	CA	2019	Upper Klamath-Trinity Rivers Fall-run ESU	Trinity River Hatchery	40.727°N, 122.795°W	562	250	01/21/2019

Table 3.2: Environmental predictors used in models detecting associations between physiological traits and environmental parameters. Abbreviations are those referenced in the manuscript. [G] indicates data was gathered from google earth. [N] indicates data was sourced from the NorWeST temperature model developed by Isaak et al., (2017) and augmented by FitzGerald et al., (2020). [P] indicates that temperature data was limited to the period of juvenile rearing based upon phenology data from FitzGerald et al., (2020). [R] indicates that data was sourced using the R package 'dataRetrieval'.

Environmental Predictor	Abbr.	Description
Latitude [G]		Latitude of the hatchery for each population
Current Annual Mean Monthly Maximum [N]	CAMax	Average of maximum monthly temperature for each river kilometer for reaches below dams
Historical Annual Mean Monthly Maximum [N]	HAmax	Average of maximum monthly temperature for each river kilometer for reaches above dams
Current Annual Mean Monthly Minimum [N]	CAMin	Average of minimum monthly temperature for each river kilometer for reaches below dams
Historical Annual Mean Monthly Minimum [N]	HAMin	Average of minimum monthly temperature for each river kilometer for reaches above dams
Current Annual Temperature Range [N]	CARange	Average differences between the minimum and maximum monthly temperature for each river kilometer for reaches below dams
Historical Annual Temperature Range [N]	HARange	Average differences between the minimum and maximum monthly temperature for each river kilometer for reaches above dams
Current Rearing Season Maximum Monthly Average [N,P]	CRMax	Average maximum monthly temperature for each river kilometer for reaches below dams, limited to the months of juvenile rearing.
Historical Rearing Season Maximum Monthly Average [N,P]	HRMax	Average maximum monthly temperature for each river kilometer for reaches above dams, limited to the months of juvenile rearing.
Current Rearing Core Maximum Monthly Average [N,P]	CRCMax	Average maximum monthly temperature for each river kilometer for reaches below dams, limited to the month of peak juvenile emergence and the subsequent month.
Historical Rearing Core Maximum Monthly Average [N,P]	HRCMax	Average maximum monthly temperature for each river kilometer for reaches above dams, limited to the month of peak juvenile emergence and the subsequent month.
Current Rearing Season Average Monthly Average [N,P]	CRAve	Average of monthly temperatures for each river kilometer for reaches below dams, limited to the months of juvenile rearing.
Historical Rearing Season Average Monthly Average [N,P]	HRAve	Average of monthly temperatures for each river kilometer for reaches above dams, limited to the months of juvenile rearing.
Migration Distance [R]	Mig.D	River length in kilometers from the hatchery to tidally influenced waters.
Migration Slope	Mig.S	The average slope of the river, calculated by dividing the distance from the hatchery to tidally influenced waters (km) by the elevation (m) on google earth.

Table 3.3: Growth Rate Data for six populations of Chinook Salmon at three acclimation temperatures. The duration (Days) is the time over which growth measures were taken. Mass, fork length and Fulton's condition factor are all reported as means and standard deviations of the observed data. Growth rate is the modeled growth rate reported as the mean and standard deviation of 28,000 draws from the posterior distribution of lowest WAIC growth model. Acclimation capacity is the mean and standard deviation of the contrast distribution of the 11 and 20°C acclimation groups.

Hatchery & Acclimation Temperature (°C)		Days	Mass (g)		Fork Length (cm)		Fulton's Condition Factor		Growth Rate (g/day)	Acclimation Capacity (g/day)
			Initial	Final	Initial	Final	Initial	Final		
Coleman	11	29	7.445 ± 0.497	11.413 ± 2.694	8.33 ± 0.75	9.73 ± 0.78	1.26 ± 0.09	1.21 ± 0.06	0.162 ± 0.021	0.107 ± 0.028
	16	29	8.415 ± 0.090	15.688 ± 3.238	8.76 ± 0.77	10.83 ± 0.74	1.23 ± 0.11	1.22 ± 0.07	0.230 ± 0.026	
	20	29	8.340 ± 0.024	17.293 ± 3.560	8.66 ± 0.58	11.07 ± 0.74	1.27 ± 0.08	1.26 ± 0.08	0.269 ± 0.026	
Elk River	11	41	6.809 ± 1.929	14.807 ± 4.854	8.23 ± 0.77	10.36 ± 1.08	1.20 ± 0.14	1.28 ± 0.07	0.174 ± 0.023	0.040 ± 0.032
	16	26	8.295 ± 2.477	13.790 ± 4.357	8.60 ± 0.77	10.10 ± 0.98	1.27 ± 0.08	1.29 ± 0.08	0.217 ± 0.039	
	20	41	6.994 ± 1.358	15.707 ± 4.958	8.04 ± 0.48	10.50 ± 1.04	1.33 ± 0.07	1.31 ± 0.07	0.214 ± 0.025	
Feather	11	42	8.229 ± 2.921	16.014 ± 4.88	8.59 ± 0.95	10.70 ± 1.02	1.24 ± 0.08	1.26 ± 0.09	0.174 ± 0.023	0.064 ± 0.042
	16	28	8.826 ± 3.880	13.168 ± 5.895	8.51 ± 1.39	9.87 ± 1.57	1.31 ± 0.09	1.26 ± 0.10	0.168 ± 0.036	
	20	28	8.441 ± 3.434	14.899 ± 5.385	8.44 ± 1.11	10.31 ± 1.32	1.32 ± 0.11	1.29 ± 0.07	0.238 ± 0.037	
Priest Rapids	11	42	7.339 ± 3.460	12.770 ± 5.849	8.42 ± 1.30	10.04 ± 1.46	1.13 ± 0.06	1.18 ± 0.05	0.133 ± 0.022	0.075 ± 0.032
	16	29	8.018 ± 2.922	14.495 ± 7.044	8.53 ± 1.19	10.30 ± 1.56	1.27 ± 0.33	1.23 ± 0.07	0.219 ± 0.035	
	20	42	7.428 ± 3.436	15.624 ± 7.702	8.35 ± 1.27	10.38 ± 1.85	1.19 ± 0.05	1.26 ± 0.06	0.208 ± 0.024	
Trask	11	42	7.795 ± 3.002	14.644 ± 5.401	8.51 ± 1.03	10.55 ± 1.24	1.20 ± 0.08	1.19 ± 0.08	0.161 ± 0.023	0.017 ± 0.033
	16	37	7.111 ± 1.954	14.771 ± 5.323	8.23 ± 0.71	10.30 ± 1.04	1.24 ± 0.08	1.29 ± 0.11	0.22 ± 0.026	
	20	42	8.623 ± 3.340	15.806 ± 6.008	8.74 ± 0.97	10.67 ± 1.21	1.22 ± 0.13	1.24 ± 0.09	0.178 ± 0.026	
Trinity	11	28	7.935 ± 3.925	9.503 ± 5.351	8.55 ± 1.43	9.00 ± 1.84	1.17 ± 0.05	1.15 ± 0.06	0.059 ± 0.032	0.059 ± 0.036
	16	54	7.189 ± 4.068	11.292 ± 9.334	8.11 ± 1.46	9.12 ± 2.37	1.21 ± 0.07	1.2 ± 0.08	0.069 ± 0.018	
	20	54	6.214 ± 3.574	12.176 ± 7.090	7.85 ± 1.40	9.64 ± 1.81	1.18 ± 0.11	1.22 ± 0.05	0.119 ± 0.018	

Table 3.4: GLMM covariate estimates of between environmental predictors and growth rate for fall-run population without Trinity. The letter superscript denotes significance (89% credible interval) between acclimation groups for a given row. The upper and lower 89% credible interval are given. Light gray text indicates no significant interaction, italics indicates weak significance (70% credible interval) and bold indicates strong significance (89% credible interval). † indicates the trend of this result differs when the Trinity hatchery growth data is included. See Supplemental Table 3.2 for environmental associations including the Trinity population.

Predictor	Abbr.	11°C Acclimation Group			16°C Acclimation Group			20°C Acclimation Group		
		Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI
Latitude		*-0.131* ^{ab†}	*-0.271*	*0.212*	0.063 ^{a†}	-0.133	0.255	**-0.216** ^{b†}	**-0.382**	**-0.050**
Current Annual Mean Monthly Maximum	*CAMax*	*-0.109* ^{a†}	*-0.248*	*0.030*	0.002 ^{ab†}	-0.188	0.192	0.090 ^{b†}	-0.055	0.234
Historical Annual Mean Monthly Maximum	*HAmax*	-0.136 ^{a†}	-0.279	0.008	0.073 ^{ab†}	-0.114	0.260	0.138 ^{b†}	-0.011	0.288
Current Annual Mean Monthly Minimum	*CAMin*	*0.096* ^{ab†}	*-0.050*	*0.245*	-0.036 ^{a†}	-0.237	0.166	**0.268** ^{b}	**0.093**	**0.442**
Historical Annual Mean Monthly Minimum	*HAMin*	0.035 ^{a†}	-0.130	0.199	*0.158* ^{a†}	*-0.049*	*0.364*	**0.193** ^{a}	**0.024**	**0.363**
Current Annual Temperature Range	*CARange*	*-0.135* ^{a†}	*-0.273*	*0.002*	0.024 ^{a†}	-0.170	0.221	0.033 ^{a†}	-0.110	0.176
Historical Annual Temperature Range	*HARange*	*-0.128* ^{a†}	*-0.266*	*0.011*	-0.008 ^{a†}	-0.201	0.187	0.038 ^{a†}	-0.102	0.176
Current Rearing Season Maximum Monthly Average	*CRMax*	*-0.136* ^{a†}	*-0.274*	*0.005*	-0.046 ^{a†}	-0.247	0.154	0.000 ^{a†}	-0.143	0.144
Historical Rearing Season Maximum Monthly Average	*HRMax*	**-0.139** ^{a†}	**-0.272**	**-0.004**	0.091 ^{a†}	-0.111	0.292	0.025 ^{a†}	-0.124	0.173
Current Rearing Core Maximum Monthly Average	*CRCMax*	0.060 ^{a†}	-0.084	0.201	-0.069 ^{a†}	-0.255	0.119	**0.323** ^{b}	**0.143**	**0.502**
Historical Rearing Core Maximum Monthly Average	*HRCMax*	0.038 ^{a†}	-0.136	0.212	-0.112 ^{ab†}	-0.084	0.308	**0.316** ^{b}	**0.138**	**0.492**
Current Rearing Season Average Monthly Average	*CRAve*	*0.103* ^{ab†}	*-0.041*	*0.248*	-0.061 ^{a†}	-0.250	0.127	**0.285** ^{b}	**0.107**	**0.459**
Historical Rearing Season Average Monthly Average	*HRAve*	0.066 ^{a†}	-0.100	0.233	*0.140* ^{a†}	*-0.063*	*0.341*	**0.232** ^{a}	**0.060**	**0.404**
Migration Distance	*Mig.D*	*-0.119* ^{a}	*-0.262*	*0.022*	-0.031 ^{ab}	-0.162	0.223	*0.107* ^{b}	*-0.042*	*0.254*
Migration Slope	*Mig.S*	0.063 ^{a†}	-0.079	0.205	0.008 ^{a†}	-0.219	0.232	-0.026 ^{a†}	-0.172	0.124

Table 3.5: Treatment measurements for critical thermal maximum (CTMax): Modeled data is the mean and standard deviation of 14,000 draws from the posterior distribution. Acclimation capacity for each hatchery was calculated as the mean difference (and standard deviation) between the 11°C and 20°C acclimation group. The remaining columns are the respective means and standard deviations of the specific fish trialed for CTMax.

Hatchery & Acclimation Temperature (°C)		Observed CTM (°C)	Modeled Mean CTM (°C)	Mass (g)	Fork Length (cm)	Fulton's Condition Factor	Count	Acclimation Capacity (°C) ΔCTM
Coleman	11	27.89 ± 0.39	28.09 ± 0.14	17.208 ± 5.147	11.45 ± 1.07	1.11 ± 0.07	22	1.93 ± 0.17
	16	29.34 ± 0.37	29.32 ± 0.15	22.925 ± 3.371	12.43 ± 0.66	1.19 ± 0.06	20	
	20	30.02 ± 0.40	30.02 ± 0.15	23.264 ± 3.764	12.32 ± 0.65	1.24 ± 0.07	20	
Elk River	11	28.05 ± 0.45	27.95 ± 0.15	26.442 ± 3.099	13.04 ± 0.45	1.19 ± 0.05	21	1.51 ± 0.21
	16	28.46 ± 0.83	28.54 ± 0.14	24.907 ± 2.965	12.70 ± 0.49	1.21 ± 0.09	20	
	20	29.14 ± 0.91	29.46 ± 0.15	26.902 ± 3.068	12.71 ± 0.43	1.31 ± 0.07	19	
Feather	11	27.78 ± 0.40	27.76 ± 0.13	25.264 ± 2.486	13.08 ± 0.44	1.13 ± 0.04	21	1.13 ± 0.20
	16	29.03 ± 0.53	29.04 ± 0.14	22.033 ± 2.337	12.32 ± 0.36	1.18 ± 0.08	23	
	20	28.74 ± 0.81	28.88 ± 0.15	23.618 ± 2.979	12.19 ± 0.45	1.30 ± 0.11	22	
Priest Rapids	11	27.87 ± 0.46	27.90 ± 0.14	18.837 ± 1.447	12.00 ± 0.25	1.09 ± 0.05	23	1.75 ± 0.19
	16	28.92 ± 0.70	28.93 ± 0.18	20.668 ± 1.456	12.23 ± 0.26	1.13 ± 0.05	20	
	20	29.56 ± 0.67	29.66 ± 0.16	23.079 ± 3.343	12.45 ± 0.37	1.19 ± 0.11	20	
Trask	11	28.15 ± 0.43	27.98 ± 0.20	25.686 ± 2.961	13.18 ± 0.47	1.12 ± 0.05	25	2.14 ± 0.19
	16	28.45 ± 0.73	28.59 ± 0.17	27.562 ± 4.239	13.15 ± 0.48	1.20 ± 0.07	20	
	20	29.99 ± 0.77	30.12 ± 0.18	26.075 ± 2.797	12.79 ± 0.40	1.25 ± 0.09	18	
Trinity	11	28.52 ± 0.18	28.41 ± 0.15	18.923 ± 5.434	11.78 ± 1.09	1.13 ± 0.04	21	0.74 ± 0.19
	16	29.19 ± 0.66	28.93 ± 0.15	18.589 ± 7.471	11.57 ± 1.52	1.14 ± 0.06	21	
	20	29.11 ± 0.97	29.16 ± 0.14	23.787 ± 5.843	12.37 ± 0.77	1.23 ± 0.09	21	

Table 3.6: GLMM covariate estimates of fifteen environmental predictor variables and CTMax for fish at three acclimation temperatures. Estimates reflect Z-score standardized model parameters. Estimate is the mean associations between a given environmental predictor and CTMax. The superscript denotes significance (89% credible interval) between acclimation groups for a given row. The upper and lower 89% credible interval are given. Light gray text indicates no significant interaction, italics indicates weak significance (70% credible interval) and bold indicates strong significance (89% credible interval).

Environmental Predictor	Abbr.	11°C Acclimation Group			16°C Acclimation Group			20°C Acclimation Group		
		Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI
Latitude		-0.026 [a]	-0.292	0.237	*-0.155* [a]	*-0.417*	*0.107*	*0.255* [b]	*-0.013*	*0.518*
Current Annual Mean Monthly Maximum	*CAMax*	-0.087 [a]	-0.359	0.201	*0.250* [b]	*-0.033*	*0.547*	*0.188* [b]	*-0.092*	*0.476*
Historical Annual Mean Monthly Maximum	*HAmax*	-0.024 [a]	-0.262	0.210	**0.271** [b]	**0.031**	**0.498**	*0.211* [b]	*-0.019*	*0.435*
Current Annual Mean Monthly Minimum	*CAMin*	-0.124 [a]	-0.394	0.160	*0.236* [b]	*-0.037*	*0.521*	0.042 [c]	-0.230	0.331
Historical Annual Mean Monthly Minimum	*HAMin*	-0.130 [a]	-0.376	0.122	*0.155* [b]	*-0.096*	*0.412*	**0.345** [c]	**0.097**	**0.600**
Current Annual Temperature Range	*CARange*	-0.063 [a]	-0.330	0.211	0.142 [b]	-0.137	0.431	0.156 [b]	-0.113	0.435
Historical Annual Temperature Range	*HARange*	0.122 [a]	-0.175	0.432	0.098 [a]	-0.206	0.404	-0.122 [b]	-0.422	0.181
Current Rearing Season Maximum Monthly Average	*CRMax*	-0.137 [a]	-0.427	0.164	0.101 [b]	-0.200	0.414	0.143 [b]	-0.153	0.451
Historical Rearing Season Maximum Monthly Average	*HRMax*	-0.128 [a]	-0.401	0.160	*0.089* [b]	*-0.191*	*0.384*	**0.287** [c]	**0.014**	**0.575**
Current Rearing Core Maximum Monthly Average	*CRCMax*	-0.135 [a]	-0.413	0.146	*0.232* [b]	*-0.045*	*0.514*	-0.047 [a]	-0.330	0.245
Historical Rearing Core Maximum Monthly Average	*HRCMax*	-0.114 [a]	-0.354	0.128	*0.211* [b]	*-0.030*	*0.457*	**0.273** [b]	**0.031**	**0.519**
Current Rearing Season Average Monthly Average	*CRAve*	-0.151 [a]	-0.444	0.151	*0.201* [b]	*-0.093*	*0.505*	-0.027 [a]	-0.325	0.281
Historical Rearing Season Average Monthly Average	*HRAve*	-0.117 [a]	-0.365	0.131	*0.162* [b]	*-0.092*	*0.412*	**0.302** [b]	**0.052**	**0.555**
Migration Distance	*Mig.D*	-0.002 [a]	-0.261	0.255	**0.265** [b]	**0.008**	**0.518**	0.133 [ab]	-0.116	0.381
Migration Slope	*Mig.S*	*0.198* [a]	*-0.113*	*0.502*	-0.154 [b]	-0.478	0.157	*-0.239* [b]	*-0.557*	*0.068*

Table 3.7: Summary metabolic data for six populations of fall-run Chinook salmon: Fish swum is the number of successful swims conducted while 'Mort.' is the number of fish that did not survive the trial. Maximum test temperature, is the highest temperature at which fish could be successfully tested. Mass, fork length and condition factor are reported as means and standard deviation of the observed data. RMR, MMR and AS values are all derived from the respective Bayesian models. Values are reported as mean and standard deviation of the model estimate calculated from repeated draws from the respective posterior distributions. Q_{10} coefficients of the RMR were calculated for each treatment (Q_{10}). For each metabolic rate, we compared the amount of metabolic capacity relative to a hatchery's metabolic capacity when acclimated to 11°C, these are reported as the mean percentage and standard deviation.

Hatchery and Acclimation Temperature		Fish Swum (n=)	Mort. (n=)	Max Test Temp. (°C)	Mass (g)	Fork Length (cm)	Condition Factor	RMR		MMR	AS			
								Q_{10}	% of 11 °C	% of 11°C	AS at T_{OPT}	T_{OPT} (°C)	% of 11°C	T_{OPT} Δ (°C)
Coleman	11°C	32	7	24	22.181 ± 4.022	12.49 ± 0.65	1.13 ± 0.07	2.50 ± 0.03	--	--	8.92 ± 0.09	18.75 ± 0.64	--	3.44 ± 1.08
	16°C	42	3	25	23.720 ± 3.254	12.70 ± 0.50	1.16 ± 0.05	2.48 ± 0.02	89.06 ± 4.28	95.42 ± 4.89	8.98 ± 0.08	20.38 ± 0.48	94.15 ± 12.00	
	20°C	45	5	25	24.720 ± 4.009	12.60 ± 0.64	1.21 ± 0.06	2.34 ± 0.02	80.00 ± 4.78	90.86 ± 4.70	8.76 ± 0.09	22.19 ± 0.89	91.64 ± 11.82	
Elk River	11°C	39	5	24	26.720 ± 3.657	13.10 ± 0.52	1.19 ± 0.05	2.36 ± 0.03	--	--	7.96 ± 0.09	17.45 ± 0.41	--	2.69 ± 0.72
	16°C	39	2	24	23.80 ± 2.950	12.50 ± 0.52	1.20 ± 0.07	2.67 ± 0.03	79.44 ± 6.75	98.86 ± 5.86	8.89 ± 0.10	18.33 ± 0.28	107.05 ± 13.00	
	20°C	44	7	25	25.320 ± 3.028	12.50 ± 0.47	1.29 ± 0.10	2.23 ± 0.02	68.88 ± 4.01	87.01 ± 4.72	7.69 ± 0.09	20.14 ± 0.57	96.68 ± 12.45	
Feather	11°C	39	4	23	25.360 ± 2.568	13.00 ± 0.44	1.14 ± 0.05	2.67 ± 0.03	--	--	10.96 ± 0.10	20.48 ± 0.69	--	-0.91 ± 0.85
	16°C	35	5	24	24.090 ± 2.591	12.70 ± 0.38	1.17 ± 0.07	2.41 ± 0.03	81.99 ± 5.88	96.90 ± 5.58	11.99 ± 0.35	25.95 ± 2.22	100.94 ± 8.88	
	20°C	38	12	25	26.080 ± 4.256	12.60 ± 0.47	1.30 ± 0.12	2.20 ± 0.03	75.74 ± 8.28	72.72 ± 4.05	7.97 ± 0.10	19.57 ± 0.48	72.44 ± 6.56	

Table 3.7 Continued:

Hatchery and Acclimation Temperature		Fish Swum (n=)	Mort. (n=)	Max Test Temp. (°C)	Mass (g)	Fork Length (cm)	Condition Factor	RMR		MMR	AS			
								Q_{10}	% of 11 °C	% of 11°C	AS at T_{OPT}	T_{OPT} (°C)	% of 11°C	T_{OPT} Δ (°C)
Priest Rapids	11°C	41	2	24	20.600 ± 3.957	12.40 ± 0.70	1.07 ± 0.04	2.74 ± 0.03	--	--	10.47 ± 0.10	20.07 ± 0.58	--	2.63 ± 1.24
	16°C	40	5	24	22.740 ± 3.461	12.60 ± 0.50	1.13 ± 0.07	2.32 ± 0.03	91.02 ± 9.71	92.03 ± 4.77	9.47 ± 0.09	20.51 ± 0.54	87.42 ± 8.46	
	20°C	41	3	25	21.670 ± 3.876	12.20 ± 0.66	1.18 ± 0.07	2.45 ± 0.03	75.85 ± 6.05	79.47 ± 5.21	8.70 ± 0.11	22.71 ± 1.11	79.22 ± 9.11	
Trask	11°C	42	5	24	23.760 ± 3.060	12.90 ± 0.49	1.10 ± 0.05	2.34 ± 0.03	--	--	7.09 ± 0.09	17.87 ± 0.61	--	3.93 ± 1.32
	16°C	38	1	25	26.600 ± 3.415	13.00 ± 0.50	1.20 ± 0.07	2.57 ± 0.03	80.94 ± 5.96	96.10 ± 5.14	6.99 ± 0.10	17.59 ± 0.33	96.51 ± 10.52	
	20°C	46	6	25	24.410 ± 5.693	12.70 ± 0.84	1.19 ± 0.08	2.55 ± 0.03	78.00 ± 5.23	103.57 ± 6.36	8.11 ± 0.09	21.80 ± 1.18	112.00 ± 15.47	
Trinity	11°C	34	2	23	20.910 ± 4.027	12.40 ± 0.79	1.10 ± 0.05	2.29 ± 0.03	--	--	8.96 ± 0.10	18.78 ± 0.93		4.81 ± 2.56
	16°C	39	0	25	23.650 ± 6.240	12.60 ± 1.08	1.15 ± 0.08	2.33 ± 0.02	94.24 ± 4.88	89.40 ± 4.62	7.79 ± 0.10	18.82 ± 0.46	84.56 ± 8.58	
	20°C	36	8	25	23.700 ± 4.422	12.60 ± 0.73	1.18 ± 0.09	2.40 ± 0.03	79.46 ± 4.63	76.22 ± 6.12	7.13 ± 0.19	23.59 ± 2.50	74.32 ± 11.71	

Table 3.8: GLMM covariate estimates of routine metabolic rate (RMR) with 15 environmental predictors: The association of each environmental predictor was assessed at three test temperatures per acclimation group. Gray text indicates no significant association. Italic text indicates a weakly significant association while bold text indicates a strongly significant association.

	11 °C Acclimation Temperature			16 °C Acclimation Temperature			20 °C Acclimation Temperature		
Env. Predictor	11°C	16°C	20°C	11°C	16°C	20°C	11°C	16°C	20°C
Latitude	0.019 ± 0.107	0.026 ± 0.105	0.032 ± 0.106	0.036 ± 0.107	0.036 ± 0.105	0.035 ± 0.106	-0.031 ± 0.107	0.004 ± 0.106	0.032 ± 0.106
CAMax	**-0.145 ± 0.099**	*-0.085 ± 0.097*	-0.038 ± 0.099	-0.019 ± 0.100	-0.038 ± 0.098	-0.054 ± 0.099	-0.063 ± 0.100	-0.070 ± 0.097	-0.076 ± 0.098
HAmax	**-0.213 ± 0.058**	**-0.166 ± 0.055**	**-0.128 ± 0.057**	-0.035 ± 0.057	*-0.063 ± 0.054*	**-0.086 ± 0.055**	**-0.129 ± 0.057**	**-0.128 ± 0.054**	**-0.128 ± 0.054**
CAMin	-0.034 ± 0.112	-0.015 ± 0.110	0.001 ± 0.111	-0.058 ± 0.112	-0.050 ± 0.110	-0.043 ± 0.111	0.034 ± 0.112	0.013 ± 0.111	-0.003 ± 0.111
HAMin	0.014 ± 0.109	0.015 ± 0.106	0.016 ± 0.107	-0.070 ± 0.108	-0.043 ± 0.106	-0.021 ± 0.107	0.020 ± 0.108	0.019 ± 0.106	0.019 ± 0.107
CARange	*-0.139 ± 0.095*	*-0.085 ± 0.093*	-0.041 ± 0.095	0.002 ± 0.095	-0.021 ± 0.093	-0.040 ± 0.094	*-0.083 ± 0.095*	*-0.081 ± 0.093*	*-0.080 ± 0.093*
HARange	**-0.169 ± 0.090**	**-0.134 ± 0.087**	*-0.106 ± 0.088*	0.032 ± 0.089	-0.012 ± 0.087	-0.047 ± 0.088	*-0.114 ± 0.089*	*-0.111 ± 0.087*	*-0.110 ± 0.087*
CRMax	-0.065 ± 0.113	-0.032 ± 0.112	-0.005 ± 0.113	-0.056 ± 0.113	-0.054 ± 0.112	-0.053 ± 0.112	0.016 ± 0.114	-0.017 ± 0.112	-0.043 ± 0.113
HRMax	-0.069 ± 0.110	-0.014 ± 0.108	0.030 ± 0.109	0.002 ± 0.109	-0.007 ± 0.108	-0.014 ± 0.109	-0.026 ± 0.109	-0.029 ± 0.108	-0.032 ± 0.108
CRCMax	-0.062 ± 0.105	-0.020 ± 0.103	0.014 ± 0.104	-0.018 ± 0.105	-0.018 ± 0.103	-0.017 ± 0.104	-0.040 ± 0.104	-0.035 ± 0.102	-0.031 ± 0.103
HRCMax	-0.024 ± 0.107	-0.015 ± 0.105	-0.008 ± 0.106	-0.077 ± 0.106	-0.056 ± 0.105	-0.039 ± 0.106	0.008 ± 0.107	-0.006 ± 0.105	-0.016 ± 0.106
CRAve	-0.032 ± 0.111	-0.004 ± 0.109	0.018 ± 0.110	-0.061 ± 0.111	-0.050 ± 0.109	-0.041 ± 0.109	0.033 ± 0.111	-0.002 ± 0.110	-0.030 ± 0.111
HRAve	0.009 ± 0.113	0.010 ± 0.111	0.010 ± 0.111	-0.076 ± 0.111	-0.048 ± 0.110	-0.026 ± 0.111	0.017 ± 0.112	0.007 ± 0.111	-0.002 ± 0.111
Mig.D	**-0.219 ± 0.063**	**-0.170 ± 0.060**	**-0.131 ± 0.061**	-0.016 ± 0.063	*-0.054 ± 0.060*	*-0.084 ± 0.061*	**-0.129 ± 0.063**	**-0.125 ± 0.059**	**-0.122 ± 0.060**
Mig.S	0.022 ± 0.110	-0.018 ± 0.108	-0.051 ± 0.110	0.032 ± 0.110	0.023 ± 0.108	0.015 ± 0.109	-0.017 ± 0.110	-0.021 ± 0.108	-0.024 ± 0.109

Table 3.9: GLMM covariate estimates of maximum metabolic rate (MMR) with 15 environmental predictors: The association of each environmental predictor was assessed at three test temperatures per acclimation group. Gray text indicates no significant association. Italic text indicates a weakly significant association while bold text indicates a strongly significant association.

	11 °C Acclimation Temperature			16 °C Acclimation Temperature			20 °C Acclimation Temperature		
Env. Predictor	11°C	16°C	20°C	11°C	16°C	20°C	11°C	16°C	20°C
Latitude	-0.098 ± 0.190	-0.119 ± 0.190	-0.132 ± 0.193	-0.081 ± 0.192	-0.130 ± 0.190	-0.159 ± 0.192	0.029 ± 0.193	0.045 ± 0.190	0.055 ± 0.192
CAMax	*0.183 ± 0.165*	**0.293 ± 0.163**	**0.359 ± 0.166**	*0.169 ± 0.166*	**0.286 ± 0.163**	**0.355 ± 0.165**	0.115 ± 0.166	*0.160 ± 0.162*	*0.187 ± 0.163*
HAmax	*0.198 ± 0.201*	*0.258 ± 0.200*	*0.293 ± 0.203*	0.105 ± 0.202	*0.185 ± 0.200*	*0.232 ± 0.202*	0.071 ± 0.203	0.104 ± 0.199	0.124 ± 0.201
CAMin	0.072 ± 0.199	0.133 ± 0.198	0.169 ± 0.201	0.115 ± 0.201	*0.209 ± 0.198*	*0.265 ± 0.200*	0.112 ± 0.201	0.144 ± 0.199	0.163 ± 0.201
HAMin	-0.081 ± 0.232	-0.100 ± 0.233	-0.111 ± 0.236	-0.034 ± 0.235	0.009 ± 0.232	0.034 ± 0.233	0.124 ± 0.234	0.158 ± 0.232	0.178 ± 0.233
CARange	*0.171 ± 0.187*	*0.263 ± 0.186*	**0.317 ± 0.189**	0.146 ± 0.188	*0.234 ± 0.186*	**0.286 ± 0.189**	0.085 ± 0.189	0.120 ± 0.185	0.141 ± 0.186
HARange	*0.213 ± 0.225*	*0.274 ± 0.225*	*0.310 ± 0.228*	0.117 ± 0.227	0.148 ± 0.225	0.167 ± 0.226	-0.029 ± 0.228	-0.023 ± 0.224	-0.019 ± 0.224
CRMax	0.122 ± 0.183	*0.226 ± 0.182*	**0.288 ± 0.185**	0.155 ± 0.185	*0.251 ± 0.182*	**0.308 ± 0.184**	0.117 ± 0.185	0.153 ± 0.181	*0.175 ± 0.182*
HRMax	0.059 ± 0.199	0.113 ± 0.199	0.146 ± 0.202	0.072 ± 0.201	0.145 ± 0.199	*0.188 ± 0.200*	0.127 ± 0.202	0.163 ± 0.198	*0.184 ± 0.200*
CRCMax	*0.137 ± 0.147*	**0.233 ± 0.145**	**0.290 ± 0.148**	*0.156 ± 0.149*	**0.288 ± 0.146**	**0.367 ± 0.148**	0.092 ± 0.150	*0.113 ± 0.147*	*0.126 ± 0.150*
HRCMax	0.004 ± 0.221	0.007 ± 0.221	0.009 ± 0.224	0.026 ± 0.222	0.093 ± 0.220	0.132 ± 0.221	0.138 ± 0.223	0.167 ± 0.220	0.185 ± 0.222
CRAve	*0.093 ± 0.132*	*0.152 ± 0.130*	*0.187 ± 0.134*	*0.133 ± 0.134*	**0.213 ± 0.130**	**0.260 ± 0.132**	0.093 ± 0.135	*0.114 ± 0.132*	*0.126 ± 0.135*
HRAve	-0.037 ± 0.190	-0.046 ± 0.189	-0.052 ± 0.192	-0.024 ± 0.191	0.035 ± 0.189	0.070 ± 0.190	0.175 ± 0.191	*0.167 ± 0.189*	*0.163 ± 0.191*
Mig.D	*0.209 ± 0.208*	*0.282 ± 0.207*	**0.326 ± 0.209**	0.120 ± 0.209	*0.194 ± 0.207*	*0.239 ± 0.209*	0.047 ± 0.208	0.083 ± 0.205	0.105 ± 0.206
Mig.S	-0.020 ± 0.201	-0.095 ± 0.201	-0.139 ± 0.204	-0.095 ± 0.204	*-0.177 ± 0.201*	*-0.226 ± 0.202*	-0.145 ± 0.203	*-0.200 ± 0.200*	*-0.232 ± 0.202*

Table 3.10: GLMM covariate estimates of aerobic scope (AS) with 15 environmental predictors: The association of each environmental predictor was assessed at three test temperatures per acclimation group. Gray text indicates no significant association. Italic text indicates a weakly significant association while bold text indicates a strongly significant association.

	11 °C Acclimation Temperature			16 °C Acclimation Temperature			20 °C Acclimation Temperature		
Env. Predictor	11°C	16°C	20°C	11°C	16°C	20°C	11°C	16°C	20°C
Latitude	-0.107 ± 0.230	-0.155 ± 0.230	-0.168 ± 0.228	-0.094 ± 0.230	-0.152 ± 0.231	*-0.210 ± 0.229*	0.073 ± 0.231	0.065 ± 0.230	0.069 ± 0.229
CAMax	0.148 ± 0.169	**0.312 ± 0.168**	**0.391 ± 0.166**	0.076 ± 0.169	*0.230 ± 0.169*	**0.337 ± 0.167**	0.052 ± 0.169	*0.151 ± 0.169*	*0.194 ± 0.167*
HAmax	*0.212 ± 0.210*	*0.293 ± 0.208*	**0.336 ± 0.207**	-0.010 ± 0.211	0.096 ± 0.211	0.183 ± 0.209	-0.013 ± 0.211	0.076 ± 0.209	0.121 ± 0.208
CAMin	0.025 ± 0.214	0.123 ± 0.213	0.162 ± 0.211	0.088 ± 0.212	*0.213 ± 0.213*	*0.305 ± 0.212*	0.069 ± 0.213	0.134 ± 0.212	0.150 ± 0.211
HAMin	-0.108 ± 0.237	-0.160 ± 0.235	-0.182 ± 0.233	-0.028 ± 0.235	0.038 ± 0.235	0.066 ± 0.234	0.168 ± 0.235	0.204 ± 0.234	*0.212 ± 0.233*
CARange	0.143 ± 0.204	*0.275 ± 0.203*	**0.340 ± 0.201**	0.044 ± 0.204	0.148 ± 0.204	*0.228 ± 0.202*	0.019 ± 0.205	0.098 ± 0.204	0.137 ± 0.202
HARange	*0.245 ± 0.229*	*0.336 ± 0.227*	**0.388 ± 0.226**	0.016 ± 0.229	0.053 ± 0.229	0.100 ± 0.228	-0.146 ± 0.229	-0.108 ± 0.229	-0.071 ± 0.228
CRMax	0.062 ± 0.200	*0.216 ± 0.199*	*0.286 ± 0.197*	0.079 ± 0.200	*0.206 ± 0.200*	*0.281 ± 0.198*	0.080 ± 0.200	0.153 ± 0.200	*0.180 ± 0.199*
HRMax	0.016 ± 0.219	0.087 ± 0.218	0.117 ± 0.216	0.004 ± 0.219	0.107 ± 0.219	0.159 ± 0.218	0.120 ± 0.219	0.184 ± 0.219	*0.207 ± 0.217*
CRCMax	0.109 ± 0.174	*0.263 ± 0.175*	**0.323 ± 0.172**	0.135 ± 0.174	**0.312 ± 0.175**	**0.434 ± 0.173**	0.049 ± 0.173	0.123 ± 0.174	0.136 ± 0.173
HRCMax	-0.038 ± 0.228	-0.053 ± 0.228	-0.058 ± 0.225	0.007 ± 0.225	0.113 ± 0.226	0.167 ± 0.225	0.139 ± 0.226	0.189 ± 0.225	0.198 ± 0.224
CRAve	0.065 ± 0.189	*0.196 ± 0.190*	*0.244 ± 0.187*	0.131 ± 0.188	**0.301 ± 0.189**	**0.409 ± 0.187**	0.070 ± 0.188	0.135 ± 0.188	0.140 ± 0.187
HRAve	-0.086 ± 0.238	-0.134 ± 0.236	-0.155 ± 0.234	-0.012 ± 0.234	0.072 ± 0.235	0.108 ± 0.235	0.159 ± 0.235	0.193 ± 0.235	0.196 ± 0.234
Mig.D	*0.238 ± 0.207*	**0.343 ± 0.206**	**0.400 ± 0.204**	0.003 ± 0.208	0.091 ± 0.208	0.179 ± 0.206	-0.050 ± 0.208	0.037 ± 0.207	0.089 ± 0.206
Mig.S	-0.014 ± 0.215	-0.148 ± 0.215	*-0.217 ± 0.213*	-0.025 ± 0.215	-0.125 ± 0.215	*-0.201 ± 0.214*	-0.075 ± 0.215	-0.170 ± 0.215	*-0.216 ± 0.214*

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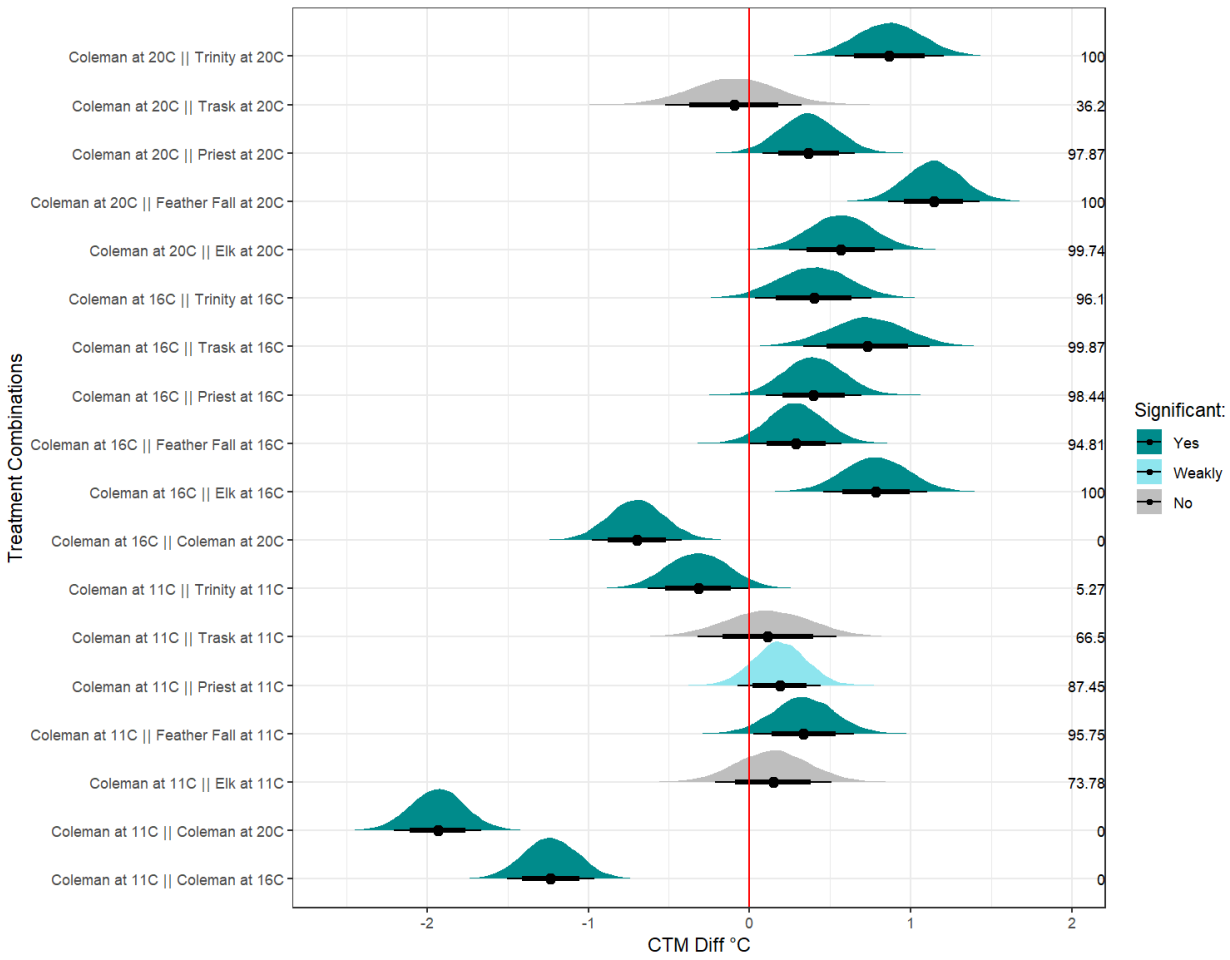
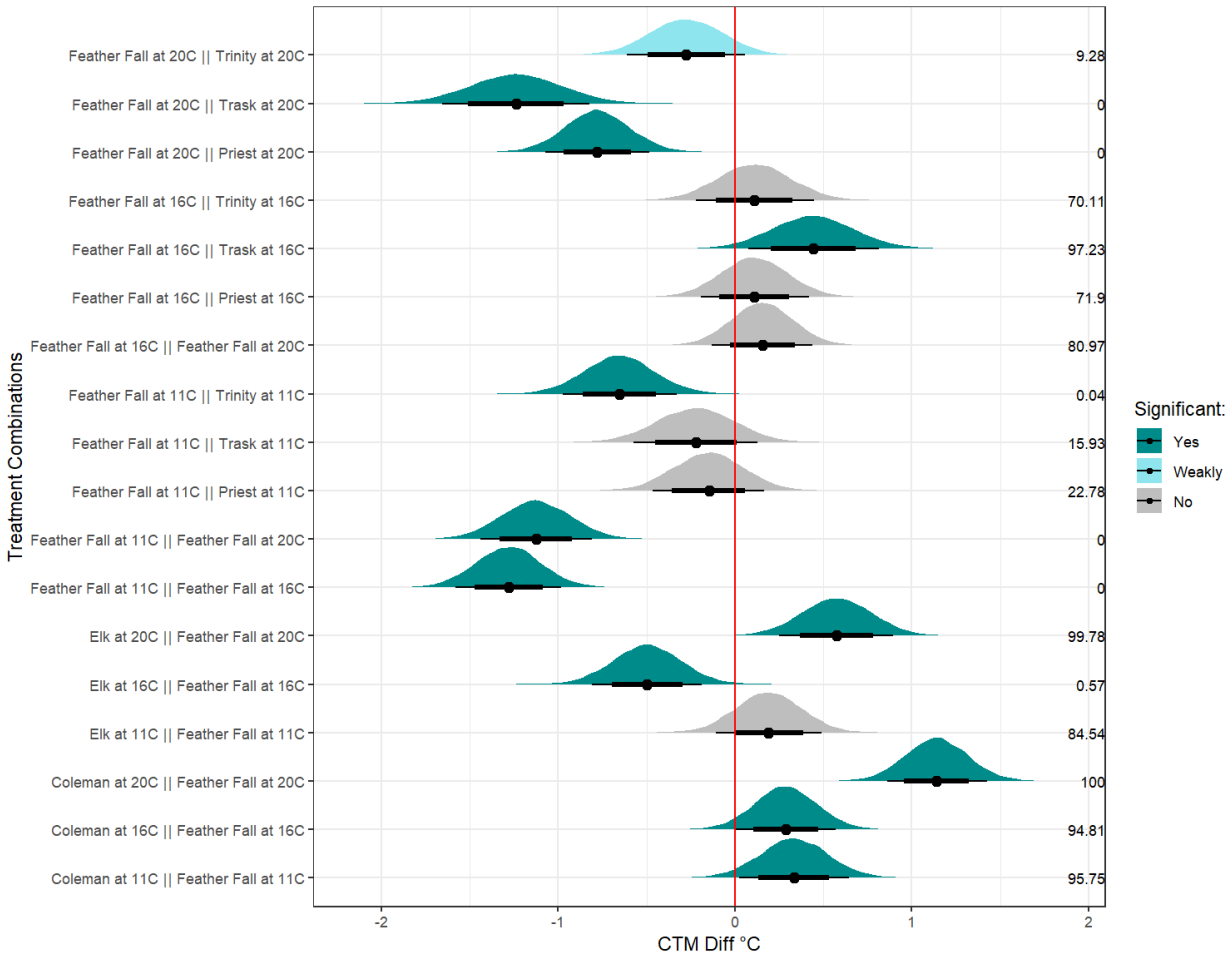
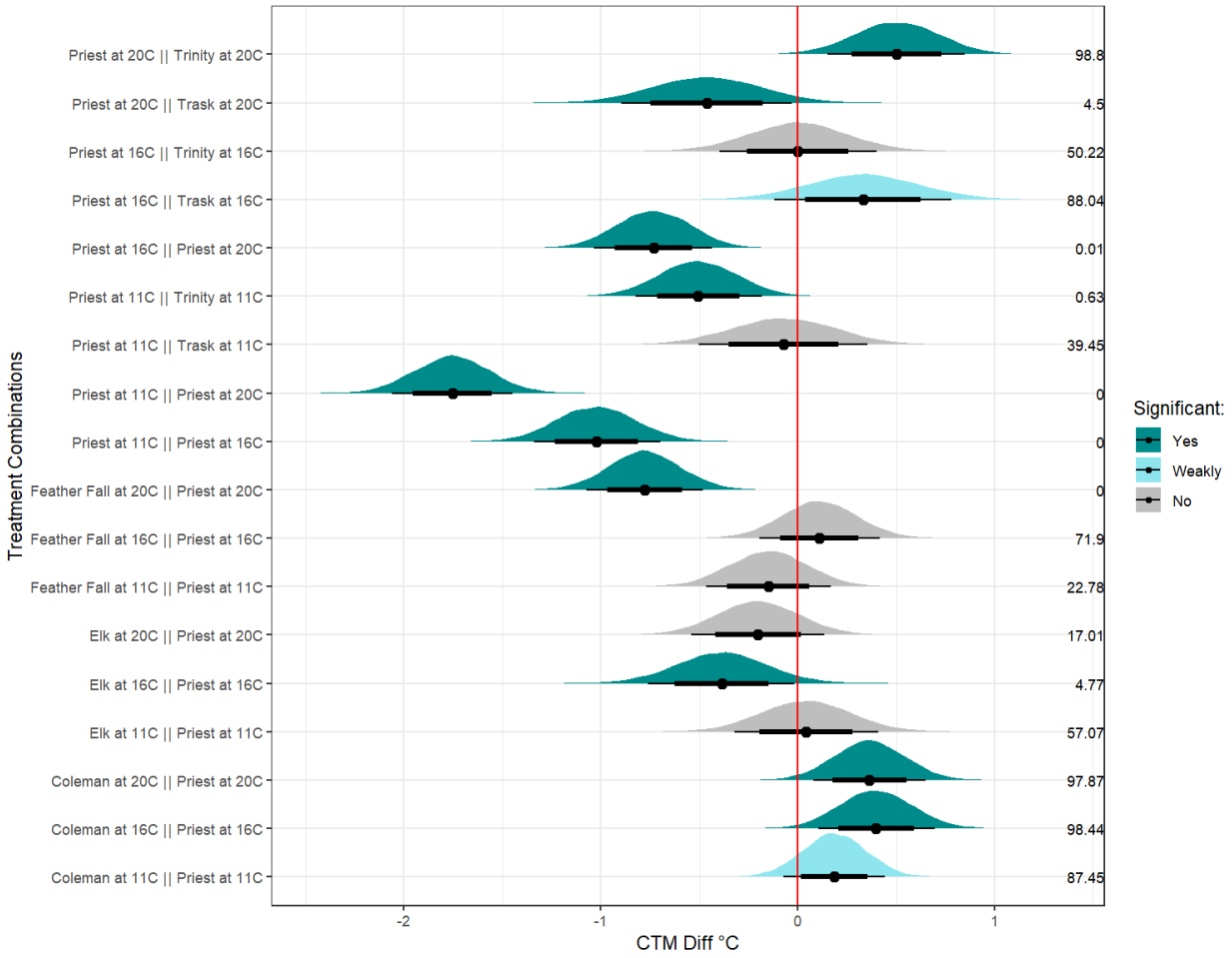


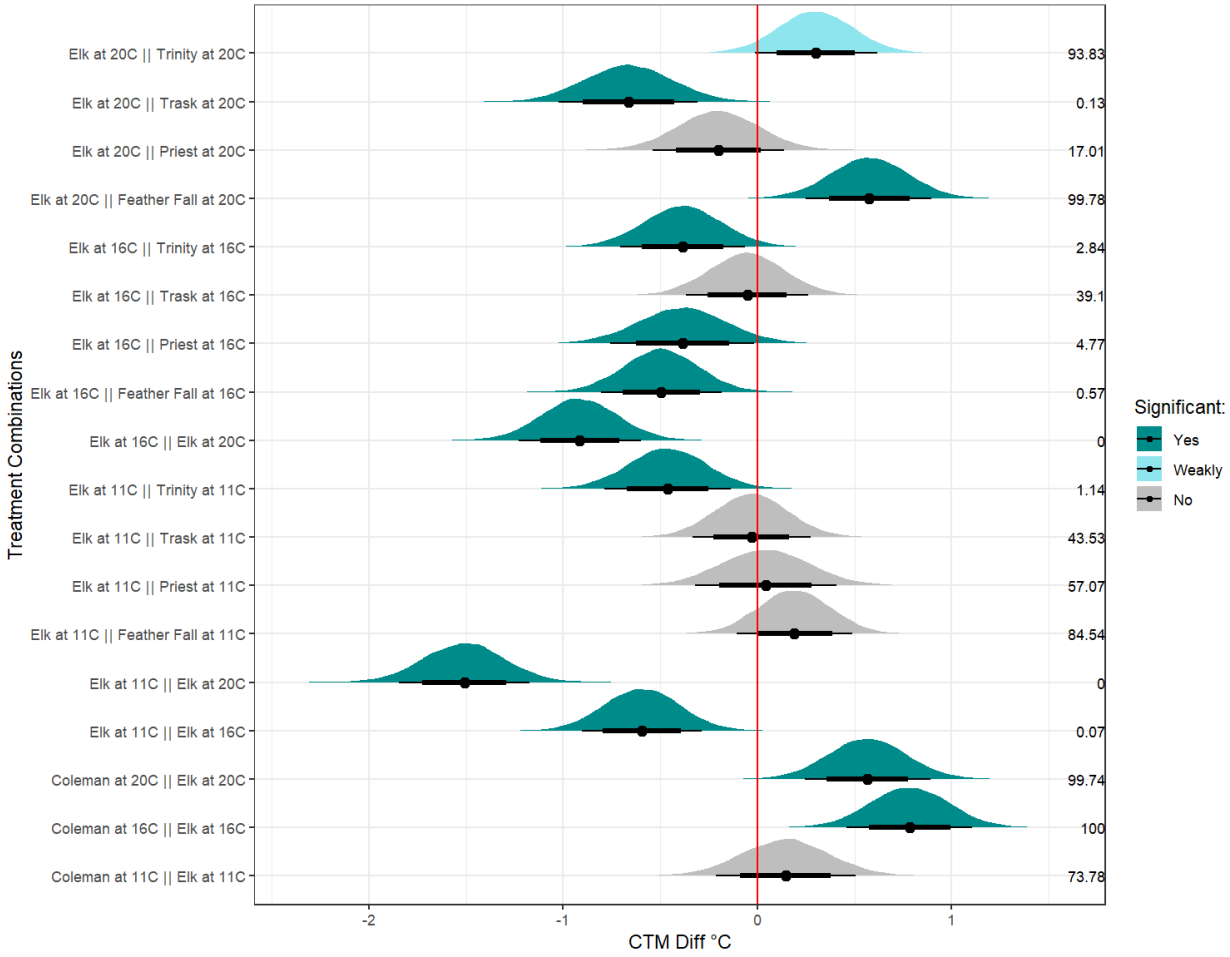
Supplemental Figure 3.1: Treatment Contrasts of CTMax values between Coleman River Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



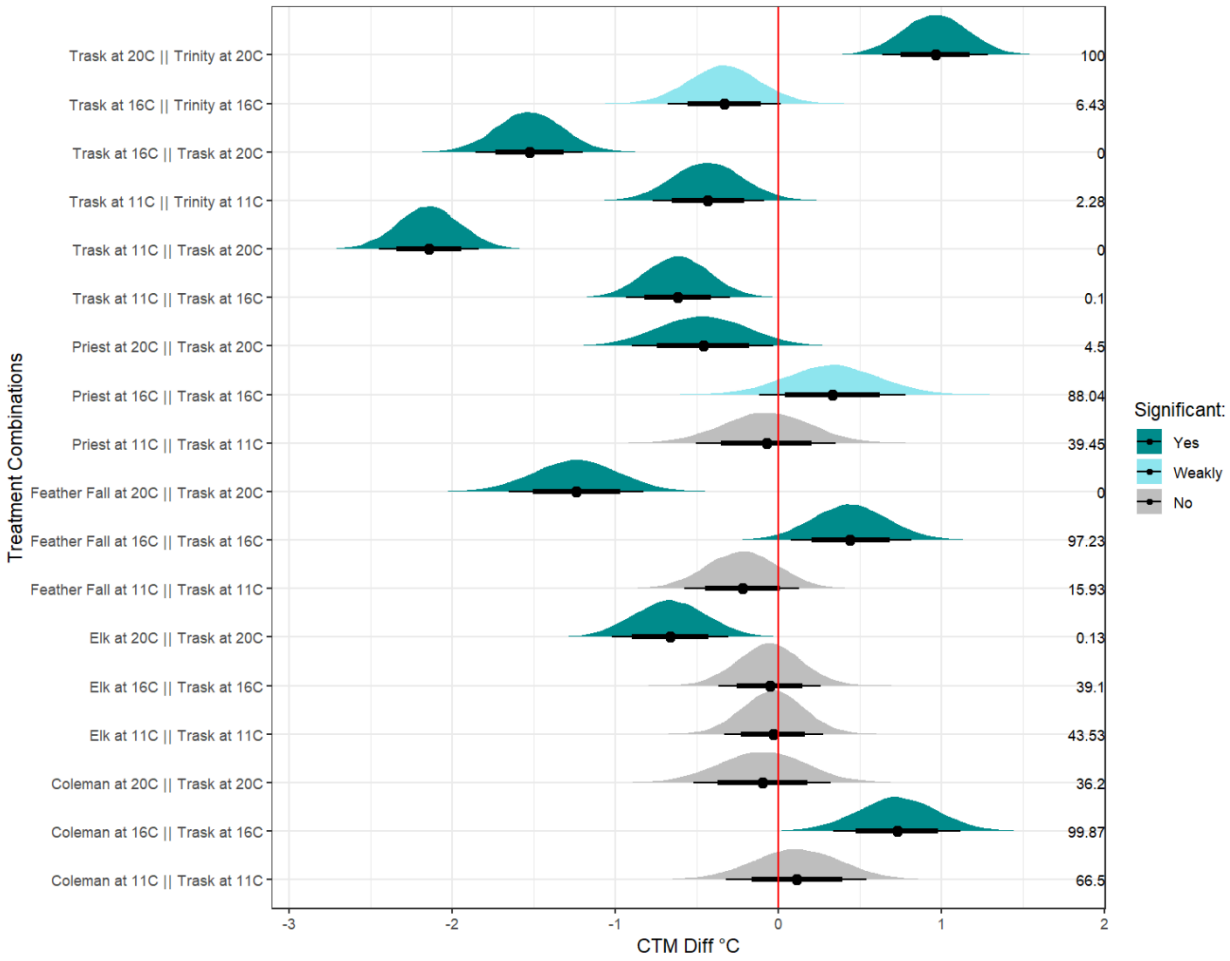
Supplemental Figure 3.2: Treatment Contrasts of CTMax values between Feather Fall-run Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



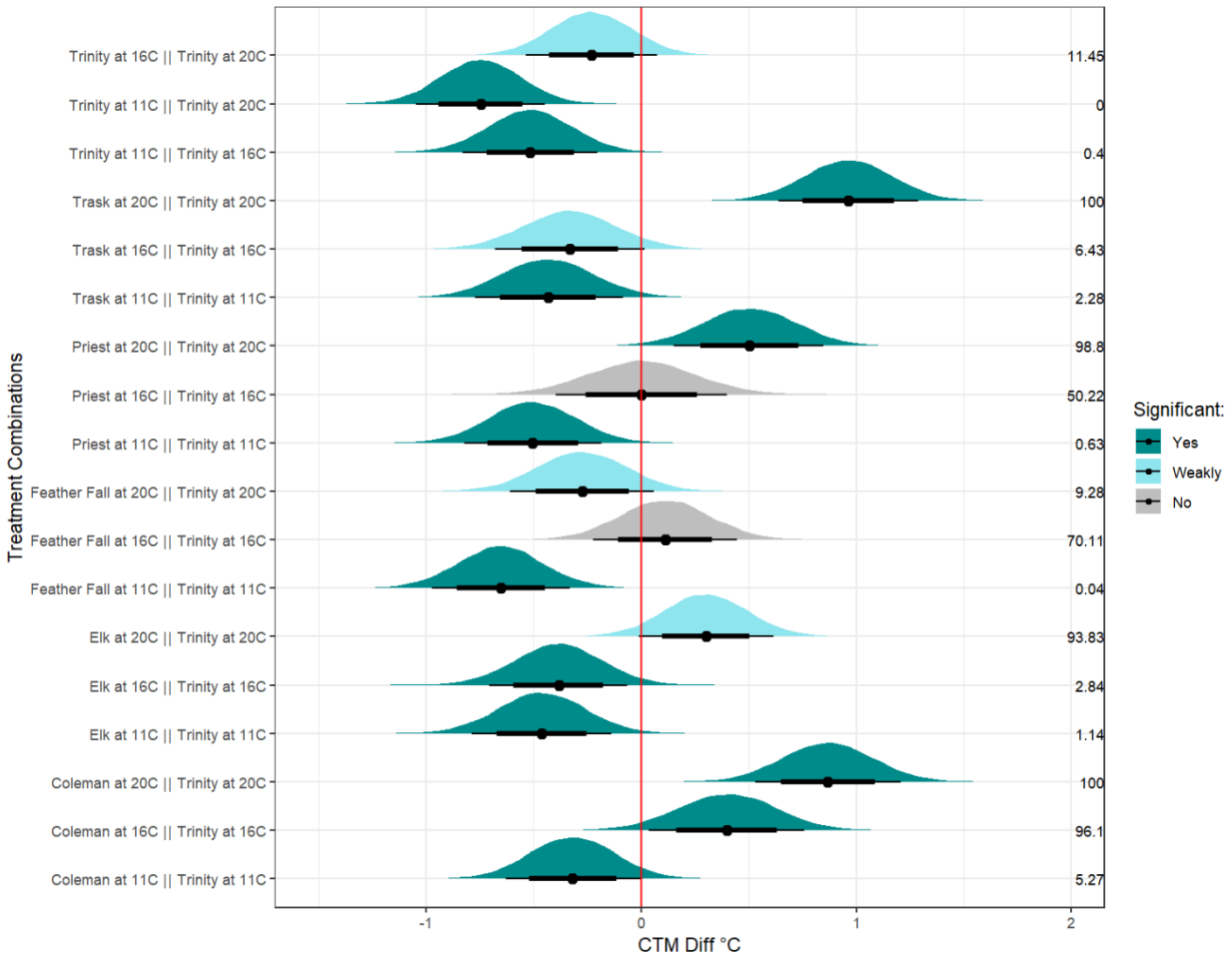
Supplemental Figure 3.3: Treatment Contrasts of CTMax values between Priest Rapids Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



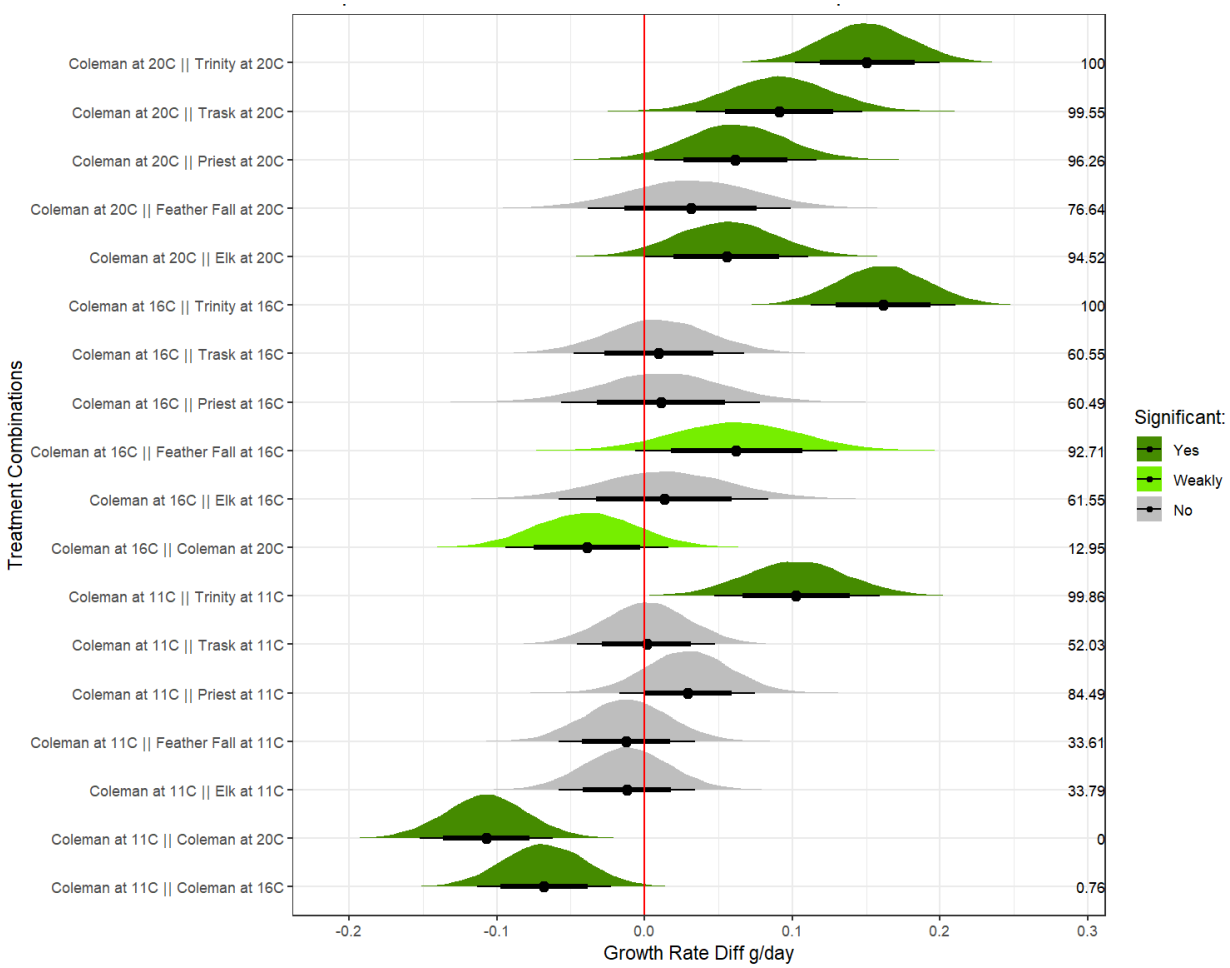
Supplemental Figure 3.4: Treatment Contrasts of CTMax values between Elk River Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



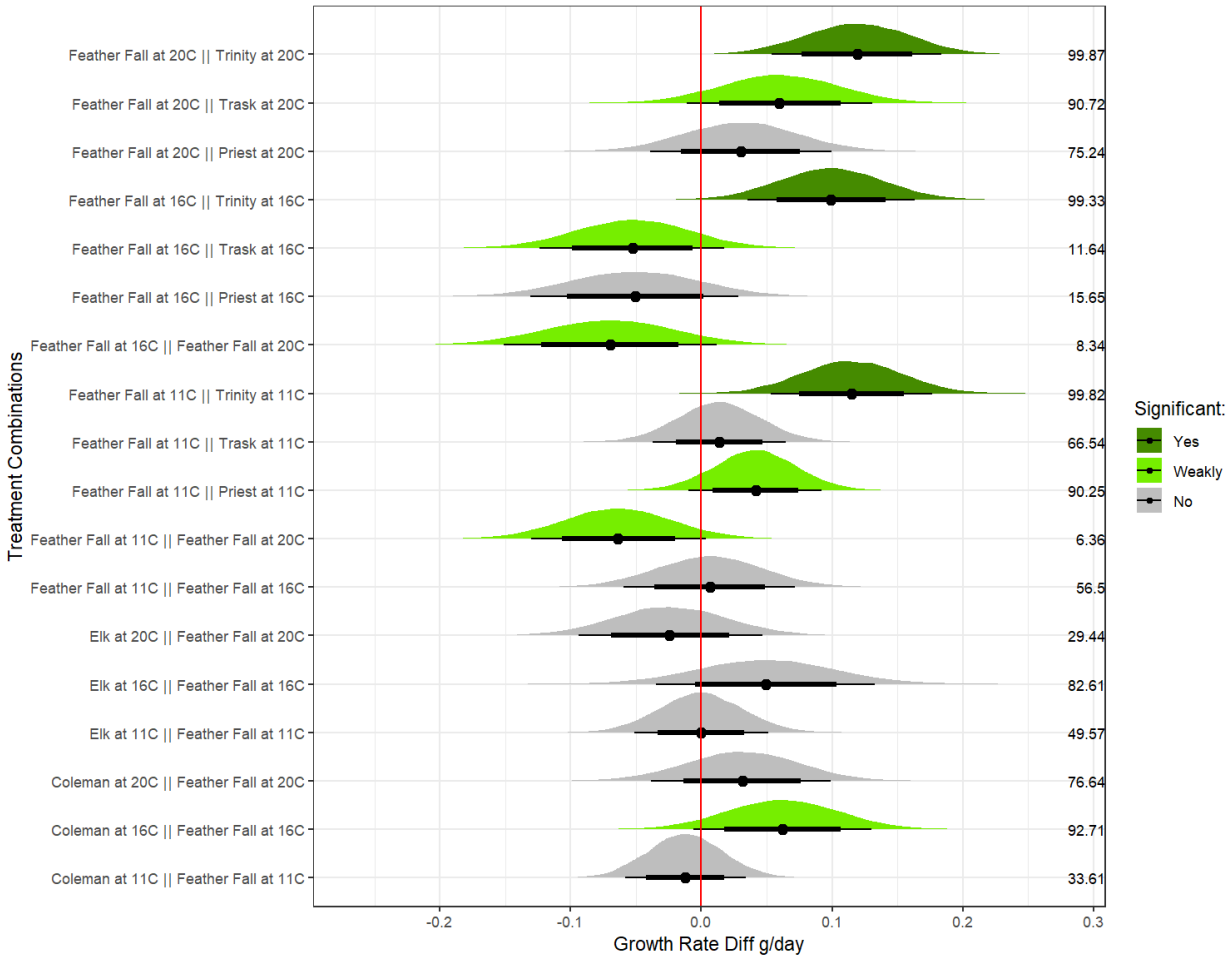
Supplemental Figure 3.5: Treatment Contrasts of CTMax values between Trask Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



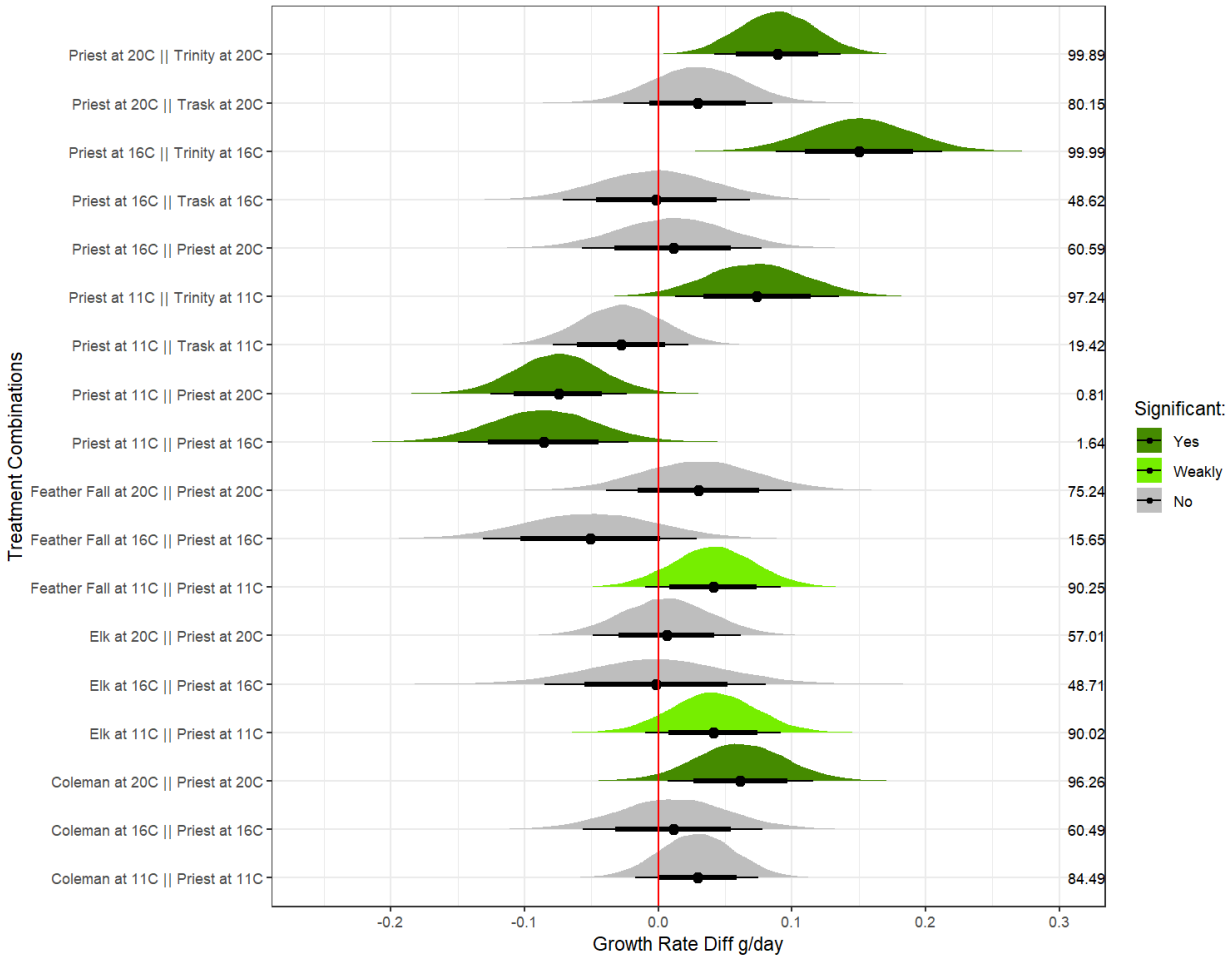
Supplemental Figure 3.6: Treatment Contrasts of CTMax values between Trinity Population and other populations: Difference is calculated as the mean CTMax value of the first population minus the mean CTMax value of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



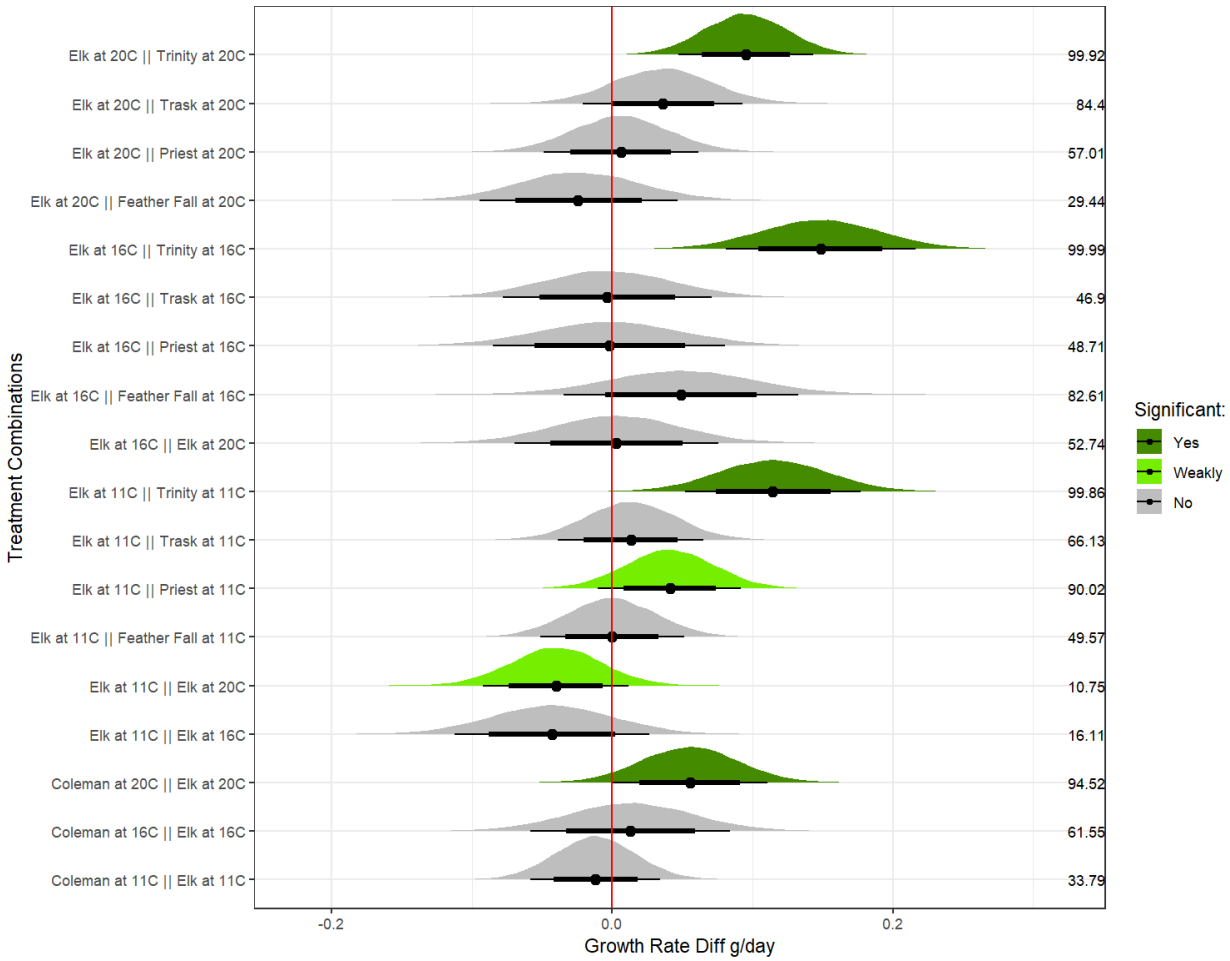
Supplemental Figure 3.7: Treatment Contrasts of Growth Rate estimates between Coleman Hatchery population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



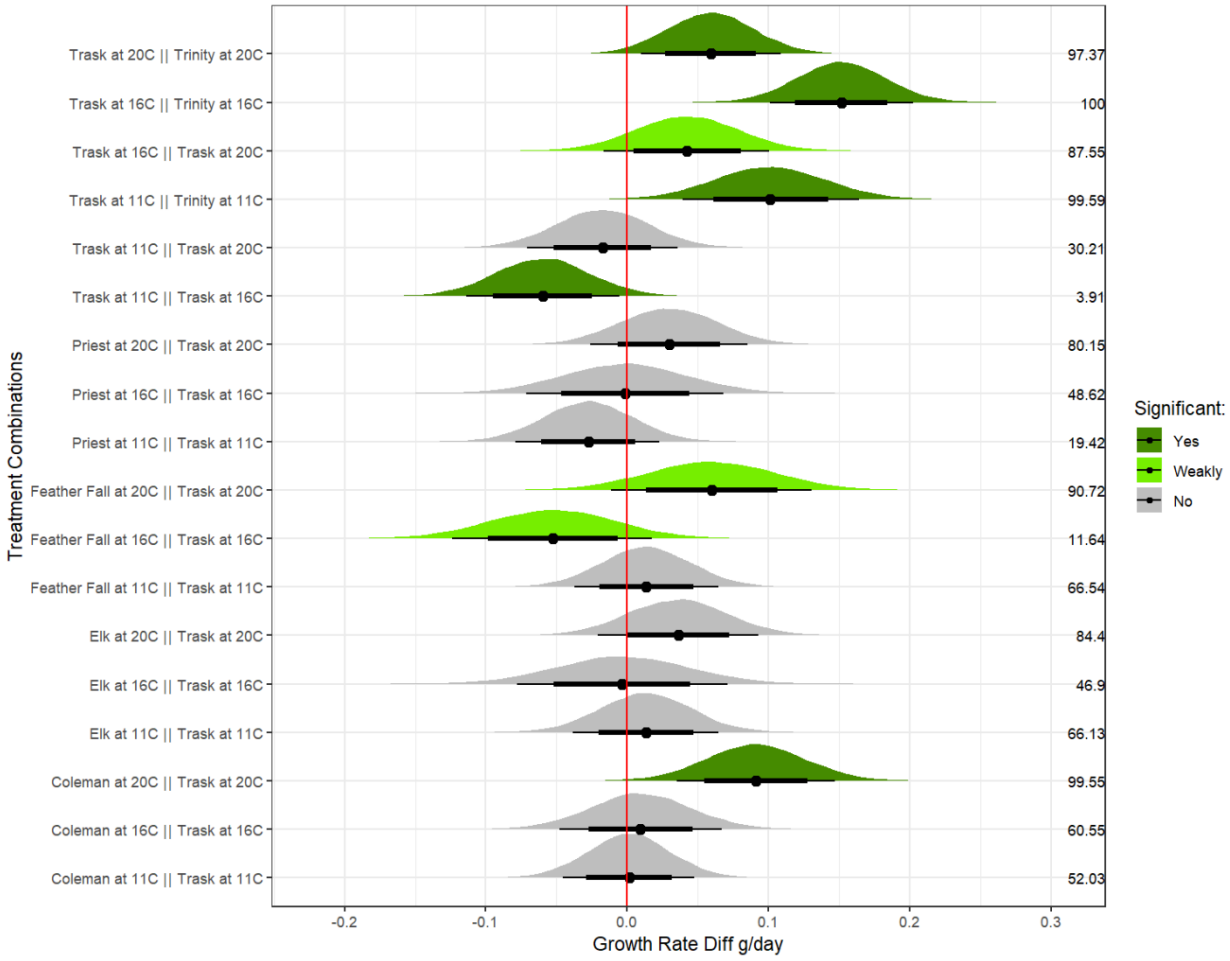
Supplemental Figure 3.8: Treatment Contrasts of Growth Rate estimates between Feather Hatchery population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



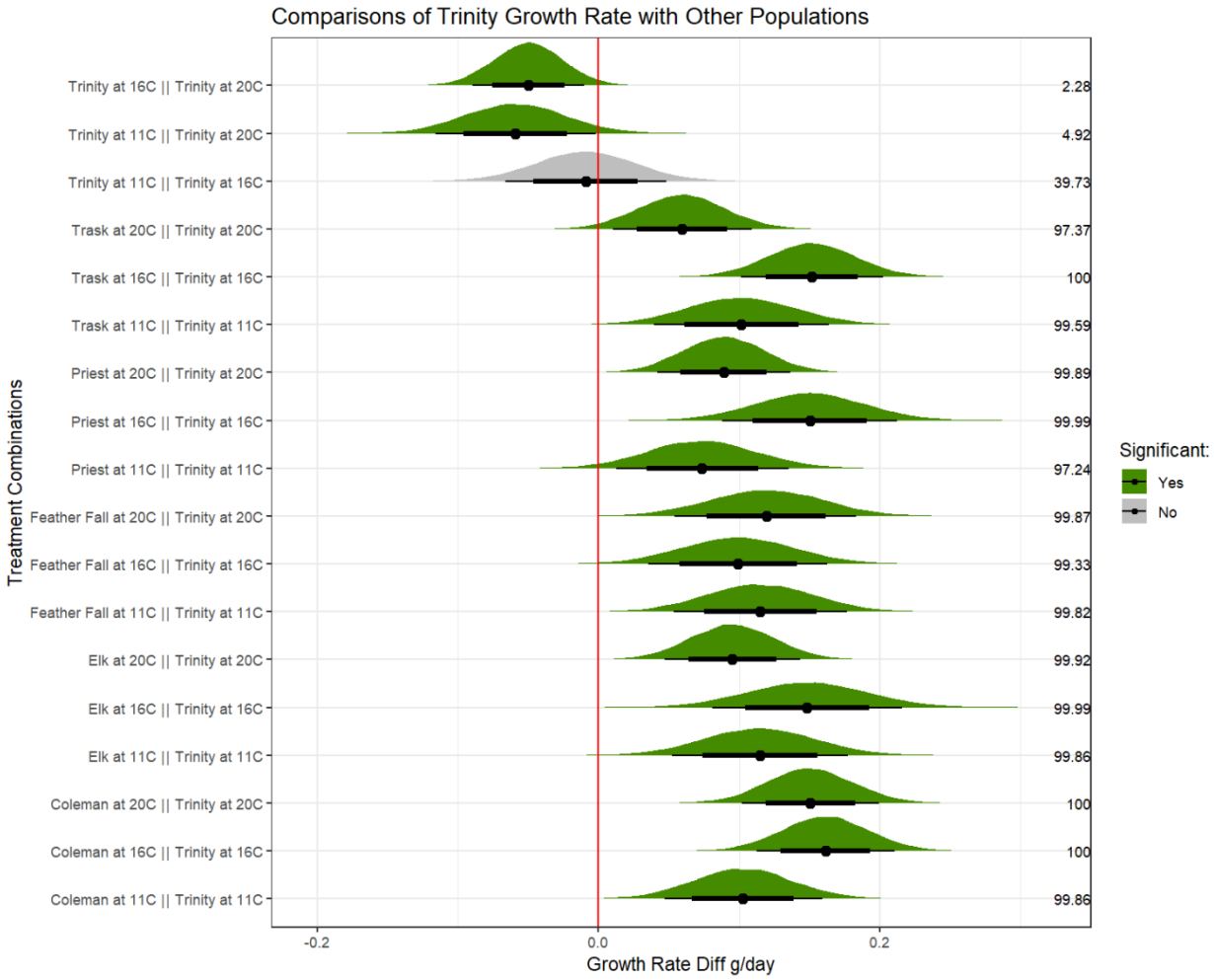
Supplemental Figure 3.9: Treatment Contrasts of Growth Rate estimates between Priest Rapids population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



Supplemental Figure 3.10: Treatment Contrasts of Growth Rate estimates between Elk River population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



Supplemental Figure 3.11: Treatment Contrasts of Growth Rate estimates between Trask population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.



Supplemental Figure 3.12: Treatment Contrasts of Growth Rate estimates between Trinity population and other populations. Difference is calculated as the mean growth rate of the first population minus the mean growth rate of second. The posterior distribution of the contrast is provided and shaded according to its significance. Significance was assigned if 94.5% of the posterior mass was above or below 0 (indicated by the vertical red line). Weakly significant is assigned if 85% of the posterior mass was above or below 0.

Supplemental Table 3.1: Summary table of all populations and test temperatures. 'Fish (n)' is the total number of fish attempted while 'Mort.' Is the number of mortalities at each temperature. Mass, fork length and condition factor are reported as the mean and standard deviation of the observed fish that underwent the trial. Accurate weights and lengths could not be obtained for mortalities.

Population	Acclimation Temp. (C°)	Trial Temp.	Fish (n)	Mass (g)	Fork Length (cm)	Condition Factor	Mort.
Coleman	11	8	3	21.707 ± 5.202	12.37 ± 0.74	1.13 ± 0.06	0
		10	3	22.797 ± 4.017	12.67 ± 0.57	1.11 ± 0.05	0
		12	4	21.903 ± 4.850	12.28 ± 0.57	1.17 ± 0.10	0
		14	3	21.360 ± 1.437	12.40 ± 0.44	1.12 ± 0.04	0
		16	3	21.253 ± 1.241	12.30 ± 0.10	1.14 ± 0.04	0
		18	4	22.775 ± 2.912	12.50 ± 0.48	1.16 ± 0.06	0
		20	4	20.875 ± 2.799	12.40 ± 0.50	1.09 ± 0.04	0
		22	4	24.778 ± 8.844	12.90 ± 1.29	1.12 ± 0.06	0
		24	8	21.780 ± 1.919	12.53 ± 0.92	1.12 ± 0.14	4
		25	1	NA	NA	NA	1
		26	2	NA	NA	NA	2
Coleman	16	8	5	21.480 ± 3.102	12.42 ± 0.58	1.12 ± 0.03	0
		10	6	23.743 ± 2.249	12.75 ± 0.48	1.14 ± 0.03	0
		12	5	22.704 ± 2.250	12.64 ± 0.51	1.12 ± 0.03	0
		14	4	24.090 ± 3.640	12.68 ± 0.61	1.18 ± 0.03	0
		16	4	24.795 ± 3.670	12.80 ± 0.57	1.18 ± 0.03	0
		18	4	23.710 ± 4.613	12.63 ± 0.71	1.17 ± 0.04	0
		20	3	22.183 ± 0.029	12.40 ± 0.10	1.16 ± 0.03	0
		22	4	25.253 ± 5.335	12.78 ± 0.60	1.20 ± 0.08	0
		24	4	25.845 ± 4.045	12.85 ± 0.60	1.21 ± 0.02	0
		25	4	23.753 ± 1.001	12.57 ± 0.06	1.20 ± 0.07	1
		26	2	NA	NA	NA	2
Coleman	20	8	4	28.485 ± 4.864	13.30 ± 0.44	1.20 ± 0.11	0
		10	4	26.373 ± 8.441	12.78 ± 1.31	1.23 ± 0.03	0
		12	5	26.048 ± 2.488	12.74 ± 0.44	1.26 ± 0.04	0
		14	5	25.748 ± 4.298	12.76 ± 0.59	1.23 ± 0.05	0
		16	6	21.483 ± 3.107	12.22 ± 0.78	1.18 ± 0.07	0
		18	4	21.705 ± 3.132	12.20 ± 0.54	1.19 ± 0.02	0
		20	5	25.818 ± 1.213	12.80 ± 0.12	1.23 ± 0.05	0
		22	4	24.690 ± 1.073	12.83 ± 0.30	1.17 ± 0.08	0
		24	4	23.433 ± 0.898	12.53 ± 0.28	1.19 ± 0.04	0
		25	4	24.128 ± 3.628	12.40 ± 0.60	1.26 ± 0.05	0
		26	3	NA	NA	NA	3
Elk River	11	8	4	27.440 ± 3.390	13.18 ± 0.65	1.20 ± 0.05	0
		10	4	29.730 ± 2.306	13.45 ± 0.41	1.22 ± 0.04	0
		12	6	28.822 ± 5.374	13.35 ± 0.67	1.20 ± 0.07	0
		14	4	23.555 ± 1.766	12.78 ± 0.17	1.13 ± 0.04	0

		16	4	28.005 ± 1.718	13.18 ± 0.19	1.22 ± 0.03	0
		18	4	27.538 ± 2.098	13.05 ± 0.34	1.24 ± 0.04	0
		20	5	23.980 ± 2.161	12.80 ± 0.45	1.14 ± 0.03	0
		22	4	26.223 ± 4.232	13.00 ± 0.67	1.19 ± 0.05	0
		24	7	24.783 ± 3.732	12.85 ± 0.70	1.16 ± 0.02	3
		25	2	NA	NA	NA	2
Elk River	16	8	4	24.658 ± 4.208	12.65 ± 0.72	1.21 ± 0.02	0
		10	5	22.408 ± 2.190	12.34 ± 0.58	1.19 ± 0.05	0
		12	3	24.680 ± 2.885	12.60 ± 0.72	1.23 ± 0.07	0
		14	4	24.000 ± 1.343	12.55 ± 0.37	1.22 ± 0.06	0
		16	4	23.968 ± 2.765	12.58 ± 0.39	1.20 ± 0.07	0
		18	5	22.552 ± 2.163	12.38 ± 0.30	1.19 ± 0.07	0
		20	4	24.530 ± 0.818	12.60 ± 0.26	1.23 ± 0.06	0
		22	5	23.342 ± 4.296	12.46 ± 0.80	1.20 ± 0.13	0
		24	5	24.776 ± 4.689	12.74 ± 0.66	1.19 ± 0.06	0
		25	2	NA	NA	NA	2
Elk River	20	8	5	26.930 ± 1.596	12.68 ± 0.38	1.33 ± 0.13	0
		10	4	27.478 ± 2.362	12.83 ± 0.34	1.30 ± 0.04	0
		12	5	27.066 ± 2.791	12.62 ± 0.51	1.35 ± 0.20	0
		14	5	24.000 ± 1.254	12.40 ± 0.50	1.26 ± 0.09	1
		16	4	22.823 ± 1.983	12.10 ± 0.18	1.29 ± 0.06	0
		18	4	23.085 ± 2.039	12.25 ± 0.33	1.25 ± 0.04	0
		20	6	25.860 ± 4.669	12.80 ± 0.50	1.22 ± 0.09	2
		22	4	25.903 ± 4.118	12.50 ± 0.70	1.32 ± 0.12	0
		24	5	25.110 ± 3.408	12.50 ± 0.52	1.28 ± 0.06	0
		25	7	24.384 ± 3.106	12.32 ± 0.51	1.30 ± 0.10	2
		26	2	NA	NA	NA	2
Feather Fall	11	8	4	23.533 ± 2.729	12.73 ± 0.32	1.14 ± 0.05	0
		10	6	25.510 ± 2.599	13.17 ± 0.43	1.11 ± 0.03	0
		12	4	26.218 ± 2.817	13.00 ± 0.41	1.19 ± 0.07	0
		14	4	24.305 ± 3.586	12.95 ± 0.60	1.11 ± 0.02	0
		16	4	24.563 ± 1.163	12.88 ± 0.24	1.15 ± 0.07	0
		18	4	25.445 ± 1.405	12.80 ± 0.29	1.21 ± 0.02	0
		20	5	26.106 ± 2.897	13.18 ± 0.61	1.14 ± 0.04	0
		22	4	25.808 ± 2.321	13.20 ± 0.22	1.12 ± 0.07	0
		23	4	26.483 ± 3.665	13.25 ± 0.66	1.13 ± 0.04	0
		24	2	NA	NA	NA	2
		25	2	NA	NA	NA	2
Feather Fall	16	8	4	25.375 ± 3.828	12.78 ± 0.59	1.21 ± 0.03	0
		10	4	26.545 ± 3.280	12.80 ± 0.38	1.26 ± 0.06	0
		12	4	23.098 ± 2.067	12.45 ± 0.17	1.20 ± 0.07	0
		14	4	22.383 ± 2.402	12.25 ± 0.35	1.22 ± 0.08	0
		16	4	24.293 ± 2.272	12.90 ± 0.36	1.13 ± 0.04	0

		18	4	24.525 ± 3.461	12.83 ± 0.34	1.16 ± 0.07	0
		20	4	23.000 ± 1.433	12.70 ± 0.26	1.12 ± 0.04	1
		22	4	23.643 ± 1.222	12.83 ± 0.28	1.12 ± 0.03	0
		24	6	23.673 ± 1.788	12.73 ± 0.39	1.15 ± 0.04	2
		25	2	NA	NA	NA	2
Feather	20	8	6	27.428 ± 8.765	12.60 ± 1.03	1.34 ± 0.12	1
		10	5	28.410 ± 3.991	12.70 ± 0.23	1.38 ± 0.15	0
		12	4	23.695 ± 3.536	12.15 ± 0.13	1.32 ± 0.19	0
		14	5	23.580 ± 1.810	12.48 ± 0.33	1.21 ± 0.08	1
		16	4	26.108 ± 2.283	12.75 ± 0.29	1.26 ± 0.11	0
		18	4	25.195 ± 1.410	12.70 ± 0.37	1.23 ± 0.09	0
		20	4	24.680 ± 3.467	12.45 ± 0.34	1.27 ± 0.08	0
		22	4	28.305 ± 4.113	12.75 ± 0.42	1.36 ± 0.10	0
		24	7	27.567 ± 2.317	12.67 ± 0.45	1.36 ± 0.03	4
		25	5	22.71	12.2	1.25	4
		26	2	NA	NA	NA	2
Priest Rapids	11	8	4	21.255 ± 3.476	12.55 ± 0.58	1.07 ± 0.03	0
		10	4	19.628 ± 3.113	12.28 ± 0.66	1.05 ± 0.02	0
		12	4	16.100 ± 0.918	11.48 ± 0.17	1.07 ± 0.04	0
		14	6	22.712 ± 3.597	12.72 ± 0.67	1.10 ± 0.02	0
		16	6	22.035 ± 4.318	12.55 ± 0.69	1.10 ± 0.06	0
		18	4	22.105 ± 2.692	12.75 ± 0.33	1.06 ± 0.05	0
		20	4	21.400 ± 4.940	12.68 ± 0.83	1.04 ± 0.05	0
		22	5	19.236 ± 5.461	12.08 ± 0.93	1.07 ± 0.04	0
		24	4	19.505 ± 3.416	12.20 ± 0.54	1.07 ± 0.05	0
		25	2	NA	NA	NA	2
Priest Rapids	16	8	6	26.678 ± 3.053	13.20 ± 0.20	1.16 ± 0.09	0
		10	4	21.360 ± 2.448	12.60 ± 0.32	1.07 ± 0.08	0
		12	4	20.368 ± 2.238	12.13 ± 0.25	1.14 ± 0.06	0
		14	4	25.528 ± 3.427	12.88 ± 0.30	1.19 ± 0.07	0
		16	4	19.413 ± 2.497	12.05 ± 0.65	1.11 ± 0.04	0
		18	4	25.270 ± 2.362	13.00 ± 0.39	1.15 ± 0.01	0
		20	4	22.773 ± 3.176	12.55 ± 0.48	1.15 ± 0.05	0
		22	5	20.698 ± 1.354	12.44 ± 0.27	1.07 ± 0.04	0
		24	5	21.464 ± 2.559	12.36 ± 0.36	1.13 ± 0.05	0
		25	3	NA	NA	NA	3
		26	2	NA	NA	NA	2
Priest Rapids	20	8	4	23.125 ± 2.352	12.53 ± 0.51	1.18 ± 0.05	0
		10	4	28.213 ± 2.853	13.15 ± 0.33	1.24 ± 0.05	0
		12	4	23.420 ± 2.418	12.60 ± 0.50	1.17 ± 0.06	0
		14	4	19.440 ± 0.777	11.78 ± 0.30	1.19 ± 0.05	0
		16	4	19.038 ± 1.863	11.73 ± 0.26	1.18 ± 0.11	0
		18	3	23.023 ± 4.496	12.63 ± 0.71	1.13 ± 0.03	0

		20	5	18.504 ± 2.001	11.76 ± 0.36	1.13 ± 0.05	0
		22	5	24.460 ± 3.389	12.74 ± 0.55	1.18 ± 0.02	0
		24	4	19.913 ± 3.001	11.88 ± 0.33	1.18 ± 0.09	0
		25	5	17.988 ± 0.143	11.45 ± 0.31	1.20 ± 0.10	1
		26	2	NA	NA	NA	2
Trask	11	8	4	22.365 ± 0.794	12.55 ± 0.13	1.13 ± 0.06	0
		10	6	23.388 ± 4.748	12.95 ± 0.70	1.07 ± 0.06	0
		12	4	24.850 ± 1.564	13.13 ± 0.29	1.10 ± 0.01	0
		14	4	22.708 ± 3.287	12.65 ± 0.61	1.12 ± 0.02	0
		16	5	24.348 ± 4.010	12.96 ± 0.62	1.11 ± 0.05	0
		18	4	23.950 ± 2.157	12.90 ± 0.42	1.11 ± 0.06	0
		20	6	24.592 ± 4.029	13.07 ± 0.62	1.10 ± 0.06	0
		22	6	23.878 ± 2.458	12.92 ± 0.34	1.10 ± 0.05	1
		24	6	23.363 ± 2.673	12.73 ± 0.39	1.13 ± 0.03	2
		25	2	NA	NA	NA	2
Trask	16	8	4	30.450 ± 4.612	13.33 ± 0.53	1.28 ± 0.06	0
		10	3	26.090 ± 5.455	13.10 ± 0.60	1.15 ± 0.08	0
		12	3	24.740 ± 2.720	12.77 ± 0.46	1.19 ± 0.04	0
		14	4	28.150 ± 1.704	13.20 ± 0.32	1.23 ± 0.10	0
		16	4	26.133 ± 1.859	13.13 ± 0.46	1.16 ± 0.05	0
		18	4	27.635 ± 5.117	13.30 ± 0.70	1.16 ± 0.03	0
		20	4	23.828 ± 1.758	12.60 ± 0.20	1.19 ± 0.09	0
		22	4	25.920 ± 1.572	12.78 ± 0.41	1.24 ± 0.06	0
		24	4	24.330 ± 1.840	12.63 ± 0.38	1.21 ± 0.04	0
		25	5	28.098 ± 2.674	13.23 ± 0.56	1.21 ± 0.07	1
Trask	20	8	4	23.285 ± 3.202	12.48 ± 0.59	1.20 ± 0.07	0
		10	4	26.063 ± 3.963	12.83 ± 0.72	1.23 ± 0.06	0
		12	4	22.273 ± 2.207	12.25 ± 0.33	1.21 ± 0.08	0
		14	6	31.822 ± 9.508	13.82 ± 1.34	1.18 ± 0.05	0
		16	4	26.378 ± 3.032	13.00 ± 0.47	1.20 ± 0.03	0
		18	4	21.830 ± 2.329	12.28 ± 0.43	1.18 ± 0.06	0
		20	5	24.070 ± 5.354	12.68 ± 0.82	1.17 ± 0.07	0
		22	6	20.577 ± 4.069	12.33 ± 0.71	1.09 ± 0.08	0
		24	7	22.184 ± 2.863	12.28 ± 0.40	1.19 ± 0.07	2
		25	6	24.490 ± 6.339	12.38 ± 0.57	1.27 ± 0.13	2
		26	2	NA	NA	NA	2
Trinity	11	8	4	21.905 ± 4.448	12.65 ± 1.02	1.07 ± 0.04	0
		10	4	23.173 ± 5.121	12.75 ± 0.93	1.11 ± 0.07	0
		12	4	19.343 ± 4.270	11.95 ± 0.88	1.12 ± 0.03	0
		14	4	19.363 ± 3.315	12.25 ± 0.68	1.05 ± 0.04	0
		16	4	22.870 ± 6.106	12.73 ± 0.91	1.09 ± 0.08	0
		18	4	22.015 ± 3.189	12.55 ± 0.65	1.11 ± 0.04	0
		20	3	16.903 ± 1.313	11.53 ± 0.31	1.10 ± 0.02	0

		22	3	20.740 ± 3.841	12.23 ± 0.81	1.13 ± 0.03	0
		23	4	20.855 ± 2.694	12.35 ± 0.71	1.11 ± 0.05	0
		24	2	NA	NA	NA	2
Trinity	16	8	4	29.825 ± 2.566	13.68 ± 0.50	1.17 ± 0.03	0
		10	3	28.063 ± 3.794	13.27 ± 0.50	1.20 ± 0.11	0
		12	4	25.915 ± 7.590	12.80 ± 1.29	1.21 ± 0.07	0
		14	4	21.903 ± 10.363	12.30 ± 1.70	1.10 ± 0.10	0
		16	4	18.383 ± 4.415	11.73 ± 1.13	1.13 ± 0.07	0
		18	4	22.275 ± 6.280	12.30 ± 1.28	1.18 ± 0.08	0
		20	4	23.850 ± 4.684	12.63 ± 0.75	1.17 ± 0.03	0
		22	4	19.688 ± 0.838	12.35 ± 0.30	1.05 ± 0.05	0
		24	4	22.505 ± 9.037	12.28 ± 1.62	1.17 ± 0.06	0
		25	4	25.183 ± 1.475	12.88 ± 0.19	1.18 ± 0.07	0
Trinity	20	8	4	21.848 ± 3.699	12.20 ± 0.68	1.20 ± 0.04	0
		10	4	24.670 ± 4.182	12.63 ± 0.53	1.22 ± 0.05	0
		12	3	28.463 ± 1.401	13.40 ± 0.26	1.18 ± 0.05	0
		14	4	28.080 ± 3.250	13.10 ± 0.50	1.25 ± 0.09	0
		16	4	27.150 ± 1.280	13.05 ± 0.17	1.22 ± 0.10	0
		18	5	23.110 ± 5.636	12.78 ± 0.64	1.09 ± 0.13	1
		20	4	18.675 ± 1.511	11.65 ± 0.29	1.18 ± 0.09	0
		22	4	21.623 ± 3.896	12.38 ± 0.91	1.14 ± 0.07	0
		24	4	20.963 ± 3.797	12.18 ± 0.85	1.16 ± 0.08	0
		25	6	23.50	12.7	1.15	5
		26	2	NA	NA	NA	2

Supplemental Table 3.2: GLMM covariate estimates of between environmental predictors and growth rate for fall-run populations, including the Trinity Hatchery. The letter superscript denotes significant difference between acclimation groups for a given row. The upper and lower bounds of the 89% credible interval are given. Light gray text indicates no significant correlation, italics indicates weak significance (70% credible interval) and bold indicates strong significance (89% credible interval).

Predictor	Abbr.	11°C Acclimation Group			16°C Acclimation Group			20°C Acclimation Group		
		Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI	Estimate	Lower 89% CI	Upper 89% CI
Latitude [G]		-0.055 [a]	-0.233	0.122	**0.491** [b]	**0.282**	**0.702**	*0.134* [a]	*-0.044*	*0.313*
Current Annual Mean Monthly Maximum [N]	*CAMax*	0.069 [a]	-0.124	0.260	**0.617** [b]	**0.424**	**0.809**	**0.368** [c]	**0.211**	**0.527**
Historical Annual Mean Monthly Maximum [N]	*HAmax*	-0.087 [a]	-0.266	0.092	**0.270** [b]	**0.043**	**0.501**	**0.265** [b]	**0.087**	**0.447**
Current Annual Mean Monthly Minimum [N]	*CAMin*	**0.270** [a]	**0.078**	**0.466**	**0.593** [b]	**0.390**	**0.800**	**0.578** [b]	**0.373**	**0.781**
Historical Annual Mean Monthly Minimum [N]	*HAMin*	**0.310** [a]	**0.072**	**0.546**	**0.702** [b]	**0.530**	**0.874**	**0.508** [ab]	**0.341**	**0.677**
Current Annual Temperature Range [N]	*CARange*	-0.009 [a]	-0.187	0.169	**0.556** [b]	**0.344**	**0.772**	**0.274** [c]	**0.115**	**0.435**
Historical Annual Temperature Range [N]	*HARange*	**-0.276** [ab]	**-0.450**	**-0.101**	**-0.532** [a]	**-0.728**	**-0.337**	**-0.179** [b]	**-0.347**	**-0.011**
Current Rearing Season Maximum Monthly Average [N,P]	*CRMax*	0.118 [a]	-0.086	0.323	**0.628** [b]	**0.449**	**0.808**	**0.334** [a]	**0.186**	**0.483**
Historical Rearing Season Maximum Monthly Average [N,P]	*HRMax*	0.116 [a]	-0.093	0.325	**0.660** [b]	**0.486**	**0.830**	**0.356** [a]	**0.208**	**0.501**
Current Rearing Core Maximum Monthly Average [N,P]	*CRCMax*	**0.249** [a]	**0.058**	**0.438**	**0.528** [b]	**0.328**	**0.729**	**0.622** [b]	**0.420**	**0.822**
Historical Rearing Core Maximum Monthly Average [N,P]	*HRCMax*	**0.266** [a]	**0.030**	**0.502**	**0.714** [b]	**0.527**	**0.901**	**0.600** [b]	**0.417**	**0.781**
Current Rearing Season Average Monthly Average [N,P]	*CRAve*	**0.304** [a]	**0.110**	**0.498**	**0.579** [b]	**0.385**	**0.775**	**0.580** [b]	**0.388**	**0.769**
Historical Rearing Season Average Monthly Average [N,P]	*HRAve*	**0.307** [a]	**0.074**	**0.540**	**0.719** [b]	**0.536**	**0.900**	**0.533** [ab]	**0.362**	**0.705**
Migration Distance [R]	*Mig.D*	*-0.122* [a]	*-0.295*	*0.052*	0.058 [ab]	-0.181	0.296	*0.135* [b]	*-0.043*	*0.314*
Migration Slope	*Mig.S*	*-0.138* [a]	*-0.339*	*0.064*	**-0.653** [b]	**-0.828**	**-0.476**	**-0.364** [a]	**-0.526**	**-0.201**