

## ARTICLE

## Freshwater Ecology

# In hot water? Assessing the link between fundamental thermal physiology and predation of juvenile Chinook salmon

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**Funding information**

California Sea Grant, Grant/Award Number: 19054; Lloyd Swift Fellowship; University of California, Davis Agricultural Experiment Station, Grant/Award Number: 2098-H; Wildlife, Fish and Conservation Biology Department at the University of California, Davis

**Handling Editor:** Jane Rogosch

**Abstract**

In light of ongoing environmental change, understanding the complex impact of interacting stressors on species, communities, and ecosystems is an important challenge. Many studies to date examine the effects of potential stressors on a single species of concern. Yet these effects often resonate throughout a community and may produce changes in ecosystem dynamics that are equally critical to species resilience. The aim of this study was to develop a mechanistic understanding of how a rapidly changing stressor, water temperature, will alter trophic interactions among ectothermic fish species. In our region, California's Sacramento–San Joaquin River Delta system, it has been speculated that the decreased survivorship of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in warming waters may be caused partly by increased predation. Temperature influences metabolic rate functions and the amount of energy available for fitness-relevant parameters (i.e., swim performance and escape response). Consequently, we hypothesized that these patterns of predation emerge due to a physiological advantage of predators over prey at warmer temperatures. To explore this, our first objective was to determine the fundamental thermal physiology of juvenile Chinook salmon and their potential predators in the Delta. Three physiological performance traits were measured for each species across a spectrum of temperatures: aerobic scope, burst speed, and the ability to burst repeatedly. For our second objective, we assessed whether the effect of temperature on these performance traits predicted the outcome of predation trials conducted across the same temperature spectrum. We found that temperature effects were species or population specific. Additionally, absolute burst swimming ability and the relative burst performance between predator and prey were stronger indicators of trophic dynamics than aerobic scope. Our analyses also confirmed that a major predator in the Delta, specifically largemouth bass (*Micropterus salmoides*), is more

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thermally adapted to higher temperatures and will likely consume salmon with an increasing frequency as waters warm. Thus, we show that an improved understanding of how fundamental thermal physiology impacts predation can provide ecosystem managers with better tools to predictively model predation upon juvenile salmon based on prevailing and future water temperatures.

#### KEYWORDS

climate change, conservation, ecophysiology, predator–prey interactions, temperature

## INTRODUCTION

Among its many known effects, climate change is leading to increases in water temperatures. This trend is forecasted to continue throughout the 21st century (Alfonso et al., 2021; IPCC, 2013), and its potential impact on aquatic and marine systems is concerning. Organisms that occupy these habitats, such as ectothermic fishes, have thermal tolerance limits based on the temperature sensitivity of biochemical mechanisms (Pike et al., 2013; Pörtner et al., 2005), which are affected by the surrounding water temperature. Extreme temperatures outside of an organism's tolerance can affect growth and reproductive potential, but also lead to physiological stress and even mortality (Boughton et al., 2007; Crozier et al., 2008; Hokanson et al., 1977; Martins et al., 2012; Pike et al., 2013). In turn, physiological responses to temperature can affect the behavior, population dynamics, and distribution of a given species. For example, known effects of temperature change include range contractions or expansions (Marras et al., 2015; Perry et al., 2005), and in extreme cases, an increase in extinction rate (Ben Rais Lasram et al., 2010; Marras et al., 2015). It has been speculated that the alterations in physiological performance due to warming conditions is directly correlated with these larger scale impacts (Marras et al., 2015; Pörtner & Knust, 2007). As a result, many studies are currently designed to understand how temperature affects organisms intrinsically, via their fundamental thermal physiology (i.e., the collection of intrinsic physiological traits that define a species' thermal capacity; Fry, 1947; Zillig et al., 2021). Yet it is unlikely that fundamental physiology alone is a sufficient predictor of a species' response to temperature. Organisms do not exist in isolation, and there is a significant gap in our understanding of how temperature interacts with ecological factors (e.g., predation, competition, disease) to constrain the fundamental thermal physiology of a species, producing its ecological thermal physiology (Brett, 1971; Zillig et al., 2021). Because climate change will undoubtedly affect both fundamental and ecological physiologies, predicting organism response to climate change requires a better understanding of how

intrinsic physiology and extrinsic ecosystem dynamics interact to influence population-specific thermal performance.

In California's Central Valley, warming conditions have led to increased focus on the complex effects of temperature on fish physiology and survivorship. This region hosts four runs of Chinook salmon (*Oncorhynchus tshawytscha*; Johnson et al., 2017), two of which are protected under state and federal endangered species acts following severe population declines (Fisher, 1994; Marine & Cech, 2004; Nehlsen et al., 1991; Yoshiyama et al., 1998). These declines have been attributed to several potential factors (reviewed in Myrick & Cech, 2004), including low survivorship in outmigrating juveniles at warmer temperatures (Buchanan et al., 2013; Kjelson & Brandes, 1989; Michel et al., 2015, 2020; Perry et al., 2010). Historically, increased juvenile mortality was assumed to result from thermal stress (e.g., Crossin et al., 2015), as water management and extreme variation in precipitation (Dettinger et al., 2011; Johnson et al., 2017; Moyle, 2002) elevated water temperatures during the spawning and rearing season of the Chinook salmon runs (Marine & Cech, 2004). Unexpectedly, however, laboratory studies reveal that some runs of Chinook salmon in this region appear thermally robust, capable of physiological growth and performance at the high temperatures often correlated with increased mortality in the wild (Marine & Cech, 2004; Poletto et al., 2017; Verhille et al., 2016; Zillig et al., 2020). It is thus unlikely that lower survival under warm conditions can be solely attributed to the direct effects of temperature on the fundamental physiology of salmon.

Alternatively, recent research on this system (e.g., Nobriga et al., 2021) suggests that warming temperatures may indirectly influence salmon survivorship, specifically via predation. Central Valley waterways are home to numerous predator species that have demonstrated top-down control on salmon populations (Erhardt et al., 2013; Lindley & Mohr, 2003; Nobriga et al., 2021; Sabal et al., 2016). Acoustic tagging of juvenile Chinook salmon in the Central Valley's Sacramento–San Joaquin River Delta (hereafter Delta) has revealed survival rates

of <5% (Buchanan et al., 2018), and it is thought that the Delta is a major survival bottleneck due to the presence of primarily non-native piscivorous predators, such as striped bass (*Morone saxatilis*) and largemouth bass (*Micropterus salmoides*) (Demetras et al., 2016; Michel et al., 2018; Nobriga et al., 2021). In addition, predation in the Delta has been shown to increase with temperatures that correspond to decreased survivorship of outmigrating Chinook salmon (Henderson et al., 2019; Johnson et al., 2017; Nobriga et al., 2021). This trend may be due to the physiology of common predators; for example, largemouth bass metabolism is highly sensitive to the range of water temperatures in the Delta, which could accelerate demand for prey as waters warm (Nobriga et al., 2021). However, to date, there has been no further exploration of whether predators are physiologically advantaged at warmer temperatures, or whether there is a link between thermal physiology and predation success.

A key next step in determining the patterns of salmon mortality in the Delta is to establish whether species-specific physiology can be used to predict trophic interactions. The fundamental thermal physiology for a given species can be measured by a variety of traits: acute and chronic thermal limits (e.g., Keefer et al., 2018; Myrick & Cech, 2004), growth rates (e.g., Cech & Myrick, 1999; Marine & Cech, 2004), and temperature-dependent metabolic indices such as aerobic scope (AS; e.g., Eliason et al., 2011; Rummer et al., 2016), cardiac physiology (e.g., Anttila et al., 2018; Eliason et al., 2011), or enzyme activities (e.g., Hochachka & Somero, 1968). These traits are often quantified in a laboratory setting and then extrapolated for management applications; however, they may not all be useful for determining the ecological thermal physiology of an organism in every context. For example, there have been discrepancies in growth rates for juvenile Chinook salmon between laboratory and field experiments (Zillig et al., 2021). These could be attributed to differences in water chemistry or the effects of disease (Myrick & Cech, 2001). Alternatively, as other studies have shown, food availability (Lusardi et al., 2020; Railsback & Rose, 1999) and competition (Reese & Harvey, 2002) may act synergistically with temperature to influence juvenile salmonid growth in the wild. Similarly, much work on salmonids has focused on AS, or the difference between maximum metabolic rate (MMR) and resting metabolic rate (RMR; e.g., Marine & Cech, 2004; Poletto et al., 2017; Verhille et al., 2016; Zillig et al., 2020). AS represents the capacity of aerobic metabolism, more than basic maintenance costs, for fitness-enhancing activities, such as feeding and swimming (Rummer et al., 2016). However, studies using AS can also produce results that do not align with trends observed in the field;

for example, AS values may indicate that salmonid populations are relatively thermally robust, but as mentioned above, their survival in the Delta decreases with warmer temperatures.

Collectively, these differences in laboratory- and field-based studies suggest that ecological factors and natural animal behaviors must be considered when designing physiological studies, to produce results that are applicable to natural settings. For predator-prey interactions specifically, other physiological measurements may be important. Among these, bursts are high-energy swimming bouts (<20 s; Domenici & Batty, 1994; Domenici & Blake, 1997; Jayne & Lauder, 1993) that are used by most fish when escaping predators or during prey capture (Domenici & Blake, 1997). Yet burst swimming in many species of fish, including salmonids, has rarely been studied. Furthermore, of the few studies on this topic, burst speed has been commonly reported (reviewed in Domenici & Blake, 1997), but other metrics such as maneuverability, burst distance, or the ability to undertake repeated bursts also warrant examination based on the behaviors observed during a predator-prey encounter. Given the life-history strategies of different fishes, it is likely that physiological performance across traits will vary not only by temperature, but by species or even population (e.g., Zillig et al., 2021). Therefore, quantifying a thermal physiological advantage ideally entails the assessment of multiple species-specific traits.

In this study, we used a multispecies, multi-trait approach to test the hypothesis that patterns of juvenile salmon mortality in the Delta occur due to a physiological advantage of their predators at warmer temperatures. To do so, our objectives were (1) to identify the optimal physiological temperatures for salmon and their common predators based on multiple performance traits and (2) to determine whether these temperatures confer a relative advantage between species in predator-prey interactions. We predicted that predation would be greatest at temperatures where predators possessed a relative physiological advantage, and lowest at temperatures where salmon performed best relative to their predators.

## METHODS

### Experimental overview

The aim of this study was to assess how predation outcomes related to physiological performance of both prey and predators. We examined two runs of juvenile Chinook salmon (fall-run [FR] and late fall-run [LFR]), which allowed us to explore how salmon populations within the same species may vary in their fundamental

thermal physiology, if at all. The Chinook salmon is a relatively wide-ranging species and includes several at-risk populations confronting thermal stress (Moyle et al., 2017; Yoshiyama et al., 1998; Zillig et al., 2021), particularly in the Central Valley, which is at the southern end of its range. Our study also examined the two key non-native predators of salmon in this system: largemouth bass and striped bass. Rainbow trout (*Oncorhynchus mykiss*) was also included as a predator because this species is known to feed on salmonids in some systems and its physiology may more closely resemble that of salmon. If fundamental thermal physiology underpins trophic dynamics, we would expect rainbow trout physiological response and subsequent predation behavior to provide a contrast with that of the other predators, which are more warm-water adapted.

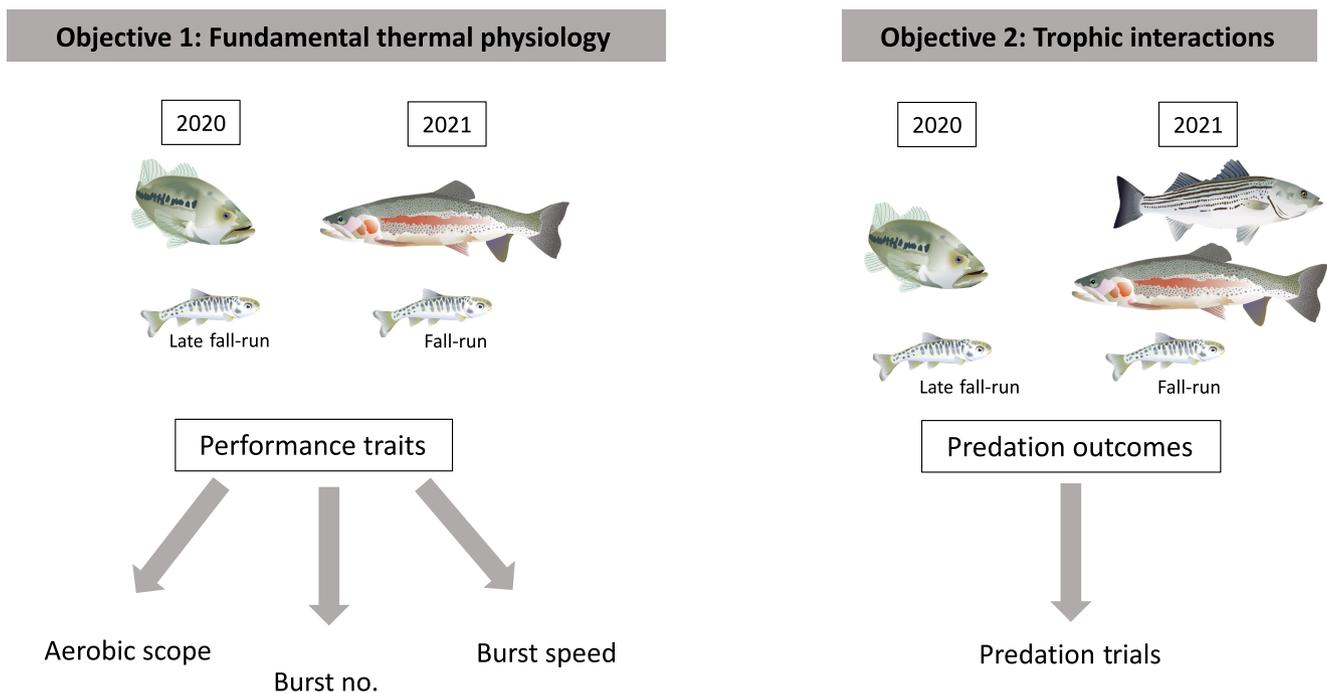
With these species, we first identified optimal physiological performance temperatures (Objective 1). Three different performance traits were measured across a temperature spectrum: AS, burst speed, and the ability to repeatedly burst (Figure 1). Measurements were taken in all species except for striped bass (see *Experimental design*). To then determine whether thermal physiological performance influenced the outcome of trophic interactions (Objective 2), we conducted predation trials across the same set of temperatures, using different combinations of salmon and predators (i.e., largemouth bass with LFR Chinook salmon; striped bass or rainbow trout with FR Chinook salmon;

Figure 1). Details regarding each component of our experiments are outlined below.

## Fish husbandry and transport

The experimental procedures for this study took place from January–July 2020 and January–May 2021 at the Center for Aquatic Biology and Aquaculture at the University of California, Davis (UC Davis). All fish care and protocols were approved by the UC Davis Institutional Animal Care and Use Committee (protocol no. 21468). In 2020, for the first set of experiments, LFR Chinook salmon ( $n = 3000$ ) were collected from the Coleman National Fish hatchery as eyed eggs (Anderson, CA), and largemouth bass ( $n = 150$ ) were obtained from The Fishery Inc. (Galt, CA). For the second set of experiments in 2021, due to egg availability, FR Chinook salmon were obtained from the Nimbus Fish hatchery (Rancho Cordova, CA) as eyed eggs ( $n = 6000$ ). Rainbow trout ( $n = 150$ ) were donated for research from the American River Hatchery (Gold River, CA) by California Department of Fish and Wildlife, and wild-caught striped bass ( $n = 77$ ) were collected via boat electrofishing in the Clifton Court Forebay. Transportation, husbandry, and rearing procedures for all fishes are outlined in Appendix S1.

After transport each year, all predators were given a 7-day acclimation period at their prior holding temperatures (largemouth bass: 16°C; striped bass and rainbow



**FIGURE 1** A schematic overview of the experimental procedures, which took place in 2020 and 2021. See *Methods* for more details (illustrations adapted from Amelia Munson, with permission).

trout: 11°C) before their water temperatures were increased by 2°C per day until they reached 18°C. This was considered the neutral temperature for the study, as it did not represent the extremes of thermal tolerance for any of the studied species (e.g., Davis et al., 2019; Gift & Westman, 1971; Heuer et al., 1983; Myrick & Cech, 2000, 2001). It has also been reported as a common temperature for the Delta during field-based studies on predation (Michel et al., 2018). We performed the same temperature ramp with the FR and LFR Chinook salmon after they were large enough to consume pelleted feed. The salmon were then allowed to grow at that temperature until they approximated the size range of out-migrants in the wild (Brandes et al., 2021; Hansen et al., 2019). All fish were given at least 3 weeks at 18°C before any experimental measurements were taken. During this time, predators were transferred to a diet of live feed (juvenile Chinook salmon or fathead minnow) to ensure that they would be able to recognize and consume prey during the predation trials.

## Experimental design

All fish were assigned to one of five different treatment groups, which reflected our test temperatures: 11, 14, 18, 22, and 25°C. These temperatures captured the range experienced by Delta system throughout much of the year (e.g., Marine & Cech, 2004; Pike et al., 2013; Poletto et al., 2017). Because of fish availability and based on previous studies (e.g., Eliason et al., 2011; Poletto et al., 2017), we aimed to test six to eight fish

per species or population at each temperature for each of the following performance traits: AS, burst capacity (i.e., speed and number of repeated bursts), and predation trial performance (Table 1). In some cases, however, incidental mortality reduced our sample size, particularly among the predators; given the limited supply of fish available, any predator excluded from the experiment due to health or behavioral reasons was not replaced.

Prior to any experimental measurements, all fishes were transferred to a holding tank for a 24-h fasting period (see exception in *Predation trials*). They were then ramped to their assigned temperature by 2°C/h and given 30 min of acute exposure at that temperature. Following the procedure, the fish were returned to 18°C via the same process. They were given 24 h to recover and were weighed and measured before being returned to their original tank. Each salmon (FR and LFR) was only used once throughout the experiments (i.e., either for AS, burst ability, or predation trial performance) and euthanized immediately after with a lethal dose of buffered tricaine methanesulfonate (0.5 g/L MS-222; Syndel, Ferndale, WA, USA). However, each individual rainbow trout and largemouth bass was tested in AS, burst ability, and predation trial performance (see striped bass exceptions below). Each predator was given 7–10 days to recover between their predation trial, AS, and burst measurements. Juvenile salmon underwent this same sequence of experiments during approximately the same time frame. Predators were then euthanized via the same methods as the salmon (MS-222; see above) at the completion of the experiments.

**TABLE 1** A summary of the fishes used in each component of this study.

Species (year)	Aerobic scope			Burst ability			Predation trials		
	<i>n</i>	Mass (g)	SL (cm)	<i>n</i>	Mass (g)	SL (cm)	<i>n</i>	Mass (g)	SL (cm)
Largemouth bass (2020)	39	277.05 (146.3–298.7)	22.7 (19.5–24.4)	39	227.09 (148.3–297.4)	22.9 (19.6–24.5)	30	221.29 (143.6–294.6)	22.4 (19.4–24.0)
LFR Chinook salmon (2020)	40	1.86 (1.17–2.57)	5.1 (4.5–5.6)	99	1.79 (0.85–2.77)	5.1 (4.4–5.9)	480	1.53 (1.33–1.72)	...
Rainbow trout [RT] (2021)	24	132.76 (94.6–177.2)	20.6 (18.5–23.4)	25	129.08 (86.4–202.0)	20.2 (18.4–22.4)	40	133.93 (60.0–192.0)	20.4 (17.0–23.1)
Striped bass [SB] (2021)	...	...	...	...	...	...	35	348.25 (210.0–482.0)	29.6 (24.3–33.2)
FR Chinook salmon (2021)	38	3.20 (0.90–7.0)	6.1 (4.1–7.7)	61	2.23 (1.05–4.62)	5.5 (4.3–7.1)	RT trials: 480; SB trials: 420	RT trials: 2.21 (1.53–4.66); SB trials: 2.61 (1.90–2.70)	...

*Note:* Sample size, mean, and range (in parentheses) of masses and standard lengths (SL) are listed when available. SLs were not taken for Chinook salmon for the predation trials to avoid excessive handling prior to the trial, but were measured for predators post-predation trial. Predation trials took place with late fall-run (LFR) Chinook salmon and largemouth bass in 2020, and fall-run (FR) Chinook salmon and either rainbow trout or striped bass in 2021.

## Swim tunnel respirometry

We used swim tunnel respirometry to quantify AS for all species across the five test temperatures in our experiment. In this study, AS was calculated as the difference between MMR and RMR. We collected both metabolic rates (RMR and MMR) based on established methodologies (Poletto et al., 2017; Verhille et al., 2016). More details on the setup and function of our swim tunnel system are available in Poletto et al. (2017). Briefly, each year of the experiment, juvenile Chinook salmon (LFR,  $n = 40$ , mean mass = 1.86 g, and mean standard length = 5.1 cm; FR,  $n = 38$ , mean mass = 3.20 g, and mean standard length = 6.1 cm) were tested in one of two 1.5-L automated swim tunnel respirometers (Loligo, Denmark), which were controlled using a single-computer system. Our predator species were tested in one of two 30-L automated swim tunnel respirometers (Loligo, Denmark), which were also controlled using a single-computer system. However, striped bass were visibly stressed by any attempted physiological tests, thrashing in the chamber and exhibiting an extremely high respiration rate and loss of equilibrium. Therefore, we only quantified AS for largemouth bass ( $n = 39$ ; mean mass = 227.05 g and mean standard length = 22.7 cm) and rainbow trout ( $n = 24$ ; mean mass = 132.76 g and mean standard length = 20.6 cm). All tunnels were surrounded by black shade material to reduce external stimuli for the fish, and infrared cameras (QSC1352W; Q-See, China) were mounted overhead each tunnel. These cameras were connected to a computer monitor to observe fish behavior during the trials.

We took metabolic measurements for RMR and MMR using intermittent respirometry (Clark et al., 2013; Poletto et al., 2017). To calculate RMR, fish were acutely exposed to their test temperature in the swim tunnels. Automatic measurements of oxygen consumption (1200-s measurement, 300-s flush) then began and were continued overnight by the AutoResp software. For the salmon in the 1.5-L tunnels, the swim tunnel impellor was reduced to its lowest rotational setting to avoid eliciting fish movements while still ensuring adequate water mixing. In the 30-L tunnels, a second submersible aquarium pump (500 L/h) was used to mix water without inducing fish movement. Measurements of RMR were typically started between 3:00 PM and 6:00 PM and continued until 7:00 AM and 9:00 AM the next day. Measurement periods were numbered  $34 \pm 12$ , and the resulting data were plotted and visually analyzed. Though unusual, measurement periods thought to result from a malfunction in the tunnel, unstable temperatures, or inexplicably high fish activity at night were discarded. The mean of the lowest

three values obtained out of all the measurement periods was then used to estimate RMR.

We measured MMR via a similar approach (1200-s measurement, 180–300-s flush). In this case, water velocity in the swimming chamber was gradually increased to swim the fish until exhaustion, although that velocity was scaled according to fish size and swimming ability. For both runs of juvenile Chinook salmon, water velocity was increased from 0 to 18 cm/s over a period of ~2 min prior to the first measurement period. For largemouth bass, water velocity increased to 30 cm/s, and for rainbow trout, to 60 cm/s during this same period. For all fish, water velocity then increased by ~10% of the previous test velocity for each subsequent measurement period. The trial was completed when the fish were exhausted and could no longer avoid impingement (see Poletto et al., 2017 for exhaustion threshold). Data were processed visually via the same methods mentioned above for the RMR. However, here the highest metabolic rate, measured over durations of at least 5 min in length, was used to determine MMR. For both MMR and RMR, background respiration in the tunnels was accounted for using control values across temperatures.

## Burst tunnel measurements

To quantify burst speed and number (hereafter “burst ability”), we used two custom burst tunnels. These tunnels were built based on a modified design by Nelson et al. (2002). Each was composed of 9.525-mm Cast Clear Acrylic Plastic, with two chambers at either end that could be opened or closed manually with a door. Both were approximately scaled to the fish species tested to ensure fishes would burst in a single plane. The salmon tunnel was 122 cm long, 7.5 cm wide, and 9.8 cm tall with a 5.6-cm fill depth. It was lined with 24 lasers (650 nm, Adafruit Industries, New York, NY, USA) along the outside of the tunnel on one side, the spacing of which ranged from 2 to 5 cm. The other side had corresponding laser detectors. The laser detectors were connected to a Raspberry Pi with code created using Python (Van Rossum & Drake, 1995). As a fish swam through the tunnel and broke a given laser beam, the time was recorded. In post-processing, this time was matched to the distance of the laser from the start of the tunnel, providing a calculation of burst velocity at that point. The larger predator tunnel was nearly identical in function and design, though at a larger scale. It was 200 cm long, 15.2 cm wide, and 25.2 cm tall with a 17.8-cm fill depth. It was also lined with 24 lasers; however, the distance between lasers was adjusted between experiment years based on the perceived burst ability of

the predators. For largemouth bass, laser distance ranged from 1 to 10 cm, and for rainbow trout, 1–5 cm. This change allowed us to increase the resolution of the laser tunnel closest to the holding chambers to capture the highest speeds of rainbow trout, which were determined to burst much faster than largemouth bass based on nonexperimental trials (A. McInturf & K. Zillig, unpublished data). High-speed cameras (GoPro Hero 6, 240 frames/s) were placed on either side of both swim tunnels to ground truth the laser readings. Temperature in the tunnels was controlled by simultaneously circulating water in the system through a chiller, via thermostat, and using a heat bar, if necessary. Water inflows were placed just above the water line in either chamber and was permitted to flow on both sides at a trickle to stabilize the temperature, oxygen, and volume of the tunnel. Water inflow did not produce a measurable current within the burst tunnel.

Prior to a given trial, individual fish were ramped to their test temperature in separate holding tanks (again, by increasing or decreasing the temperature at a rate of 2°C/h). The temperature in the burst tunnel was set to match the test temperature. Following the temperature ramp and 30-min acute exposure period in the holding tank, a fish was placed in one of two of the starting chambers and given 5 min to recover from handling prior to the initial burst. A trial consisted of repeated bursts (<30 s apart) across the tunnel until the fish was exhausted or had reached the maximum number measured (25 bursts), which had been determined as a likely upper bound for performance based on pilot trials conducted with nonexperimental largemouth bass (A. McInturf & K. Zillig, unpublished data). We elicited a given burst by tapping the side of the chamber with a small polyvinyl chloride (PVC) pipe to startle the fish, and then opening the chamber door and pinching the fish tail simultaneously. In cases where fish did not burst the full length of the tunnel, we noted the distance at which it had stopped before startling the fish again with the PVC pipe to swim the remainder of the tunnel. Human error and failures to burst (i.e., refusal to leave the chamber) were also recorded and excluded from the analysis. A fish was considered exhausted when it failed to burst from the chamber following the pinch and PVC stimulus three times.

As in the swim respirometry, striped bass were easily stressed by this procedure and this species was excluded from burst trials. Bursting methods were identical for the remaining species: largemouth bass ( $n = 39$ ; mean mass = 227.09 g and mean standard length = 22.9 cm), rainbow trout ( $n = 25$ ; mean mass = 129.08 g and mean standard length = 20.2 cm), FR ( $n = 61$ ; mean mass = 2.23 g and mean standard length = 5.5 cm), and LFR juvenile Chinook salmon ( $n = 99$ ; mean mass = 1.79 g and mean standard length = 5.1 cm). All fish were given a minimum of 10 attempts to burst, and a

“failure to burst” threshold was determined based on trials with nonexperimental fish (A. McInturf & K. Zillig, unpublished data). For the predators, a failure to burst was classified as any movement less than 0.50 m from the starting chamber; for salmon, as refusal to leave the chamber. Failed burst attempts were then discarded.

After the data were collected, the number of bursts in each trial was confirmed by written records and the corresponding Python code output. Given the possibility of an unnaturally high-speed reading due to premature disturbance of the lasers in the tunnel, any physiologically infeasible outliers were removed (e.g., burst velocity >400 cm/s for rainbow trout—Domenici & Blake, 1997; 50 m/s for Chinook salmon and largemouth bass). For a given individual fish, we calculated the mean burst speed by taking the average of these maximum speed recordings for each successful burst throughout the trial.

## Predation trials

Predation trials took place with largemouth bass (predator) and LFR Chinook salmon (prey) from May to July 2020, and with striped bass, rainbow trout (predators) and FR Chinook salmon (prey) in March–May 2021. Predators were fasted 72 h before each trial to avoid satiation during the trial. Juvenile salmon were also fasted for 24 h. Due to fish availability, we tested a total of 40 rainbow trout (mean mass = 133.93 g and mean standard length = 20.2 cm), 30 largemouth bass (mean mass = 221.29 g and mean standard length = 22.4 cm), and 35 striped bass (mean mass: 348.25 g and mean standard length = 29.6 cm). Trials with each predator species were distributed as evenly as possible across our five test temperatures. All trials were identical in procedure. On the first day of each trial, we introduced 12 juvenile salmon (2020: LFR, mean mass = 1.53 g; 2021: FR, mean mass = ~2.40 g) into each predator tank. Tanks were 1 m in diameter, and aerated ambient (18°C) well water flowed into each tank at a rate of ~1.5 L/min throughout the trials. Water inflows were submerged slightly below the water line, to reduce available shelter for the juvenile salmon and avoid surface water disturbance. Following established protocols (Davis et al., 2019), each predation tank was surrounded by a white vinyl curtain to eliminate visual stimuli and create consistent arena lighting. Predators were placed in separate holding tanks, to eliminate the possibility of predation events before the trial began. Holding tanks were equal to the predation tanks in size, water flow and exchange rates, and temperature. All predation and holding tanks were randomly assigned by test temperature (11, 14, 18, 22, and 25°C), and salmon and predators had their temperatures ramped simultaneously. After the 30-min acute exposure period following the

temperature ramp, predators were transferred from the holding tank to a predation tank corresponding to their assigned temperatures. Fish were gently netted into buckets underwater and similarly released into their predation tanks in order to minimize handling stress and eliminate air exposure.

All fish were left with minimal human disturbance for the rest of the trial, which ranged from 48 to 72 h depending on the latency of the predator species to consume prey. Largemouth bass and striped bass, which often consumed prey within the first 24 h, had 48-h trials. Rainbow trout would frequently eat nothing in the first 24 h, and so were provided 72-h trials. Regardless of the trial length, surviving salmon in each tank were counted independently by two researchers every 24 h. In cases where the researchers did not agree, the same tank was reevaluated via the same process until a consensus was reached. These checks were performed silently and with minimal disturbance of the tank, to reduce any impact on the ongoing trials. Water temperatures were monitored every 3 min throughout the trial by loggers (Onset HOBO, Bourne, MA, USA) moored in the external tank standpipes, to ensure test temperature stability. At the conclusion of the trial, largemouth bass and rainbow trout were weighed, measured, and returned to their holding tanks. To reduce stress due to any unnecessary handling, striped bass were returned immediately to their holding tanks.

## Data processing and statistical analysis

We performed our statistical analysis using R Studio version 4.0.2 (R Core Team, 2020) and the lme4 (Bates et al., 2015) and MASS packages (Venables & Ripley, 2002). Plots were generated using the ggplot2 package (Wickham, 2016). We analyzed each set of experiments (predation trials, AS, and burst ability) using a combination of linear models (LMs) and generalized linear models (GLMs).

For each run or species of fish that was tested for physiological performance traits (LFR Chinook salmon, FR Chinook salmon, largemouth bass, and rainbow trout), we created three models (i.e., AS, burst speed, and burst number) with the same fixed effects predictors: test temperature and fish mass. For AS, based on previous studies (i.e., Baird et al., 2020; Poletto et al., 2017; Verhille et al., 2016), we used a LM with both a continuous and quadratic term for temperature as a fixed effect to account for nonlinearity between temperature and AS. We included mass as a continuous fixed effect to account for the possibility that our fish had grown over the course of the experiment. We analyzed burst speed

using linear regression with those same predictors, although with temperature as a continuous linear variable (without the quadratic term). We also used a Poisson regression model to determine the effect of temperature and fish mass on burst number, because this response variable was based on count data.

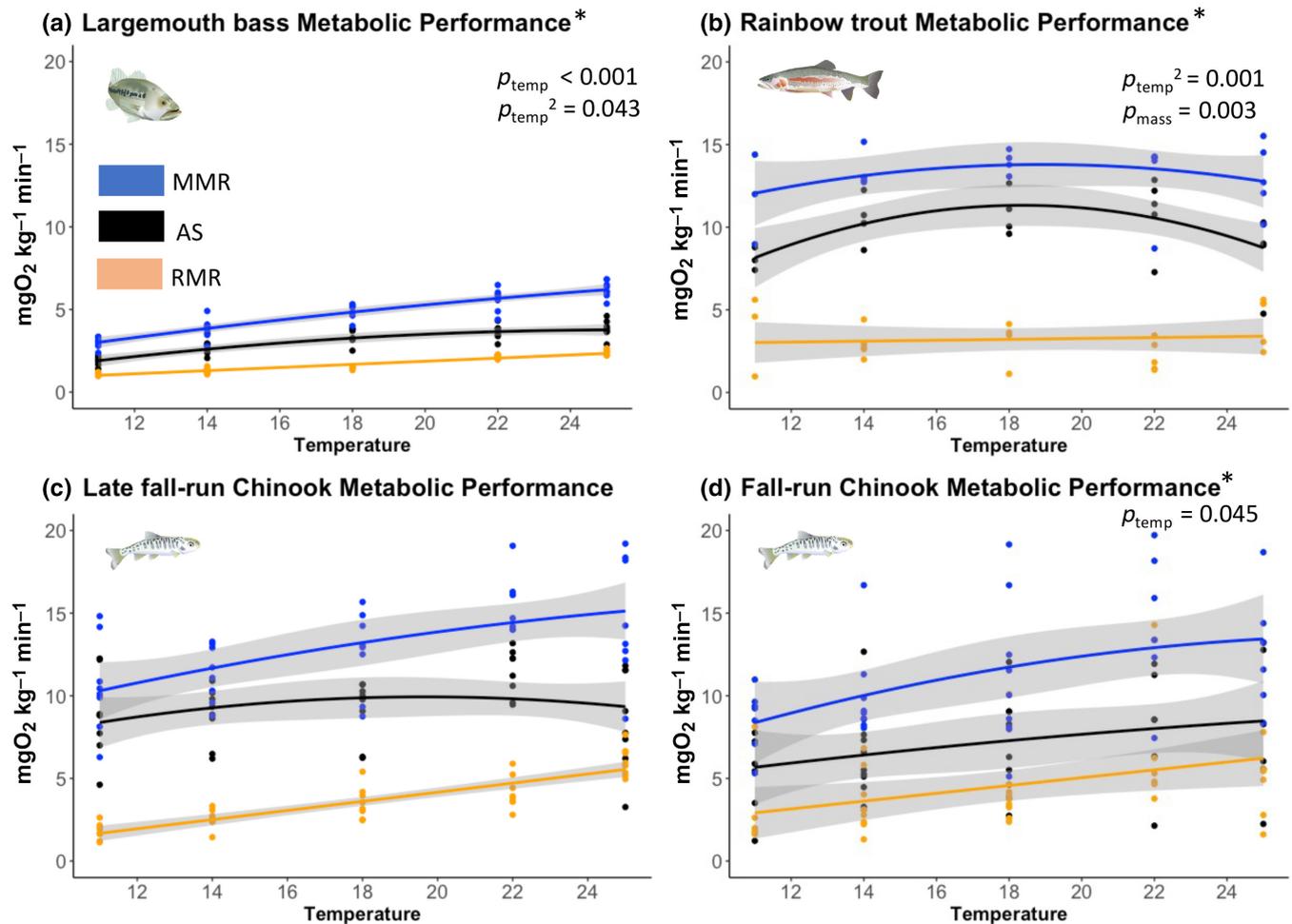
For our predation trials, we were first interested in examining whether temperature or other factors influenced the number of salmon consumed. Our count data for this response variable were overdispersed relative to a Poisson distribution, so we analyzed the predation trial results from the largemouth bass, striped bass, and rainbow trout trials using a negative binomial GLM. Because both prey size and water temperature can influence predator consumption rate (Michel et al., 2018), our fixed effect predictors included test temperature as a continuous variable, as well as average salmon mass and the mass of the predator in each tank. Both continuous mass variables were mean-centered and scaled.

We then evaluated whether predation trial outcome was influenced by relative difference in performance between salmon and their predators. To do so, we calculated the proportional difference in AS, burst number, and burst speed for LFR and FR salmon as compared with largemouth bass and rainbow trout, respectively. Striped bass were excluded from this component of our analysis because we had no data on their AS and burst ability. To compare differences in performance (i.e., AS, burst speed, or burst number), we computed the mean performance value at each temperature for all species, and then divided the value for salmon by that of the predator and subtracted by 1 to yield the proportional difference in performance. We then created three negative binomial GLMs with number of salmon eaten as the response variable. Each model had either the relative difference in AS, burst speed, or burst number as a fixed effect predictor.

## RESULTS

### Swim tunnel respirometry

As predicted, the effect of temperature on AS varied by fish species or population (Appendix S2: Table S1). For juvenile Chinook salmon, there was no significant effect of temperature on LFR AS (Appendix S2: Table S2; Figure 2c), while there was a positive correlation between these two variables for FR (Appendix S2: Table S3; Figure 2d;  $p = 0.045$ ). Both predator species tested (largemouth bass and rainbow trout) also showed a significant response in AS to temperature. Temperature had a significant quadratic effect on largemouth bass AS



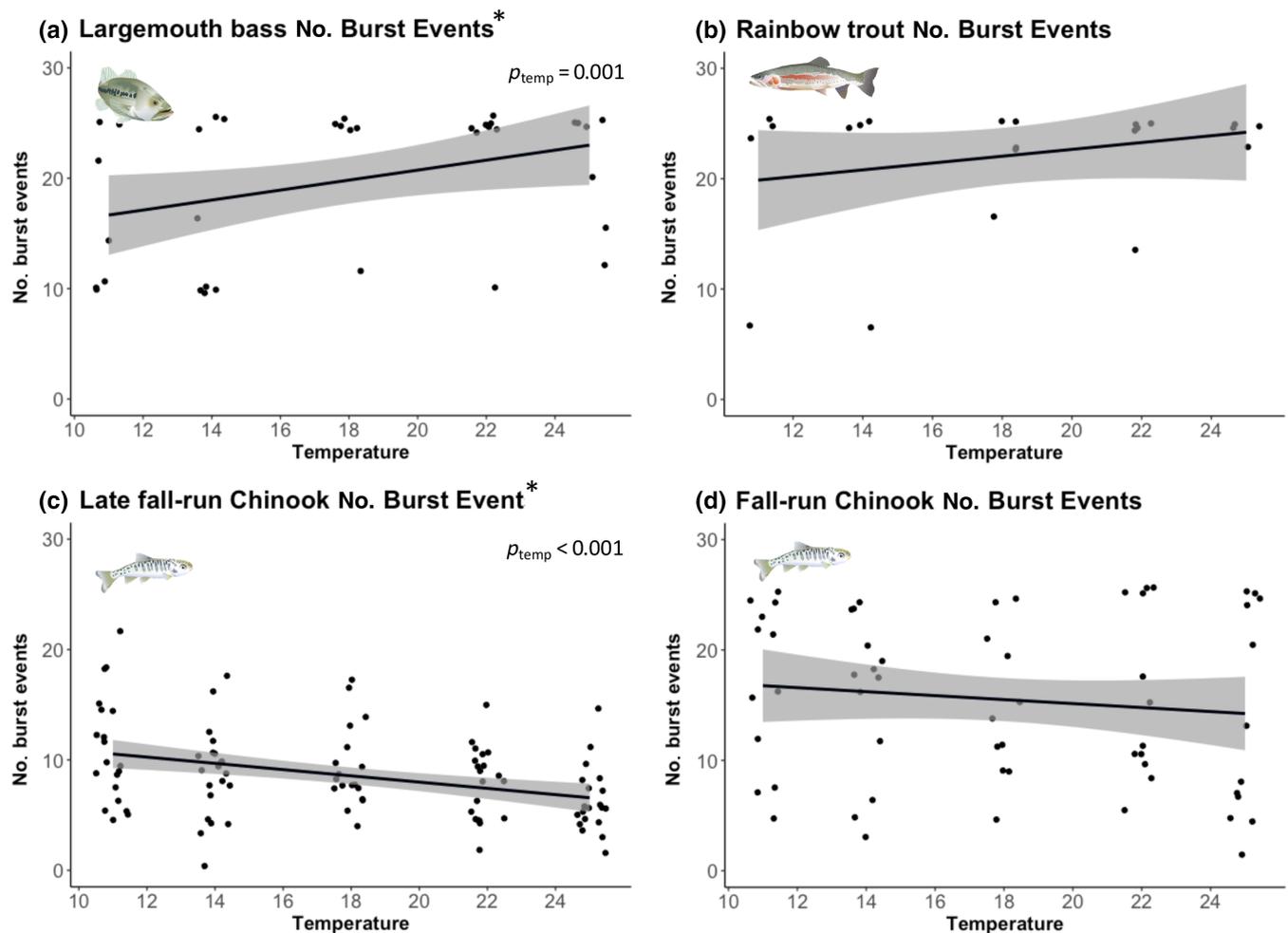
**FIGURE 2** Aerobic scope (AS) thermal performance curves as a function of water temperature (in degrees Celsius) for (a) largemouth bass, (b) rainbow trout, (c) late fall-run Chinook salmon, and (d) fall-run Chinook salmon. AS is denoted in black, resting metabolic rate (RMR) in orange, and maximum metabolic rate (MMR) in blue. Asterisk indicates a statistically significant relationship, with the  $p$  value of significant predictors reported on the graph (see details of models in text).

(Appendix S2: Table S4; Figure 2a;  $p = 0.043$ ), with a peak at the upper range of test temperatures. Conversely, there was a significant negative effect of higher temperatures on rainbow trout AS (Appendix S2: Table S5;  $p = 0.001$ ), which peaked at  $\sim 18^\circ\text{C}$  (Figure 2b). Our rainbow trout model also suggested that there was a significant positive effect of mass ( $p = 0.003$ ), which we did not observe in any of the other fish species.

### Burst tunnel measurements

In contrast to AS, we observed significant effects of temperature on both burst speed and number in LFR juvenile Chinook salmon (Appendix S2: Table S6; Figures 3c and 4c) but not in FR (Appendix S2: Table S7; Figures 3d and 4d). For LFR, temperature affected burst speed and number differently; there was a significant positive effect of

temperature on burst speed (Figure 4c;  $p < 0.001$ ), but a negative effect on burst number (Figure 3c;  $p < 0.001$ ). Salmon mass was not a significant predictor in either model. Burst speed between the two salmon populations was comparable (range LFR: 18.35–137.73 cm/s; range FR: 32.62–157.58 cm/s). Among our predators, rainbow trout burst ability was not significantly affected by temperature (Appendix S2: Table S8). However, rainbow trout consistently reached the highest burst speeds among all tested species (range: 142.10–350.63 cm/s; Figure 4b), and 75% of individuals undertook at least 20 repeated bursts (Figure 3b). Burst speeds for largemouth bass were more like those of the salmon, ranging from 22.59 to 66.03 cm/s. In parallel with the results of our predation and AS models, both burst speed and number were positively correlated with temperature for largemouth bass (Appendix S2: Table S9; Figures 3a and 4a;  $p = 0.006$  and  $0.001$ , respectively).



**FIGURE 3** The number of repeated bursts performed as a function of water temperature (in degrees Celsius) for (a) largemouth bass, (b) rainbow trout, (c) late fall-run Chinook salmon, and (d) fall-run Chinook salmon. Asterisk indicates a statistically significant relationship, with the  $p$  value of significant predictors reported on the graph (see details of models in text).

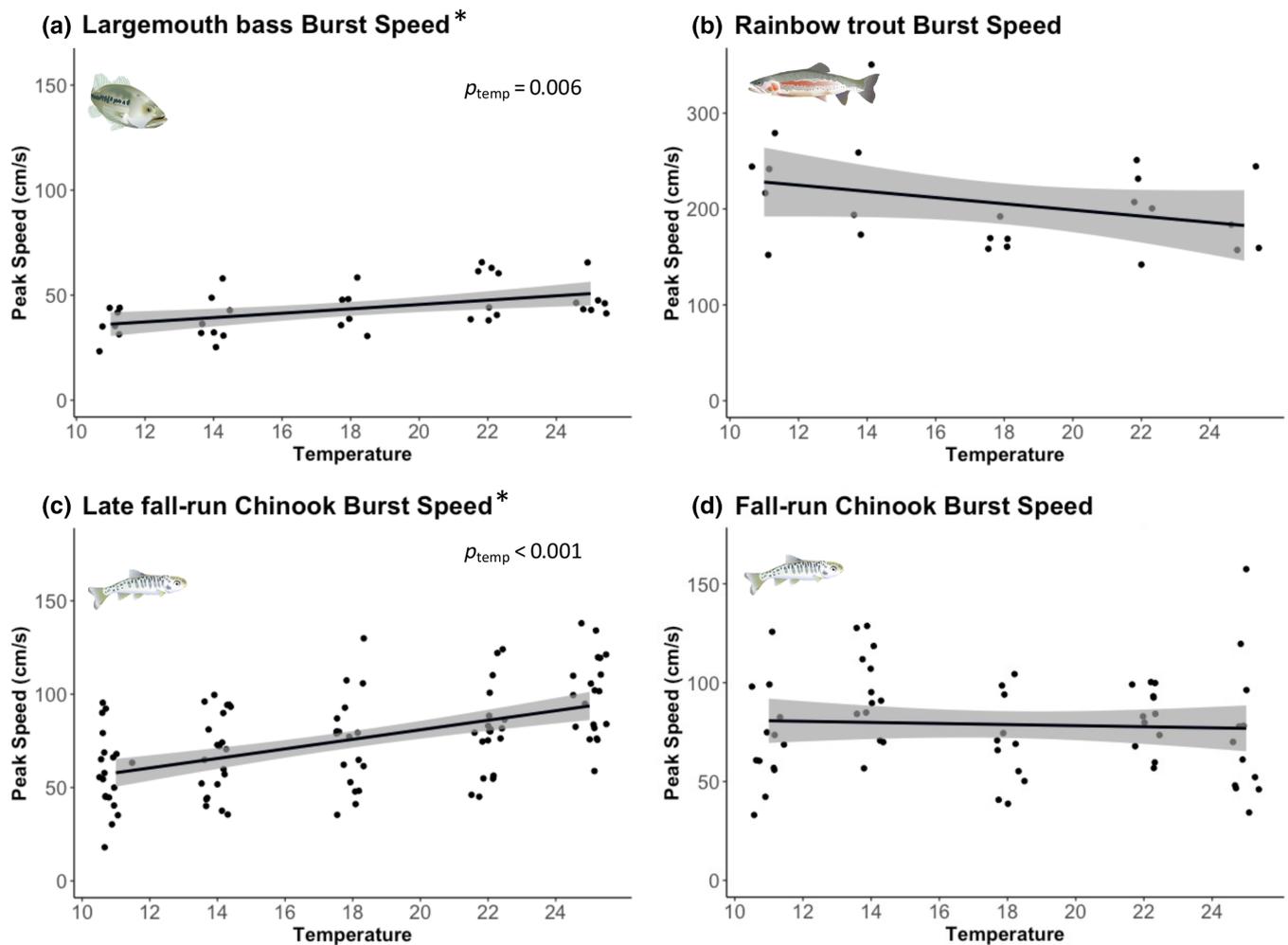
## Predation trials

We measured the number of juvenile Chinook salmon that were eaten in a total of 115 predation trials. There was a positive correlation between number of salmon eaten and temperature for largemouth bass ( $p = 0.015$ ), which were tested with LFR Chinook salmon. Thus, a larger number of salmon were consumed at the upper end of our tested water temperature range (22–25°C) than the lower (11–14°C). However, most largemouth bass consumed relatively few salmon (mean: 1.83; range: 0–12). There was no effect of predator mass or juvenile Chinook salmon mass in this model (Appendix S2: Table S10; Figure 5a).

For our other two predators (rainbow trout and striped bass), we observed no significant predation response to temperature. Both were tested with FR juvenile Chinook salmon. For striped bass, we found a significant negative correlation between the number of salmon eaten and average salmon mass per tank (Appendix S2: Table S11; Figure 5b). The average number of salmon consumed per

trial was also higher than with largemouth bass (mean: 2.49; range: 0–10). None of our predictors were significant in explaining variation in rainbow trout predation (Appendix S2: Table S12; Figure 5c), which may be due in part to the large number of trials in which rainbow trout failed to consume any salmon (mean: 0.38; range: 0–5). Of 40 rainbow trout tested, only 8 ate at least one salmon, in contrast to 19 of 30 largemouth bass and 26 of 35 striped bass. Of these, 12 largemouth bass and 18 striped bass consumed multiple salmon, compared with just 3 rainbow trout.

We also analyzed how the mean difference in relative performance between predator and prey affected the outcome of predator–prey interactions. To do so, we compared the physiological performance of each predator–prey pairing in our study for which we had sufficient data. There was no effect in performance difference for any of our physiological performance traits (i.e., AS, burst number, and burst speed) on the predation trials with rainbow trout and FR Chinook salmon. For our largemouth bass and LFR Chinook salmon



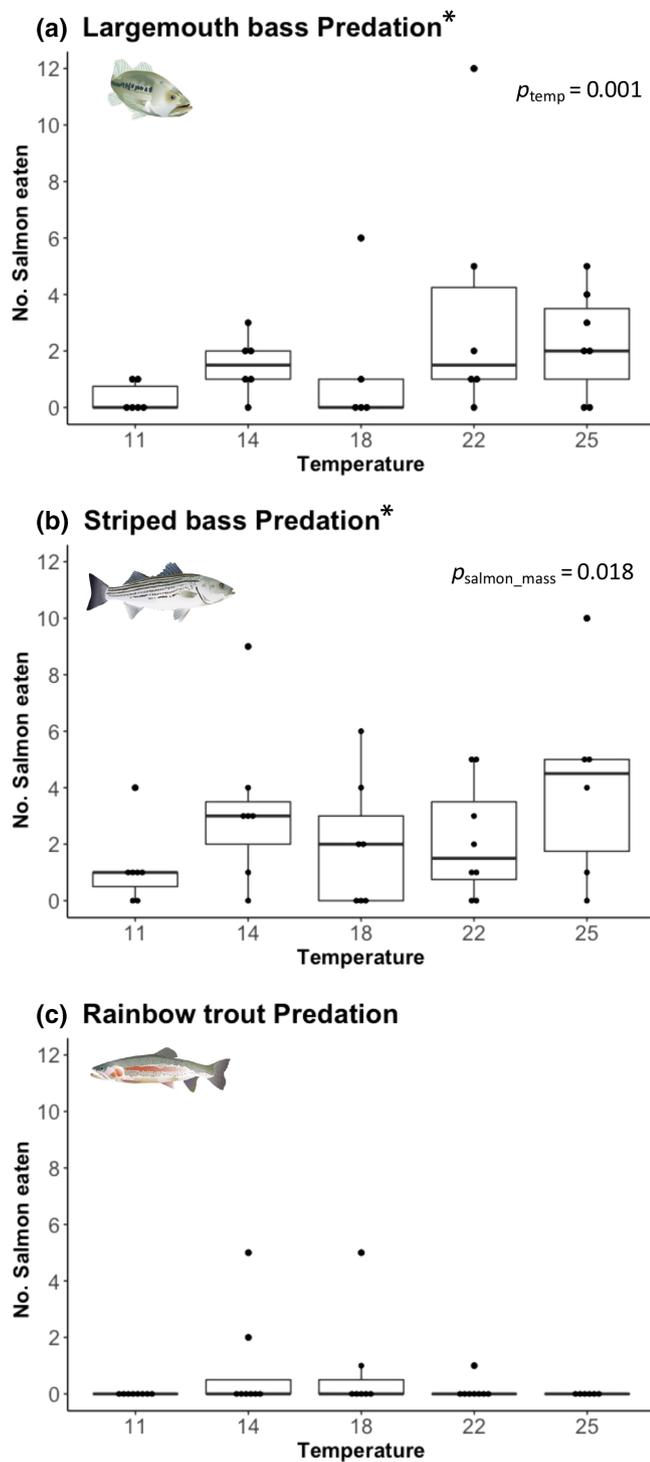
**FIGURE 4** Maximum burst speed exhibited as a function of water temperature (in degrees Celsius) for (a) largemouth bass, (b) rainbow trout, (c) late fall-run Chinook salmon, and (d) fall-run Chinook salmon. Asterisk indicates a statistically significant relationship, with the  $p$  value of significant predictors reported on the graph (see details of models in text).

trials, the performance difference in burst number was negatively correlated with the outcome of predation trials (Appendix S2: Table S13;  $p = 0.010$ ). In other words, this indicates that relative increases in bass burst number, compared with those of salmon, were correlated with a larger number of salmon consumed. The other predictors (relative AS and relative burst speed) were not significant in their respective models.

## DISCUSSION

The integration of physiology, behavior, and ecology is becoming increasingly important as we forecast the effects of climate change on fisheries and ecosystems (Horodysky et al., 2015). While warming water temperatures will undoubtedly impact organisms via their fundamental thermal physiology, the resulting change on extrinsic ecological dynamics, like predator–prey interactions, remains

understudied. Yet predator–prey interactions depend on underlying physiological mechanisms, which are likely to be affected by the thermal environment for ectothermic fishes (Grigaltchik et al., 2012). Because species can respond differently to similar temperature changes, disproportionate changes in predator or prey physiological performance can alter predation or evasion success, respectively (Grigaltchik et al., 2012). In the Delta, current research on juvenile salmon already suggests that there may be a positive correlation between predation rate and temperature (Johnson et al., 2017; Nobriga et al., 2021). We aimed to determine whether this trend is due to an advantage conferred by the fundamental physiologies of predators versus prey. However, identifying a physiological advantage was challenging and highly dependent on the metric examined. Among our predators, largemouth bass performed best physiologically at the warmest test temperatures, which also corresponded to the highest predation rates. Our results were less conclusive for rainbow trout.



**FIGURE 5** Number of salmon eaten as a function of water temperature (in degrees Celsius) during predation trials conducted during 2020 and 2021. Results are shown for (a) largemouth bass, which were tested with late fall-run Chinook salmon, (b) striped bass, and (c) rainbow trout, both of which were tested with fall-run Chinook salmon. Asterisk indicates a statistically significant relationship, with the  $p$  value of significant predictors reported on the graph (see details of models in text).

Though they showed a response to temperature in AS, these predators were thermally robust in burst ability and generally less predacious. Similarly, there were differences between populations of salmon. LFR Chinook showed no effect of temperature on AS, but a potential trade-off between burst speed and number of bursts with temperature. Alternatively, FR Chinook showed a significant positive effect of temperature on AS, but were thermally robust in their burst abilities. It is challenging to discern the drivers of these differences; for example, whether they emerged due to the hatchery environment or innate characteristics of each run. Regardless, our results suggest that the mechanistic factors underlying temperature-dependent predation rates could vary even among populations of the same species.

Salmonids are thought to require cooler waters to survive and grow ( $<16^{\circ}\text{C}$ ; Marine & Cech, 2004; Yates et al., 2008), and they are often managed accordingly (US Environmental Protection Agency, 2003). Consequently, it is hypothesized that a lack of thermal tolerance by juvenile Chinook salmon is among the potential factors that limit juvenile salmon production at warm temperatures in the Delta. However, our results join an increasing body of evidence (e.g., Poletto et al., 2017; Zillig et al., 2021) suggesting that the fundamental thermal physiology of salmonids is not the major force driving this trend. While we observed variation between FR and LFR Chinook depending on the performance metric examined, salmon physiological response was often thermally robust. We instead found support for field-based hypotheses (Nobriga et al., 2021) that survivorship in the Delta depends on a physiological advantage obtained by predators in warming waters. This was most evident in largemouth bass, for which AS, burst number, and burst speed significantly increased with temperature. This species also consumed significantly more salmon at our two highest temperatures (22 and  $25^{\circ}\text{C}$ ), and our results were consistent with previous work indicating a positive relationship between temperature and food intake in this species (Lemons & Crawshaw, 1985). Similarly, while we were unable to obtain physiological data for striped bass, previous studies suggest that they possess a higher AS near  $20^{\circ}\text{C}$  (Lapointe et al., 2014), and we observed predation more frequently at all but our lowest temperature ( $<14^{\circ}\text{C}$ ). By contrast, the response to increased acute temperature exposure differed for the rainbow trout. These predators generally tolerated a wide variety of temperatures, which has also been observed in previous research (Chen et al., 2015; Verhille et al., 2016). Only their AS was significantly affected by temperature and highest at around  $18^{\circ}\text{C}$ , which also corresponded to

the middle range of temperatures where they most frequently consumed salmon (Figure 5c). While a physiological advantage was difficult to determine for this species, our results do match our prediction that they are physiologically similar to the other salmonids in this study based on their broad thermal tolerance.

Taken together, our results suggest that the fundamental physiology of predators can often provide valuable insight into where predation may occur. Largemouth bass are structure-oriented, non-native ambush predators (Michel et al., 2018), and our analyses indicate that their physiology is well-adapted to exploit prey items at warmer temperatures that occur in the Delta's nearshore habitats and later during the salmon outmigration season. Striped bass are also more physiologically suited to warmer waters (Lapointe et al., 2014), but their ability to consume salmon across trial temperatures suggests that they can contribute to smolt predation in all but the coldest pelagic habitats where they are found. Largemouth and striped bass are two of the most impactful piscivorous predators of salmon in the Delta (Michel et al., 2018; Nobriga et al., 2021), and their physiological and ecological performance at warmer temperatures warrants concern for juvenile salmon survival in a changing climate.

Conversely, rainbow trout are unlikely to be a major threat to salmon in the Delta at any temperature. Unfortunately, it remains unclear whether this can be attributed to similarities between the thermal physiologies of predators and prey, which might reduce any discernable advantage for either species. Rainbow trout demonstrated a reluctance to consume salmon during predation trials, despite their voraciousness for live feed (including salmon) in the holding tank. The lack of predation in our trials may be more reflective of their ecological role in the wild, where they typically feed on invertebrates (Elliott, 1973; Tippets & Moyle, 1978; C. Michel, personal communication, 2019). In the Delta specifically, it is often suggested that rainbow trout predation is limited, although quantification is difficult and may be underestimated. Rainbow trout do consume salmon fry in other systems (Beauchamp, 1995; Ginetz & Larkin, 1976), including Central Valley rivers (Merz, 2002), and in the laboratory (Mazur & Beauchamp, 2003). Consequently, there may also have been an effect of our study design preventing them from doing so in our experiments. For example, rainbow trout may have responded more strongly than the other predators to handling or acute temperature exposure, and this would not have been accounted for in our consistent methodologies for each tested species.

While we were able to establish conclusions about predation based on general physiological response to temperature, a key challenge we encountered was

determining which, if any, physiological performance trait best predicted trophic interactions. The degree to which thermal response differs between traits could affect the use of species-specific fundamental thermal physiology as a tool for predicting ecological outcomes. Of our performance traits, we found one that showed a similar relationship to temperature as the outcome of predation trials for both predators and prey: number of repeated bursts. This was further supported when we calculated the relative difference in performance between largemouth bass and LFR Chinook salmon; an increase in relative largemouth bass ability to repeat burst corresponded with an increase in number of salmon consumed. Though it is hypothesized to have a substantial influence on the outcome of predator-prey interactions (Domenici & Blake, 1997; Taylor & McPhail, 1985; Webb, 1986), burst swimming has not been integrated as a routine measurement in physiological research, and there are not yet common protocols across studies. For determining fundamental thermal physiology, there has been a widespread focus on AS, which is thought to define the capacities of an organism to undergo fitness-enhancing activities. However, AS did not appear to correlate with predation trial outcomes based on our results, which may be due to a behavioral trade-off. Whereas aerobic capacity is useful for steady (continuous) swimming (Blake, 1983), fast-starts (<1 s) or bursts (<20 s) are often used by predators when attacking prey, or prey when evading predators (Domenici & Blake, 1997). Furthermore, attack or evasion speed may not be the most critical component of a successful capture (Domenici & Blake, 1997). Webb (1986) found that prey speed was submaximal in response to predator attacks that were not followed by a chase. This suggests that the ability to undertake repeated bursts in pursuit of prey (or during escape from a predator) is likely more deterministic in a predator-prey encounter than burst speed.

It is difficult to disentangle the mechanisms underpinning the predation trial outcomes; specifically, whether predation at a given temperature emerged due to increased vulnerability of salmon, or a disproportionate increase in performance by predators. Existing studies indicate that it may be a combination. For example, Higham et al. (2006) found that largemouth bass maximize fluid speeds while suction feeding by increasing their swimming speeds, thus reducing chances of prey escape. Based on our results, this could suggest that the higher speeds and higher number of bursts at warmer temperatures by largemouth bass, coupled with a reduction in the number of bursts by LFR Chinook salmon, led to increased salmon consumption in warmer waters during the predation trials. Consequently, it is probable that the ecological outcomes depend in large part on the advantage obtained via burst abilities at a

given temperature. If this is the case, the outcomes of predator–prey situations, such as in the predation trials, will likely vary by salmon population examined given their differential burst capacity. For instance, because FR Chinook salmon were more thermally robust in both burst metrics, we may have observed fewer of them consumed if they, rather than the LFR individuals, had been combined with largemouth bass in the predation trials. In general, and as proposed in previous work (Poletto et al., 2017; Verhille et al., 2015, 2016), our study challenges the use of a single physiological trait for determining the fundamental thermal physiology of a species and predicting ecological outcomes. We recommend future physiological studies expand beyond traditional measurements and explore other physiological variables that may have more predictive power for ecosystem interactions. Some that may be potentially meaningful, but were beyond the scope of our study, include mean burst distance and acceleration capacity, and repeatability of burst performance over larger timescales and between individuals.

Given the degree to which response to temperature varied by performance trait within and between species, our conclusions should be considered in the context of our experimental design. Perhaps most importantly, while many of our results are also supported by field-based research, we conducted this study in the laboratory using primarily hatchery-raised fishes (except for striped bass) and extrapolating beyond these conditions should be done with caution. For example, although we ensured that all predators were consuming live feed in the weeks prior to the predation trials, the behaviors exhibited by captive largemouth bass may differ from those of their wild counterparts. They also may not be directly comparable to those of the wild-caught striped bass in our study. Similarly, the juvenile salmon were reared in captivity and not exposed to predators prior to the predation trials to avoid habituation. It is possible that prey naïveté (Cox & Lima, 2006; Michel et al., 2018; Sih et al., 2010) impacted the outcomes of these trials by shaping juvenile salmon behavior. Yet for juvenile salmon in the Delta, it is worth noting that many are hatchery-raised; Barnett-Johnson et al. (2007) estimate that over 80% of Sacramento and San Joaquin salmon taken from ocean fisheries are of hatchery origin. These juvenile salmon also encounter more non-native than native predator species (Michel et al., 2018), including largemouth and striped bass, to which they may not yet have evolved to respond appropriately (see Kuehne & Olden, 2012). Future studies should examine the impact of prey naïveté on predation of outmigrating juvenile salmon, but our decision to choose potentially naive prey in this study is reflective of the composition of fish communities in this system.

From a physiological standpoint, an additional consideration is that we chose to acclimate all our study fishes at the same temperature (18°C) before acutely exposing them to their test temperatures for each trial. This falls in the range of temperatures where optimal growth for juvenile salmon has been observed in laboratory studies (i.e., Cech & Myrick, 1999; Marine & Cech, 2004). Previous research has found that exposure temperature, rather than duration of thermal exposure (acute vs. acclimation), influences swimming performance (Kirby et al., 2020; Poletto et al., 2017). However, we cannot exclude the possibility that this acclimation temperature influenced our results, particularly as temperature is known to affect acute thermal tolerance and growth rate (Zillig et al., 2020). Similarly, Zillig et al. (2020) has also shown that growth and thermal tolerance vary by population in response to the same increases in temperature, which we also observed in our study. Such variation appears strongest in the juvenile life stage (Pörtner & Farrell, 2008; Zillig et al., 2021). Simultaneously, predator assemblages and activity also differ among watersheds, thus producing varying effects on salmonid ecological thermal physiologies (Zillig et al., 2021). Future work is therefore required to examine fundamental and ecological thermal physiology of salmon runs from other watersheds. Finally, we conducted our predation trials with a single predator per tank to remove any conspecific cues. However, in the wild, predation behavior is also influenced by intraspecific dynamics, such as competition. While it is unclear the degree to which rainbow trout predate on juvenile salmon, previous studies on hatchery-raised salmonids (Fenderson et al., 1968) suggest that the lack of competition or social cues may also explain the differences in rainbow trout feeding behavior during the predation trials versus in the holding tanks, which is related to the captive environment in which the trout were raised. Understanding such intraspecific dynamics, and how they interact with environmental factors like temperature, requires further study to improve our ability to assess predation.

We also controlled for other potentially interactive effects that would be present in a non-captive environment. For instance, existing work by Nobriga et al. (2021) suggests that habitat may influence the relative impact of predators with different behavioral strategies. Relevant to our study, largemouth bass, an ambush predator, rely on camouflage from surrounding vegetation during predator–prey interactions, whereas more pelagic striped bass tend to consume prey in open water. Given the lack of available shelter in the tanks, our predation trials may have been better suited to the natural behaviors of the latter predator. This design may have simultaneously increased vulnerability of salmon to predation, as we provided no cover to use as refuge from predators. Furthermore, both bottom roughness (Michel

et al., 2020) and river inflows (Nobriga et al., 2021) are known to influence predation in the Delta, and how these variables interact with temperature is the focus of ongoing research. Other factors pertaining to fish fitness, such as differential susceptibilities to disease, were also not considered in this study but certainly influence the outcome of predator–prey interactions in the wild. We cannot predict how salmon or predators would have responded if we had not controlled for such factors, and future studies should consider their additive effects on ecosystem dynamics.

## CONCLUSION

The Delta is an ecosystem that has already been dramatically altered and faces further threat at the forefront of environmental change. Increasing water temperatures and predation by non-native piscivorous predators directly correlate to low survival of outmigrating juveniles, which is a major contributor to the decline of salmon runs in this region (Buchanan et al., 2013; Michel et al., 2015, 2020; Perry et al., 2010). Yet, prior to this study, there remained a gap in our knowledge of the physiological mechanisms of this mortality. Our results suggest that fundamental thermal physiologies of predators and prey play a role in shaping predator–prey outcomes. Further, our results suggest that care should be taken in using lab-based performance traits to predict ecological outcomes based on species-specific fundamental thermal physiology. Ideally, the relative advantage in physiological performance between predators and prey should also be considered. Furthermore, given the consistency with which burst ability specifically predicted the outcome of predation trials, we recommend future physiological studies expand their focus to the mechanisms underlying such ecologically relevant behaviors (e.g., see Lehman et al., 2017). With the continuing miniaturization of tools such as accelerometers, these metrics can also be examined in the field, offering more realistic insight into how fishes are going to respond to future temperature change. From a management perspective, our results suggest that the relationship between temperature and predation is complex and should be considered in conjunction with other potential factors influencing predator population dynamics. Along with other studies (i.e., Marras et al., 2015), we found support for the prediction that non-native species such as largemouth bass will experience increasing success in the Delta because their thermal window of physiological performance is shifted toward warmer temperatures, as opposed to that of native salmonids. In addition, because temperature can affect fish distribution in response to thermal preferences

(Callihan et al., 2014; Díaz et al., 2007; Michel et al., 2020), we have shown that combining physiological and ecological approaches can yield useful insight into where predation hotspots may be occurring based on our understanding of predator and prey physiology. Such predictions can produce actionable results; for example, managers could hypothetically improve the survival of juvenile salmonids by adjusting the magnitude of river flow entering the Delta, which affects water temperature along primary outmigration routes (Michel et al., 2020; Nobriga et al., 2021). Finally, it has been suggested that salmon in the Delta are at the southern range of the species distribution and may serve as indicator populations for how warming can affect predator–prey interactions (Nobriga et al., 2021; Zillig et al., 2021). However, as we have shown, both fundamental physiology and temperature-driven ecological outcomes are trait-, species- and population-specific. We conclude by advocating for more studies linking temperature, physiology, and ecosystem dynamics in other systems, incorporating novel approaches to understand both fundamental and ecological physiologies across a wide variety of species.

## AUTHOR CONTRIBUTIONS

Alexandra G. McInturf, Ken W. Zillig, Nann A. Fangue, and Cyril J. Michel contributed to the conception of the study. Alexandra G. McInturf secured funding, collected data, wrote the manuscript, and performed statistical analyses. Ken W. Zillig assisted in collecting data and writing the manuscript. Katherine Cook, Jacqueline Fukumoto, Anna Jones, and Emily Patterson also assisted in data collection and cleaning. Dennis E. Cocherell helped organize data collection and experimental setup and advised on husbandry practices. Cyril J. Michel reviewed the manuscript and statistics. Damien Caillaud supervised statistical analyses and reviewed the manuscript. Nann A. Fangue supervised data collection and statistical analysis and assisted in writing and reviewing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## ACKNOWLEDGMENTS

The authors would like to thank the researchers who volunteered their time to assist in data collection: Sarah Baird, Anna Steel, Kirsten Sheehy, Amelia Munson, Lea Pollack, Scott Burman, and Aviva Blonder. Sarah Baird was also invaluable in providing guidance on fish husbandry and data collection protocols and helped review the methods section of the manuscript. David Ayers offered guidance in contextualizing the results of the study, and Amelia Munson provided the fish illustrations for our figures. We also thank the managers of CABA (Linda Deanovic and Matt Stone) for facilitating this study

throughout its duration. Finally, thank you to Heidi Dewar, Evan Batzer, Matt Nobriga, Steve Lindley, and two anonymous reviewers for their thoughtful comments on the manuscript.

## FUNDING INFORMATION

Alexandra G. McInturf acknowledges funding from California Sea Grant's Delta Science Fellowship (grant number 19054). Nann A. Fangue would like to acknowledge funding from the University of California, Davis Agricultural Experiment Station (grant number 2098-H). Jacqueline Fukumoto was supported by the Lloyd Swift Fellowship, granted through the Wildlife, Fish and Conservation Biology Department at the University of California, Davis.

## CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (McInturf et al., 2022) are available from Zenodo: <https://doi.org/10.5281/zenodo.6545470>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** McInturf, Alexandra G., Ken W. Zillig, Katherine Cook, Jacqueline Fukumoto, Anna Jones, Emily Patterson, Dennis E. Cocherell, Cyril J. Michel, Damien Caillaud, and Nann A. Fangue. 2022. "In Hot Water? Assessing the Link between Fundamental Thermal Physiology and Predation of Juvenile Chinook Salmon." *Ecosphere* e4264. <https://doi.org/10.1002/ecs2.4264>