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Interpopulation variation in thermal physiology among seasonal runs of Chinook salmon

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Abstract

Conservation of species facing environmental change requires an understanding of interpopulation physiological variation. However, physiological data are often scarce and therefore pooled across populations and species, erasing potentially important variability between populations. Interpopulation variation in thermal physiology has been observed within the Salmonidae family, although it has not been associated with seasonally distinct migratory phenotypes (i.e., seasonal runs). To resolve whether thermal physiology is associated with life-history strategy, we acclimated four Sacramento River juvenile Chinook salmon (*Oncorhynchus tshawytscha*) populations (Coleman fall-run, Feather River fall-run, Feather River spring-run, and Sacramento River winter-run) exhibiting different seasonal migratory phenotypes (fall-, spring-, and winter-run), at 11, 16, and 20 °C and assessed variation in growth rate, critical thermal maxima, and temperature-dependent metabolic traits. We identified population differences in the physiological parameters measured and found compelling evidence that the critically endangered and endemic Sacramento River winter-run Chinook population exhibits thermal physiology associated with its early-migration life-history strategy. Acclimation to warm temperatures limited the growth and metabolic capacity of winter-run Chinook salmon, highlighting the risk of future environmental warming to this endemic population.

Key words: conservation physiology, ecophysiology, fish, thermal tolerance, metabolism, aerobic scope, climate change

Introduction

The role that interpopulation variation plays in successful conservation and management of at-risk species is gaining increasing attention (Gayeski et al. 2018; Waples and Lindley 2018; Zillig et al. 2021). Furthermore, a population's physiological response to environmental warming may predict vulnerability to climate change (Stillman 2003; Sandblom et al. 2016; Chen et al. 2018). Identifying populations poised for extinction or those resilient to environmental change will enable resource managers to tailor conservation approaches to a population's specific requirements (Gayeski et al. 2018), facilitate evolutionary rescue (Aitken and Whitlock 2013; Carlson et al. 2014), and anticipate environmental risk factors. Management actions must often import estimates of physiological performance to produce conservation criteria for individual populations. The lack of population-specific data leads to collective management of distinct populations, which may ignore local habitat characteristics, physiologies, or life-history strategies, and ultimately may fail to provide adequate protection against environmental stochasticity (Gayeski et al. 2018; Zillig et al. 2021).

Salmonid fishes inhabit a wide variety of environments and exhibit complex life-history strategies that promote interpopulation variation. Therefore, they have become a focus of interpopulation variation research (Gamperl et al. 2002; Eliason et al. 2011; Chen et al. 2013; McDermid et al. 2013; Stitt et al. 2014; Sparks et al. 2017). Populations may exhibit genetic and phenotypic adaptations suited to environmental characteristics unique to their spawning, rearing, and migratory environments (Eliason et al. 2011; Chen et al. 2013). With many populations of salmonids facing extirpation and extinction (Gustafson et al. 2007; Moyle et al. 2017), understanding the capacity for different life-history strategies to exhibit predictable thermal physiology is critical to effective management of conservation-reliant species facing rapid environmental change.

The greatest concentration of at-risk Pacific salmonid populations is in California, USA, with over 50% of evolutionarily significant units (ESUs) expected to be extinct within 50 years (Moyle et al. 2017). Threats to Pacific salmonids (*Oncorhynchus* spp.) are diverse and often temperature-dependent (Crossin et al. 2008; Moyle et al. 2017; Zillig et al. 2021). Cold water is essential for successful salmonid reproduction and recruitment (Quinn 2018); therefore, salmonids are sensitive to the warming effects of climate change and local anthropogenic stressors. For instance, construction of hydropower dams reduces and homogenizes spawning and rearing habitat, depriving returning adults access to cold headwater streams and constraining juveniles to low-elevation, channelized habitat (McClure et al. 2008). Interactions between

climate (e.g., increasing water temperature, drought severity, reduced snowpack) and anthropogenic effects (e.g., dams, invasive species, habitat degradation) have been identified as key factors driving population declines (Moyle et al. 2013, 2017). Despite awareness of these threats, there is a lack actionable data on the thermal physiology of salmonids in California (Zillig et al. 2018).

Chinook salmon (*Oncorhynchus tshawytscha*) are the dominant anadromous salmonid in California. Of the six Chinook salmon ESUs in California, three are native to the Sacramento River and are named after the season of adult freshwater entry (winter-, spring-, or fall/late fall-run). These different migratory phenotypes or "runs" use the Sacramento watershed year-round and may be composed of multiple, or in the case of winter-run, a single population (Moyle et al. 2017). Early migration (winter- and spring-run) enabled returning adults to access high-elevation, cold-water habitat accessible due to winter precipitation and spring snowmelt. Subsequently, juveniles of the different runs exhibit different rearing and outmigration phenologies. Spring-run fish typically adopted a stream-type life history, hatching in the fall and winter, spending 3–15 months in cold mountain streams protecting them against summer extremes. Winter-run juveniles hatch earlier, during summer months and outmigrate 5–10 months later. Historically, they would have reared in the cold, stable spring-fed systems of the Southern Cascade Mountains. Finally, fall-run fish typically exhibit an ocean-type life-history strategy, departing low-elevation streams a few months after emergence and rearing in floodplains and estuaries (Yoshiyama et al. 1998, 2001; Moyle 2002). Anthropogenic modification of California's Central Valley watershed has impacted the ecology of Chinook salmon by restricting habitat and altering historical temperature and flow regimes (Waples et al. 2008; Thompson et al. 2012). Specifically, Central Valley rim dams have eliminated access to cold water spawning and rearing habitat, leading to 80% declines in historical habitat for spring-run and a complete loss for winter-run populations (Yoshiyama et al. 2001; Quiñones et al. 2015). Remaining early-migrating populations are constrained to the low-elevation habitat of the Sacramento River and must contend with summer water temperatures, made tolerable through regulated cold-water releases from upstream reservoirs (Johnson and Lindley 2016). Proposed conservation actions, via reintroduction (Lusardi and Moyle 2017; USFWS 2018) or habitat restoration (Hause et al. 2022), require matching the thermal environment to a population's thermal physiology. Determining interpopulation variation in thermal physiology is an essential step in preparing salmonid conservation for environmental change. However, prior research on interpopulation variation in salmonid thermal physiology (Eliason et al. 2011; Chen et al. 2015; Verhille et al. 2016; Poletto et al. 2017) has not examined the relationships between seasonal migratory phenotypes and thermal physiology.

We sought to determine whether different seasonal runs of juvenile Chinook salmon exhibit interpopulation variation in thermal physiological traits consistent with their migratory phenotype (early or late adult migration). We conducted a robust suite of physiological experiments on four populations of Chinook salmon, belonging to one of three seasonal runs. We quantified temperature-dependent growth rate, acute thermal tolerance (critical thermal maxima, CT_{max}), and metabolic performance (routine, maximum, and aerobic scope (AS)) to assess differences in thermal performance and acclimation capacity between seasonal runs. We hypothesized that different seasonal runs are locally adapted and would possess thermal tolerance, growth capacity, and metabolic performance suited to their life-history strategies. For instance, winter-run Chinook salmon uniquely spawn during summer months, and historically reared in stable, cold, spring-fed systems, while fall-run populations spawn during the autumn months at lower elevations when temperatures are typically warmer and less stable. We predicted that juveniles from early-migrating populations (spring- and winter-run) when compared to late-migrating fall-run populations would exhibit reduced thermal performance when acclimated to warmer temperatures (e.g., slower growth, reduced metabolic capacity), indicating potential local adaptation to historically cold juvenile rearing habitats. Understanding thermal physiology associated with seasonal migratory phenotypes will aid in predicting how different populations will respond to environmental change and conservation actions.

Methods

Data collection

This experiment was conducted from 2017 to 2019, and sampled hatchery produced Chinook salmon smolts from the Sacramento River winter-run, Coleman fall-run, Feather River fall-run, and Feather River spring-run populations. Populations were selected due to being the dominant contributors of their respective run types to the ecosystem. Fish were reared in a common garden with each population being reared under the same acclimation temperatures (11, 16, and 20 °C), spanning a range of temperatures experienced by Sacramento River Chinook salmon (FitzGerald et al. 2020). This research was approved by an Institutional Animal Care and Use Committee and the use of endangered and threatened species was authorized via a California Endangered Species Act memorandum of understanding (Fangue_SRWR_CHN_123118, Zillig_CVSR_CHN_123119) and 10(a)(1)(A) permit 17299-2 M.

Fish husbandry

Fish from the Coleman population were acquired as eggs and trucked to 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 (~1–2 g) and trucked to the CABA in a 765 L tank. All fish were held at 11–13 °C until placed within their experimental tanks (two tanks per acclimation temperature, n = 55–70 per tank). Acclimation temperatures (11, 16, or 20 °C) were achieved by increasing tank temperature by ~1.5 °C per day and held constant for the duration of the experiment (4–9 months). Each pair of

acclimation temperature and population was reared in two replicate 470 L cylindrical tanks. Fish were exposed to natural photoperiods and fed continuously with ad libitum rations, updated biweekly, to account for fish growth. Fish were acclimated for at least 3 weeks prior to any experimental data collection. Additional husbandry specifications are in Table S1.

Growth

Growth measurements were initiated in mid to late spring when all populations would still be rearing prior to outmigration. Growth data were gathered every 2 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 5-gallon (1 gallon = 3.785 L) bucket until measured. Fish were air exposed for ~15–20 s to measure mass (±0.01 g; Ohaus B3000D) and fork length (±0.1 cm) and then placed into a second bucket for recovery before returning to their original treatment tank. Fish were netted and measured by the same experimenter across all sampling days.

Growth measurements were conducted until CT_{max} and metabolic experiments began. CT_{max} and metabolic experiments necessitated size selection and therefore biased any further collection of growth data. 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. Growth rate was calculated as the estimated marginal trend time on fish mass based upon the best performing model (Lenth 2020).

Critical thermal maximum

CT_{max} values were quantified according to established methods (Becker and Genoway 1979). The CT_{max} bath was a 1 m × 2 m × 20 cm fiberglass tray. Within this tray were placed six covered 4 L Pyrex beakers. Beakers were filled with 2.5 L of well water and aerated with an airstone to ensure both adequate oxygen saturation and circulation of water. 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 throughout the CT_{max} bath. Water temperature within each beaker warmed at 0.33 °C per minute.

Fish of appropriate size ($n = 253$ total, 12.4 cm ± 0.76 standard deviation (SD)) were selected from treatment tanks and transferred to separate tanks for fasting. Fish acclimated to 20 or 16 °C were fasted for 24 h and 11 °C fish were fasted for 48 h to account for their slower metabolic rate. Once fasted, fish were individually netted and transferred into the 4 L beakers. Fish were given 30 min to acclimate to their beaker after which the CT_{max} trial was started.

During the CT_{max} trial, beaker temperature was measured every 5 m 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 CT_{max} endpoint was loss of equilibrium (Beitinger et al. 2000; Fangue et al. 2006); when this point was reached, fish were removed and returned to a recovery bath at their acclimation temperature and the temperature of the CT_{max} beaker was recorded. Fish that did not fully recover within 24 h were not included in analysis (6% of individuals). After 24 h recovery, fish were euthanized using a buffered solution of MS-222 (0.5 $g \cdot L^{-1}$) and subsequently weighed (wet mass ± 0.01 g) and measured (fork length ± 0.1 cm).

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 sump into an aerated water bath surrounding each swim tunnel, and then returned to the sump. Sumps were supplied with nonchlorinated freshwater from a designated well and aerated with airstones. The temperature of the sump (and therefore the swim tunnels) was maintained (±0.5 °C) by circulating water through a heat pump (model DSHP-7; Aqua Logic Delta Star, USA) using a high-volume water pump (Sweetwater SHE 1.7 Aquatic Ecosystems, USA). In addition, each sump contained a thermostatically controlled titanium heater (TH-800; Finnex, USA). 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 $cm \cdot s^{-1}$) 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 maximum metabolic rates (MMRs) were captured using intermittent respirometry (Brett 1964). Flush pumps (Eheim 1048A, Germany) for each tunnel pumped aerated freshwater 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 3 min once the flush pump was activated. Oxygen saturation data from AutoResp™ were transformed to oxygen concentra-

tion using the following equation:

$$(1) \quad [O_2] = \frac{\%O_2Sat}{100} \times \alpha(O_2) \times BP$$

where $\%O_2Sat$ is the oxygen saturation percentage reported from AutoResp™, αO_2 is the coefficient temperature-corrected oxygen solubility (mg $O_2 \cdot L^{-1} \cdot mm\ Hg^{-1}$), and BP is the barometric pressure (mm Hg). Oxygen concentration (mg $O_2 \cdot L^{-1}$; eq. 1) was measured every second and regressed over time; the coefficient of this relationship (mg $O_2 \cdot L^{-1} \cdot s^{-1}$) was then converted to metabolic rate (mg $O_2 \cdot kg^{-1} \cdot min^{-1}$; eq. 2):

$$(2) \quad MR = R \times V \times M^{-1} \times 60$$

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 (Table 1).

Routine metabolic rate

Prior to routine metabolic rate (RMR) trials, fish were fasted to ensure a postprandial state. Fish reared at 16 or 20 °C were fasted for 24 h, while fish acclimated to 11 °C were fasted for 48 h. Fish were then transferred into a swim tunnel respirometer between 13:00 and 17:00. After 30 min at their acclimation temperature, the temperature was adjusted at 2 °C·h^{-1} to the test temperature (8–26 °C). Automated intermittent flow respirometry began 30 min after the test temperature was achieved and continued overnight. Measurement periods ranged from 900 to 1800 s in duration; flush periods were 180–300 s. Periods varied in length in response to fish size and test temperature to ensure oxygen saturation was kept high (>80%) during the 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 infrared 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). RMR measurements were concluded by 08:00 ± 40 min.

Maximum metabolic rate

MMR was elicited using a modified critical swimming velocity protocol (Poletto et al. 2017). Tunnel speed was increased gradually from 0 to 30 cm·s^{-1} over a ~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 (~0.5 body length (BL)·s^{-1}). Fish were swum until exhausted and unable to swim. Swimming metabolism was measured by sealing the tunnel for approximately 16 min of the 20 min measurement period. When a fish became impinged upon the back screen (>2/3 of body in contact with screen), the tunnel velocity was stopped for ~1 min and then gradually returned to the original speed over 2 min. A fish was determined to be exhausted if it became impinged twice within the same velocity step. At this point, the tunnel impellor was stopped to allow for recovery. The highest metabolic rate measured over a minimum of 5 min 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. 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 subacute thermal persistence (Table S2). Data from fish that did not survive the trial or recovery were not used in analysis. After a 24 h recovery period, fish were euthanized in a buffered solution of MS-222 (0.5 g·L^{-1}). Measurements for mass (g), fork length (cm), and total length (cm) were taken, and Fulton's condition factor was calculated.

AS was calculated as the difference between a fish's RMR and MMR. Thermal optima (T_{OPT}) were defined as the temperature when AS was maximized and calculated as the root value of the derivative of the quadratic function describing the relationship between AS and test temperature for a given treatment.

Statistical analyses

All statistical analyses were conducted in R (version 4.0.2) using the package brms (Bürkner 2017) to construct Bayesian generalized linear mixed effect models (CT_{max}, growth rate, RMR, MMR, and AS). 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 weakly regularizing priors. Final models were selected using Watanabe–Akaike information criterion (WAIC) and 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 (Table S3). The CT_{max} model additionally included fixed effects for fish mass (g) and age (days post-hatch) as both fish mass and fish age can influence upper thermal tolerance (Chen et al. 2013; Turko et al. 2020). Growth rate was measured by modeling mass as a linear function of time (days) with an additional fixed effect for the starting mass of each treatment group and a random effect for rearing tank to account for unmeasured sources of variation. Metabolic models assessed linear, quadratic, logarithmic, and exponential forms. The RMR model used log-transformed RMR values to fit an exponential function and included noninteracting fixed effects for swim tunnel and fish age. The MMR model was fit to the log-transformation of swim temperature with noninteracting fixed effects for swim tunnel, Fulton's condition factor, and fish age. The AS model was defined by a second-order polynomial function of test temperature and an additional fixed effect for Fulton's condition factor and swim tunnel. Mass, condition factor, test temperature, and all response variables were centered and scaled to SDs (Z scores). The predictor variables for time (growth

Table 1. Metabolic performance data for four populations of Sacramento River Chinook salmon, including resting metabolic rate (RMR), maximum metabolic rate (MMR), and aerobic scope (AS).

Hatchery and acclimation temperature		Fish tested (n)	Max. test temp. (°C)	Mass (g; μ ± SD)	Fork length (cm; μ ± SD)	Fulton's condition factor (μ ± SD)	RMR (μ ± SE)	MMR (μ ± SE)	AS (μ ± SE)		
							% of 11 °C	% of 11 °C	AS at T_{OPT} (mg O_2·kg^{-1} ·min^{-1})	T_{OPT} (°C)	% of 11 °C
Coleman fall-run	11 °C	32	24	22.18 ± 4.022	12.5 ± 0.65	1.13 ± 0.071	—	—	9.28 ± 0.11	18.72 ± 0.65	—
	16 °C	42	25	23.72 ± 3.254	12.7 ± 0.50	1.16 ± 0.048	88.9 ± 4.46	94.2 ± 5.44	8.93 ± 0.09	20.32 ± 0.53	90.4 ± 11.83
	20 °C	45	25	24.72 ± 4.009	12.6 ± 0.64	1.21 ± 0.060	79.7 ± 4.92	89.7 ± 4.86	8.71 ± 0.11	22.41 ± 1.26	88.2 ± 11.58
Feather fall-run	11 °C	39	23	25.36 ± 2.568	13.0 ± 0.44	1.14 ± 0.054	—	—	11.14 ± 0.14	20.78 ± 0.89	—
	16 °C	35	24	24.09 ± 2.591	12.7 ± 0.38	1.17 ± 0.067	81.9 ± 5.60	94.4 ± 6.43	12.02 ± 0.41	26.17 ± 2.52	98.1 ± 9.93
	20 °C	38	25	26.08 ± 4.256	12.6 ± 0.47	1.30 ± 0.118	74.4 ± 7.89	69.6 ± 4.72	8.07 ± 0.12	20.1 ± 0.75	73.1 ± 7.31
Feather spring-run	11 °C	37	24	25.12 ± 3.079	13.0 ± 0.54	1.14 ± 0.081	—	—	11.41 ± 0.11	18.32 ± 0.29	—
	16 °C	37	24	25.15 ± 4.629	12.9 ± 0.61	1.17 ± 0.084	76.8 ± 7.00	82.6 ± 5.49	9.59 ± 0.11	18.98 ± 0.41	83.9 ± 8.00
	20 °C	39	24	24.65 ± 4.024	12.4 ± 0.55	1.28 ± 0.092	61.9 ± 4.48	71.3 ± 4.18	8.42 ± 4.81	26.27 ± 87.59	78.2 ± 11.44
Sacramento winter-run	11 °C	39	24	21.59 ± 2.214	12.2 ± 0.38	1.19 ± 0.109	—	—	11.34 ± 0.10	19.20 ± 0.46	—
	16 °C	44	25	21.45 ± 2.512	12.2 ± 0.44	1.17 ± 0.061	79.8 ± 4.29	94.5 ± 3.96	11.54 ± 0.10	18.66 ± 0.24	100.2 ± 7.80
	20 °C	42	25	21.14 ± 4.811	12.0 ± 0.84	1.21 ± 0.110	69.2 ± 4.19	80.7 ± 4.29	9.78 ± 0.12	18.02 ± 0.21	83.5 ± 7.81

model) and fish age (days post-hatch; MMR, RMR, and CT_{max} 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). We attributed significance to treatment groups and predictor variables if the 94.5% of the posterior distribution did not include 0. Treatment comparisons for CT_{max} and growth rate are provided in Figs. S1–S8.

The T_{OPT} is the temperature at which AS is maximized; values for the T_{OPT} were calculated using 500 simulated datasets randomly sampled from the posterior distributions of the AS model. T_{OPT} was calculated by fitting a quadratic equation to each AS sample and calculating the root of the first derivative.

Finally, we also estimated a treatment group's capacity to preserve metabolic activity by quantifying the percentage of a population's 11 °C RMR, MMR, and AS that was maintained when that population was acclimated to 16 or 20 °C. For a given test temperature, we used the 11 °C acclimated metabolic rate as the divisor and the 16 or 20 °C acclimated metabolic rate as the dividend to determine the proportion of 11 °C acclimated metabolic rate maintained after acclimation to 16 or 20 °C. This process was repeated across all test temperatures, and the resulting proportions averaged and scaled out to produce the percentage of metabolic capacity maintained after acclimation (Table 1).

Results

Growth

Fish mass increased over the trial duration in all treatments and the resulting growth rates were significantly influenced by acclimation temperature and population (Table 2). Fall-run populations and spring-run exhibited positive relationships between growth rate and acclimation temperature. The winter-run population demonstrated increasing growth from 11 to 16 °C but was the only population to exhibit reduced growth when acclimated to 20 °C (Fig. 1A).

Critical thermal maxima

Thermal tolerance differed significantly among populations in both absolute value of CT_{max} (27.8–29.8 °C) and response to acclimation temperature (Table 2). Populations demonstrated a significant increase in CT_{max} between fish acclimated from 11 to 16 °C, with Coleman fall-run and Sacramento winter-run populations exhibiting additional statistically significant increases in CT_{max} with acclimation to 20 °C (Fig. 1B). The CT_{max} of Feather River spring-run did not increase further when acclimated to 20 °C, while the CT_{max} of Feather River fall-run decreased slightly (−0.3 °C) although this was statistically significant. Metabolic trials were conducted at test temperatures approaching lethality and the maximum test temperature reflects a subacute thermal limit (23–25 °C), which increased with acclimation temperature (Table 1).

Metabolic performance

Routine metabolic rate

RMR increased exponentially with test temperature in all treatment groups. Within each population, warm acclimation reduced RMR (Fig. 2). This effect was greatest at the warmest test temperatures. Winter- and spring-run Chinook salmon populations exhibited greater proportional reductions in RMR when acclimated to 16 and 20 °C. Fall-run populations shared similar proportional reductions in RMR (Table 1).

Maximum metabolic rate

MMR was best fit as a function of the log (base 2) of the test temperature, thereby defined as an increasing, monotonic relationship (Fig. 2). Acclimation to higher temperatures typically depressed MMR regardless of population although to varying degrees. The Feather River populations exhibited the greatest reductions in MMR capacity with the winter-run and Coleman fall-run populations preserving a greater proportion of MMR capacity when acclimated to 20 °C (Table 1). The effect of acclimation temperature on MMR was negatively associated with test temperature with the greatest reductions in MMR occurring at the highest test temperatures (Fig. 2), a result that parallels the effect of acclimation temperature on RMR.

Aerobic scope

AS of all treatments increased with test temperature, reached a T_{OPT}, and in some treatments declined as test temperatures exceeded T_{OPT} (Fig. 2). Across all populations, acclimation to higher temperatures (16 or 20 °C) reduced overall AS (Table 1). The strength of the acclimation response varied between populations. For instance, Coleman fall-run demonstrated the lowest response to acclimation temperature, while Feather fall-run exhibited the greatest reduction of their 11 °C AS when acclimated to 20 °C (Table 1). This decline in metabolic capacity generally increased with test temperature.

T_{OPT} was sensitive to acclimation temperature. As acclimation temperatures increased, Coleman fall-run and Feather spring-run elicited T_{OPT} at warmer temperatures, but with reduced AS capacity. Winter-run was unusual, demonstrating a decrease in T_{OPT} (19.2–18.0 °C) when the acclimation temperature was increased from 11 to 20 °C. Feather fall-run acclimated to 16 °C and Feather spring-run acclimated to 20 °C exhibited unusually high T_{OPT} values (26.2 and 26.3 °C, respectively).

Winter-run mortality

On 17 October 2018, one tank of 20 °C acclimated winter-run Chinook salmon suffered an outbreak of columnaris and subsequent mortality ($n = 7$). The mortality of this tank is hypothesized to be a result of thermal stress after being reared at 20 °C for 202 days. Collection of growth data and CT_{max} data preceded disease onset by 107 and 41 days, respectively,

Table 2. Growth and critical thermal maxima (modeled mean and standard error) from four populations of Sacramento River Chinook salmon.

			Growth rate	Critical thermal maxima	
Hatchery and acclimation temperature			Growth rate (g·day^{-1})	Critical thermal maximum (°C)	Fish tested (*n*)
Coleman fall-run	Coleman National Fish Hatchery	11 °C	0.162 ± 0.018	29.6 ± 0.21	22
		16 °C	0.229 ± 0.023	29.2 ± 0.13	20
		20 °C	0.266 ± 0.023	29.8 ± 0.13	20
Feather fall-run	Livingston Stone National Fish Hatchery	11 °C	0.171 ± 0.019	27.8 ± 0.13	21
		16 °C	0.172 ± 0.030	28.9 ± 0.12	23
		20 °C	0.240 ± 0.031	28.7 ± 0.13	22
Feather spring-run	Feather River Fish Hatchery	11 °C	0.139 ± 0.021	27.8 ± 0.13	21
		16 °C	0.214 ± 0.021	29.0 ± 0.12	22
		20 °C	0.250 ± 0.031	29.1 ± 0.14	20
Sacramento winter-run	Feather River Fish Hatchery	11 °C	0.118 ± 0.014	28.1 ± 0.12	22
		16 °C	0.168 ± 0.021	28.9 ± 0.15	17
		20 °C	0.094 ± 0.011	29.6 ± 0.21	9

and are presumed to be unaffected. Three fish from the infected tank were used in metabolic trials in the 3 weeks preceding the outbreak. Infection at time of experiment is possible; however, their metabolic rates were not unusual. To compensate for lost fish, six previously tested individuals were reacclimated to 20 °C for at least 40 days and retested. Fish were not individually marked; therefore, we are unable to determine the prior acclimation temperature or trial date for these recovered fish. To evaluate the potential impact of disease exposure, we conducted our statistical analysis without potentially sick or reacclimated fish, yielding a 0.15 °C increase in T_{OPT} for the affected treatment. Therefore, we consider the impact of disease on our results to be marginal.

Discussion

We compared four Chinook salmon populations from the Sacramento River (CA) to assess whether differences in seasonal migratory phenotype are associated with population-specific traits in thermal physiology. Comparative growth rate, CT_{max}, and metabolic performance (RMR, MMR, and AS) measured across three acclimation temperatures (11, 16, and 20 °C) indicated pronounced differences in thermal physiology among populations with important implications for conservation under a changing climate.

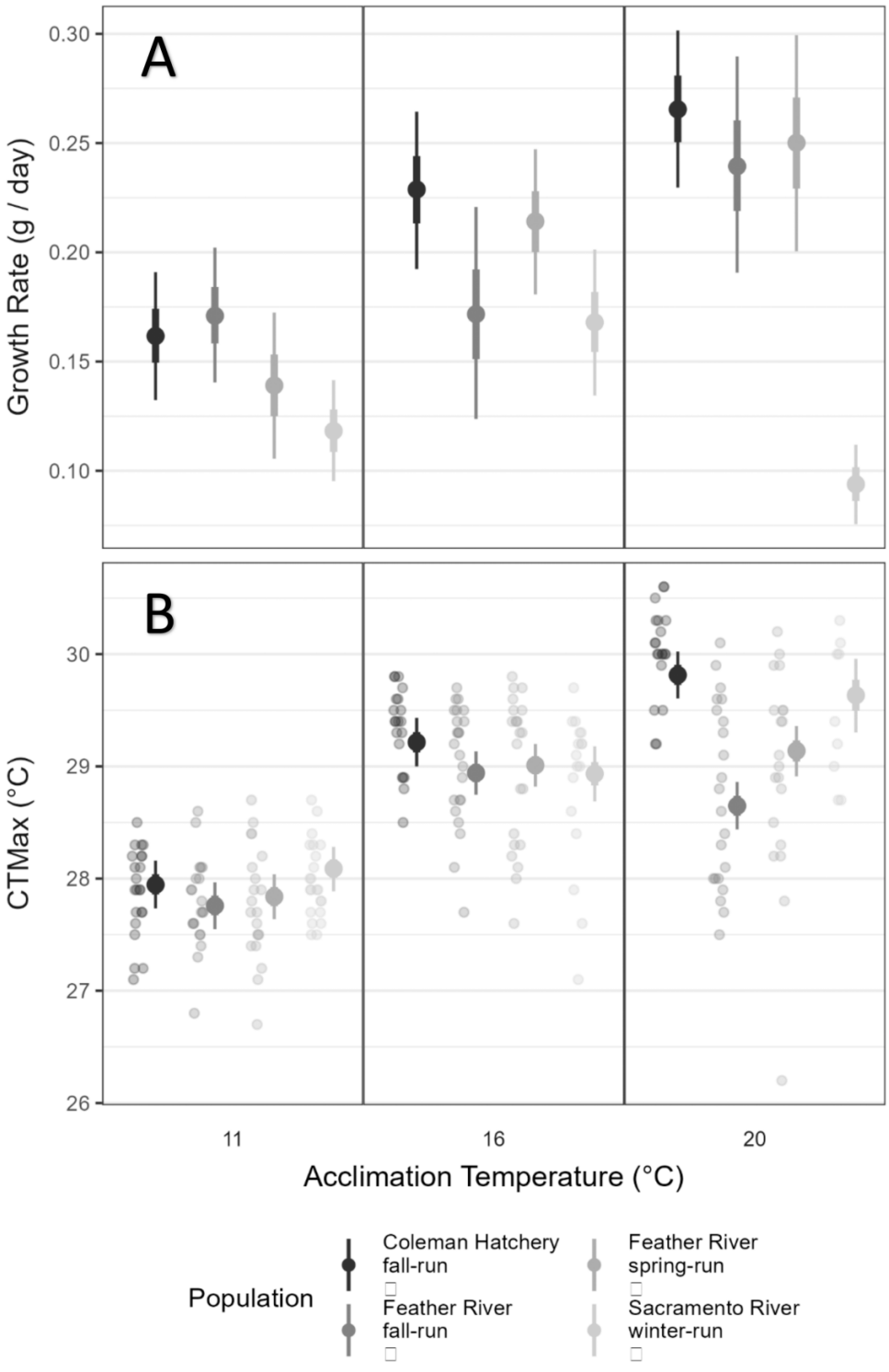
Differential timing in migration is well documented among anadromous fish (Leggett and Carscadden 1978; Hansen and Jonsson 1991; Jonsson et al. 1991) and specifically Pacific salmonid species (Taylor 1991; Smoker et al. 1998; O'Malley et al. 2013), as is intraspecific variation in thermal physiology among populations (Eliason et al. 2011; Chen et al. 2013, 2015, 2018; Adams et al. 2022). However, relationships between thermal physiology and salmonid life-history strategy are rarely studied but are necessary to predict population responses to environmental change (Zillig et al. 2021).

Variation in adult migration timing and juvenile rearing strategies maximizes the likelihood for juvenile recruitment. Among Sacramento River Chinook salmon, early adult migration facilitated populations to access perpetually cold stream- or snowmelt-fed tributaries via seasonally exclusive migratory routes. Once deposited in these cold, thermally stable, high-elevation streams, juvenile winter- and spring-run Chinook salmon could rear for 3–15 months prior to outmigration. Oppositely, fall-run juveniles, deposited at low elevations, leave their streams rapidly (1–7 months) to rear in productive estuaries and floodplains (Yoshiyama et al. 1998; Moyle 2002), which are typically warmer and more thermally variable.

We predicted that if winter- and spring-run populations were locally adapted to historical environmental conditions (i.e., colder temperatures), they would exhibit reduced growth and AS when acclimated to a warm temperature (e.g., 20 °C). Indeed, the winter-run demonstrated a significant decline in growth rate and a reduced metabolic T_{OPT} when acclimated to 20 °C, consistent with our hypothesis. In contrast, winter-run acclimated to 20 °C possess acute thermal tolerances (CT_{max}) similar to the other studied populations, a result consistent with work on brown trout (*S. trutta*) that did not find an association between CT_{max} and migration phenotype (Desforges et al. 2021).

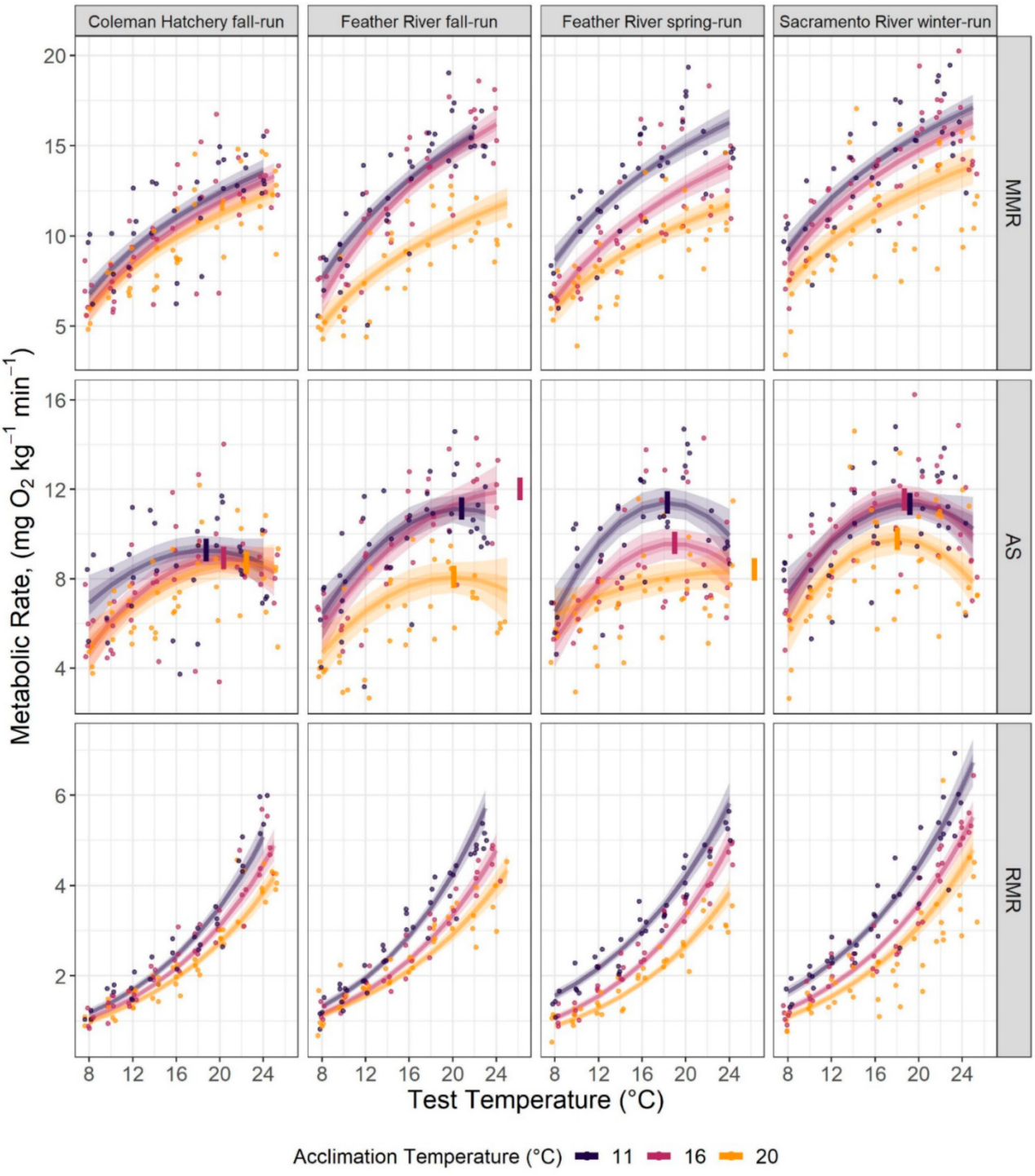
Metabolic performance of winter-run salmon varied considerably from other populations. T_{OPT} are generally accepted to increase with acclimation (Schulte et al. 2011; Huey et al. 2012). The inverse relationship between acclimation temperature and T_{OPT} indicates that winter-run may be uniquely vulnerable to climate warming due to limited acclimation plasticity in a warming environment. Limited winter-run Chinook salmon AS at warm temperatures may explain their reduced growth rate and subsequent disease outbreak when reared at 20 °C and portend their impending extinction in the wild (Katz et al. 2013; Moyle et al. 2017). In California, climate change impacts on drought (Diffenbaugh et al. 2015) and snow pack (Hamlet et al. 2005) are expected to increase river water temperatures. Winter-run embryos hatch in early summer (May–July) and juveniles must withstand summer conditions. Recently, drought conditions (Durand

Fig. 1. Critical thermal maximum (CT_{max}) and growth rates of four populations of Sacramento River Chinook salmon acclimated to three temperatures. (A) Modeled growth rates ($g \cdot day^{-1}$). (B) Observed (jittered individual points) and model estimate CT_{max} values (°C). Mean model estimate is represented by the offset large point, while the 50% (thick) and 89% (narrow) credible intervals are represented by the whiskers.



et al. 2020; Williams et al. 2022) have limited necessary dam releases, exacerbating summer maximum water temperatures and extending the period where temperatures exceed 20 °C in the Sacramento River. Even if temperatures remain below winter-run CT_{max} values (28–30 °C), limited growth and declining metabolic capacity exhibited when fish were acclimated to 20 °C highlight the challenge of preserving this unique and endemic population in a warming future. Preserving cold-water habitat, even in non-natal environments, is necessary to protect this unique popula-

Fig. 2. Metabolic rates for four populations of Sacramento River Chinook salmon reared at three acclimation temperatures. Individual fish (points) were tested at only one acute 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 and are jittered for visibility, while lines are the trait estimates derived from the lowest Watanabe–Akaike information criterion (WAIC) model. Shaded regions represent the 50% (dark) and 89% (light) credible intervals. Thermal optima (T_{OPT}) are indicated by the vertical segments on the AS plots.



tion (Phillis et al. 2018). Additionally, conservation plans seeking to reintroduce winter-run salmon (USFWS 2018) should select habitats that minimize or avoid warm-water conditions.

The thermal physiology of the Feather River spring-run, another early-migrating population, was more similar to the Feather fall-run than the earlier-migrating winter-run, contrary to our hypothesis. Genetic studies on the Feather River

spring-run indicate genetic introgression with the sympatric Feather River fall-run (Lindley et al. 2004), although differentiation remains, specifically among genes hypothesized to influence run timing (O'Malley et al. 2013; Meek et al. 2020). Both populations exhibited unusually high T_{OPT} values (Feather River fall-run: 26.17 °C when acclimated to 16 °C; Feather River spring-run: 26.27 °C when acclimated to 20 °C). We consider these extreme values to be an artifact of our method of T_{OPT} calculation, although they do reflect AS values that do not decline as temperatures become critical. Our CT_{max} values and growth rates indicate considerable similarity in both spring- and fall-run Feather River populations. Whether these similarities are due to recent genetic homogenization or local adaptation to the Feather River is unknown. Future physiological studies on genetically distinct spring-run populations from Deer and Mill Creeks, CA (Meek et al. 2020), could determine whether the spring-run phenotype contains unique thermal traits and whether the thermal physiologies of Feather River spring- and fall-run are introgressed. From a conservation perspective, the results of our study indicate that juvenile Feather River spring- and fall-run Chinook salmon should respond to rising temperatures similarly.

In contrast to Sacramento River winter-run Chinook salmon, the geographically proximal Coleman fall-run is the most thermally tolerant population studied herein, possessing the highest CT_{max} and fastest growth rates when acclimated to 20 °C. Furthermore, they appear capable of preserving their metabolic rates across acclimation temperatures, a trait shared with the Mokelumne River Hatchery (Poletto et al. 2017), which may benefit an ocean-type life history that rears in thermally fluctuating estuaries and floodplains. The Feather fall-run population does not exhibit the same amount of metabolic resilience, a possible effect of introgression with the early-migrating spring-run. Differences among fall-run populations could reflect hatchery practices, genetic diversity, or local adaptation. Future research exploring the genetics and transcriptomics of thermal physiology (e.g., Tomalty et al. 2015) may allow for identification of thermally robust genotypes and selective drivers for thermal performance. Expanding our understanding of these mechanisms is relevant to predicting population resiliency in a future of rapid environmental change (Zillig et al. 2021).

In agreement with other metabolic research on Central Valley salmonids (Verhille et al. 2016; Poletto et al. 2017), our work affirms that juvenile Sacramento River Chinook salmon are capable of maintaining near-optimal AS and MMR at near-lethal temperatures. Past work on adult Pacific salmonids have typically found descending aerobic performance at sublethal temperatures (Lee et al. 2003; Eliason et al. 2011), even among populations otherwise adapted to warm temperature (Chen et al. 2015) results that supported the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis (Pörtner et al. 2017) that predicts that thermal limits are bounded by oxygen acquisition and delivery. Our results indicate that some juvenile Chinook salmon populations are capable of peak oxygen absorption at temperatures approaching lethality, thereby challenging the ubiquity of the OCLTT hypothesis.

Physiological compensation to environmental warming may predict climate vulnerability (Sandblom et al. 2016). By conducting physiological tests across acclimation temperatures, we were able to determine population variation in compensatory capacity. For instance, acclimation to 20 °C reduced overall metabolic performance but varied in severity among populations. Coleman fall-run exhibited the smallest acclimation effect, while other populations exhibited greater reductions in MMR and AS capacity when acclimated to 20 °C (Table 1). RMR rate also decreased with acclimation temperature, potentially due to thermal metabolic compensation (Somero 1969; Johnston and Dunn 1987; Evans 1990). When viewed as a response to high-temperature acclimation, a reduction in RMR would preserve organisms' absolute AS despite a reduction in MMR due to warm acclimation. While overall AS would be maintained, there could be fitness trade-offs (i.e., reduced somatic growth, development, or immune function). Effective preservation of AS is evident in the Coleman fall-run population where overall AS at 20 °C is 88.2% of the AS of 11 °C acclimated fish. Another fall-run population from the Mokelumne Hatchery also exhibited metabolic stability. Warm acclimation to 19 °C induced matching declines in RMR and MMR across test temperatures relative to fish acclimated to 15 °C. The result was equivalent AS regardless of acclimation temperature (Poletto et al. 2017). This metabolic stability was not observed among the Feather River fall-run, spring-run, and Sacramento River winter-run populations, and indicates that when exposed to warmer water temperatures, these populations will generally exhibit declining metabolic capacity. While limited compensation may be expected for early-migrating populations, which historically reared in colder, more thermally stable streams (Moyle et al. 2017), the lack of metabolic compensation in Feather River fall-run diverges from the response observed among the Coleman and Mokelumne fall-run populations (Poletto et al. 2017). This result highlights the challenges of prescribing single management temperature targets across geographically proximal Chinook salmon populations (Zillig et al. 2021).

The populations used in this study were all of hatchery origin and interpopulation variation may include aspects of hatchery selection. Hatchery populations have exhibited rapid declines in reproductive capacity and population fitness in the wild (Araki et al. 2008), possibly due to adaptive or acclimatory pressures in hatcheries (Woodworth et al. 2002; Chittenden et al. 2010), effective population size (Wang et al. 2002), spawning and release strategies (Lusardi and Moyle 2017; Sturrock et al. 2019), and history of hatchery supplementation (Sturrock et al. 2019). Despite the unknown impacts of hatchery production on thermal physiology, decades of hatchery supplementation ensure that even unsupplemented wild populations in California are genetically homogenized with hatchery populations (Williamson and May 2005; Barnett-Johnson et al. 2007). Therefore, understanding the thermal physiology of hatchery genotypes remains pertinent to identifying unique wild populations that may preserve novel variation in thermal physiology.

Physiological data are becoming increasingly valuable for species conservation and climate change planning (Madliger et al. 2016; Patterson et al. 2016). For salmonids, which ex-

hibit an array of life-history strategies, diversity of phenotypes offers resilience against environmental stochasticity (Hilborn et al. 2003; Schindler et al. 2010). Current management frameworks (U.S. Environmental Protection Agency 2003) propose single temperature thresholds for identifying thermally impaired rivers and triggering management responses (e.g., increasing reservoir releases) and are applied across species (Zillig et al. 2021). This framework may be at odds with our results indicating that the critically endangered winter-run populations express distinctly different physiological responses than other nearby Chinook salmon populations. Understanding how physiology differs between populations and its relationship with life-history strategies can allow for run-specific environmental regulation that conserves distinct migratory phenotypes and other intraspecific traits. 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).

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Data availability

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Code availability

All statistical analyses were conducted in R (version 4.0.2) and using published packages.

Author contributions

KWZ conceptualized, conducted, and analyzed the research and authored the manuscript. RAL assisted in data acquisition, editing, and project design. DEC assisted in experimental logistics, methodology, and fish husbandry. NAF contributed to idea generation, critical editing, and advising.

Competing interests

The authors declare that there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2022-0133.

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