CWB Review of Literature regarding Thermal Tolerances of California Salmonids

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Variation in Thermal Eco-physiology among California Salmonids: Implications for Management

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SCOPE AND PURPOSE

California salmonids are under increasing environmental strain. Drought, climate change, and anthropogenic need for increasingly limited water resources have pushed many salmonid species into a precarious position (Moyle et al. 2008; Quinones & Moyle 2014). Moyle et al. (2017) found that nearly 75% of all salmonids in California will likely be extinct within the next 100 years if present trends continue. Similarly, Moyle et al. (2013) found that fish requiring cool water in California were particularly vulnerable to climate change and future extinction. These papers highlight a major limiting factor on the future persistence of salmonids in California: increasing water temperature.

Current thermal criteria for salmonid management in California is governed by a disparate set of water quality standards and temperature requirements implemented differently across regional boards. The water quality objective applied in most regional boards for the protection of fisheries is to constrain increases in water temperature to no more than a 5 °F (2.8 °C) increase above the "natural receiving water temperature". However, a lack of a readily available historical data and agreed upon procedure for calculating "natural receiving water temperature" has made this criterion difficult to implement[1]. The United States Environmental Protection Agency (USEPA) – Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards (Region 10) is the most thorough body of work that exists to-date examining appropriate temperature thresholds for salmonids. They were designed as a guidance tool for streamlining the establishment of temperature criteria in Oregon, Washington, Idaho, and Alaska (U.S. Environmental Protection Agency 2003). Within EPA Region 9, notably the state of California, the Region 10 guidelines have been used to assess water quality conditions for salmonids. Additionally, some of the Region 10 guidelines, have been implemented by NMFS in some portions of their Biological Opinions (National Marine Fisheries Service 2009, 2016) and they are often recommended by the California Department of Fish and Wildlife for streams with salmonid habitat. However, they have not wholesale been adopted in California and the suitability of the Region 10 guidelines to California systems, and specifically Central Valley salmonid populations, is currently debated.

California represents the southernmost range extent for nearly all the native salmonid species. Historic and current environmental conditions (e.g. climate, temperature, urbanization) in California's Central Valley are considerably different (e.g. greater stochasticity, temperature, levels of urbanization) than those in the Pacific Northwest, EPA Region 10 area. California salmonid populations may have developed traits and behaviors adapted to California-specific conditions, primarily temperature regimes, and these conditions may be different, rare or absent across other parts of the native species range. To that end, California salmonids may exhibit a range of temperature-dependent performance traits (e.g. differences in recruitment, disease vulnerability, swimming performance) closely matched to the environmental selection pressures experienced at local or regional scales and differing from salmonid populations farther north. For

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[1] There are some specific numeric temperature water quality objectives in certain Basin Plans applied in addition to this narrative objective in some locations (e.g. instantaneous temperatures between 55 and 70F along the Sacramento River – cite to RB5 plan) however the majority of salmon bearing rivers and streams only have the narrative water quality objective.

example, Verhille et al. (2016) found that Tuolumne River *Oncorhynchus mykiss* populations can maintain 95% of maximum aerobic output at 24.6 °C, greater than other previously studied *O. mykiss* populations (see Fry 1948; Chen et al. 2015). The potential for local adaption, and therefore interpopulation variation, of salmonids may complicate application of the Region 10 guidance criteria to California populations.

Due to increasing global temperatures and anthropogenic environmental change, climatic extremes, such as the drought conditions spanning 2012 – 2016, are anticipated to continue, if not increase in magnitude and frequency (Tansey et al. 2014). Therefore, a review of the literature specific to California salmonid thermal performance is necessary in order to implement management guidelines that will aid in salmonid protection and recovery. It is the purpose of this review to summarize research pertaining to the thermal eco-physiology of California salmonid species, focusing on data from California populations but including other west-coast populations when data specific to California are sparse. This review will synthesize the literature to address the questions below and provide insight on potential methodologies and thermal indices necessary to protect these iconic fishes in an era of rapid climatic change.

- Will the existing Region 10 guidelines offer protection to Central Valley salmonids?
- Which physiological and ecological metrics or indices are of value to promote the effective and sustainable management of salmonids with respect to water temperature?
- Is there enough information available to set temperature criteria for California salmonids? If not, what is required?

OUTLINE

- Introduction
    - EPA Region 10 Guidance
    - California's Central Valley
    - Life History Diversity in the Central Valley
- Life Stages, Development, and Thermal Constraints
    - Egg Development
    - Egg-Fry Development
    - Juveniles
    - Smoltification
    - Adults
- Thermal Ecology of Salmonids
    - Quantifying River Temperature and Temperature Metrics
    - Acclimation and Adaptation
    - Watershed Variation
    - Growth and Metabolism
    - Biotic Interactions and water temperature
        - Predation
        - Competition
        - Disease
        - Ecotoxicology
- Recommendations and Conclusions
    - Recommendations
    - A Caution on Singular Approaches: Laboratory versus Field Studies

    - Management Metric
    - Region 10 Application
    - Accounting for Thermal Ecology
- Appendix

INTRODUCTION

In 2001, Myrick and Cech produced a thorough review of the thermal tolerances of Central Valley populations of Chinook salmon and steelhead trout. Since this time, the literature on salmonid thermal tolerance has continued to evolve, and critical advances in our understanding of the variety of ecological and physiological factors that influence thermal performance among populations and between species have emerged. It is the purpose of this review to summarize the body of work surrounding thermal physiology and ecology of salmonids in California with emphasis on the literature and synthetic interpretations since 2001.

As ectotherms, fish are strongly influenced by temperature. Environmental temperature establishes physiological rate processes (e.g. the speed of metabolism) and influences ecological interactions on scales ranging from local to regional. Therefore, understanding the mechanisms underlying thermal performance and capacity is crucial to predicting species responses particularly in the era of climate change (See Appendix: Biological Scales).

Aspects of fish thermal physiology are acted upon by natural selection as any other trait. Across taxa, thermal physiology has been shown to reflect ecological differences. Work on brook trout (*Salvelinus fontinalis*; Stitt et al. 2014) and sockeye salmon (*O. nerka*; Eliason et al. 2011, Chen et al. 2013) have demonstrated that a fish population's thermal physiology closely reflects the environmental conditions under which it evolved. Fangue et al. (2006) and Stitt et al. (2013) demonstrated that interpopulation variation in thermal tolerance is aligned along a latitudinal gradient with low latitude populations showing thermal performance at higher temperatures than populations at higher latitudes. Sauter et al. (2001) found differences in thermoregulatory behavior between two seasonal runs of Chinook salmon. In an era of climatic change and associated shifts in species distributions, understanding the influence of biogeography on the capacity for thermal performance as well as adaption are essential for effective conservation and management.

Salmonids are a good case-study for elucidating the various ways temperature structures biological interactions across spatial and temporal scales. Native to the northern latitudes and considered to be cool water species, salmonids consist of both anadromous and freshwater-resident species, many of which have adopted life-history strategies which include long migrations to suitable habitat for spawning and rearing. In an era of increasing global temperatures, salmonids are suffering significant population declines (Moyle et al. 2017) with water temperature as a primary factor influencing current trends. In California and elsewhere, rising temperatures compounded with habitat-loss and habitat modification, and genetic introgression with domesticated strains, are leading to widespread losses in abundance and diversity (Van Doornik et al. 2013; Muhlfeld et al. 2014; Moyle et al. 2017).

EPA Region 10 Guidance

The Region 10 temperature guidance was drafted by the Region 10 USEPA office which includes the states of Alaska, Washington, Idaho and Oregon. The Region 10 document was designed to provide temperature guidance thresholds for the conservation of native salmonid populations (U.S. Environmental Protection Agency 2003). The Region 10 guidance was developed with the best available science at the time, largely focusing on research derived from USEPA Region 10 salmonid populations, though a handful of California-based studies were also included.

In the absence of California-specific temperature guidance, Region 10 Guidance was recommended for use in California. Where applied, the Region 10 guidance provides a suite of temperature thresholds for environmental managers to ensure that water bodies do not exceed temperatures harmful to salmonids (Table 1). Some of these metrics have been incorporated into Biological Opinions governing the operation of California dams. If implemented, Region 10 guidelines, may be employed in California during summer months when river temperatures are generally highest in order to prevent loss during migration and rearing (U.S. Environmental Protection Agency 2003). When river temperatures exceed specific temperature thresholds, dam operators may be instructed to release cooler water from reservoirs to reduce river temperatures in order to protect specific populations.

Current water quality objectives for the management of state water temperature stipulates that water discharge must not increase ambient temperature more than 5°F (2.78 °C) above natural receiving water temperatures. This regulation would likely be protective, however precise knowledge of what constitutes “natural receiving water temperature” is difficult, if not impossible, to define due to the lack of tributary specific historical data. Due to large scale climatic shifts achievable water temperatures are generally increasing through time in California (Cayan et al. 2006). Projected temperatures are expected to increase between 1.7 °C and 5.8 °C over the next century and California streams have been modeled to increase 0.8 °C for each 1 °C of increase in the air temperature (Cayan et al. 2006; Null et al. 2013). The warming of water temperature is also exacerbated during relative periods of low flow (Chang & Bonnette 2016) as experienced in the 2012-2016 California drought. Furthermore, climatic conditions that cause drought conditions (low precipitation, high temperatures) are very likely to occur in the next century (Diffenbaugh et al. 2015). In summary, shifts in ‘natural receiving water temperature’ of waterbodies further complicates the baseline upon which current management guidelines operate. Therefore, updating California’s thermal management regulations may be warranted.

The management framework of the Region 10 guidance criteria recommends river temperatures for all salmonids irrespective of species, or seasonal run[2]. However, there is growing evidence to suggest that different species of salmonids vary in their temperature tolerances (Cech & Myrick 1999; Myrick & Cech 2001; Richter & Kolmes 2005; Verhille et al. 2016) as do different populations of the same species (Sauter et al. 2001; Eliason et al. 2011; Chen et al. 2013; Stitt et al. 2013). In California’s Central Valley there are typically overlapping life stages, species and runs present most months of the year (see California’s Central Valley below) and any temperature threshold must protect the most sensitive species and/or life stage present at any given time. Region 10 guidance thresholds are given as a maximum 7-day average of daily

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[2] Exceptions include temperatures specific to bull trout (*Salvelinus confluentes*) and a single temperature specific for steelhead smoltification. Bull trout are extirpated from California.

maximums (7DADM). An easily applied metric that may lack important biological relevance, see Management Metric below for deeper discussion.

Table 1: Region 10 Guidance Criteria for Salmon and Trout

Salmonid Uses During the Summer Maximum Conditions	Criteria
Bull Trout Juvenile Rearing	12°C (55°F) 7DADM
Salmon/Trout "Core" Juvenile Rearing *(Salmon adult holding prior to spawning, and adult and sub-adult bull trout foraging and migration may also be included in this use category)*	16°C (61°F) 7DADM
Salmon/Trout Migration plus Non-Core Juvenile Rearing	18°C (64°C) 7DADM
Salmon Trout Migration	20°C (68°F) 7DADM. Plus a provision to protect and, where feasible, restore the natural thermal regime
Salmonid Uses	**Criteria**
Bull Trout Spawning	9°C (48°F) 7DADM
Salmon/Trout Spawning, Egg Incubation, and Fry Emergence	13°C (55°F) 7DADM
Steelhead Smoltification	14°C (57°F) 7DADM

Modified from U.S. Environmental Protection Agency (2003). 1) "7DADM" refers to the Maximum 7 Day Average of the Daily Maximums; 2) "Salmon" refers to Chinook, Coho, sockeye, pink and chum salmon; 3) "Trout" refers to steelhead and coastal cutthroat trout

California's Central Valley

The Central Valley of California is currently home to two native species of anadromous salmonids, Chinook salmon (*O. tshawytscha*) and Steelhead trout (*O. mykiss*). Within Chinook salmon, the Central Valley, hosts four seasonal runs: fall, late-fall, winter and spring. Winter-run Chinook are endemic to California. *O. mykiss* exists within the Central Valley in both resident (rainbow trout) and anadromous (steelhead) forms. These different species and runs differ in migration timing as well as duration of freshwater residency (Moyle et al. 2017). They also show differences in some aspects of thermal capacity (more detail below).

Threats to Chinook salmon and steelhead trout within the Central Valley are multifaceted. Global climatic change has altered precipitation patterns and increased surface temperatures (Moyle et al. 2017). Anthropogenic modifications to the Sacramento-San Joaquin watershed have restricted habitat access, altered flow patterns, channelized riparian zones and negatively affected water quality through increasing temperatures and environmental toxins (Moyle et al. 2017). Finally, most fall-run Chinook salmon populations within the Central Valley are genetically homogenized due to hatchery strays (Johnson et al. 2012). This loss of genetic diversity has reduced population resilience and adaptive potential (Williamson & May 2005). Likewise, Central Valley steelhead show reduced genetic diversity due to hatchery reared strays (Pearse & Garza 2015; Moyle et al. 2017).

Life History Diversity in the Central Valley

Within seasonal runs, salmonids also exhibit variation in life-history. Juveniles may spend different amounts of time rearing in freshwater prior to out-migration, or at sea prior to adult freshwater emigration. For instance, Hodge et al. (2016) revealed that *O. mykiss* exhibited 38 different life-history strategies within the Klamath River basin alone (see also, Shapovalov & Taft 1954). Despite these findings, there has been little research investigating potential differences in temperature sensitivity between geographically and temporally sympatric salmonids that exhibit different life-history strategies.

Chinook salmon exist as multiple seasonal-runs (Figure 1) constituting a diversity of migration phenology (Nehlsen et al. 1991). Fall-run Chinook salmon migrate into fresh water through the fall season and spawn upon arrival at natal habitat. Winter-run Chinook salmon begin migration during the winter months and arrive at their spawning grounds in late spring and spawn in early summer (May-June). Egg incubation and juvenile emergence takes place throughout the summer. Finally, spring-run Chinook salmon begin their migration in late March, over-summer as adults, and spawn during fall. When considering application of Region 10 guidelines to California, it is important to note that those guidelines were primarily derived from data on fall-run Chinook (but also spring-run Chinook to a lesser extent). Considering the diversity of life history strategies in the Central Valley, management guidelines in California populations should strongly consider differences in run timing and the potential for adaptation to different thermal regimes.

Steelhead also exhibit variation in migration phenology. In the Central Valley, adult steelhead trout migrate during winter and spawn between February and April. However, in the Klamath River basin and other Northern California coastal rivers, two seasonal runs of steelhead (winter and summer) are present. Summer steelhead, which are of greater conservation concern (Moyle et al. 2017), migrate through spring, maturing over summer in cold, deep reaches at high elevations and spawn during winter (Klamath Mountains Province ESU: January through March, Northern California ESU: December through February). Winter steelhead enter freshwater with their gonads fully mature, allowing them to reproduce quickly. Winter steelhead migrate to freshwater from November to April and reproduce shortly after arriving to respective spawning grounds. Differences in run timing (early vs. late) in both steelhead trout and Chinook salmon have been shown to be the result of genetic mutations, believed to have occurred once in each species, and disseminated by positive selection of straying individuals (Prince et al. 2017).

This variety of migration phenology ensures adult salmonids experience a range of temperature conditions contingent on their time and place in California river systems. Comparative work revealing differences in temperature sensitivity among different salmon or steelhead runs is not well studied in California, so specific differences and associated mechanisms in thermal capacity between runs currently remain unknown. Based on the current literature, however, characterization and consideration of population-specific thermal performance is needed to support or refute the utility of Region 10 guidance for California salmonids moving forward.

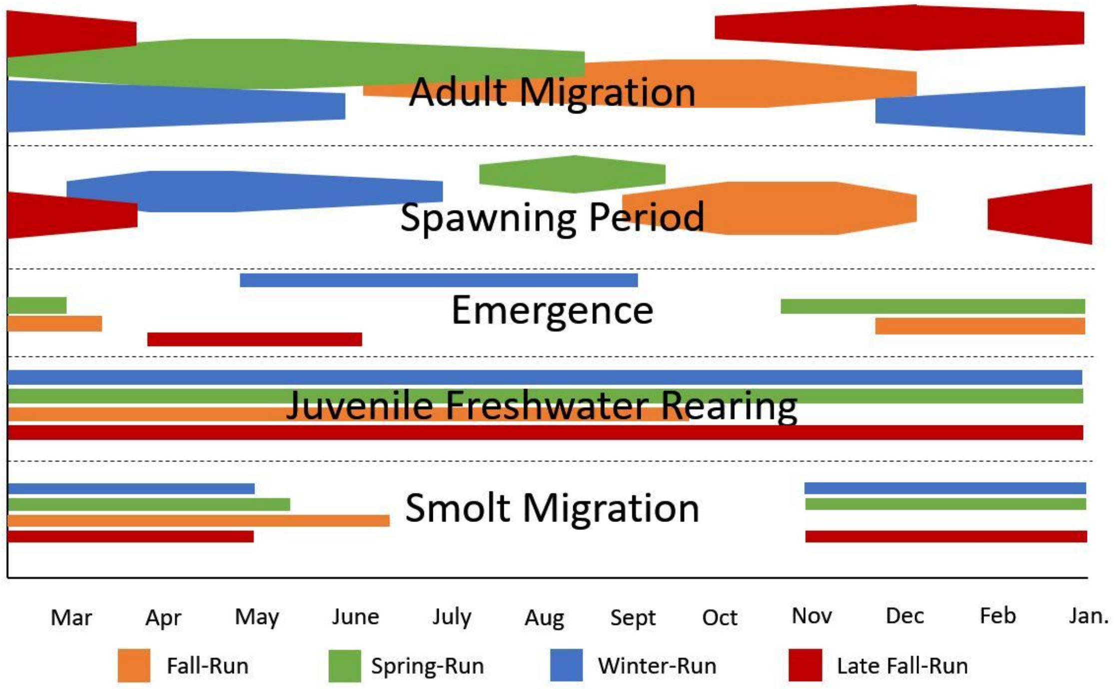

Figure 1: Chinook Salmon Presence in the Sacramento River by Life-stage and Seasonal Run. Information modified from Myrick & Cech (2001) and Moyle (2002).

LIFE STAGES, DEVELOPMENT, AND THERMAL CONSTRAINTS

Within species, salmonids also exhibit variation in thermal performance by age class. Anadromy requires that salmon spend several distinct life stages in fresh water. These different life stages have different thermal requirements, each varying by species (Murray & McPhail 1988). In general, eggs and embryos are most sensitive to thermal conditions, requiring cold, stable temperatures for proper incubation and development (Myrick & Cech 2001; Moyle 2002). Post-hatch alevin are mobile but remain hidden within substrate to avoid predation, generally exhibiting a greater tolerance of temperatures than during egg incubation (Myrick & Cech 2004). Upon absorption of the yolk-sac, parr become predatory and seek new habitats to support exogenous feeding. Departing natal streams, parr begin out-migration and undergo smoltification prior to ocean entry. Adults are considered less thermally plastic than juveniles (Pörtner & Farrell 2008). In short, the thermal performance capacity of salmonids differs strongly between life stages and between different species and runs (Tables 2.1-2.3).

It is important to understand that the magnitude and duration of thermal exposure both influence a fish's performance metrics. Typically, as magnitude of thermal stress increases, duration of tolerance decreases. Therefore, both facets of thermal exposure are important when evaluating thermal performance data (see Appendix: Acute vs. Chronic).

Table 2.1: Thermal Metrics for Central Valley Anadromous Salmonids

		Chinook Salmon				Steelhead Trout		
		Fall CS	**Late-Fall**	**Spring**	**Winter**		**Metric**	**Citations**
Life Stage	**Egg**	10-14°C[1] 13.3-13.9°C[2]	Unknown	Unknown	13.3°C[2]	Unknown	**Minimal Mortality (<10%)**	[1] Richter and Kolmes 2005 [2] Myrick and Cech 2001
	Alevin	Unknown	Unknown	Unknown	Unknown	Unknown	**Minimal Mortality (<10%)**	
	Juvenile	17-20°C[3] 15.3°C[4]†	Unknown	Unknown	Unknown	19-20.5°C[5]	**Optimal Growth**	[3] Myrick and Cech 2002 [4] Rich 1987 [5] Myrick and Cech 2005
		28.8°C @ 19°C[6]	Unknown	Unknown	Unknown	27.5-29.6°C @ 11-19°C[7]	**Critical Thermal Maximum**	[6] Cech and Myrick 1999 [7] Myrick and Cech 2005
	Smolt	<17°C[8,2]	Unknown	Unknown	Unknown	Unknown	**Successful Smoltification**	[8] Marine and Cech 2004
	Adult	21-24°C[9]‡*f* 19-21[10,11]‡	Unknown	23°C[9] ‡*f*	Unknown	Unknown	**Migration Success**	[9] Strange 2010 [10] Hallock 1970 [11] Williams 2006

Laboratory conditions (satiation rations, clean water etc.) should be assumed unless marked by a † representing 'field-like' laboratory conditions or ‡ representing date quantified from field observations. *f* represents populations tested were from the Klamath River Basin.

Table 2.2: Thermal Metrics for Central Valley Anadromous Salmonids Compared to Northern Populations

		Chinook Salmon				**Steelhead Trout**		
		Fall	**Late-Fall**	**Spring**	**Winter**		**Metric**	**Citations**
Life Stage	**Egg**	10-14°C[1] 13.3-13.9°C[2]	Unknown	Unknown	13.3°C[2]	***4-10°C[1]*** ***7-10°C[2]***	**Minimal Mortality (<10%)**	[1] Richter and Komes 2005 [2] Myrick and Cech 2001
	Alevin	***15.1-16.5°C[3,4,5]***	Unknown	Unknown	Unknown	***>15°C[6]***	**Minimal Mortality (<10%)**	[3] Garling & Masterson 1985 [4] Geist et al. 2006 [5] Beacham & Murray 1990 [6] Rombough 1988
	Juvenile	28.8°C @ 19°C[7]	Unknown	Unknown	Unknown	27.5-29.6°C @ 11-19°C[8]	**Critical Thermal Maximum**	[7]Cech and Myrick 1999 [8]Myrick and Cech 2005
		17-20°C[9] 15.3°C[10†]	Unknown	***15.6°C [11]***	Unknown	19-20.5°C[12] ***13.3-16.5°C[13†]***	**Optimal Growth**	[9] Myrick and Cech 2002 [10] Rich 1987 [11] McCullough 1999 [12] Myrick and Cech 2005 [13] Wurtsbaugh 1977
	Smolt	<17°C[14,2]	Unknown	***12-15°C[2]***	Unknown	***12-13°C[2]***	**Successful Smoltification**	[14] Marine and Cech 2004
	Adult	21-24°C[15‡ *f*] 19-21[16,17‡]	Unknown	23°C[15 ‡ *f*] ***21-22°C[18‡]***	Unknown	***19-21°C[2,19‡]***	**Migration Success**	[15] Strange 2010 [16] Hallock 1970 [17] Williams 2006 [18] Alabaster 1988 [19] Keefer et al 2009

Bolded metrics represent those measured in populations from Washington, Oregon, Alaska or Idaho. Non-bolded metrics are those collected from California populations. Laboratory conditions (satiation rations, clean water etc.) should be assumed unless marked by a † representing 'field-like' laboratory conditions or ‡ representing date quantified from field observations. *f* represents populations tested were from the Klamath River Basin.

Table 2.3: Aerobic Scope Measures for Salmonid Populations

Species	**Population**	**Life Stage**	**Acclimation Temperature**	**Tested Temperatures**	**Opt. Thermal Window**	**Citation**
O. mykiss	Tuolumne, CA	Juvenile	13 °C	13 - 25°C	17.8-24.6 °C	Verhille et al. 2016
O. mykiss	Australia	Juvenile	15°C	8 - 25 °C	12.8-18.6 °C	Chen et al. 2015
O. mykiss	Northern	N/A	N/A	10 - 22 °C	20.5-22.4 °C	Fry 1948
Chinook	Mokelumne, CA	Juvenile	15 °C & 19 °C	12 - 26 °C	Not Reported	Poletto et al. 2017

Table of measured aerobic scope values for Chinook and *O. mykiss* strains. 'Tested Temperatures' indicates the temperatures over which aerobic scope was quantified. 'Opt. Thermal Window' represents the range of temperatures at which aerobic potential is 95% of maximum. For more information on the aerobic scope metric see Appendix: Physiological Metrics.

Egg Development

One of the most thermally sensitive stages of the salmonid life-cycle is the embryonic stage. Myrick & Cech (2001) reviewed multiple studies to determine that Central Valley Chinook salmon eggs could withstand temperatures ranging between 1.7 °C to 16.7 °C, with mortality increasing dramatically toward the extremes. Central Valley winter- and spring-run Chinook salmon populations are most at risk of high temperatures as they typically spawn earlier and therefore are exposed to warmer water conditions due in part to California's Mediterranean climate. Myrick & Cech (2001) presented chronic thermal limits between 13.3 -13.9 °C for fall-run Chinook and 13.3 °C for winter-run Chinook, below which egg mortality was minimal. The authors also concluded that Sacramento River fall-run Chinook eggs were not more thermally tolerant than northern populations from Oregon and Washington. However, work conducted by Heming (1982), found that a fall-run Chinook population from British Columbia had declining egg survivorship at 12 °C and Richter & Kolmes (2005) reported optimal incubation temperatures ranging from 10-14 °C in summarizing multiple studies on Chinook populations from northern states.

Richter & Kolmes (2005) summarized a body of work suggesting that optimal steelhead egg incubation temperatures are between 4-10 °C, with mortality increasing with temperature to 15-16 °C. Similarly, Myrick & Cech (2001) determined that the viability window for *O. mykiss* eggs is relatively narrow (5-10 °C), when compared to Chinook salmon. Furthermore, *O. mykiss* appears to exhibit strain-level differences in thermal tolerance. Similar to Chinook salmon, the level of variation that may exist within California populations of *O. mykiss* has not been thoroughly explored.

Recent modelling work by Martin et al. (2017) showed that laboratory studies may have overestimated the lethal temperature of developing winter-run Chinook salmon eggs by ~ 3C°. While this is a theoretical explanation, that as of yet, has not been empirically demonstrated, this work has important implications for the studies referenced above and for management of thermal regimes because most studies on thermal tolerances of salmon eggs are conducted in the laboratory. Martin et al. (2017) suggest that this discrepancy is due to differences in oxygen availability between environments. The laboratory setting can be generally categorized as an ideal environment with high levels of oxygen versus actual field conditions that may exhibit low oxygen conditions. Their work is particularly relevant to winter-run Chinook salmon conservation. A 1999 USFWS report identified 13.3 °C as a conservative thermal threshold for the protection of winter-run eggs and embryos. This data was collected in a laboratory setting, and while 13.3 °C is not lethal, it may not be protective under natural, fluctuating in-river conditions.

Egg-Fry Development

Similar to eggs during incubation, post-hatch salmonid alevin are also susceptible to thermal conditions. However, the research on alevin thermal tolerances is sparse when compared to eggs or juveniles. The Region 10 guidelines, while prescriptive for "Fry Emergence" do not report alevin thermal limits in their determination of temperature thresholds. This is likely due to the in-river proximity and temporal overlap between rearing alevin and developing embryos that would make differential thermal management impossible between life stages. However, there is a considerable shift in thermal tolerance that occurs between eggs and alevin.

Very little is known about the thermal limits of Chinook salmon alevin, especially within California. Work by Geist et al. (2006) found that a specific population of Snake River Chinook salmon alevin from Idaho survived rearing temperatures up to 16.5 °C, furthermore there was no significant difference in survival between 16.5 °C and 13 °C. However, survival fell precipitously when alevin were reared at 17.0 °C indicating a thermal limit for this population. The authors note that 16.5 °C exceeds the implemented Region 10 threshold of 13 °C, and that this may represent local adaption to historically warm river temperature experienced by this population (Geist et al. 2006). Somewhat consistent with this result is analysis of Velsen (1987) data on Pacific salmon embryos. Summarized by Beacham & Murray (1990), alevin from five pacific salmon species were incubated at temperatures ranging from 2 °C to 16 °C. Only Coho salmon (*O. kisutch*) exhibited greater than 50% mortality when reared at 16 °C. Alevin from the Great Lakes showed reduced survival when reared at 15.1 °C (Garling Jr. & Masterson 1985) further supporting increased thermal performance when compared to eggs.

Steelhead alevin are also poorly studied. Rombough (1988) found that Washington steelhead trout alevin had greater thermal tolerance than embryos with less than 5% mortality when reared at temperatures between 6-15 °C. Furthermore, it is indicative that steelhead alevin are capable of withstanding temperatures exceeding Region 10 thresholds. However, a lack of studies may be cause of caution due to evidence of impressive interpopulation variation within *O. mykiss* alevin. Stonecypher et al. (1994) found that two Idaho rainbow trout strains had significantly different survival rates to the alevin life stage (40% vs. 9%) when reared at 2 °C, although both populations exhibited minimal mortality (<10%) when reared at 7 °C. Furthermore, the authors found that of four trout populations tested, the survival of the two domesticated strains was greatly reduced at 2 °C, suggesting that domestication can influence thermal performance traits.

Temperature is an important factor in the early developmental rates of salmonids. Relatively warmer water temperature can enhance the rate of development and ultimately influence fry size, timing of exogenous feeding, and viability (Murray & Beacham 1986; Rombough 1988). However, warmer incubation temperatures during the egg stage have also been shown to reduce length and mass of pink salmon fry (*O. gorbuscha*, Murray & Beacham 1986) steelhead trout (Rombough 1988) and Chinook salmon (Fuhrman et al. 2018). Fuhrman et al. (2018) found that hatchery populations from Oregon and Washington exposed to warmer temperature (~10 °C) regimes emerged earlier and less developed than fish reared at cooler temperatures (~5 °C). Emergence at a smaller size or earlier stage of development also increases predation risk during development and may inhibit competitive interactions between conspecifics (Fuhrman et al. 2018). Mortality associated with reduced size at hatching may be an indirect consequence of warmer water temperature.

Juveniles

Within the salmon literature the term juvenile is applied broadly from emergent individuals without yolk sacs to parr prior to smoltification. Complicating this, individuals may remain as juveniles for variable time periods and within diverse habitats. In general, there are two broad but predominate life-history strategies: ocean-type and stream-type. Ocean-type juveniles migrate to the ocean within the first year while the stream-type life history will remain in freshwater for at least one summer. The stream type life history extends residence time in freshwater exposing juveniles to higher water temperatures during summer, suggesting that the strategy may be less successful particularly under future climate scenarios. Within the Central

Valley, fall and late fall-run fish are more likely to be ocean-type while winter and spring-run salmon exhibit more stream-type strategies. However, within all runs a mixture of these two general life-histories exist (Moyle et al. 2017). Central Valley steelhead exhibit both ocean and stream-type strategies, though most juveniles remain in freshwater for one or two years prior to smoltification while others do not migrate (i.e. resident rainbow trout). Currently, there are a lack of studies looking at thermal performance of juvenile salmonids that exhibit different life history strategies.

Chinook salmon juveniles have been broadly studied in terms of their thermal tolerance and performance. Growth studies on Central Valley fall-run populations have indicated that 17-20 °C yields optimal growth when fish are fed to satiation in a laboratory setting (Cech & Myrick 1999; Myrick & Cech 2002, 2004). However, Rich (1987) reared American River fall-run Chinook from the Nimbus National Fish Hatchery using river water and found that growth rates declined when fish were reared at temperatures exceeding 15.3 °C. Myrick & Cech (2001) attributed this discrepancy to potential effects of disease or water chemistry between trials conducted in the laboratory and those using river water.

Acute and chronic lethal temperatures for Central Valley salmonids have also been extensively studied and reviewed by Myrick and Cech (2001). The chronic maximum temperature a fish can survive can be determined by determining the incipient upper lethal temperature (IULT). The IULT for Chinook juveniles from Mokelumne Hatchery 24 °C (Hanson 1997), and 24 °C for the American River (Rich 1987). Poletto et al. (2017) exposed Mokelumne river fall-run Chinook to gradual warming (over several hours) during aerobic scope experiments, and observed mortality at 26 °C. Acute thermal tolerances for Chinook salmon are somewhat higher. Cech & Myrick (1999) reported fall-run American river juveniles acclimated at 19 °C exhibited a critical thermal maximum (CTM) of 28.8 °C. There is also evidence for differences in CTM between populations of Chinook juveniles. Unpublished data by Zillig et al. found differences in CTM between populations of Central Valley Chinook and populations from Oregon. Furthermore, populations differed in effect of acclimation in improving CTM (Zillig et al. unpublished data).

Steelhead are less well studied than Chinook. Washington steelhead reared in a laboratory but fed according to natural conditions had optimal growth rates when acclimated to13.3 °C and 16.5 °C when fed satiation rations (Wurtsbaugh 1977; WDOE 2002). Contrasting this result are those of Myrick and Cech (2005) which found that the growth of American River hatchery steelhead in California was greatest at 19 °C when acclimated under laboratory conditions and fed until satiation as opposed to 11 or 15 °C. This is consistent with Sullivan et al. (2000) which concluded that 20.5 °C is an appropriate 7DADM limit for Pacific Northwest juvenile steelhead growth. The discrepancy between these reported optimal growth rates may be due to differences in ration treatments between studies, interpopulation variation in growth rate, or a combination of both.

Comparing critical thermal tolerance between populations indicates capacity for interpopulation variation in steelhead trout. When acclimated to a natural thermal regime below 16 °C, wild Feather River steelhead juveniles had a CTM of 30.8 °C, meanwhile hatchery reared juveniles acclimated to 16 °C had a CTM of 29.4 °C. This results indicates a potential loss of thermal tolerance associated with domestication (Myrick & Cech 2000a). There is also some evidence for interpopulation variation among steelhead populations as the Nimbus steelhead strain, when acclimated to 15 °C had a CTM of 28.4 °C. The same population had a CTM of 29.6 °C when acclimated to 19 °C (Myrick & Cech 2005).

Smoltification

The transition from freshwater tolerance to saltwater tolerance for juvenile salmonids requires essential developmental processes involving concerted shifts in gill morphology, metabolic demand, body pigmentation, and behavior (Hoar 1988). Unlike some fish which show a fluid, repeatable process of salt water tolerance, smoltification for nearly all juvenile anadromous salmonids (excepting steelhead trout) is a single event, which is only reversed when, as adults, individuals return to freshwater. Marine & Cech (2004) conducted work on juvenile fall-run Chinook salmon from the Sacramento River by investigating gill Na^+/K^+-ATPase, and blood salinity as indices of smoltification. Their work demonstrated that when acclimated and reared at warm temperatures (17-20 °C, 21-24 °C) Chinook salmon smolts suffered impaired smoltification (reduced osmoregulatory capacity) and increased rates of predation when compared to fish reared at 13-16 °C. Sauter et al. (2001) compared the thermal preference of two seasonal Chinook runs, spring- and fall-run, from Washington. The results revealed a significant change in thermal preference between runs during smoltification. Fall-run smolts drastically altered thermal preference (from a high of 17.7 °C to 11.2 °C) which was correlated with their approach to maximal saltwater tolerance. Conversely, spring-run Chinook smolts preferred 16.6 °C with no associated change in thermal preference associated with smoltification. The authors interpreted differences between spring- and fall-run Chinook runs to reflect the different environmental conditions experienced during smoltification. Research investigating differences in smoltification traits of California runs and populations is currently lacking.

Steelhead trout appear to be much more reliant on cold water during smoltification. For instance, in a steelhead population from Washington, Adams et al (1973, 1975) found that smoltification failed to occur at temperatures exceeding 11 °C. Richter & Kolmes (2005) reviewed several papers on steelhead populations from the Pacific northwest to indicate that steelhead smoltification was impaired at temperatures exceeding 13.6 °C. They also note the finding by McCullough et al. (2001a) that smoltification thresholds appeared different between seasonal runs (13 °C for winter-run steelhead [Hoar 1988] and 13.6 °C for summer-run [Zaugg & Wagner 1973])

With respect to smoltification, there is an additional complication related to developmental phenology. Successful smoltification and migration into the ocean, can only occur if a salmon enters saltwater during a limited smoltification window (Hoar 1988). Arrival to saltwater too early or too late can impair successful transition and is considered a cause of increased predation and related mortality among salmonid smolts (Hoar 1988). The onset and duration of the smoltification window is to some degree temperature-dependent. Zaugg & Wagner (1973) indicated that water temperature and photoperiod moderate the onset of smoltification and the optimal window for transition. Their work measured gill Na^+/K^+ATPase as a proxy for smoltification and found that manipulations of photoperiod and temperature regimes could alter the development of saltwater tolerance on the order of several months. This may be a looming problem in California, where water temperature is expected to rise, yet migration distance and photoperiod are fixed for a given population. Furthermore, efforts to truck or otherwise transport juvenile salmonids (Lusardi & Moyle 2017) may interfere with effective saltwater transition by exposing fish to saltwater outside of the optimal smoltification period. There is some work that indicates that different populations may have different smoltification profiles. Beakes et al. (2010) looked at the traits of juvenile salmonids undergoing smoltification between two different California populations. They found differences in the size necessary to smolt with juvenile steelhead from Coleman National Fish Hatchery smolting at larger sizes than juveniles in Scott Creek. In summarizing, the authors found the result consistent with local adaptation to differences in food availability and growth potential between the two watersheds. Proper smoltification and saltwater adjustment is crucial to the success of juvenile salmonids. Therefore, understanding how different species, runs or populations vary in their smoltification parameters would greatly inform management strategies that assist juvenile salmon during migration.

Adults

As adults, anadromous salmonids spend most of their lives in the ocean, a period which is not covered by Region 10 guidelines. Therefore, this review will focus on the thermal performance and ecological considerations of adult salmon during their return to freshwater. Warm water temperatures can impact adult salmon by preventing upstream migration. Strange (2010) used temperature sensing biotelemetry tags to determine at which temperatures adult Klamath River basin Chinook salmon initiated or stopped migration. This study included 16 spring-run and 2 fall-run adults and demonstrated that fish would reinitiate upstream migration when temperatures were below 21-24 °C. Strange converted these results into a 7DADM value of 23 °C and notes that this is considerably warmer than values reported from northern populations, Goniea et al. (2006) found reduced migrations by fall-run Columbia River Chinook at 20 °C, while Mccullough (1999) concluded from several populations of salmon from the Pacific Northwest that 21 °C prevented adult upstream migration. This was also corroborated by later reviews (McCullough et al. 2001; Richter & Kolmes 2005). Strange (2010) suggested that the results from more northerly populations were possible evidence of local adaptation to warmer water temperatures in the Klamath River basin. Hallock et al. (1970) reported that water temperature exceeding 19 °C inhibited migration of Chinook salmon in the San Joaquin River, however in 2004 over 500 adults migrated up the San Joaquin River at temperatures exceeding 21 °C (daily average; Williams 2006). In regards to steelhead trout, Richter & Kolmes (2005) summarized multiple studies from the Pacific Northwest to conclude that 21 °C was a temperature that would inhibit upstream migration by steelhead adults. However, work by Keefer et al. (2009) indicated that 19 °C may pose a migratory barrier for Columbia River steelhead, with adults utilizing thermal refugia until water temperatures declined. Given the capacity for interpopulation differences more research is certainly needed to determine the thermal barriers for Chinook salmon and steelhead trout within the Central Valley. Within Chinook salmon, research determining the thermal barriers to adult migration between seasonal runs would illuminate differences between populations that are relevant for management.

THERMAL ECOLOGY OF SALMONIDS

The Region 10 guidelines may be imperfect for effective management of Central Valley salmonids because it: does not differentiate by species or run, relies on studies conducted largely on northern populations and uses the 7DADM metric. Furthermore, the Region 10 thresholds may be unattainable under certain environmental conditions (e.g. drought) or in specific areas where temperatures are uncontrollable (e.g. too far from dam). A large body of research has developed in the past two decades identifying causes of variation in the thermal performance of salmonids. Some of these causes are intrinsic genotypic differences between populations or species, others are a result of the phenotypic plasticity of salmonids applied to diverse and dynamic ecological conditions. These factors may offer predictive insight into environmental conditions where the Region 10 guidelines may be unprotective, overly conservative or impossible to satisfy.

Quantifying River Temperature and Temperature Metrics

Considerable debate has occurred regarding the best thermal metric relating river temperature to salmonid response. Due to its simplicity, the 7-day average daily maximum (7DADM) is broadly applied by managers (alternatively referred to as maximum weekly maximum temperature, MWMT). However, the 7DADM may not be the most biologically relevant temperature metric to use. The 7DADM is a running average over a 7-day period of the daily peak temperature and, therefore, it does not protect against a single high daily peak temperature nor does it offer an indication of temperature duration or rate of change. A temperature metric that captures multiple aspects of temperature stress (e.g. absolute temp, duration, rate of change) would provide managers greater flexibility and nuance when making decisions about water releases. Alternative metrics that could be applied include degree days, weekly or daily averages, daily maximums, or quantification of the 24-hour temperature cycle experienced by fish. To date we are not aware of work conducted to evaluate different metric, or combinations of metrics, in their reliability or accuracy to protect salmon and conserve water resources.

Acclimation and Adaptation

An organism’s thermal capacity is a multifaceted product of physiological traits, behavioral responses and environmental conditions, both contemporary and historical. An organism’s life history may expose it to temperature fluctuations at multiple temporal and spatial scales. The strategies by which organisms adjust to fluctuations in their thermal environment fall under two broad categories: acclimation and adaptation. The Region 10 guidelines provide static thermal thresholds to manage river temperatures. However, salmon and their thermal performance are dynamic, enabling response to environmental conditions on short time-scales via acclimation and across generations via adaptation. This juxtaposition may introduce and obscure pitfalls to salmonid management. Therefore, considering the role of acclimation and adaptation in interpreting thermal performance for management thresholds is important.

Acclimation refers to the process by which an individual organism may adjust to changing environmental conditions (Narum et al. 2013). It is well documented that salmonids acclimate to local water temperatures. Acclimation to warmer water temperature typically improves upper thermal tolerance. For instance, Myrick & Cech (2000b) found significant acclimation effects in the CTM of Mt. Shasta and Eagle Lake populations of rainbow trout reared at temperatures between 10 °C and 25 °C. For instance, Mt. Shasta rainbow trout had CTMs of 27.6, 28.6, 29.6, 31.0 and 32.0 °C at acclimation temperatures of 10, 14, 19, 22, and 25 °C respectively. Similarly, juvenile steelhead from the Nimbus hatchery on the American river were reared at three temperatures (11, 15 and 19 °C) and had CTMs of 27.5, 28.4 and 29.6 °C, indicating a clear response to acclimation (Myrick & Cech 2005). Chen et al. (2013) found the same pattern among nine populations of Fraser River sockeye salmon reared at 10, 14 and 16 °C. Each population demonstrated significant increases in CTM as the acclimation temperature increased. Furthermore, comparisons between Chinook salmon from Coleman National Fish Hatchery and the Elk River and Trask Hatcheries in Oregon demonstrated differences in acclimation capacity between populations (Zillig et al. unpublished). These differences may have important ramifications for how salmonid populations cope with changes in the thermal landscape. Population differences in acclimation response are an indicator of which populations may be at most at risk to alterations in the thermal landscape.

Adaptation refers to genetic adjustment of a lineage of organisms constituting a population or species. In this context, the forces of mutation, genetic drift and natural selection tune organismal traits to increase biological fitness in response to environmental conditions (Narum et al. 2010, 2013). While operating across generations, adaption can be important on management timescales and an important part of effective conservation. Ashley et al. (2003) coined "Evolutionarily Enlightened Management" to represent the acceptance that species will evolve to future conditions or those imposed via management actions. Addressing the role of evolution in salmonid management is important as there is evidence of rapid adaption, specifically due to domestication by hatcheries. In their review of hatchery effects on salmonids, Araki et al. (2008) synthesize works demonstrating that hatcheries produce fish that are less fit than their wild counterparts. Furthermore, they found that fitness loss can develop rapidly, in as few as one or two generations (Araki et al. 2007). The loss of adaptive traits can be profound in terms of future adaptive potential. In a meta-analysis of bird species, Bradshaw & Holzapfel (2008) found that in response to a changing thermal landscape, birds could fluidly adapt their phenology but thermal physiological traits were rigid. Whether salmonids show similar restrictions on trait evolution to climatic changes is unknown, but if so, would imply that lost thermal physiological traits may be unlikely to reappear. Tangentially, Prince et al. (2017) deduced through genetic analysis that the early migrating phenotype exhibited by spring- and winter-run Chinook as well as summer steelhead, evolved only once per species, not repeatedly per population as previously thought. In the case of the winter-run Chinook, extinction would mean likely permanent loss of that seasonal phenotype.

Research into the standing diversity in thermal or phenological traits amongst populations is an important avenue for study as diverse phenotypes should be considered a conservation resource to be protected in order to enhance species resilience. Genetic studies conducted by Williamson & May (2005) on Central Valley populations of Chinook salmon, however, have indicated a reduction in genetic diversity between populations when compared to similar work on other Chinook populations. The authors attribute this loss of diversity to homogenization of wild populations via hatchery release of reared salmon. Reduction in genetic diversity reduces the adaptive capacity of populations as there are fewer genetic resources upon which natural selection can act. Ultimately, this suggests that homogenization of salmonid populations in the Central Valley and possibly elsewhere will reduce adaptive potential in face of a changing climate. As future river temperatures are expected to increase, understanding the adaptive and acclimatory capacity of California's salmonid populations may offer additional management levers leading to long-term conservation benefits.

Watershed Variation

Interpopulation variation between salmon populations is produced through combination of life-history strategies that reduce gene flow and environmental heterogeneity that spans broad scales. Pacific salmonids occupy a large latitudinal band of coastal habitat, ranging historically from the Arctic to southern California. Additionally, throughout this range, individual rivers and tributaries vary widely in environmental characteristics, producing a diversity of habitats. Life history plasticity enable salmon to adapt and occupy most accessible river systems, while spawn site fidelity and homing behavior reduce regional gene-flow and stimulate genetic drift between even geographically proximate populations.

Watersheds can exhibit variation across several environmental gradients that influence salmonid biology. Water source (Nichols et al. 2014), discharge volume, riparian habitat (Webb & Zhang 1997; Moore et al. 2006), level of dissolved nutrients (Selbie et al. 2009; Ranalli & Macalady 2010), turbidity and other characteristics can all vary between and within watersheds and this has important implications for salmonid response. For instance, Lisi et al. (2013) demonstrated that environmental characteristics such as watershed steepness, size, and the presence of lakes accounted for variability in spawn timing of Alaska sockeye salmon, primarily through moderation of river temperature.

Furthermore, variation of environmental characteristics within a watershed allows different salmonid runs to occupy distinct niches. Historically, salmon migrated and spawned throughout the length of a river, with more thermally tolerant populations occupying lower elevations, while upper reaches contained populations adapted to ~~a~~ more physically demanding migrations and colder water (Myrick & Cech 2004). To that end, (Eliason et al. 2011) demonstrated that differences between populations of Sockeye salmon from the Fraser river in multiple traits (heart mass, aerobic scope, heart rate) correlated strongly with environmental conditions associated with the migratory routes and spawning grounds of each populations. Specifically, populations that migrated further and had to pass hydraulically challenging river features had increased heart mass while those that populations native to warmer habitats had improved aerobic, cardiac and heart rate scopes at warm temperatures. It is conceivable that Central Valley salmonids would demonstrate similar population-specific adaptation to historical local environmental conditions. Dams and other barriers to migration have increased the complexity of predicting salmonid thermal performance. Dams have reduced access to most of California's high elevation salmonid rivers, reducing watershed heterogeneity and forcing multiple phenotypes and species to overlap (Botsford & Brittnacher 1998; Lindley & Mohr 2003). The result of this cohabitation has led to problems maintaining reproductive isolation between different salmonid populations, as well as managing populations displaced from historical habitat and associated environmental conditions (e.g., winter- and spring-run Chinook). The existence of populations-specific thermal traits, the influence of recent (last 200 years) habitat modification, and the rate of current adaptation to modern conditions is all unknown for Central Valley salmonids.

Growth and Metabolism

Laboratory studies on physiology can elucidate the baselines and optima of thermal capacity, but it is important to recognize that interactions with the environment also influence temperature tolerance. Stream temperature can strongly influence the growth and survival of salmonids, but ectotherms have shown a capacity to compensate for increases in stream temperature when abundant food resources are available. Bioenergetic theory stipulates that ectotherm growth is a function of energy consumed versus energy expended or lost (Railsback & Rose 1999). Energy loss is generally dictated by metabolic activity which increases positively with temperature. As temperature increases so do metabolic outputs such as egestion, excretion, and costs associated with digestion (Hanson et al. 1997). Under such circumstances in the wild, salmonids or other stream fishes must seek out thermal refugia to reduce energy expenditure or compensate with increased food consumption. Otherwise, an energy deficit will occur, leading to reduced growth rates with potential consequences for fitness, including death (see Beakes et al. 2010).

Most stream ecosystems are naturally oligotrophic (Myrvold & Kennedy 2015), suggesting that behavioral thermoregulation and movement to thermal refuges is an effective strategy to deal with rising stream temperature (see Welsh et al. 2001). However, in productive ecosystems (i.e., spring-fed rivers, tailwaters below dams, floodplains, coastal lagoons, etc.), salmonids may be able to compensate for increases in stream temperature with food consumption. The phenomenon has been shown to occur in numerous tightly controlled laboratory studies where salmonids are fed to satiation and exposed to warming temperature regimes. For instance, Foott et al. (2014) found that California juvenile Coho salmon reared at mean study temperatures of 16.3 °C and 21.3 °C exhibited similar growth rates when fed to satiation. Additionally, experimental fish did not show a stress response at warmer water temperatures, as measured by plasma cortisol level. Empirical evidence for growth compensation in natural ecosystems has been less frequent. However, Bisson et al. (1988) found exceptionally high rates of juvenile Coho salmon production in Washington streams exhibiting temperatures up to 29.5 °C and speculated that food was a causative mechanism supporting observed rates of production. Railsback & Rose (1999) found that food consumption was the primary determinant of salmonid growth during summer (as opposed to temperature) and Weber et al. (2014) used reach specific food web data and bioenergetic models to accurately predict salmonid growth rates in several streams in the John Day River Basin. Work by McCarthy et al. (2009) on wild populations of steelhead in tributaries of the Trinity River found that high water temperatures and reduced feeding rate reduced growth, sometimes yielding weight loss. Their models indicated that reduced growth may occur at temperatures as low as 15 °C and that increased food availability or quality would expand the window of viable temperatures. Their conclusions were extrapolated to indicate that under future warming conditions steelhead in food-limited systems may suffer. In a field experiment, Lusardi et al. (in prep) found food to be the proximal factor affecting juvenile Coho salmon growth during summer, across a longitudinal gradient of temperature and food density in a California stream. Specifically, they found that juvenile Coho growth peaked at a maximum weekly maximum temperature of 21.1 °C. Dodrill et al. (2016) modeled a similar response in rainbow trout, concluding that warmer temperatures resulted in reduced growth, unless accompanied by increases in prey availability and prey size. This body of work demonstrates that the intrinsic productivity of a river system, and subsequent prey availability, can have important implications on whether a given salmonid population will thrive, cope or suffer with increasing water temperatures. Food availability and productivity can vary through time and between systems and therefore offers a powerful predictor for inter-populations variation of in-field thermal capacity.

The diet of salmonids is entirely composed of ectothermic organisms. As such, water temperature will influence the ecology and physiology of salmonid prey. Annual changes in water temperature and flow regime have been shown to alter the phenology, abundance and community assemblage of aquatic macroinvertebrates (Boulton et al. 1992; Bonada et al. 2007; Lusardi et al. 2016; Peterson et al. 2017) and phenological shifts in food availability have been shown to have population-level effects on predator species, such as juvenile salmonids (Møller et al. 2008; Thackery et al. 2010). In extreme cases, termed 'phenological mismatch', shifts in the timing of species interactions can lead to population decline and species endangerment (Møller et al. 2008). Phenological mismatch is of greatest concern for species which are specialist predators or rely upon historically reliable but ephemeral food resources (Visser et al. 1998; Green 2010; Kudo & Ida 2013). Due to the seasonality of the freshwater stage of juvenile salmonids, temperature-induced phenological shifts in macroinvertebrate prey abundance may influence the carrying capacity of in-river habitats.

Biotic Interactions and water temperature

Predation

Exposure to elevated water temperature on both acute and chronic time scales has been demonstrated to influence predation risk in juvenile salmonids. Acute thermal exposure can also influence predation risk. Coutant (1973) exposed Columbia basin juvenile salmonids to brief thermal shocks (26-30 °C) and documented increased predation. For juvenile rainbow trout exposure times of ~90 seconds or greater to 30.5 °C were linked to increased risk of predation, while for a 30 second exposure to 28 °C was enough to increase predation risk on juvenile Chinook salmon above control treatments. The results indicate that short exposures to sub-lethal temperatures can strongly influence predation risk of juvenile salmonids.

In the Central Valley, Marine and Cech (2004) examined the influence of temperature on predation risk by rearing juvenile Chinook salmon from the Sacramento River at three temperature regimes (13–16 °C, 17–20 °C, and 21–24 °C) and exposing them to a predator (striped bass, *Morone saxatilis)*. They found that fish reared under the highest temperature regime were preferentially consumed by striped bass. Petersen & Kitchell (2001) modeled the bioenergetics of three predators of juvenile salmonids (northern squawfish, *Ptychocheilus oregonensis*, smallmouth bass, *Micropterus dolomieu,* and walleye, *Stizostedion vitreum*) in the Columbia River, and found that predation by all three increased during climatic warm periods. This is consistent with laboratory studies by Vigg & Burley (1991) who found that temperature-dependent consumption rate of northern squawfish increased exponentially across a temperature gradient (8-21.5 °C). These results indicate that elevated river temperatures could increase predation on juvenile salmonids.

Temperature can also influence sub-lethal effects of predation. Kuehne et al. (2012) conducted semi-natural stream experiments observing changes in direct mortality, behavior and physiological traits of salmon exposed to predation by smallmouth bass. Predation and control experiments occurred over 48 hours at 15 °C and 20 °C. There were no observed differences in direct predation, however salmon occupying warmer water exhibited reduced growth demonstrating an effect of the multiple stressors (predation and temperature). Predation, through both lethal and sub-lethal effects can have a substantial effect on salmonid populations (Erhardt et al. 2018). Thermal management of salmonid predators may offer a powerful lever in conserving Central Valley salmonids.

Competition

As temperature increases, salmonids will experience an increase in metabolic energy demands (Elliot 1994). This will increase competition between conspecifics for food resources, potentially reducing habitat carrying capacity. There will also be changes in competitive dynamics between species. Reese & Harvey (2002) tested the effect of Sacramento pikeminnow (*Ptychocheilus grandis*) on the growth and behavior of juvenile Eel River steelhead in artificial streams and found that at elevated temperatures (20-23 °C), growth of dominant steelhead juveniles was reduced by 50% when exposed to pikeminnow. Similarly, Gordon (1987) found that when redside shiner (*Richardsonius balteatus*) and steelhead trout were reared together at warm temperatures (19-22 °C), production of steelhead declined by 54%, steelhead suffered no loss in production at cool temperatures (12-15 °C). Wenger et al. (2011) who modeled the impact of future climate scenarios on four species of Wester trout found that climactic increases in temperature were expected to reduce habitat due to enhanced competitive interactions. Together, these studies suggest that warming water temperature may strongly and negatively influence competitive interactions between salmonids and other fishes (Bear et al. 2007).

Disease

The role of temperature in structuring disease response in salmonids appears to be complex and species specific. In a USEPA report, Fryer & Pilcher (1974) investigated how temperature influences the virulence of multiple salmonid diseases. Their work demonstrated a positive relationship between temperature and disease virulence and subsequent salmonid mortality. Recent work by Dietrich et al. (2014) found that Chinook salmon held at 19-20 °C suffered increase mortality to *Aeromonas salmonicida*, when compared to juveniles held at 11 °C. Additionally, work on Klamath River juvenile Chinook and Coho salmon revealed increased fish mortality associated with myxozoan parasite, *Ceratonova shasta,* infection as temperatures increased from 13° C to 21° C (Ray et al. 2012). However, there are exceptions to this relationship. For instance, the virulence of *C. shasta* in rainbow trout appeared temperature-independent (Fryer & Pilcher 1974). Research on Kokanee salmon (*O. nerka*) exposed to infectious hematopoietic necrosis virus revealed a maximum mortality window between 12 °C to 15 °C. Above and below these temperature, mortality was reduced (Fryer & Pilcher 1974). In another study, Sanders et al. (1978) infected three species of salmonids with bacterial kidney disease and found differences in temperature-dependent fish mortality between Coho salmon and steelhead trout, but no effects on sockeye salmon.

There is also an ecological role in determining how river temperature regimes influence disease. Chiaramonte et al. (2016) found that juvenile Coho salmon, Chinook salmon, and steelhead trout from the Klamath River suffered reduced mortality and infection by *C. Shasta,* when utilizing thermal refugia. Here, thermal refugia acted simultaneously as a refuge from disease and warmer water conditions which could influence other aspects of ecophysiology. With the onset of climate change, such cold-water refugia will become increasingly important, but presumably reduced as water temperatures generally increase and thermal habitat is lost. Quantification of available cold-water refugia within a given river system is an integral part of any assessment to determine the thermal risk potentially associated with resident salmonids. The Region 10 guidelines do not explicitly seek to quantify or integrate thermal refugia into its threshold temperatures, but it does state that natural cold water refugia should be preserved if not restored to protect salmon.

Ecotoxicology

In a foundational review, Cairns et al. (1975) found that the interaction of temperature and environmental toxins can pose a serious but variable threat to aquatic organisms. The interacting effects of temperature and toxins may be synergistic, additive, or antagonistic and, further, may be acutely lethal or induce chronic pathologies. Laetz et al. (2009) tested several mixtures of pesticides on Coho salmon and found that mixtures typically synergized to increase mortality, and that some chemicals when exposed alone were sub-lethal but became lethal when combined. Hodson & Sprague (1975) exposed Atlantic salmon (*Salmo salar*) to varying concentrations of zinc at three temperatures (3, 11, 19 °C) and found that when exposed to lethal concentrations, fish acclimated to 19 °C died faster than fish acclimated to 11 or 3 °C. However, fish at warm temperature required higher concentrations to yield 50% mortality. The authors attribute this counterintuitive result to temperature-dependent metabolic processes for absorbing and removing zinc from the site of action. Similarly, Dietrich et al. (2014) found that increasing temperature (11 °C vs. 19-20 °C) increased the toxicity of an organophosphate and juvenile Chinook salmon mortality, while Macek et al. (1969) found that susceptibility of rainbow trout to 15 individuals toxins also increased with temperature (1.6, 7.2 and 12.7 °C).

Environmental toxins can interact with other ecological processes to influence thermal capacity. Arkoosh et al. (2001) studied juvenile Chinook salmon from the Puget sound, exposing fish to common agricultural toxins and then to the pathogen *Vibrio anguillarum.* Their work demonstrated that exposure to toxins increased the susceptibility of Chinook salmon to infection by *V. anguillarum*. Toxins can also indirectly influence rearing salmonids by damaging primary producers and macroinvertebrates, limiting food availability in stream ecosystems (Macneale et al. 2010). Finally, toxins can also interact with important developmental processes. Dietrich et al. (2013) exposed Chinook salmon smolts to common chemicals used in forest fire flame retardants. Exposure to high concentrations were acutely lethal, but lower concentrations negatively influenced smolt saltwater tolerance. How exposure to toxins influence thermal limitations of smoltification is currently unknown.

The effects of environmental toxins on thermal tolerances may vary by toxin, concentration, developmental stage and species. Negative synergistic effects of multiple toxins are also possible. Furthermore, the effect of toxins on the thermal tolerance of salmonids may not end when exposure ceases, and instead may be permanent. Therefore, river systems that are known to have a high prevalence of toxins should be individually evaluated, and populations of salmonid within should be considered less thermally tolerant than populations from unpolluted waterways. Furthermore, future water quality standards will likely become more difficult to maintain making pollution management an important strategy for protecting salmonids from increasing water temperatures.

CONCLUSIONS AND RECOMMENDATIONS

Recommendations

California salmonids are of great conservation concern. Populations within California are subject to multiple environmental and anthropogenic threats; however, the unifying concern is increasing water temperature. Increasing water temperature may be caused by drought, climate change, municipal or agricultural water needs or habitat alteration. Increasing water temperature can impair salmonid embryo development, salt water transition, and alter competition, predation and disease dynamics. Maintaining appropriate water temperatures requires conserving and strategically releasing cold water resources, resources which could be applied to municipal and agricultural water needs associated with California's growing populations and economy. Balancing cold-water needs and effectively managing salmonid populations now and into the future requires understanding the thermal physiology and ecology of salmon in order to produce regulatory frameworks which enable the conservation of both salmon and water for California.

A Caution on Singular Approaches: Laboratory versus Field Studies

An important caveat in any salmonid temperature study is the inherent difference between results collected in the field from those in the laboratory. The common dichotomy is that field studies provide ecological relevance while sacrificing mechanistic understanding due to confounding and uncontrolled variables versus laboratory studies which provide detailed understanding of organisms divorced from the complexities of the natural world. We posit that both strategies as well as modeling approaches are required for a functional understanding of thermal biology of salmonids.

The majority of studies incorporated into the Region 10 guidelines, as well as those reviewed in Myrick & Cech (2001) and Richter & Kolmes (2005) are laboratory studies the bulk of which pertain to northern populations. Fish used in these studies, unless otherwise stated, are typically fed to satiation and housed in clean, highly-oxygenated water. They are typically unperturbed by biotic interactions (predation and competition), kept free of disease, naïve to environmental toxins, and do not experience the full range of abiotic conditions apparent in natural habitats. Given the role of all these factors in influencing thermal physiology, the reported laboratory thermal metrics should be considered representative of optimum performance, and could be elevated from what would be expected under natural conditions (i.e. exposure to predators, disease, food quality and quantity, etc.).

Work directly testing the effect of laboratory conditions on the thermal capacity to fish relative to wild counterparts has not be conducted. However, laboratory experiments have attempted to explore individual factors (hypoxia, feed restriction, disease) on the performance of juvenile salmonids (Brett et al. 1969; Eliason & Farrell 2014). Martin et al. (2017) demonstrated via modeling that reduced oxygen abundance in the field, explained a 2-3 °C discrepancy in the thermal tolerance of winter-run Chinook eggs measured in the laboratory but empirical measurements are needed to confirm this hypothesis. With respect to current research, laboratory studies on the influence of disease and toxins on thermal performance have indicated reduced thermal capacity (Ray et al. 2012; Dietrich et al. 2014). The implications of the results to a natural or field setting strongly suggest that wild fish suffering from infection or environmental toxins will have reduced thermal limits and perform poorly at higher temperatures than if unperturbed.

Management Metric

Evaluating the efficacy of the 7DADM metric versus alternative metrics is an important step in ensuring that salmon are conserved. While application of a 7DADM is useful due to its simplicity, it may be that multifaceted metrics are necessary to adequately capture the complexity of salmonid thermal biology. We believe that pairing highly resolved thermal performance data from salmonid populations in California with modeling of hypothetical river temperatures could produce a tool capable of evaluating the effectiveness of multiple potential metrics. Proposed metrics (e.g. degree days, 7DADM, daily average, etc.) could be evaluated for making protective management decisions (e.g. triggering dam releases when necessary) as well as minimizing the risks of false-positives (wasting cold water) or false-negatives (exposing salmon to high water temperatures). Furthermore, simulation of this kind could identify environmental conditions where specific management metrics are prone to error, information essential for preparation for a future of increasing environmental stochasticity. This work would bolster confidence that a chosen management metric, such as 7DADM is robust to environmental change and adequately protecting salmonid populations.

Region 10 Application

Water temperature management is a driving factor in effectively protecting California salmonids. However, water temperature must be understood and managed as an environmental factor that is entangled with most every facet of the salmonid life-cycle. With respect to the utility of Region 10 guidelines, they will likely offer a conservative, protective set of thermal limits for Central Valley salmonids because they are derived predominantly from northern putatively cold-adapted populations and because 'too cold' is less lethal than 'too hot' for salmonids exposed to the ranges of temperatures considered here. However, discrepancies do exist (e.g. adult migration) and lack of data exploring interpopulation variation in thermal performance or even run-specific data on winter-, spring- and late-fall run Chinook salmon highlight the potential for further discrepancies either to the detriment of salmon or to the efficient use of water resources.

Furthermore, there will likely exist conditions where adherence to the Region 10 guidelines will become impossible or where thermally-manageable zones will shrink. Environmental conditions such as drought and increasing atmospheric temperatures raise ambient water temperatures, possibly in excess of what can be effectively controlled through dam releases. Prolonged periods of drought, as seen between 2012 and 2016, reduce available cold-water resources and make compliance increasingly difficult. Under such conditions a thorough understanding of California salmonid thermal physiology and ecology will improve management flexibility and positive outcomes for salmonid conservation.

For Central Valley Chinook salmon, the Region 10 recommended temperature for salmon/trout spawning, egg incubation, and fry emergence of 13 °C 7DADM will likely be effective as they are consistent with temperature thresholds currently applied by a biological opinion for winter-run Chinook on the Sacramento River (56 °F (13.3 °C) as a daily maximum between Balls Ferry and Bend Bridge (National Marine Fisheries Service 2009). The application of the Region 10 guideline of 13 °C for the spawning, incubation and emergence of steelhead/rainbow trout is likely adequate, but sub-optimal, for Central Valley populations, optimal rearing temperatures are between 5-10 °C (Myrick & Cech 2001; Richter & Kolmes 2005) and ~16 °C is critical (Velsen 1987). Alevin of both Chinook salmon and steelhead trout will likely be protected by the Region 10 guidelines. Alevin of both species from northern populations appear be more thermally tolerant than eggs with thermal capacity exceeding temperatures prescribed for fry emergence by the Region 10 criteria. However, there is a lack of studies on the thermal performance of alevin from California and the Central Valley.

Fall-run juvenile Chinook salmon from California appear to be thermally tolerant in excess of Region 10 recommended thresholds for core and non-core juvenile rearing of 16 °C or 18 °C 7DADM, respectively. However, there appears to be little work on the influence of temperature on growth rate or acute or chronic thermal limits associated with winter-, spring- or late fall-run Chinook. Given the sensitive state of the winter- and spring-runs as well as their extended residency in the Central Valley, understanding how temperature influences their growth and performance is essential to evaluating how Region 10 guidelines will affect them. Juvenile steelhead appear to be equally if not more thermally tolerant than juvenile Chinook. However, there is evidence for interpopulation variation in steelhead thermal physiology and so attention should be paid to at-risk populations or those from unique habitats. The Region 10 guidance does not provide a specific smoltification threshold for Chinook salmon. This is cause for concern as

Marine & Cech (2004) found that reduced smoltification success when Central Valley Chinook were reared at temperatures exceeding 17 °C. Furthermore, there is some evidence for considerable differences in smoltification thermo-regulatory behavior between seasonal runs amongst northern populations (Sauter et al. 2001). Research identifying thermal smoltification thresholds for spring- and winter-run salmon should be conducted to ensure that proposed management strategies will be protective. The Region 10 threshold for steelhead smoltification is 14 °C 7DADM. This would likely be protective for Central Valley populations. The Region 10 guideline for adult migrating salmonids is 20 °C 7DADM. There is little research on thermal barriers to migration for Central Valley salmonid populations and comparisons of work conducted on more northern populations imply potential for interpopulation variation. Management of the adult life-stage of Chinook salmon is further complicated by the presence of four seasonal runs which migrate at different times throughout the year.

For most life-stages and species for which thermal performance data exists, the Region 10 guidelines appear protective against temperature-induced mortality, but may be sub-optimal, either managing water too be warm or too cool. In both cases, exposure to sub-optimal temperatures can yield sub-lethal detrimental physiological and ecological effects (see Appendix: Thermal Performance Curves). Growth rates and predator avoidance rates can diminish, competitive dynamics can be skewed away from salmonids and diseases may change in virulence. Given the context of the Central Valley and predicted climatic changes, understanding of sub- or indirectly lethal effects of managed thermal regimes is important to properly conserving California's salmonids.

Accounting for Thermal Ecology

The Central Valley contains a broad array of environmental conditions both natural and anthropogenic. It is our view that protection of the most at-risk salmonid populations will require understanding of how their specific ecological landscape influences their thermal performance. It is known that salmonid populations can vary in thermal capacity due to intrinsic physiological (e.g. species, life-stage, run-timing) traits and extrinsic ecological (e.g. prey availability, habitat quality, migration distance) factors. Factors combine to determine optimal, adequate and critical temperatures for developing, rearing and out-migrating juvenile salmonids. Furthermore, future climate conditions and anthropogenic water demands will make the Region 10 values increasingly difficult and costly to achieve. Therefore, we recommend that for populations of important commercial, ecological or evolutionary value that more nuanced, population specific and ecologically holistic protections are designated. In fact, this approach will be necessary to manage salmonids in California in a future warmer climate where meeting Region 10 guidance will become increasingly more difficult.

For a given river system, optimizing the thermal landscape will require data addressing both ecological and physiological traits. There are several data gaps that would provide actionable knowledge for river managers. Research detailing the thermal performance, tolerances and diversity of the late-fall-, spring- and winter-runs of Central Valley Chinook salmon would ensure that management guidelines will protect those populations and allow for predictions to be made for future climate scenarios. Special focus should be applied to winter- and spring-run Chinook due to their loss of historical spawning habitat, critically low population numbers and listing status. Another important data gap is the potential for adaptation in key traits such as embryo and larval survival, growth rate, smoltification success and smoltification phenology.

Finally, studies designed to quantify the difference in thermal performance between laboratory and field studies would reduce error in anticipating performance of wild fish based upon laboratory studies.

To answer these questions and provide actionable population-specific datasets for Central Valley salmonid management, we recommend two tiers of data collection. The first is a comprehensive collection of a few, high-throughput or passively-collected traits. This work would identify salmonid populations that may be disproportionately advantaged or disadvantaged by future climate or anthropogenic changes or left unprotected by Region 10 guidelines. This survey could be limited by a triage process of expert opinion and will identify populations for the second wave of investigation. The second suite of tests would assess important physiological and ecological parameters necessary to determine optimal thermal limits for each population so that managers are presented with current and defensible data in order to conserve remaining populations in the Central Valley.

First tier traits are primarily environmental in order to determine habitat quality and predict suitability under different climatic regimes. These include water temperature and quality, system productivity and salmonid redd characteristics such as temperature and dissolved oxygen and population diversity sampled from carcass surveys. The second tier of experiments would be conducted on a subset of those evaluated in tier one. Possible criteria for further experimentation may include systems with unusual temperature profiles, high or low genetic diversity, systems with low productivity or poor water quality (low O2, high toxins etc.). These populations and their resident systems would be physiologically evaluated with both laboratory and field experiments and following success, additional populations would be explored. Lab experiments would quantify CTM, growth, aerobic scope, genetic diversity and smoltification physiology (see Appendix: Physiological Metrics). Field experiments would include both measures of salmonid performance in the field as well as quantification of habitat quality. In river experiments of salmonid performance would include growth, diet and population metrics while habitat quality would be evaluated by prey abundance, predator assemblage and presence of cold-water refugia. We feel that quantification of these parameters both in the field and wild would enable detailed models to be constructed that may allow predictive assessment of additional riparian systems with reduced experimental work. This modeling could evaluate salmonid population viability under future climate scenarios or water management regimes.

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APPENDIX

For ectothermic organisms, such as salmonids, temperature represents the foundational variable which parameterizes biological interactions from the molecular to the ecosystem scales (Hochachka & Somero 2002). The quantity of research on the role of temperature in structuring patterns of life is vast, therefore prior to evaluating the specific relationship between temperature and California salmonids it is important to summarize what is known about the role of temperature both physiologically and ecologically.

Biological Scales

Temperature influences organisms across spatial scales from molecules to ecosystems. This is important to consider because thermal capacity can influence an organism's ability to thrive, tolerate, or adjust to environmental temperatures which span multiple biological scales. Fundamentally, temperature is a measure of the kinetic energy of particles. Increasing or decreasing temperature respectively increases or decreases the chaotic motion of particles. On the molecular level, temperature influences the velocity and frequency at which molecules interact and subsequently the rates of chemical reactions. At this scale, temperature defines the functioning of proteins, the speed of enzymatic reactions, the permeability and pliability of cellular membranes and the solubility of molecules (Hochachka & Somero 2002). On the organismal level, temperature influences growth rate, digestion, and development (Angilletta 2009). At the scale of ecosystems, organisms experience a variable thermal landscape from which to occupy different thermal habitats. The dispersal of organisms through the thermal landscape structures predator-prey dynamics, the spread of pathogens, reproductive efficacy, progeny dispersal, growth, and, ultimately, fitness. When evaluating the thermal performance of organisms, the influence of temperature across scales must strongly be considered. Physiological studies illuminate how temperature affects organisms from the bottom-up while ecological studies can explore top-down effects.

Acute vs. Chronic

Temperature is rarely a static environmental variable. Instead, it is dynamic across multiple time scales. For many organisms, temperature fluctuates diurnally and seasonally. For ectotherms, response to temporal thermal change is a constant process of adjustment. Subject to environmental temperature, ectotherms like fish must be physiologically capable of coping with thermal change as there are fitness costs associated with failing to do so. Physiological responses to environmental temperatures fall into two categories: chronic and acute (Hochachka & Somero 2002; Schulte et al. 2011). Chronic temperature change occurs on a time scale fitting acclimation: several days to weeks. Therefore, an organism's viability in response to a chronic temperature condition relies upon its ability to acclimate its internal biological processes. Conversely, acute temperature change occurs on a time scale too rapid for acclimation, usually seconds to days. On this scale, organismal viability is determined by the organism's intrinsic capacity to tolerate temperature change in the moment. An organism's physiological capacity to survive either acute or chronic temperature exposures is derived from an assortment of physiological traits. Neither acute nor chronic temperature exposure alone can adequately explain an organism's thermal tolerance. Therefore, when considering organismal temperature performance, both aspects of thermal capacity should be assessed.

Thermal Performance Curves

Environmental temperature has a ubiquitous influence on the biology of organisms, operating, often oppositely, on a variety of different mechanisms across biological scales (Hochachka & Somero 2002). Thermal Performance Curves (TPC, Figure 2) provide holistic insight into the emergent influence of temperature on relevant organismal traits that may otherwise be absent when investigated on the cellular or molecular scale (Schulte et al. 2011). In fishes, it has been widely reported that performance of a given physiological trait (e.g. swimming speed, metabolic rate, heart rate, growth) changes across a range of temperatures. When the relationship between temperature and trait performance is plotted it creates a TPC. Most TPCs share a common shape. At low temperatures performance is typically low. As temperature increases, so does trait performance, peaking at an intermediate value. Past this peak, performance in the trait quickly declines (Huey & Stevenson 1979). The absolute magnitude of these curves is impacted by ration but the relative performance between populations and/or species derived in the lab may be translatable to the relative performance in the field. Points along TPCs can provide a suite of information about how temperature influences a given physiological trait including: optimal temperatures, optimal thermal windows, sub-optimal and critical temperatures. Additionally, the relative shape, height, skew, and alignment of a TPC across a thermal spectrum may provide additional insight into the influence of temperature on physiological performance (Farrell 2016). Comparisons of TPCs between groups (i.e. species, populations, acclimation groups) can provide understanding as to how a trait may be influenced by thermal adaptation or acclimation (Eliason et al. 2011). For further information on TPCs see Schulte et al. (2011)

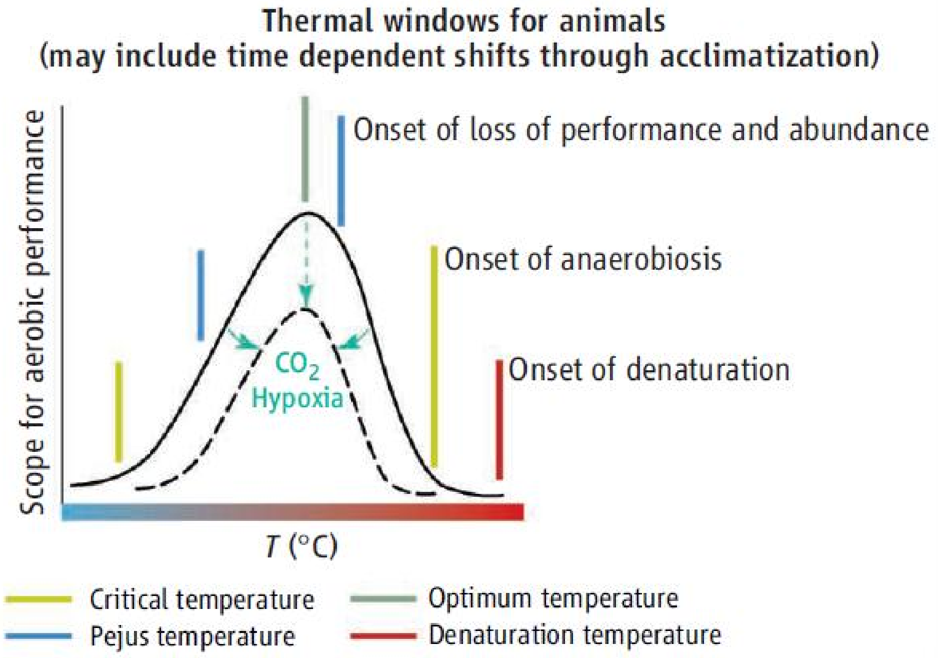

Figure 2: Thermal Performance Curve Modified from Pörtner and Farrell (2008). Shows optima, pejus (turning worse) and critical temperatures for an ectotherm across a thermal gradient. Additional environmental factors such as CO_2 or hypoxia can modify the TPC and therefore the associated optima, pejus and critical temperatures.

Physiological Metrics

The field of ecophysiology has developed a large suite of experimental methodologies that reveal different aspects of an organism's thermal profile. As described above, thermal physiology is constituted by a complex and dynamic set of traits which are influenced by factors spanning the sub-cellular, organismal, and ecosystem scales. To adequately characterize the thermal physiology of an organism, population, or species, a broad array of experimental methodologies (both laboratory and field) should be implemented. Below we introduce several commonly assessed physiological traits and address their application as well as shortcomings.

Critical Thermal Maximum/Minimum, i.e. Lethal Limits

Physiological thermal limits can be determined with critical thermal maximum/minimum (CTMax/CTMin) experiments. CTMs assess the upper or lower lethal temperature for an organism undergoing acute thermal exposure. For fish, experiments are conducted by quickly increasing or decreasing the surrounding water temperature (~.3 °C*min^{-1}). The CTM is the water temperature at which ecological death occurs (i.e., the inability to maintain equilibrium and an upright orientation) (Becker & Genoway 1979).

Critical thermal limits under chronic temperature exposure can also be quantified. Chronic thermal maximum/minimum experiments are used to determine at what temperature long-term exposure to elevated or lowered water temperatures results in mortality. Generally, water temperature is directionally modified slowly (~1 °C*day^{-1}) and daily mortalities are recorded (Fields et al. 1987). These experiments can reveal the upper or lower thermal bounds of acclimation in a laboratory setting.

Aerobic Scope

Aerobic scope is a measurement of aerobic metabolism and is calculated by determining the differential rate of oxygen uptake by a fish in a resting state and at a state of maximum exertion (Clark et al. 2013). These measurements are iterated across an ecologically relevant thermal gradient to produce a TPC describing the influence of temperature on aerobic metabolism. Measuring aerobic scope can provide insight into how environmental temperature influences the energy budget available for growth, migration, development, and immune response, as examples. Detailed information into the measurement of aerobic scope and its application to eco-physiological research can be found in Clark et al. (2013) and Norin & Clark (2015).

Temperature Dependent Growth Rate

Growth rate is a widely measured trait and conceptually simple to acquire. Growth rate can be measured both in laboratory or field settings, provided an appropriate sampling strategy. In fish, typically mass and length are repeatedly measured over time to assess how experimental (Geist et al. 2006) or field (Jeffres et al. 2008) conditions influence growth . These two metrics can be combined to produce condition factor. Condition factor is conceptually similar to the body-mass index (BMI) used in humans, and captures the proportional relationship between mass and length. Growth studies can reveal what temperatures or combination of environmental variables lead to enhanced or reduced growth. While simple to measure, the sheer number of growth x condition permutations (e.g. acclimation temperature, age, feed ration, or food quality, etc.) make standardization and comparison between studies difficult. Growth studies when compared across temperatures can provide insight into the conditions which yield optimal growth. While field studies represent realistic environments, other environmental variables besides temperature can often influence growth (e.g. density, species interactions, food, etc.). Conversely, laboratory studies offer a highly controlled environment but ultimately lack many of the factors which can influence growth in a natural environment. As such, it should be noted that field growth conditions and laboratory growth conditions are rarely equivalent. Growth data from both types of studies should only be carefully compared and used to inform management.

Preference

Ectotherms inhabiting a thermally heterogeneous environment may occupy a variety of thermal conditions. Selection of any given temperature may be determined by several factors including, endogenous energy stores, developmental stage, availability of prey, predation risk and competition. Thermal preference is typically measured by exposing a fish to a thermal gradient and recording the fish's position within the gradient. The temperature region where a fish resides is its thermal preference. Thermal preference may or may not be the same as the optimal growth temperature or the aerobic scope derived metabolic optimum. Therefore, temperature preference offers holistic insight into thermal capacity that includes physiological traits as well as environmental conditions and behavioral responses. For examples of temperature preference studies in California see (Welsh et al. 2001; Cocherell et al. 2014).

Heart Rate

Heart rate is an important physiological metric for understanding thermal tolerance. For fishes, it is theorized that capacity for thermal tolerance is determined by an individual's ability to supply tissue with oxygen (Pörtner & Knust 2007). Heart rate represents an important factor in determining an organism's oxygen delivery capacity and therefore, their aerobic scope and thermal capacity. Heart rate can be measured non-invasively on captive fish via a submerged electrocardiogram (Casselman et al. 2012). Two important aspects of heart physiology that can be measured in this way are maximum sustained heart rate and occurrence of heart arrhythmia. Sustained maximum heart rate can identify the range of temperatures at which a fish exhibits maximal oxygenation, while the onset of arrhythmia implies cardiac failure and upper thermal limits (Muñoz et al. 2014). (Cech & Myrick 1999)

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