

Oversummer growth and survival of juvenile coho salmon (*Oncorhynchus kisutch*) across a natural gradient of stream water temperature and prey availability: an *in situ* enclosure experiment

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Abstract: Conservation efforts for Pacific salmon (*Oncorhynchus* spp.) increasingly prioritize maintenance of cool water temperatures that protect all freshwater life stages. However, development of appropriate temperature standards requires a robust understanding of the interactions among water temperature, ecosystem productivity, and fish performance. We used a series of *in situ* enclosures to examine how natural spatiotemporal gradients in thermal conditions and prey availability affected the summer growth and survival of age-0+ coho salmon (*Oncorhynchus kisutch*). Coho salmon absolute growth rates peaked at a mean daily average water temperature (mean T) of 16.6 °C and an associated maximum weekly maximum temperature (MWMT) of 21.1 °C. Juvenile growth under these thermal conditions was sixfold greater than the growth rates observed for conspecifics rearing in the coolest study reach (mean T = 13.0 °C; MWMT = 16.0 °C). Even at the highest rearing temperature (mean T = 18.1 °C; MWMT = 24.0 °C), growth rates remained positive and above the study-wide average, although overall survival was reduced. Among the predictor variables examined, invertebrate prey abundance was the predominant factor influencing age-0+ coho salmon growth. These results suggest that abundant prey resources may mitigate the negative effects of elevated water temperature on fish growth in riverine environments. Given the likelihood of increasing stream temperatures with climate change, productive ecosystems may provide critical refuges for juvenile salmonids.

Résumé : Les efforts de conservation des saumons du Pacifique (*Oncorhynchus* spp.) accordent une priorité croissante au maintien de températures de l'eau fraîches, qui protègent les poissons à toutes les étapes de la vie en eau douce. L'élaboration de normes de température convenables nécessite toutefois une bonne compréhension des interactions entre la température de l'eau, la productivité des écosystèmes et la performance des poissons. Nous avons utilisé une série d'enclos en place pour examiner l'influence de gradients spatiotemporels naturels des conditions thermiques et de la disponibilité de proies sur la croissance et la survie estivales de saumons cohos (*Oncorhynchus kisutch*) d'âge-0+. Les taux de croissance absolus des saumons cohos atteignaient un maximum à une valeur moyenne de la température de l'eau quotidienne (T moyenne) de 16,6 °C et une valeur maximum de la température maximum hebdomadaire (MTMH) associée de 21,1 °C. La croissance des juvéniles dans ces conditions thermiques était six fois plus grande que les taux de croissance observés pour les congénères croissant dans le tronçon étudié le plus frais (T moyenne = 13,0 °C; MTMH = 16,0 °C). Même à la température de croissance la plus élevée (T moyenne = 18,1 °C; MTMH = 24,0 °C), les taux de croissance demeuraient positifs et supérieurs à la moyenne pour l'ensemble de l'étude, malgré une survie globale plus faible. Parmi les variables prédictives examinées, l'abondance de proies invertébrées est le facteur qui influençait de manière prédominante la croissance des saumons cohos d'âge-0+. Ces résultats donnent à penser que des ressources de proies abondantes pourraient atténuer les effets négatifs de températures de l'eau élevées sur la croissance des poissons en milieu fluvial. Étant donné la forte probabilité d'augmentation des températures des cours d'eau en raison des changements climatiques, les écosystèmes productifs pourraient offrir des refuges critiques aux salmonidés juvéniles. [Traduit par la Rédaction]

Introduction

Efforts to conserve at-risk populations of anadromous Pacific salmon (*Oncorhynchus* spp.) often center on the restoration of physical habitat attributes (e.g., stream sinuosity, pool frequency and depth, large wood abundance) associated with enhanced juvenile production in fresh water. However, there is growing recognition

that restoration and protection of suitable hydrologic and thermal regimes will be critical to the long-term viability of many salmonid populations (Mantua et al. 2010; He and Marcinkevage 2017; Obedzinski et al. 2018). This is especially true in California (USA), where numerous salmon stocks are listed as threatened or endangered under the US Endangered Species Act (ESA), and

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extant populations are universally challenged by both anthropogenic impacts and extreme climatic conditions (Moyle et al. 2013, 2017).

Water temperature is a key environmental variable that influences juvenile salmonid production through direct and indirect pathways. While direct adverse effects of elevated stream temperatures can be acute (i.e., lethal) due to extreme thermal stress, more frequently effects are chronic (i.e., sublethal) and associated with short-duration exposure to small or moderate increases in temperature. Chronic effects can include reduced growth and development (Martin et al. 1986; Reeves et al. 1989), altered behavior (Goniea et al. 2006), increased susceptibility to disease (Becker and Fujihara 1978; Miller et al. 2014), or changes in life-history phenology (Kovach et al. 2013; Spence and Dick 2014). Furthermore, water temperature can indirectly influence juvenile salmon growth and production via changes in riverine food web structure (e.g., rates of primary and secondary production) or by increasing the frequency of negative density-dependent interactions such as competition and predation (Wenger et al. 2011; Lehman et al. 2017).

Coho salmon (*Oncorhynchus kisutch*) are recognized as the most temperature-intolerant of the Pacific salmonids and experience thermal stress at water temperatures as low as 16 °C (Brett 1952). Laboratory studies have demonstrated that juvenile coho salmon growth and performance are optimized at temperatures between 11.4 and 14.5 °C (e.g., Coutant 1977; Reiser and Bjorn 1979; Bell 1986), and field observations generally confirm a relationship between cool thermal regimes and the presence of juvenile coho salmon (Welsh et al. 2001). However, fish growth rates in nature are determined by the interactions among water temperature, prey availability, and the energetic costs of living in a lotic environment. Thus, for juvenile salmonids, enhanced trophic resources may offset the metabolic costs associated with elevated water temperature to some extent (Brewitt et al. 2017), when temperatures remain below the critical thermal maximum (estimated range 27 to 29 °C for wild coho salmon; Konecki et al. 1995). There is increasing evidence that juvenile coho salmon can occupy and persist in ostensibly thermally stressful habitats when food resources are abundant. For example, Osterback et al. (2018) reported positive growth by juvenile coho salmon in a central California coastal freshwater lagoon despite mean daily water temperatures > 20 °C and attributed these results, in part, to high standing stocks of invertebrate prey. It is also likely that local adaptation and (or) acclimation contribute to the ability of coho salmon populations at the southern end of their North American range (i.e., California) to cope with elevated and highly variable thermal regimes.

While the effects of stream temperature on juvenile salmonid growth and performance have been extensively studied (e.g., Brett 1952; McCullough 1999; Myrick and Cech 2004), it remains uncertain how ecosystem productivity influences the interaction between water temperature and salmon performance (Myrvold and Kennedy 2015). Several authors have called for a broader understanding of how prey availability influences salmonid persistence in the wild (e.g., Weber et al. 2014; Lusardi et al. 2016, 2018), particularly where high water temperatures may limit growth and production. To address this knowledge gap, we used a series of *in situ* mesocosms to quantify differences in the oversummer growth and survival of juvenile (age-0+) coho salmon across a natural gradient of stream temperature and prey abundance. Our aim was to examine whether enhanced food availability mitigated the adverse effects of elevated water temperature on the summer growth and survival of age-0+ coho salmon. This work has implications for contemporary salmonid conservation and recovery efforts and for predicting the response of salmonids to future climate change.

Methods

Study system

This study was conducted in a 10 km segment of Big Spring Creek and the Shasta River within the Klamath River watershed in northern California, USA (Fig. 1). The Shasta River (watershed area = 2070 km²) originates in the Scott Mountains and flows northward ~93 km before joining the Klamath River. The climate is semi-arid and characterized by cool, wet winters and warm, dry summers. Annual precipitation averages 48.3 cm (water years 1981–2015, GHCND rainfall gage USC0004 49866; <http://www.ncdc.noaa.gov>) and occurs as both rain and snow, primarily between October and April. Mean monthly maximum air temperature ranges from ~7 °C in January to 33 °C in July. Historically, favorable thermal conditions for Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon, and steelhead (anadromous *Oncorhynchus mykiss*) in the Shasta River basin were maintained by large-volume volcanic spring sources that provided year-round inputs of cool, nutrient-rich water. Prior to water development in the Shasta River basin, the largest natural spring complex (Big Springs) provided a steady flow of 2.9 m³·s⁻¹ of 11–12 °C water to the mainstem Shasta River (Mack 1960) and accounted for more than half of the 5.7 m³·s⁻¹ historical (unimpaired) summer base flow (NRC 2004; Null et al. 2009).

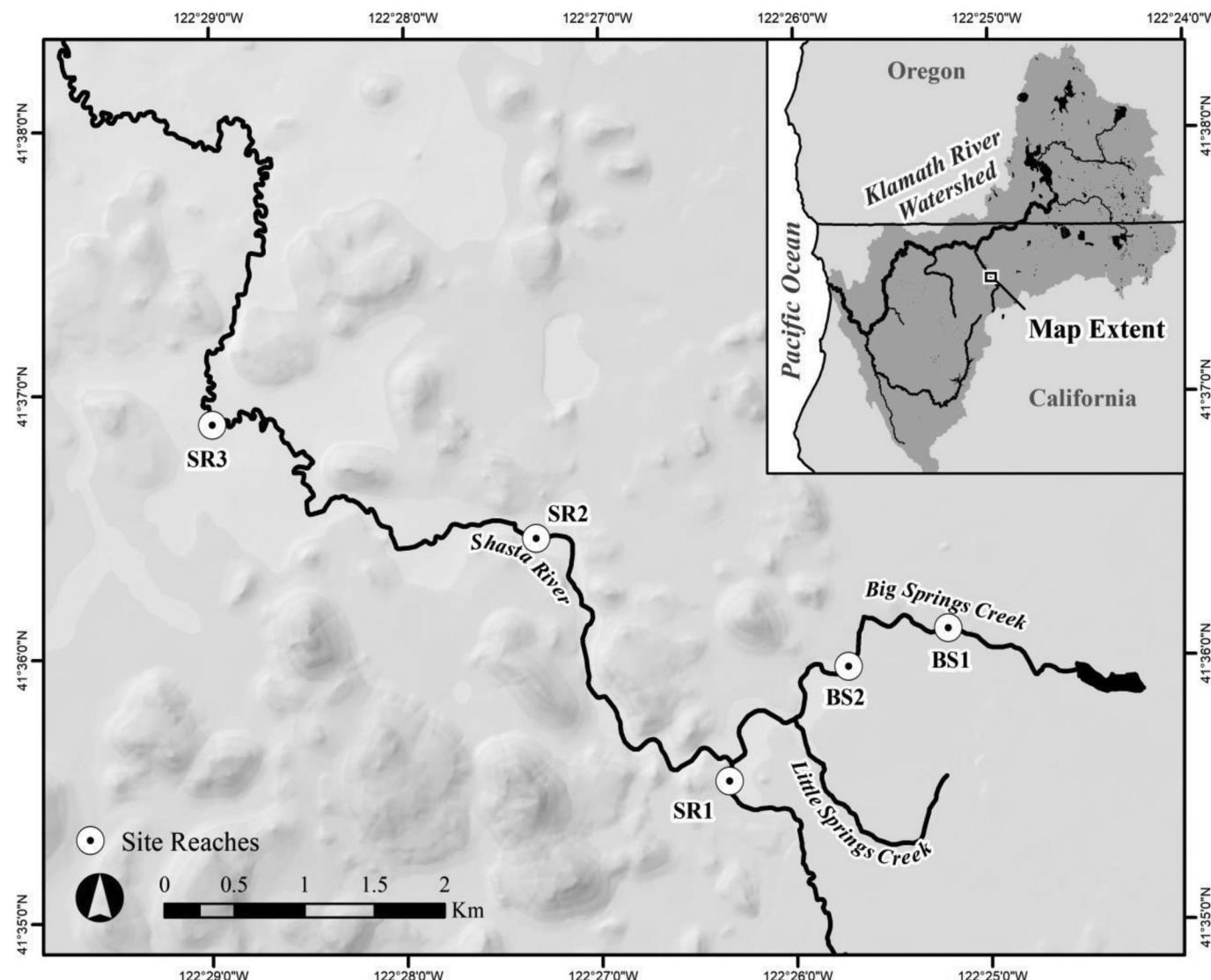
Land-use change and intensive water management have adversely affected salmonids and other native cold-water fishes in the Shasta River basin (NRC 2004). The construction of Dwinell Dam on the mainstem Shasta River (river kilometre (rkm) 65.4) in 1928 eliminated access to more than 22% of the historical salmon spawning and rearing habitat (Wales 1951). Downstream of Dwinell Dam, the Shasta River flows predominantly through a low-gradient alluvial valley with little riparian shading. The dominant land use is agriculture, and widespread water abstraction (and subsequent tailwater returns of warm water) during the April to October irrigation season result in highly altered summer streamflow and temperature regimes that are generally unfavorable for salmonids, and juvenile coho salmon in particular (Jeffres and Moyle 2012; Moyle et al. 2017). The Southern Oregon/Northern California Coast (SONCC) coho salmon evolutionary significant unit, which includes the Shasta River population, is listed as threatened under the US ESA. The federal SONCC coho salmon recovery plan (NMFS 2014) explicitly identifies summer stream temperatures as a critical stressor affecting the Shasta River population.

Experimental design

We used *in situ* mesocosms (hereinafter enclosures) to examine how natural gradients of stream water temperature and prey availability in the Shasta River basin affected the oversummer performance of age-0+ coho salmon. Our experiment, which began on 9–10 July 2013 and was terminated on 8–9 September 2013 (63 days), was conducted during the summer dry period when stream discharge in the Shasta River basin is low, water temperature is elevated, and juvenile salmonid mortality is presumed to be high (Chesney et al. 2009; Nichols et al. 2013; NMFS 2014).

Our study was carried out in five 50 m study reaches in the Shasta River basin (Fig. 1). The study reaches were chosen to represent a gradient in thermal conditions, and reach selection was informed by previous research in the watershed (e.g., Jeffres et al. 2009; Nichols et al. 2013). Four study reaches, coded BS1, BS2, SR2, and SR3, were located 0.5, 2.7, 5.9, and 10.0 km, respectively, downstream of natural cold-water spring sources. A fifth study reach (coded SR1) was located on the mainstem Shasta River ~200 m upstream of the Big Springs Creek confluence and was not influenced by major spring sources (Fig. 1). In each of the five study reaches, we constructed five replicate enclosures (254 cm long × 133 cm wide; area = 3.4 m²), resulting in 25 enclosures total. The enclosures were constructed by hammering T-posts into the streambed in a rectangular pattern and encircling the perimeter

Fig. 1. Location map showing study reach locations on Big Springs Creek and the Shasta River (Siskiyou County, California, USA).



of the T-posts with heavy delta knotless netting (6.35 mm aperture; Memphis Net and Twine Co., Inc., Memphis, Tennessee, USA). Tube sandbags (12.6 cm diameter \times 152.4 cm long; mass \sim 30 kg) were used to form a seal between the bottom of the perimeter netting and the natural streambed. The net walls of each enclosure extended vertically from the streambed to a height $>$ 60 cm above the water's surface. Enclosure walls were permeable to most drifting invertebrates but not fishes. While we recognize that enclosure walls may have inhibited the drift of some invertebrate taxa, such effects were likely minimal due to the relatively large aperture size of the enclosure netting, and any realized effect was expected to be similar among enclosures and across study reaches. The natural streambed served as the bottom of each enclosure and the tops of each enclosure were open to permit insect emergence and inputs of allochthonous material. However, a small amount of fluorescent cordage was strung across the tops to deter roosting behavior and (or) entry by aerial predators. To minimize the potential influence of upstream enclosures on water velocity and the delivery of organic material (e.g., detritus and drifting invertebrates) to downstream enclosures, we constructed each enclosure with its long axes parallel to streamflow, and the in-stream position of each successive enclosure was offset (i.e.,

river left, midchannel, and river right) longitudinally within the study reach.

Biotic and abiotic conditions

We quantified a select set of physical and biological parameters during the 63-day experiment to characterize differences in rearing conditions within and among study reaches. Stream water temperature was continuously recorded at 15 min intervals using HOBO Pro v2 (Onset Computer Corporation, Bourne, Massachusetts, USA) data loggers affixed to the upstream-most enclosure in each study reach. Water velocity ($\pm 0.01 \text{ m s}^{-1}$) and depth ($\pm 0.01 \text{ cm}$) were measured within each enclosure near the midpoint of the experiment (day 31; 10–11 August 2013) using a Marsh-McBirney Flo-Mate (Hach Co., Loveland, Colorado, USA) velocity meter attached to a top-setting wading rod. We visually estimated the percentage cover ($\pm 5\%$) provided by aquatic macrophytes (predominantly shortspike watermilfoil (*Myriophyllum sibiricum*) and white-water crowfoot (*Ranunculus aquatilis*)) within each enclosure at the midpoint of the experiment.

Benthic invertebrate sampling

As a measure of prey availability in each study reach, benthic invertebrates were collected at the start (day 0), midpoint (day 31),

and end (day 63) of the experiment. Although juvenile coho salmon are known to preferentially forage in the water column rather than from the benthos (e.g., [Nielsen 1992](#)), invertebrate drift is roughly proportional to benthic invertebrate density and thus a suitable proxy for prey availability ([Hildebrand 1974](#); [Hammock and Wetzel 2013](#); [Kennedy et al. 2014](#)). Within the Shasta River, [Lusardi et al. \(2018\)](#) reported a positive relationship between invertebrate density and invertebrate drift. Benthic invertebrate samples were collected proximate (but external) to each enclosure to avoid disrupting conditions and biota inside the experimental units. On each sample date, we randomly selected four transects within each study reach and used a modified Hess sampler (335 μm mesh; sample area = 0.12 m^2) to collect three benthic samples along each transect (25%, 50%, and 75% wetted width). The three samples were combined in the field to produce one composite sample per transect and resulted in four composited invertebrate samples per study reach on each sample date. All samples were preserved in 90% ethanol.

In the laboratory, benthic invertebrate samples were processed using a subsampling procedure (Folsom plankton splitter or [Caton \(1991\)](#) gridded tray) to randomly extract a minimum of 500 organisms. In cases where a sample contained fewer than 500 organisms, all invertebrates were removed. Invertebrates were subsequently dried at 60 °C for ≥48 h and weighed on an analytical balance (± 0.01 g). Dried samples were ashed in a muffle furnace at 475 °C for ≥90 min, cooled to room temperature, and reweighed to determine ash-free dry mass (AFDM, g). We did not determine the taxonomic composition of invertebrate samples.

Coho salmon growth and performance

On 8 July 2013, 150 subyearling (age-0+) coho salmon were obtained from Iron Gate Fish Hatchery (California Department of Fish and Wildlife, Hornbrook, California, USA), located on the Klamath River, ~21 rkm upstream of the mouth of the Shasta River. Hence, the juvenile coho salmon used in our study were a local stock and presumed well-adapted to local environmental conditions, including the thermal regime. During the 60 days preceding our study, our experimental fish were exposed to water temperatures in the hatchery that ranged from 8.3 to 14.4 °C (mean = 12.2 °C). Fish were transported to the study area in insulated and oxygenated 114 L plastic containers. After a 24 h holding period, individual fish were anesthetized using a buffered solution of tricaine methanesulfonate (MS-222), weighed (wet mass ± 0.1 g), measured for fork length (FL; ± 1.0 mm), and distinctively marked using a 12.5 mm × 2.1 mm, 134.2 kHz full-duplex passive integrated transponder (PIT) tag (Biomark Inc., Boise, Idaho, USA). Following PIT tagging, fish were separated into two size groups based on the distribution of fork lengths: 70–78 mm (small; mean FL = 75 mm) and 79–90 mm (large; mean FL = 82 mm). Three individuals from each size group were then randomly selected, positively identified via PIT tag number, and assigned to each enclosure ($n = 6$ fish per enclosure; density = 1.8 age-0+ coho salmon· m^{-2}). While this density is high relative to what would be expected basin-wide, juvenile coho salmon densities > 2.0 individuals· m^{-2} have been documented in the watershed (e.g., Big Springs Creek; [Jeffres et al. 2009](#)). Coho salmon were acclimated to water temperatures at each reach prior to being transferred to experimental enclosures on 9–10 July 2013. There were no significant differences in initial FL or mass among study reaches or among enclosures within reaches at the start of the experiment (nested analysis of variance (ANOVA), $p > 0.52$ for all variables).

During the experiment, each enclosure was cleared of external debris, inspected for physical damage, and checked for the presence of dead fish at least every 2 days. Two enclosures (one each in study reaches SR2 and SR3) were damaged and all fish escaped; consequently, these enclosures were excluded from all subsequent analyses. Individuals found dead during the experiment were not replaced, as coho salmon survivorship was a response

variable of interest. We acknowledge that live fish remaining in enclosures where mortalities occurred may have experienced enhanced growth rates due to reduced density, and we accounted for this possibility by using enclosure as a random effect in the analysis (see Data analysis section). On 8–9 September 2013 (after 63 days), surviving fish in each enclosure were collected using a backpack electrofisher, whereupon they were anesthetized, identified via PIT tag number, and weighed to determine final mass.

Data analysis

We extracted the average, maximum, and minimum stream temperature for each day of the experiment and used these data to calculate the mean daily average water temperature (mean T) and mean diel variation (mean ΔT) at each study reach. Additionally, we converted each time series to 7-day moving averages and calculated maximum weekly average temperature (MWAT), maximum weekly maximum temperature (MWMT), and maximum weekly minimum temperature (MWMInT). These summary metrics were subsequently used to model the effect of water temperature on coho salmon growth (see Model development). Benthic invertebrate density (no. individuals· m^{-2}) and biomass (g AFDM· m^{-2}) were extrapolated based on the area of streambed sampled and the fraction of each sample processed in the laboratory. Invertebrate density and biomass samples collected from each study reach at the start, midpoint, and end of the experiment ($n = 12$) were averaged to produce an overall estimate of food availability during the study period. Averaging the invertebrate density data allowed us to regress invertebrate density against coho salmon growth, a response variable for which we had a single measurement per fish across the experiment. The response of age-0+ coho salmon during the experimental period was assessed in terms of absolute growth in mass (G , g·day $^{-1}$) and proportion mortality, with enclosures within study reaches serving as replicate experimental units. While our analysis averaged across potentially important temporal variation in juvenile coho salmon growth and its predictors, a major advantage is that the fish remained undisturbed for the entire experiment.

Statistical differences in invertebrate density, invertebrate biomass, and coho salmon absolute growth rates between reaches were assessed using ANOVA with a significance level (α) of 0.05. Each variable was transformed (natural-log) to meet assumptions of normality and to correct for heteroscedasticity. Significant ANOVAs were followed by Tukey's honestly significant differences (HSD) tests. ANOVAs were run in JMP Pro version 12.0 (SAS Institute Inc., Cary, North Carolina, USA).

Model development

Environmental predictors of coho salmon growth and mortality

We used an information-theoretic approach ([Burnham and Anderson 2002](#); [McElreath 2016](#)) to examine how select environmental parameters contributed to the growth and survival of age-0+ coho salmon across all study reaches. Candidate models were compared using Akaike's information criteria adjusted for small sample size (AIC_c; [Burnham and Anderson 2002](#)). Statistical significance was assessed based on the relative ranking of the models and whether the 95% confidence intervals of environmental parameter estimates overlapped zero. Models exhibiting a delta (Δ) AIC_c value > 2.0 were considered dissimilar ([Bolker 2008](#)). All model comparisons were conducted in R ([R Core Team 2015](#)).

For each set of models considered, enclosure was included as a random effect to account for individual enclosure effects within study reaches. For all models, each fixed effect variable was scaled using the "scale" command in R to ensure that all parameters could be estimated and were of similar magnitude ("scale" subtracts the mean and divides by standard deviation; [Becker et al. 1988](#)). To demonstrate effect sizes for the environmental variables

Table 1. Abiotic and biotic variables associated with each study reach.

Variable	Study reach				
	BS1	BS2	SR1	SR2	SR3
Distance from springs (km)	0.5	2.7	NA ^a	5.9	10
Mean depth (cm)	50.1±1.9	46.1±2.4	38.7±1.0	35.8±4.7	40.3±2.4
Mean velocity (m·s ⁻¹)	0.07±0.02	0.13±0.01	0.09±0.01	0.16±0.04	0.32±0.05
Temperature (°C)					
Mean T ^b	13.0±0.03	14.8±0.01	18.1±0.1	16.6±0.1	17.1±0.1
Range ^c	11.1–16.1	11.1–19.2	13.1–24.7	12.3–21.6	13.3–20.9
Mean ΔT ^d	3.9±0.49	5.2±0.66	6.7±0.86	5.1±0.65	3.2±0.41
MWAT ^e	13.3	15.7	19.9	18.0	18.7
MWMT ^f	16.0	18.9	24.0	21.1	20.6
Mean macrophyte cover (%)	0	65±19.0	85.4±1.2	100	7.8±2.1
Mean invertebrate density (individuals·m ⁻²)	32 019±2 408	39 451±6 129	51 474±7 469	64 106±9 597	34 219±4 997
Mean invertebrate biomass (g·m ⁻²)	2.8±0.5	3.4±0.6	9.9±3.4	7.8±1.4	5.3±1.1

Note: Mean values are presented ±1 standard error. Water depth and velocity were measured and macrophyte cover was visually estimated (±5%) inside each enclosure ($n = 5$ at each study reach) at the midpoint of the experimental period. Water temperature was continuously recorded (15 min intervals) at a single location in each study reach. Invertebrate density and biomass values for each study reach represent the mean of 12 samples (four transects × three sample dates; see Methods).

^aStudy reach SR1 was located upstream of the Big Springs Creek – Shasta River confluence and was not influenced by source springs.

^bMean daily average water temperature ($n = 63$ days).

^cRange is the instantaneous minimum and maximum water temperature values recorded during the study.

^dMean ΔT represents the average diel variation ($n = 63$ days).

^eMaximum weekly average temperature.

^fMaximum weekly maximum temperature.

considered, we made predictions using models that received substantial AIC_c support ($\Delta\text{AIC}_c \leq 5.0$) across the range in environmental predictors.

We employed a three-step model development process to determine drivers of coho salmon growth in our study. First, we examined a set of candidate models to specifically assess whether invertebrate density or invertebrate biomass was the best proxy for coho salmon food availability (see online Supplementary material¹). Since the model with invertebrate density performed conclusively better than other candidate models (Table S1¹), all subsequent analyses used invertebrate density as the measure of prey availability. Second, again using coho salmon absolute growth rate as the response variable, we compared eight models to assess the influence of the summary temperature metrics derived in our study (Table S2¹). AIC_c did not strongly differentiate between different potential temperature metrics, although minimum temperature models (m3 and m7) and mean ΔT (m8) received substantially less weight (Table S2¹). Therefore, we used mean T as our primary water temperature metric for all subsequent analyses because it adequately captures the range of thermal conditions experienced during the entire study period. However, we also report MWMT values because of the broad application of this temperature metric by regulatory agencies throughout the western USA (EPA 2003) and its prevalence in the ecological literature (e.g., Welsh et al. 2001; Moore et al. 2013; Mauger et al. 2017).

In the final step, we compared 11 models of coho salmon growth rate: (m1) an intercept model, (m2) an invertebrate density model, (m3) a temperature model (mean T), (m4) a water velocity model, (m5) a water depth model, (m6) a percentage aquatic macrophytes model, (m7) an invertebrate density plus temperature (MWMT) model, (m8) an invertebrate density plus velocity model, (m9) an invertebrate density plus depth model, (m10) an invertebrate density plus percentage aquatic macrophytes model, and (m11) an invertebrate density by temperature interaction model (see Table 2). The invertebrate density by temperature interaction model was included because both predictor variables have been shown to interact to affect salmonid growth in both laboratory experiments (Wurtsbaugh and Davis 1977) and bioenergetics model simulations (Railsback and Rose 1999). Invertebrate density was included

in most models to prevent the strong association between invertebrate density and coho salmon growth from masking the effects of other variables on growth (McElreath 2016). Furthermore, because the influence of temperature on fish growth is nonlinear over wide temperature ranges (e.g., Fonds et al. 1992; Cotton et al. 2003), we assessed the shape of the relationship between growth and temperature in our analysis by examining box and whisker plots of the residuals from the invertebrate density model (i.e., the top-ranked growth model) against temperature (Fig. S1¹). This analysis suggested a possible nonlinear response of coho salmon growth to temperature. As such, a quadratic temperature model was also fit, but it did not perform well and was therefore not included in the model comparison. We used the R packages lme4 (Bates et al. 2015) and nlme (Pinheiro et al. 2018) to fit the growth rate models with a Gaussian distribution of error.

Coho salmon mortality data were also analyzed using multimodel inference; however, we used generalized linear models (GLMs) rather than mixed effects Gaussian models because the response variable was a proportion (McElreath 2016). Models included an intercept-only model (null) and a model with MWMT as a predictor. We used a binomial distribution of error for both the null and temperature models because models with this distribution substantially outperformed beta-binomial models in terms of AIC_c in a preliminary analysis. Maximum likelihood estimation was used to fit beta-binomial mortality models (bbmle package, mle2; Bolker 2016), while binomial models were fit using the glm command in R.

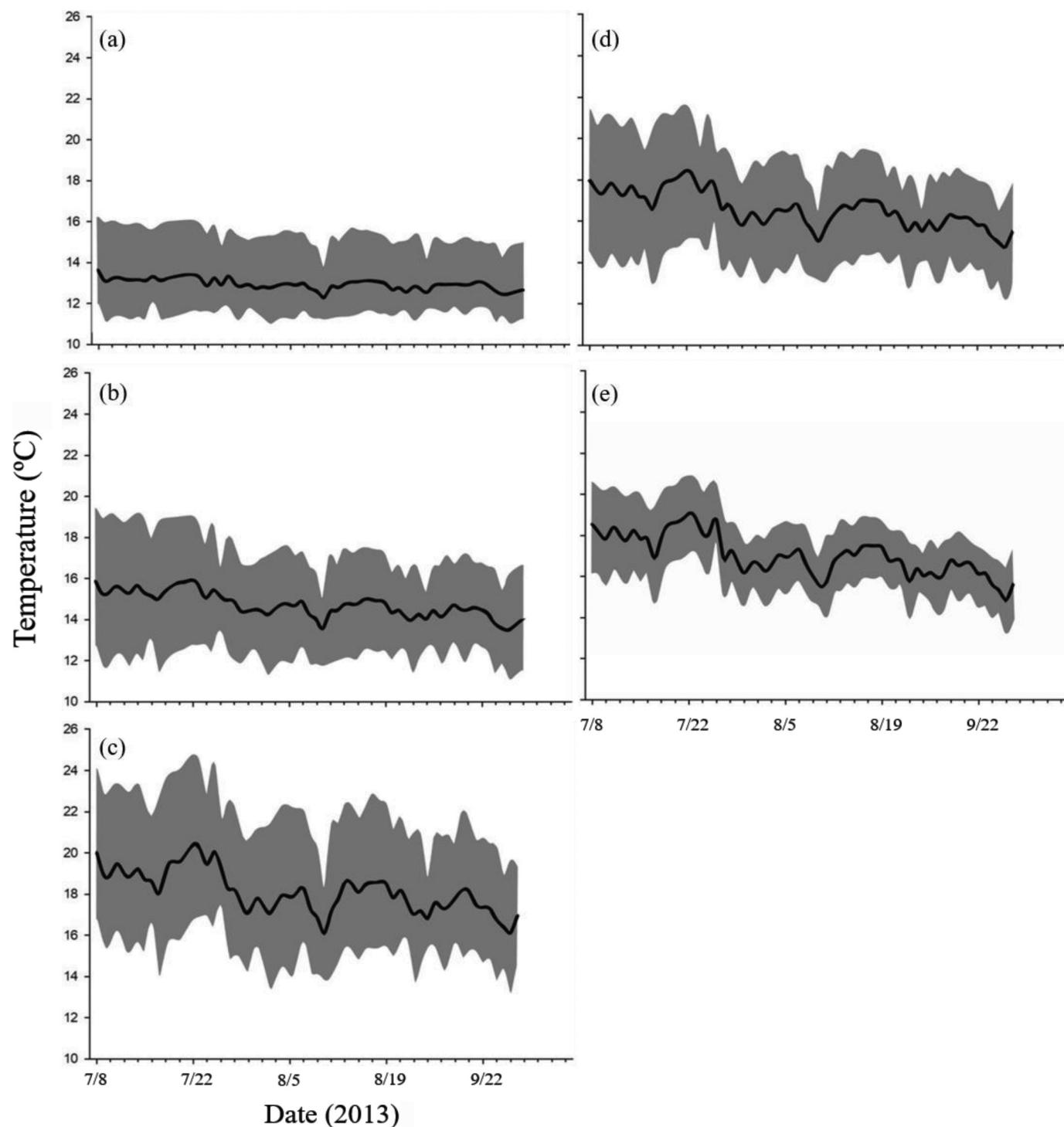
Results

Biotic and abiotic conditions

Physical habitat characteristics were variable both within and among the five study reaches. Aquatic macrophyte coverage ranged from 0% (reach BS1) to 100% (reach SR2) of the stream channel (Table 1). Water depth averaged 42.2 cm (±1 standard error (SE) = 2.6 cm) across all enclosures (range = 21.3–56.5 cm; $n = 25$), and reaches BS1 and SR2 were significantly different from all other reaches (ANOVA, $F_{[4,20]} = 4.47$, $p < 0.01$; Tukey's HSD, $p < 0.05$; Table 1). Water velocity also differed among study reaches, as SR3

¹Supplementary data are available with the article through the journal Web site at <http://nrcsciencepress.com/doi/suppl/10.1139/cjfas-2018-0484>.

Fig. 2. Time series of daily maximum, mean, and minimum water temperatures during the study period at each study reach: BS1 (a), BS2 (b), SR1 (c), SR2 (d), and SR3 (e).

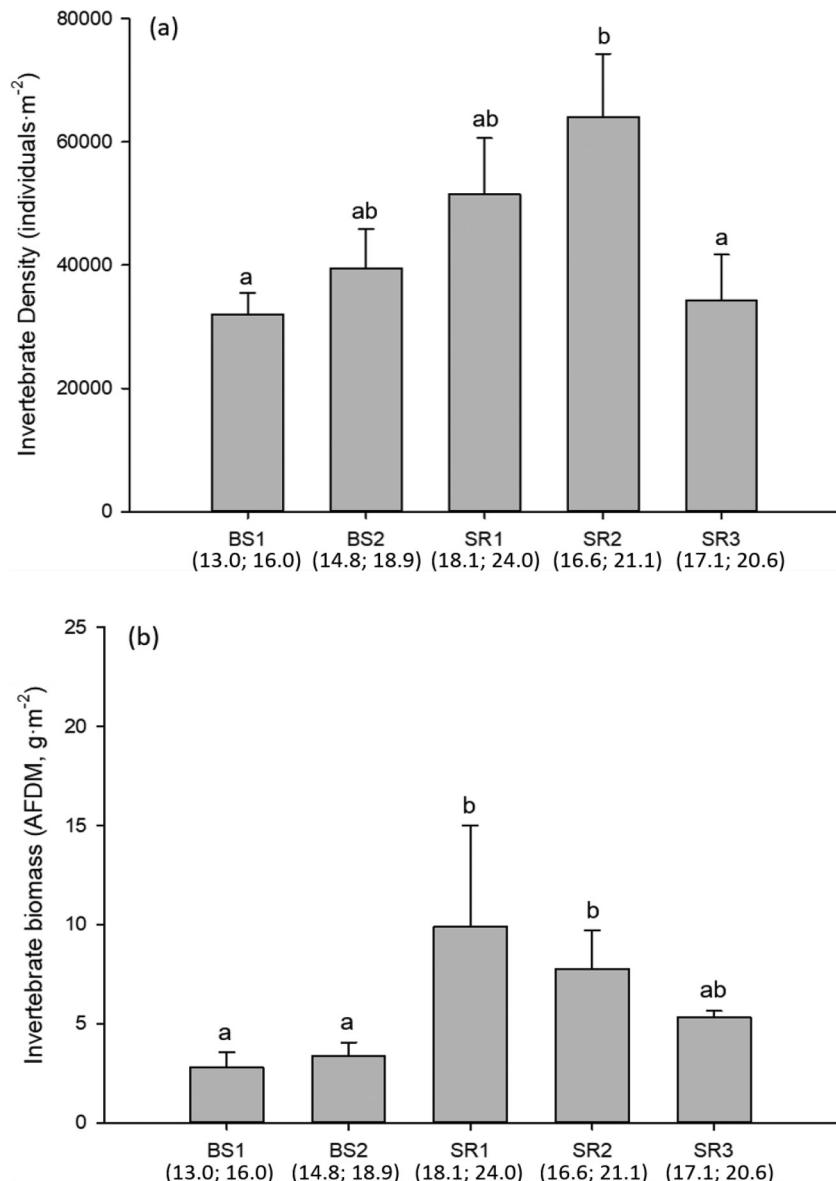


exhibited significantly higher velocity at the midpoint of the experiment relative to the other four reaches ($F_{4,20} = 8.9$, $p < 0.01$; Tukey's HSD, $p < 0.05$; Table 1).

Stream water temperature was variable across all study reaches (Table 1), but each time series exhibited a similar temporal pattern of decline during the study period (Fig. 2). Mean T values ranged from 13.0 to 18.1 °C, and MWMT values ranged from 16.0 to 24.0 °C. Four of the five study reaches exhibited MWMT values above 18 °C (Table 1). The highest mean T and MWMT values occurred at SR1,

which was located on the mainstem Shasta River above the Big Springs Creek confluence, and thus was not influenced by cool water delivered by Big Springs Creek. Maximum diel temperature fluctuations occurred at SR1 ($\Delta T = 8.5$ °C) on 17 July (day 8 of our study), BS2 ($\Delta T = 7.4$ °C) on 10 July (day 1 of our study), and SR2 ($\Delta T = 7.3$ °C) on 17 July (day 8 of our study). In contrast, study reaches BS1 ($\Delta T = 4.8$ °C) and SR3 ($\Delta T = 4.8$ °C) exhibited substantially less thermal variability, with maximum diel fluctuations occurring on 10 July (day 2 of our study; Fig. 2).

Fig. 3. Mean (+1 standard error) invertebrate density (a) and biomass (b; AFDM = ash-free dry matter) at each enclosure study reach. Different lowercase letters above the bars indicate statistically significant differences between reaches (ANOVA followed by Tukey's honestly significant different test, $p < 0.05$). Study reaches sharing the same letter are not different. Parenthetical values under each study reach are the mean daily average water temperature (mean T) followed by maximum weekly maximum temperature (MWMT) observed during the study period. Note: SR1 is located upstream of Big Springs Creek and was not influenced by major spring sources.



Benthic invertebrates

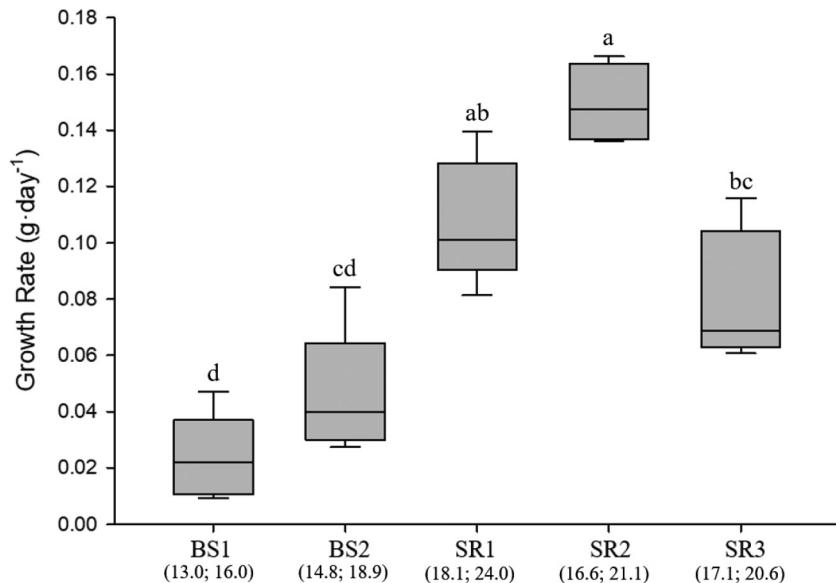
There were significant differences in both invertebrate density ($F_{[4,53]} = 3.96, p < 0.01$; Tukey's HSD, $p < 0.05$; Fig. 3a) and invertebrate biomass ($F_{[4,53]} = 7.21, p < 0.01$; Tukey's HSD, $p < 0.05$; Fig. 3b) among the five study reaches. Mean invertebrate density was greatest at SR2 (mean \pm SE = $64\ 106 \pm 9597$ individuals·m⁻²) and lowest at BS1 ($32\ 019 \pm 2408$ individuals·m⁻²), a 2.0-fold difference. Even greater variation occurred among individual samples. Maximum invertebrate density during the entire study period was recorded at SR2 during August ($139\ 434$ individuals·m⁻²), while the lowest density ($20\ 122$ individuals·m⁻²) was observed at BS1 during July, a 6.9-fold difference in abundance. Mean invertebrate biomass was greatest at SR1 (9.88 ± 3.37 g AFDM·m⁻²) followed by SR2 (7.76 ± 1.37 g AFDM·m⁻²), whereas the lowest mean invertebrate biomass was observed at BS1 (2.77 ± 0.45 g AFDM·m⁻²; Fig. 3b). Invertebrate density and biomass were positively associ-

ated, but not strongly so (linear regression, $r^2 = 0.34, p < 0.01$), indicating a decoupling between the two variables.

Coho salmon growth and performance

We recovered 113 (75.3%) of the 150 age-0+ coho salmon initially placed in our experimental enclosures. Of the 37 unrecovered fish, 31 individuals escaped (confirmed via subsequent detections on stationary PIT tag antenna arrays located in the basin), four carcasses were recovered from SR1, and two carcasses were removed from SR3. We found a significant difference in coho salmon absolute growth rate among reaches (ANOVA, $F_{[4,15]} = 32.38, p < 0.01$; Tukey's HSD, $p < 0.05$; Fig. 4). Mean absolute growth was greatest at SR2 (0.15 ± 0.01 g·day⁻¹), followed by SR1 (0.11 ± 0.01 g·day⁻¹), and lowest at BS1 (0.02 ± 0.01 g·day⁻¹). Age-0+ coho salmon reared at study reaches SR2 and BS1 exhibited a mean change in mass of 9.1 and 1.4 g, respectively, a 6.5-fold difference in growth. Nearly all

Fig. 4. Absolute growth rate of age-0+ coho salmon reared in experimental enclosures at five different locations in the Shasta River basin (center line, median; box limits, upper and lower quartiles; whiskers, maximum and minimum interquartile range). Different lowercase letters above box and whiskers indicate a statistically significant difference between study reaches (ANOVA followed by Tukey's honestly significant different test, $p < 0.05$). Study reaches sharing the same letter are not different. Parenthetical values under each study reach are the mean daily average water temperature (mean T) followed by maximum weekly maximum temperature (MWMT) observed during the study period. Note: SR1 is located upstream of Big Springs Creek and was not influenced by major spring sources.



coho salmon (106 of 113; 93.8%) recovered at the end of the 63-day experimental period exhibited positive absolute growth rates. The exception to this trend occurred at reach BS1 (the reach with the lowest mean T , MWMT, and invertebrate density; Table 1) where 7 of 29 fish (24.1%) exhibited absolute growth rates ≤ 0.0 g·day $^{-1}$ during the study.

Model comparisons

The top-ranked model describing the absolute growth of juvenile coho salmon during our experiment included scaled invertebrate density as the lone parameter (AIC_c weight = 67.0%), and all models that included a parameter for invertebrate density received >99% of the AIC_c weight (Table 2). The parameter estimates for scaled invertebrate density were positive and did not overlap zero (parameter estimate = 0.04, 95% CI = 0.03 to 0.05), indicating a reliably positive effect of invertebrate density on coho salmon absolute growth rate (Fig. 5). Model estimates for coho salmon growth were 4.1 times greater at SR2 than at BS1, the reaches with the highest (64 106 individuals·m $^{-2}$) and lowest (32 019 individuals·m $^{-2}$) overall invertebrate densities, respectively. The food + temperature model received some AIC_c weight ($\Delta AIC_c = 1.6$, AIC_c weight = 30%; Table 2), indicating an additive effect of increasing water temperature on age-0+ coho salmon growth. The parameter estimates for both factors were positive and did not overlap zero (food parameter estimate = 0.03, 95% CI = 0.02 to 0.04; temperature parameter estimate = 0.02, 95% CI = 0.01 to 0.03). A plot of the residuals from the invertebrate density model against mean T confirmed that the influence of temperature was positive, but showed a possible nonlinearity between growth and temperature (Fig. S1¹). Mean coho salmon growth peaked at a mean T of 16.6 °C and MWMT of 21.1 °C. Mean absolute growth rates from low to high values were 0.02 g·day $^{-1}$ at BS1 (mean T = 13.0 °C; MWMT = 16.0 °C), 0.05 g·day $^{-1}$ at BS2 (mean T = 14.8 °C; MWMT = 18.9 °C), 0.07 g·day $^{-1}$ at SR3 (mean T = 17.1 °C; MWMT = 20.6 °C), 0.11 g·day $^{-1}$ at SR1 (mean T = 18.1 °C; MWMT = 24.0 °C), and 0.15 g·day $^{-1}$ at SR2 (mean T = 16.6 °C; MWMT = 21.1 °C) (Fig. 5). Thus, while coho salmon growth remained positive (and above average) at the highest mean T (18.1 °C) and MWMT (24.0 °C) (reach SR1; Table 1),

Table 2. Model comparison for juvenile coho salmon growth rate.

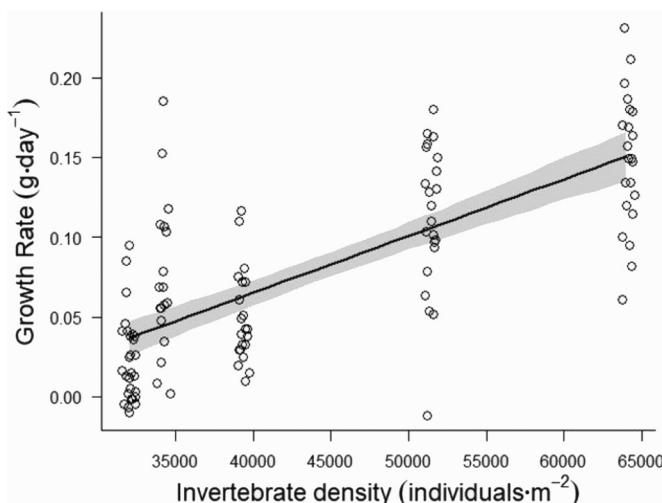
Model	df	ΔAIC_c	AIC_c weight
$G \sim D$	4	0	0.670
$G \sim T + D$	5	1.6	0.302
$G \sim Velocity + D$	5	8.2	0.011
$G \sim P_{Macro} + D$	5	9.3	0.006
$G \sim Depth + D$	5	9.9	0.005
$G \sim D + T + D \times T$	6	11.1	0.003
$G \sim T$	4	12.5	0.001
$G \sim P_{Macro}$	4	12.6	0.001
$G \sim Depth$	4	17.3	<0.001
$G \sim$ (Intercept only)	3	20.1	<0.001
$G \sim Velocity$	4	29.1	<0.001

Note: The model parameter G represents absolute growth rate of age-0+ coho salmon (g·day $^{-1}$), D is invertebrate density, T is mean daily average water temperature (mean T), and P_{Macro} is the proportion of the stream channel occupied by aquatic macrophytes. df is the degrees of freedom, and ΔAIC_c is the difference in AIC_c between the model of interest and the top-ranked model.

absolute growth was maximized at a mean T of 16.6 °C and MWMT of 21.1 °C (reach SR2; Table 1). Neither water velocity nor depth were a strong predictor of coho salmon growth (Table 2).

While coho salmon mortality was generally low during our experiment, mortality was elevated at SR1, the study reach with the highest MWMT (Fig. 6). In order of increasing MWMT values at each study reach, mean mortality rates were 0.0% at BS1 (MWMT = 16.0 °C), 0.0% at BS2 (MWMT = 18.9 °C), 6.7% at SR3 (MWMT = 20.6 °C), 0.0% at SR2 (MWMT = 21.1 °C), and 13% at SR1 (MWMT = 24.0 °C). The MWMT model received markedly more AIC_c support than the intercept model ($\Delta AIC_c = 6.2$, 95.9% of the AIC_c weight; Table 3). The temperature parameter was positive and did not overlap zero (parameter estimate = 0.57, 95% CI = 0.10 to 1.03), indicating that age-0+ coho salmon mortality reliably increased with MWMT (Fig. 6).

Fig. 5. Absolute growth rates of age-0+ coho salmon reared in experimental enclosures as a function of overall invertebrate density (prey availability). Invertebrate density represents the mean invertebrate density at each enclosure study reach. Shaded area represents the 95% confidence interval of the model.



Discussion

Our study describes how natural spatiotemporal gradients in thermal conditions, prey availability, and select environmental factors affected the growth and survival of enclosure-reared age-0+ coho salmon during the critical summer period. We found that variability in food resources (invertebrate prey densities) among study reaches most strongly explained the growth of age-0+ coho salmon during the summer low flow period, across mean T values ranging from 13.0 to 18.1 °C and MWMT values ranging from 16.0 to 24.0 °C. Even at the highest temperatures observed during our study (mean T = 18.1 °C; MWMT = 24.0 °C), juvenile coho salmon growth rates were positive and above the study-wide average, although mortality rates peaked at this elevated temperature. Our results indicate that ecosystem productivity may help buffer the negative effects of elevated water temperature on juvenile salmonid growth and survival, with important implications for climate change.

We found that juvenile coho salmon growth rates peaked at a mean T of 16.6 °C and MWMT of 21.1 °C and were six times greater than those observed at the coolest reach (BS1), which exhibited a mean T of 13.0 °C and MWMT of 16 °C. Previous studies have suggested that optimal stream temperatures for coho salmon growth are less than those in our experiment. McCullough (1999) reported that juvenile coho salmon growth was maximized at 15 °C, while Hicks (2002) proposed that weekly average temperatures of 14–15 °C would likely be the most beneficial for coho salmon growth. Moyle (2002) suggested an optimal temperature range between 12 and 14 °C for juvenile coho salmon populations in California, while Stenhouse et al. (2012) recommended an instantaneous maximum temperature of 15.5 °C for coho salmon in the Shasta River (our study system). Differences in growth and temperature across disparate studies and geographies may be a function of local adaptation and (or) acclimation. However, the aforementioned recommendations suggest that water temperatures exceeding ~16 °C likely constrain juvenile coho salmon growth and, by extension, diminish habitat suitability to some degree. The results of our study, however, are inconsistent with these recommendations.

To reconcile our findings with reported temperature optima, we propose that abundant trophic resources can help mitigate the negative effects of elevated water temperature on juvenile salmonid growth, particularly in cases where instantaneous maximum temperatures remain well below upper thermal limits and (or) where

Fig. 6. Mortality of age-0+ coho salmon reared in experimental enclosures as a function of maximum weekly maximum temperature (MWMT). Points represent mean fish mortality in each replicate enclosure. Shaded area represents the 95% confidence interval of the model.

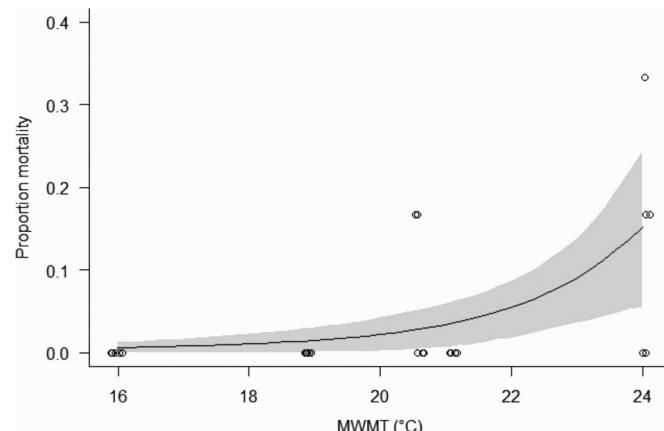


Table 3. Comparison of the temperature and null model used to estimate mortality of juvenile coho salmon.

Model	df	ΔAIC_c	AIC_c weight
$P_{\text{Mort}} \sim T$	2	0	0.959
$P_{\text{Mort}} \sim (\text{Intercept only})$	1	6.3	0.041

Note: P_{Mort} is proportion mortality and T is temperature (MWMT). df is the degrees of freedom, and ΔAIC_c is the difference in AIC_c between the model of interest and the top-ranked model.

sufficient diel temperature fluctuations occur. There are clear metabolic trade-offs between water temperature and prey consumption (Hanson et al. 1997). Growth of ectotherms is a function of the amount of energy consumed and net energy expended through respiration, in addition to metabolic costs associated with egestion and excretion. Energy consumption is dictated by prey availability (capture efficiency), while energy expenditure increases with temperature and discharge, primarily through intensified respiration. Most salmon-bearing streams are oligotrophic and abundant food sources are typically rare, particularly at temperate latitudes (Myrvold and Kennedy 2015). Consequently, factors other than food (both physiological and ecological) often constrain salmonid growth in many riverine ecosystems, and this may explain the paucity of empirical evidence directly linking juvenile salmonid growth to food abundance.

Nevertheless, a few field studies have provided evidence that food availability influences juvenile salmonid growth and (or) habitat selection. Bisson et al. (1988) reported robust rates of coho salmon production in several Washington (USA) streams where maximum temperatures ranged from 24.5 to 29.5 °C, and the authors hypothesized that food resources played an important role in those observations. Railsback and Rose (1999) found that variability in the summer growth of rainbow trout (resident *O. mykiss*) in the Sierra Nevada of California was a function of food availability rather than temperature, and Boughton et al. (2007) demonstrated that augmented food resources enhanced the growth rate (but not survival) of juvenile steelhead reared in enclosures in a southern California stream. In an experiment conducted in artificial channels adjacent to a British Columbia stream, enhanced food availability enabled juvenile coho salmon to expand foraging ranges into higher-velocity habitats where energy expenditures were presumably greater (Rosenfeld et al. 2005). In another study, Rosenfeld and Raeburn (2009) found that prey availability associ-

ated with different habitats accounted for differences in juvenile coho salmon growth rates. Our work builds on these studies and demonstrates that coho salmon can grow rapidly at a mean T of 16.6 °C (and MWMT of 21.1 °C) when prey resources are abundant.

We acknowledge that the results obtained in our experiment were likely influenced by the use of enclosures, which prohibited dispersal by juvenile coho salmon in response to stressful thermal conditions (i.e., behavioral thermoregulation). Moreover, it is probable that elements of the thermal regime beyond mean T and MWMT are important determinants of habitat suitability for juvenile salmonids. Despite diel temperature fluctuation not playing a prominent role as a predictor of age-0+ coho growth in our study, such thermal variability is presumed to reduce heat stress and metabolic demand. Chesney et al. (2009) described age-0+ coho salmon rearing at weekly maximum temperatures up to 22.4 °C in the Shasta River when sufficient diel thermal fluctuations occurred (i.e., daily minimum temperatures of ~13 °C) and speculated that rearing at elevated water temperatures was also facilitated by abundant trophic resources. Substantial diel thermal fluctuations (ΔT up to 8.5 °C) occurred during our study, possibly enabling juvenile coho salmon to recover from prior thermal stress and perhaps reducing overall study mortality, although such fluctuations were not indicative of growth. The role of diel thermal fluctuations on juvenile coho salmon growth in the wild has not been extensively studied, but should be examined more closely, particularly as it interacts with prey availability.

Our findings add to a growing literature showing juvenile coho salmon can persist and grow in environments with elevated water temperatures when sufficient food is available. While a broader understanding of the interactions between water temperature and food availability can provide context in understanding potential limiting factors on salmonid population viability, the results presented here should not be misconstrued as an endorsement of high water temperatures in lieu of functioning stream and riparian habitat. Elevated water temperatures have been shown to negatively affect obligate cold-water species through different pathways, both direct and indirect (Morita et al. 2015). However, there is mounting evidence that fish often reside in locations that exceed purported thermal optima when such locations (or nearby habitats) exhibit thermal heterogeneity over time and (or) space (Brewitt et al. 2017). Movements between thermally heterogeneous environments are often cyclical, with salmonids dispersing from physiologically optimal cold-water habitat to warmer water to seek enhanced foraging and growth opportunities (Brewitt et al. 2017; Osterback et al. 2018). Conversely, juvenile salmonids rearing at more northern latitudes have been shown to disperse from cooler to warmer habitats to accelerate metabolic processes and growth (Armstrong et al. 2013).

Watersheds are context-specific environments characterized by a range of physical and biological factors that interact to influence the growth, distribution, and fitness of salmonids. An improved understanding of these interactions, and specifically the role that food webs play in supporting salmonid rearing, is critical for successful conservation and management of imperiled salmonid populations. Our results suggest that enhanced food resources may allow juvenile salmonids to persist in habitats that would be deemed suboptimal based on temperature criteria alone. This may be particularly true in watersheds with intrinsically high rates of secondary production or in highly productive seasonal habitats such as coastal freshwater lagoons (e.g., Bond et al. 2008; Hayes et al. 2008; Osterback et al. 2018). Several recent studies have called for a broader inclusion of prey availability into salmonid habitat selection and suitability models (e.g., Wipfli and Baxter 2010; Weber et al. 2014), and the results presented here strongly support this recommendation.

The potential for highly productive habitats to ameliorate the negative effects of high stream temperature has important implications for salmonid conservation and management under cli-

mate change (Lusardi et al. 2016; Moyle et al. 2017). Elevated water temperatures have been shown to strongly limit the distribution and abundance of salmonids (Roper et al. 1994; Welsh et al. 2001; Myrick and Cech 2004) with potentially important fitness consequences (Angilletta et al. 2008). Climate change is predicted to further increase stream water temperature (Morrill et al. 2005; Isaak et al. 2012), affecting salmonids and other cold-water fishes in numerous ways. Wenger et al. (2011) projected nearly a 50% decline in cold-water trout habitat throughout the western United States by 2080. Salmonids at the southern edge of their native range are particularly vulnerable to climate change because water temperatures regularly approach purported thermal tolerances in many streams (Katz et al. 2013; Moyle et al. 2017). Our findings, therefore, suggests that food availability may offset negative effects of increasing water temperature in highly productive ecosystems.

The climate refugia literature to date has largely focused on ecosystems that provide cold-water habitats (e.g., Isaak et al. 2015). We suggest that habitats with inherently high rates of secondary production, such as spring-fed rivers, floodplains, seasonal lagoons, and estuaries, will likely become increasingly important to the viability of salmonids under future warming scenarios, and such habitats should be emphasized in climate-adaptation strategies. In general, however, these habitats are comparatively rare, understudied, and have often experienced considerable change due to water development and urbanization, particularly in California (Moyle et al. 2017). Further research is warranted to assess the ability of such habitats to support juvenile salmonids and possibly buffer the effects of climate warming on salmonid populations.

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