

Central California Coast Steelhead Regional Temperature Study

Technical Review Panel Recommendations



May 2023

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Report availability

This report is available on Valley Water's Regional Temperature Study website (<https://www.valleywater.org/learning-center/healthy-creeks-and-ecosystems/steelhead-regional-temperature-study>) and SFEI's projects website (www.sfei.org/projects).

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Steelhead trout (photo courtesy of Oregon State University via Wikimedia Commons)

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Technical Review Panel

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1. Introduction

1.1 Background

In South San Francisco Bay, the Santa Clara Valley Water District (Valley Water) owns and operates water supply facilities on several creeks for urban and agricultural users. Many of these creeks support steelhead trout (*Oncorhynchus mykiss*) belonging to the Central California Coast (CCC) Distinct Population Segment (DPS), which is listed as threatened by the National Marine Fisheries Service (NMFS) under the Endangered Species Act (NMFS 2016). In 2018, the San Francisco Bay Regional Water Quality Control Board (RWQCB) recommended revising the Clean Water Act Section 303(d) list of impaired water bodies in California to include Los Gatos Creek downstream of Lexington Reservoir (henceforth called lower Los Gatos Creek), which is one of the creeks managed by Valley Water for water supply. The RWQCB concluded that periods of elevated water temperature on lower Los Gatos Creek were inconsistent with supporting cold freshwater habitat and steelhead migration. Both are beneficial uses of the creek (RWQCB 2019).

The listing of lower Los Gatos Creek as temperature impaired was based on water temperature measurement comparisons with several water temperature evaluation guidelines. The water temperature measurements used in the assessment were collected hourly at 32 locations on lower Los Gatos Creek between 2000 and 2012 (RWQCB 2019). The temperature evaluation guidelines used to assess impairment to steelhead were:

- 7DADM: The 7-day average daily maximum temperature, which is the rolling seven-day average of daily maximum temperatures compared to a threshold of 20°C (68°F) for the period March 11 through June 15 (steelhead out-migration period) (Shapovalov and Taft 1954; USEPA 2003).
- Lethal: Days for which the temperature, at any time, exceeded 24°C (75.2°F) from March 1 through October 31 (Carter 2008; Moyle 2002; USEPA 1977), a temperature associated with lethality for steelhead.
- MWAT: The maximum weekly average temperature from March 1 through October 31 (summer rearing for steelhead) at each station for each year compared to 19.6°C (67.3°F) (Sullivan et al. 2000).
- 7DAVG: The rolling seven-day average temperature from March 1 through October 31 (summer rearing for steelhead) compared to 17 °C (62.6°F) (Sullivan et al. 2000).

The RWQCB concluded that lower Los Gatos Creek should be listed as impaired for temperature because the values for 7DADM, MWAT, and 7DAVG were found to exceed the guideline temperature thresholds approximately 17% of the time (see RWQCB 2019 for more details).

In a letter to the State Water Resources Control Board (SWRCB) on April 30, 2020, Valley Water provided comments on the initial recommendation for listing Los Gatos Creek as temperature impaired (Valley Water 2020). The review indicated that the temperature thresholds used in the listing decision were inappropriately applied to Los Gatos Creek for several reasons:

- Valley Water pointed out that only temperature data from the summer and fall were assessed, and omitted data from the entire steelhead out-migration period. This omission could potentially inflate the proportion of temperature exceedances.
- Valley Water also stated that the steelhead temperature thresholds were inappropriate because they were developed for rivers in Washington, Oregon, and Idaho (USEPA 2003). They further stated these metrics would not be directly applicable to Los Gatos Creek, which naturally experiences warmer temperatures than Pacific Northwest rivers.
- Valley Water concluded that the choice of temperature evaluation guidelines is critical in determining temperature impairment for steelhead. Furthermore, they concluded higher temperature thresholds, currently available in peer-reviewed literature from studies conducted in watersheds similar to Los Gatos Creek, could have been used, resulting in a different outcome regarding impairment.
- Valley Water therefore suggested that the SWRCB direct the RWQCB to work with Valley Water on a regional scientific study to determine appropriate temperature evaluation guidelines for CCC steelhead. The results of the study would be directly used for a future assessment of the suitability of Los Gatos Creek for steelhead survival and migration.

On October 20, 2020, the SWRCB approved the recommendation by the RWQCB to revise the Clean Water Act Section 303(d) list of impaired water bodies in California to include lower Los Gatos Creek due to elevated water temperatures impairing cold freshwater habitat (COLD) and migration (MIGR) beneficial uses (SWRCB 2021). The listing resolution also states that Valley Water intends to coordinate with the RWQCB and interested stakeholders in conducting a two-year temperature study that assesses regionally-appropriate temperature evaluation guidelines for water bodies with CCC steelhead affected by Valley Water operations. The resolution states that the results could potentially be useful for reassessing the listing of Los Gatos Creek as temperature impaired during a future listing cycle. The State Water Board submitted this listing decision as part of the 2018 303(d) List to the United States Environmental Protection Agency (USEPA). USEPA accepted this listing decision thereby agreeing with the listing of Lower Los Gatos Creek for temperature.

Following the release of the SWRCB resolution regarding the lower Los Gatos Creek listing, Valley Water and the RWQCB worked to define the goals and desired outcomes of the regional temperature study (RTS). Through a series of conversations, it was decided that the RTS would focus on:

- identifying available temperature data related to the requirements for CCC steelhead

both within the Valley Water service area and throughout the DPS;

- conducting initial analyses of water temperatures suitable for CCC steelhead throughout the DPS; and
- developing recommendations for scientific studies that could be used to refine protective temperature evaluation guidelines for cold freshwater habitat (COLD) and migration (MIGR) beneficial uses, as well as spawning (SPWN), that are directly applicable to CCC steelhead, as opposed to the Pacific Northwest. Study recommendations could then be implemented after the completion of the RTS, and findings of these studies used to assist the RWQCB with future temperature listing evaluations.

1.2 Overview of the Regional Temperature Study (RTS)

The RTS included the following participants:

- Valley Water - the lead organization who developed the RTS work plan, coordinated with the RWQCB to set goals and desired outcomes, and provided funding for advisors and consultants.
- Technical Review Panel (TRP) - the TRP consisted of four renowned and impartial scientists with expertise in ecology of California fishes, temperature criteria for salmonids, and hydrology/water temperature modeling. The TRP convened several times over the course of the RTS to review work products and give input on protective temperatures for CCC steelhead (details provided below). San Francisco Estuary Institute (SFEI) was contracted by Valley Water to assemble the TRP and facilitate the TRP meetings and work products.
- RWQCB - coordinated with Valley Water throughout the study on goals and desired outcomes, reviewed the study work plan, and attended TRP meetings.
- Other regulatory agencies - representatives from NMFS, USEPA, California Department of Fish and Wildlife (CDFW), North Coast Regional Water Quality Control Board (NCRWQCB), and SWRCB attended TRP meetings and provided input on study goals and desired outcomes.
- The public – were invited to the final TRP meeting and provided input on TRP recommendations.

The RTS consisted of two distinct phases over the two-year time period:

- Phase 1 focused on information gathering and preliminary analyses. Within this phase, Valley Water engaged Stillwater Sciences to identify and use existing data sets to evaluate stream temperatures within the CCC DPS and how they might influence the presence, density, and the body condition of CCC steelhead. Stillwater also recommended studies that could be used to refine temperature evaluation guidelines for CCC steelhead (see Stillwater 2023).

- Phase 2 focused on the TRP convening several times (with regulatory agency representatives and the public, and in private) to review RTS work products, assess the key considerations for protective temperatures for CCC steelhead, and develop ideas for studies that could help provide useful information for refining protective temperature guidelines for CCC steelhead.

To help focus the TRP's efforts within the RTS, Valley Water and the RWQCB developed the following three Guiding Questions:

1. What key factors must be considered when determining protective temperatures that support CCC steelhead cold freshwater habitat (COLD), migration (MIGR), and spawning (SPWN) beneficial uses in the study area (e.g., life stages, thermal adaptation and acclimation, food availability, predation by and competition with other fish species, disease, seasonal habitat conditions, etc.)
2. Valley Water, San Francisco Bay RWQCB, and other regulatory agencies are seeking to improve the thresholds associated with protective temperatures that support CCC steelhead COLD, MIGR, and SPWN beneficial uses in the study area. What information could improve the protective temperature thresholds?
3. What new data collection and/or experimental or modeled data analyses should be considered for providing information that could improve the protective temperature thresholds for CCC steelhead in the study area? How should the analyses be prioritized?

Here, "protective temperatures" are defined as temperatures that support steelhead and are beneficial as they perform the necessary activities for completing their life cycle. Protective temperatures, however, need not be optimal temperatures that maximize an activity because winter temperatures, for example, may be naturally below an optimal temperature for an activity. "Protective temperature thresholds" are therefore defined herein as the temperatures or temperature ranges that, when exceeded, would result in impairment to activities necessary for completing their life cycle.

1.3 Overview of this Recommendations Memo

This memo contains the TRP's answers to the above Guiding Questions. Thoughts are provided on the key factors that need to be considered when assessing protective temperatures for CCC steelhead. Also, details are provided on recommended field, laboratory, and modeling studies that could help refine protective temperature guidelines for COLD, MIGR, and SPWN beneficial uses of CCC steelhead. These recommendations can be used to guide future research priorities for Valley Water, RWQCB, SWRCB, USEPA, and other interested parties.

2. Guiding Principles for Assessing Protective Temperatures for Steelhead

Establishing protective temperatures for CCC steelhead begins by establishing clear guidance on the species-specific physiological and ecological traits as they relate to temperature impacts over a full steelhead life cycle (Quinn 2018). Therefore, we developed a set of Guiding Principles for the RTS, presented below, that reflect our thoughts on the traits of steelhead that need to be considered. These Guiding Principles provide the foundation for our answers to the Guiding Questions regarding protective temperatures for CCC steelhead in the subsequent section.

Guiding Principle #1 - Fundamentals of fish thermal physiology need to be appreciated and acknowledged so that the existing knowledge base for CCC steelhead trout can be placed within this broader context, and knowledge gaps identified.

Steelhead trout are ectotherms and cannot internally regulate their body temperature independent of their environment, as do endotherms such as birds and mammals. All the same, behavioral preferences for thermal microhabitats are possible and are evident in steelhead and other salmonids; these may lead to behavioral thermoregulation (Keefer et al. 2018). For example, behavioral thermoregulation has been observed in the short-term selection of habitats dominated by cool groundwater inputs by adult migrating steelhead (Farrell et al. 2009), and over the long-term by selecting the time of year that up-river migration occurs (Eliason et al. 2011; Quinn 2018). Steelhead populations that can spawn in winter months when stream temperatures are cooler are a good example of this latter strategy, and they may be genetically adapted to such conditions. However, while behavioral selection of cool water temperature has benefits (e.g., a reduction in the energy needs for basal life), there are trade-offs (e.g., absolute swimming speed is reduced and remaining at a cooler temperature for too long could result in thermal acclimation, see below) (Spina 2007).

Like all salmonids, steelhead need oxygen for all activities, even the very brief burst activities that delay oxygen usage until after the activity when metabolic costs are repaid (Lee et al. 2003; Zhang et al. 2018). The maximum rate at which an individual salmonid can supply oxygen for activities above its basic (or basal) needs is called its aerobic scope. Thus, oxygen is apportioned to activities within the constraint of maximum aerobic scope, including the oxygen cost of growth. Indeed, thermal dependence of growth is correlated with metabolic scope (i.e., oxygen availability for activity) (Neubauer & Anderson 2019). Therefore, knowing metabolic scope as a function of temperature is a very valuable predictive tool (Farrell et al. 2008), as are growth rate, swimming performance, and survival.

Maximum aerobic scope at a given temperature is typically observed (measured) during sustained swimming activity, or following burst swimming activity, or after eating a large meal

(post-prandial) (Little et al. 2020). Strains of *O. mykiss* with higher aerobic performance have been shown to have higher hypoxic tolerance (Zhang et al. 2018). Aerobic performance is limited at temperature extremes that are several degrees below those temperatures that are acutely lethal (e.g., CT_{max}) (Farrell 2016; Adams et al. 2022), and the thermal limitation on aerobic scope could therefore have direct ecological relevance if it were known for CCC steelhead. That said, the interaction of changing metabolic rates, other metabolic support systems (e.g., cardiac performance or energetics), and species ecological requirements may ultimately result in genetically-based adaptations to tolerating higher temperatures.

Thus, it is now possible to routinely measure the temperature dependence of aerobic scope, as well as the basic oxygen needs of salmonids, both in laboratory and field settings. Figure 1 illustrates a thermal performance curve (TPC), the graphical relationship between temperature and biological rate processes. Aerobic scope is a form of TPC. The shape of a TPC, and that for aerobic scope, can vary among species (adaptation; Farrell et al. 2009) and with acclimation temperature (typically a period of weeks at a single temperature; Adams et al. 2022). As a metabolic activity, growth too has a TPC, which may differ from that for aerobic scope, as can the oxygen cost of other activities such as eating a meal (Adams et al. 2022). Regardless, a certain level of aerobic scope is required to perform any activity. How fish apportion and prioritize aerobic scope among their many activities is important (Farrell 2016).

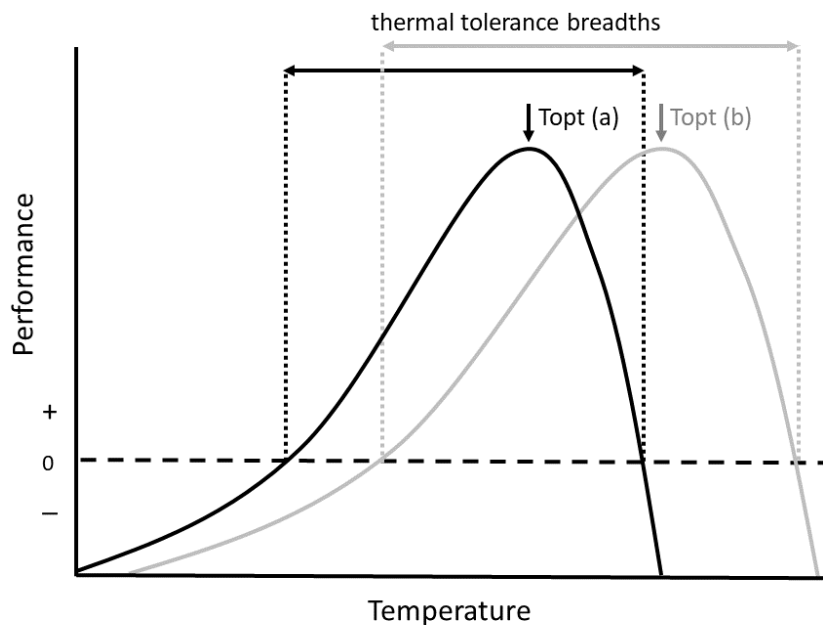


Figure 1. Hypothetical thermal performance curves (TPC). a) TPC for population acclimated or adapted to a mid-temperature range. b) TPC of a warm-acclimated or warm-adapted population with a broader thermal tolerance. A different TPC exists for different activities, populations, species, and life stages. Peak performance is not necessarily equal between curves, but is shown as equal here for demonstration purposes.

Finally, the CCC steelhead temperature tolerance study conducted as part of the Regional Temperature Study (Stillwater Sciences 2023) suggests a TPC for fish condition that differs from that published for more northern populations. By examining *O. mykiss* throughout the DPS range, the study showed habitat water temperatures ranging from 12 to 20°C. Moreover, the body condition of nearly all fish examined was determined to be in “good condition” regardless of temperature when evaluated against a larger database of fish size collected from southeastern Alaska through central California. The authors, therefore, suggested that despite being exposed to water temperatures higher than those often considered by regulators as optimal for growth (e.g., 18°C), fish routinely consumed enough prey to account for the increased basal metabolic demands associated with higher temperatures or that these fish had increased aerobic capacity compared to more northern populations (Stillwater Sciences 2023). The authors further noted that *O. mykiss* can experience increased growth rates at higher temperatures if there is enough prey available, but there was no ability to test this within the Stillwater Sciences data analysis due to lack of information on prey availability. Regardless of the exact mechanisms, the Stillwater Sciences study showed that CCC *O. mykiss* are doing well with respect to growth and condition at water temperatures higher than would be considered protective of Pacific Northwest populations.

Guiding Principal #2 - The difference between thermal adaptation and thermal acclimation needs to be recognized and considered in setting temperature guidelines.

Fish genetics set the limits of environmental conditions in which fish can or cannot live, and they are adapted to tolerate and survive a certain range of temperatures. Consequently, the expectation and experimentally determined reality is that different fish species are adapted to exist in and thrive at different ranges of water temperature. This variability in thermal ranges extends to different populations and stocks of the same species, as well as subspecies (Fangue et al. 2006; Fangue et al. 2008; Schulte et al. 2011; Eliason et al. 2011; Chen et al. 2015; 2018; Zhang et al. 2018; Adams et al. 2022).

A population of fish can also adapt to local temperature conditions over time if they are genetically isolated, as alluded to in the EPA Region 10 Guidance for Pacific Northwest State and Tribal Temperature Water Quality Standards (USEPA 2003) report used as guidance for the lower Los Gatos Creek temperature impairment listing. Today, many examples exist of different TPCs among closely related fish species. Notably, the redband trout (*O. mykiss gairdneri*), a rainbow trout subspecies which has been geographically isolated in desert conditions for many generations, is far more tolerant of high temperature than its founding *O. mykiss* relatives common to coastal PNW (Chen et al. 2015; 2018). In addition, sockeye salmon (*O. nerka*) populations in the Fraser River, Canada have TPCs for aerobic scope, heart rate, and cardiac output that appear to be tailored to the upstream migration conditions that they typically encounter (Eliason et al. 2011; 2013). Also, killifish that extend over the eastern coasts of Canada and the United States have two subpopulations with different TPCs, and a hybrid zone between them (reviewed in Schulte et al. 2011).

The clear implication of thermal adaptation within a species is that protective temperature ranges must be based on data collected from that species using relevant or appropriate surrogate populations or stocks. Extrapolating from other species, populations, or stocks may provide only generalities rather than site-specifics.

Layered on to these genetic differences is phenotypic plasticity, which is the ability of an individual fish to reversibly acclimate to given temperatures over periods of days to several weeks at that new temperature via biochemical adjustments. Phenotypic plasticity, naturally, is constrained by a fish's genetics. Moreover, a fish may not fully express its maximal performance potential at a given acclimation temperature, which is the basis of TPCs. Many activities do have a thermal optimum, the temperature at which that activity is best performed, and not all activities have the same thermal optimum (e.g., egg fertilization vs. larval growth). Thermal acclimation can shift the thermal optimum for a TPC. It can also shift maximum performance. Warm acclimation can benefit fishes, for example, by increasing peak heart rate and increasing the body temperature threshold for the onset of cardiac arrhythmia (Farrell 2016). Thus, warm acclimation benefits life supporting activities. Yet, protective temperatures need not be optimal temperatures for an activity. Winter temperatures, for example, may be naturally below an optimal temperature for an activity. An optimal temperature then acts as a 'central' reference point within a protective temperature range.

Taken together, a fish's thermal acclimation and adaptation responses are shaped by their evolutionary history and by local thermal regimes and it is the interplay between these two processes that define a fish population's ultimate sensitivity to environmental temperatures.

Short term (acute) temperature exposures similarly affect the rate at which activities can be performed. Cold temperatures slow swimming speed and slow digestion rate, for example, whereas a warmer fish can swim faster and digest a meal faster. Nevertheless, there are limits to acute exposures of temperature extremes. In fact, fish can resist such thermal extremes for only a few minutes. These extreme temperature limits are called the critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}), for extreme cold and hot, respectively. Therefore, life at CT_{max} is very much time limited. While CT_{max} and CT_{min} values are generally several degrees beyond functional TPCs, they are useful thermal indices for species comparisons because they can be easily measured experimentally and they are positively correlated with thermal sensitivity.

Guiding Principal #3 - Acclimation temperature can alter the resistance to thermal extremes as well as the thermal performance of activities.

In general, CT_{max} and CT_{min} increase with acclimation temperature (Chen et al. 2015). The changes in CT_{max} and CT_{min} with acclimation temperature act as the upper and lower boundary conditions for life-supporting activities, as illustrated by the thermal tolerance polygon (or Fry polygon) in Figure 2. The performance of life supporting activities lie within the bounding

polygon, indicating that some activities are more thermally sensitive than others, having higher or lower thermal limits than other activities. For example, in Figure 2 the reproduction activity generally has a lower thermal range than digestion. The shape and size of these polygons also change with life stage, where stages from eggs to adults have unique thermal sensitivities.

While thermal polygons are a well-established principle for understanding the relationship between acclimation temperature and fish activities, the USEPA (2003) report only briefly touched on them. Informed thermal criteria for salmonids should take advantage of such information, which has become increasingly available in the literature. However, such information is lacking for steelhead in Los Gatos Creek and throughout the CCC DPS.

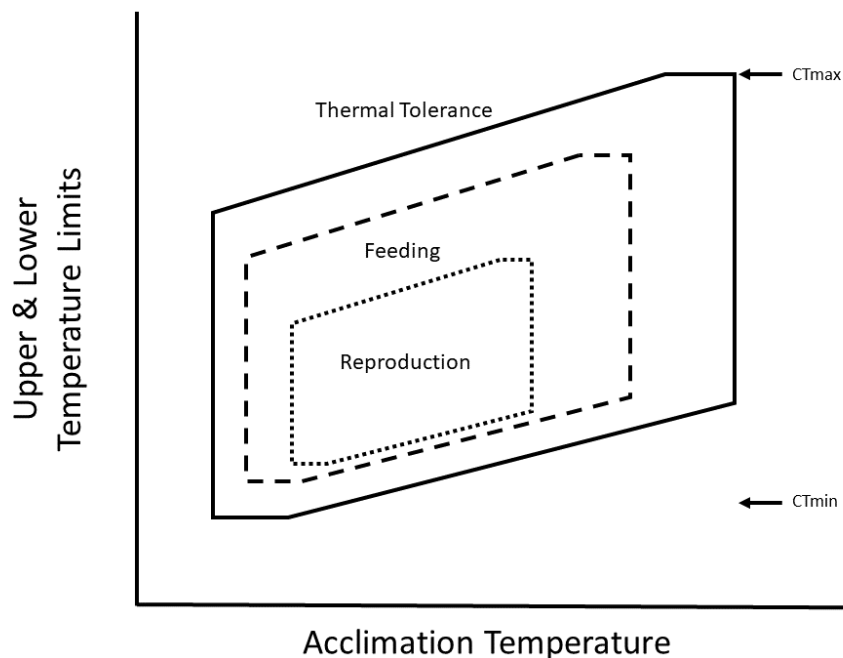


Figure 2. Thermal tolerance polygon (or Fry polygon) showing the relationship between upper and lower temperature limits (range) for given functions (e.g., reproduction, feeding or thermal tolerance) versus acclimation temperature.

Guiding Principal # 4 - A basic understanding of optimal temperatures and the limits for their application is needed.

Optimal temperatures are those that allow maximum physiological performance for a given activity, such as swimming, feeding, or reproducing. Indeed, different activities may have different optimal temperature ranges. Juvenile salmonids, for example, may forage most efficiently at a higher temperature than is optimal for digestion, so it may pay to find cooler water (e.g., a spring inflow) after a foraging bout. It is therefore imperative to have population-specific TPCs that span a fish's full thermal range at hand when establishing biologically relevant temperature guidelines.

Fixation on a single temperature is dangerous for several reasons. The first reason for not using a single number is that a TPC may not have a distinct peak such as that shown for adult salmon, to which a single optimal temperature (T_{opt}) can be reliably assigned (Lee et al. 2003; Eliason et al. 2011; 2013). For example, a California stock of steelhead has a remarkably flat TPC for aerobic scope, with a plateau extending to around 24°C (Verhille et al. 2016). Other fish species also show broad plateaus for aerobic scope TPCs (Fangue et al. 2008; reviewed in Zillig et al. 2021; Poletto et al. 2017; Ferreira et al. 2014), with brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) having broader peaks than those of sockeye salmon, for instance (Farrell et al. 2009). The width of the T_{opt} plateau can even vary with acclimation temperature (Ferreira et al. 2014).

The second reason relates to ecological relevance. Under natural conditions, fishes living in temperate climates rarely spend their life at a T_{opt} for any single activity. For example, seasonal changes, short term warm and cool weather conditions, and diel meteorological conditions all result in notable water temperature variations that dictate the TPCs. Therefore, there are ecologically relevant trade-offs to optimizing a TPC. Growth at colder winter temperatures will typically be slower than during warmer summer temperatures in part because fish are living at a sub-optimum temperature for aerobic scope. Fish may have to choose to experience sub-optimum elevated temperatures for their survival by seeking out cold water refuges (e.g., springs) during the warmer periods of the year. Migrating adult salmon do this to conserve body stores of energy en route to spawning areas (Hinch et al. 2022). Conversely, by selecting supra-optimum habitat temperature a fish can benefit from the higher photosynthetic rate (and food availability) that it supports. For sockeye, in such instances, the warmer waters may also contain predators with a higher T_{opt} who therefore have an overall advantage.

Ultimately, a temperature range should be used as a guide for assessing protective temperatures for CCC steelhead over their full life cycle rather than a single, fixed T_{opt} value.

3. Technical Review Panel Answers to the Guiding Questions

Guiding Question #1: What key factors must be considered when determining protective temperatures that support CCC steelhead coldwater freshwater habitat (COLD), migration (MIGR), and spawning (SPWN) beneficial uses in the study area (e.g., life stages, thermal adaptation and acclimation, food availability, predation by and competition with other fish species, disease, seasonal habitat conditions, etc.)?

We think that there is a set of primary and secondary factors that need to be considered when determining protective temperatures for CCC steelhead:

Primary factors

- **Gene flow** - Accounting for gene flow (the movement of genes into and out of a population) and hybridization among populations is important when assessing protective temperatures. Understanding gene flow will help to determine the degree to which genetic diversity can be affecting CCC steelhead adaptations to temperature in locations throughout the DPS range. Quantifying genetic diversity includes assessing gene flow among CCC sub-populations and among CCC steelhead and steelhead from adjacent Distinct Population Segments, requiring a thorough knowledge of population structure of these fish.
- **Thermal adaptation and acclimation** - As stated above in the Guiding Principles, adaptation and acclimation are key to understanding protective temperatures for CCC steelhead because there can be considerable variability within a regional population. It is important to determine how traits such as metabolism, swimming performance, and aerobic capacity are different in CCC steelhead sub-populations that are adapted or acclimated to different temperatures. In addition, it is important to consider the range of temperatures each fish encounters on hourly, daily, weekly, and longer basis, together with factors such as food supply that influence their condition and overall ability to survive. It would also be useful to predict how fish will respond to increasing temperatures caused by a warming climate.
- **Life stage** - There is a need to consider how temperatures affect the ability of steelhead to complete their life cycle (e.g., what are the impacts of temperatures that reach the upper limits of tolerance?). There is also the need to consider what parts of a fish's life cycle are at play when temperatures are high. For example, during adult migration, steelhead are both swimming long distances and preparing for reproduction. It is important to understand how temperature affects an adult's ability to migrate to spawning grounds and an adult female's fecundity. It is also important to understand that duration of exposure to high temperatures affects each life stage differently.
- **Disease** - Understanding the impact of temperature on diseases that can be harmful to steelhead is an important data gap. Overall, disease severity caused by parasites in salmonids is heavily influenced by factors such as exposure concentration and duration, water temperature, and parasite virulence (Barrett and Bartholomew 2021). Many salmonid diseases can become virulent above 15.6 to 16°C (Jeffries et al. 2012; Lehman et al. 2020), and disease-induced mortality increases as temperatures rise toward the limit of salmonid growth (Richter and Kolmes 2005). However, the survival of the parasite *Myxobolus cerebralis*, the causal agent for salmonid whirling disease, has a lower presence of the mature parasite stage at higher temperatures (El-Matbouli et al. 1999). Conversely, harmful fungi such as *Saprolegnia parasitica*, which infects wounds on and eggs in salmonids, can show good growth at high water temperatures (Kitancharoen et al. 1996).

Secondary factors

- **Food availability** - Food availability and sources are important considerations when assessing protective temperatures for CCC steelhead. These fish can tolerate warmer temperatures when food is abundant, but juveniles can be absent from waters that exceed 25-26°C, even for short periods (Moyle et al. 2017). Yet, a study of hatchery steelhead from Washington (Connolly and Petersen 2003) found that under food-limited conditions, smaller juvenile steelhead were in poorer condition than larger steelhead at lower temperatures, but that the opposite was true at higher temperatures. Hence, the study suggests there can be a physiological advantage to being a small steelhead when temperature is elevated and food is scarce.

Abundant invertebrates, an important food source, are important to sustain a population of rapidly growing juvenile steelhead. Thus, there is a definite trade-off between warmer temperatures that can increase invertebrate production and feeding rates of fish, and decreased juvenile steelhead survival rates. The appetite of steelhead decreases at supra-optimal temperatures (Adams et al. 2022), as does growth rate (Myrick and Cech 2004), but these temperature thresholds are very much stock-specific. Smith and Li (1983) observed that, despite the increased energetic cost and potential stress, juvenile CCC steelhead moved into fast flowing riffles at relatively high temperatures because of high food availability.

- **Predation and Competition** - The susceptibility of juvenile salmonids to predation and their ability to compete for resources is sensitive to ambient water temperature (Zillig et al. 2021; McInturf et al. 2022). Native and non-native predators present in the CCC steelhead range with a higher temperature tolerance than steelhead could cause steelhead to behaviorally avoid warm waters because of predation risk. In a test of competitive dynamics, Reese and Harvey (2002) found that elevated temperatures (20–23°C) coupled with predation by and competition with Sacramento pikeminnow (*Ptychocheilus grandis*) reduced the growth of juvenile steelhead by 50% compared to their condition at elevated temperatures when pikeminnow were not present. However, steelhead growth was not affected by the presence of pikeminnow when juvenile steelhead were reared at lower temperatures (15-18°C). In a similar study, Reeves et al. (1987) showed that the growth rate of juvenile steelhead reared with redbside shiner (*Richardsonius balteatus*) at elevated temperatures (19–22°C) decreased by 54% compared with times when redbside shiner were absent. At lower temperatures (12-15°C), they found that growth rate was independent of redbside shiner presence. In general, sublethal effects of temperature on predation and competition risk for salmonids is poorly studied. Such effects deserve further research for setting CCC steelhead temperature guidelines because these effects may represent a considerable portion of thermally influenced biotic interactions (Zillig et al. 2021).
- **Oxygen** - Impacts of dissolved oxygen concentration on steelhead needs to be considered when assessing protective temperatures for CCC steelhead because temperature and the amount of oxygen in water are correlated. Temperature is

negatively correlated with dissolved oxygen concentration for most habitats occupied by steelhead (the concentration of oxygen dissolved in water decreases as temperature increases). However, low dissolved oxygen levels alone can have many negative impacts on fish development and performance (Carter 2005), as well as increasing the toxicity of contaminants such as ammonia, zinc, lead, and copper that are lethal to salmonids (Colt et al. 1979; Davis 1975). Further, while groundwater contributions to or hyporheic processes in streams often create cool water microhabitats (refugia) occupied by salmonids when ambient water temperature is high during summer months, these cold water sources can have low dissolved oxygen concentrations that limit their habitat value (Baker et al. 2000). In general, thermally-stressed salmonids often encounter a trade-off between thermal relief and increasing exposure to low dissolved oxygen waters, which can delay movement into refugia until river temperatures reach lethal thresholds (Kurylyk et al. 2015)

Guiding Question #2: Valley Water, San Francisco Bay Regional Water Quality Control Board, and other regulatory agencies are seeking to improve the thresholds associated with protective temperatures that support CCC steelhead COLD, MIGR, and SPWN beneficial uses in the study area. What information could improve the protective temperature thresholds?

Overall, we feel that there are still many data gaps regarding protective temperatures for CCC steelhead that should be addressed through focused studies that examine the range of factors influencing the thermal tolerance of steelhead specific to the CCC DPS. Foremost, USEPA (2003) is badly outdated and has been largely supplanted by peer-reviewed research findings over the intervening two decades; the USEPA report is especially weak in its coverage of intraspecific differences in thermal performance within the salmonid species, including steelhead. For example, the temperatures for migration for cold-adapted populations will be lower than for warm-adapted populations. Therefore, data need to be generated specifically for stocks to which the temperature guidelines will be applied.

As described above in the answer to Guiding Question #1, there is a range of factors that need to be considered when assessing protective temperatures for CCC steelhead. Yet, the amount of information available on these factors that is directly useful for determining CCC steelhead protective temperature thresholds is very limited. Thus, existing CCC steelhead genetics provide only limited information about genetic diversity and population structure (Garza and Pearce 2008). More information is needed not only on genetics but also on distribution, ecology, and behavior. There is also a paucity of information regarding how thermal adaptation and acclimation, life stage, and disease factors affect CCC steelhead protective temperature thresholds. For the environmental factors that need to be considered, there is some existing information about the tradeoffs CCC steelhead experience to get food at high temperatures (see Smith and Li 1983), but overall, there is currently little information about how protective temperatures for CCC steelhead are affected by food abundance, biotic factors (e.g., predation and competition), and oxygen availability. To effectively evaluate the impacts of temperature or

other factors in a given field or laboratory study, condition factor must be assessed in laboratory and field studies. Condition factor of a fish can give insight into how it is adapted or acclimated to an environment when evaluating physiology or behavior. Understanding how global warming affects water temperatures that CCC steelhead experience is also an important need.

Guiding Question #3: What new data collection and/or experimental or modeled data analyses should be considered for providing information that could improve the protective temperature thresholds for CCC steelhead in the study area? How should the analyses be prioritized?

There are four types of studies that provide useful information for addressing key data gaps and improving protective temperature standards for CCC steelhead:

- **Habitat conditions assessment** - Habitat conditions include physical habitat that support the various fish life stages (e.g., migration, spawning, egg incubation, rearing). Typical physical habitat conditions include flow, depth, velocity, substrate (natural and artificial), and cover. Other important habitat conditions to consider include water temperature and other water quality measures (e.g., dissolved oxygen). Developing a spatially and temporally appropriate water quality monitoring program that compliments fish population assessments would help define baseline conditions and provide information to support future management actions.
- **In situ experiments** - Observational data collection in the field or during experiments conducted in natural settings. Field experiments require careful design and execution to answer the specific hypothesis. Laboratory experiments are often remarkably helpful in developing field experiments.
- **Laboratory experiments** - Experiments conducted in isolated systems are useful for measuring factors of fish physiology and behavior. Laboratory experiments should consider observed conditions in nature, with the range of temperatures used reflecting those found within the CCC DPS. Further, test subjects should be sourced from varying populations, as physiology can vary between groups. To best understand the impact of temperature on *O. mykiss*, experiments should be performed on multiple life stages including eggs, juveniles, and adults. The focus should be on the life stages when temperature extremes are experienced in the first instance.
- **Mathematical modeling** - Data collected in the habitat conditions assessment would be used to develop models that can predict spatial and temporal responses of juvenile and adult steelhead to changing habitat conditions and temperatures. Potential models should be identified early in the process to ensure the appropriate data are collected to support model development.

Prioritizing studies should consider balancing the difficulty and cost of conducting each study with the value of the information or impact the study will provide. An Impact-Difficulty matrix,

Figure 3, can be used as a guide to assist decision-makers in identifying studies given available resources. Here, impact is defined as providing useful information for helping develop appropriate protective temperature evaluation guidelines for CCC steelhead. For example, studies with a relatively low degree of difficulty and a high, medium, or low impact could be considered the highest priority (shown in green below), whereas high and moderate cost projects with a low impact could be considered the lowest priority (shown in red below). Medium priority projects (shown in yellow) occupy the remainder of the matrix.

Impact	high			
	moderate			
	low			
		high	moderate	low
		Difficulty or Cost		

Figure 3. Impact-Difficulty matrix and classes (red indicates low priority, yellow indicates medium priority, and green indicates high priority).

Study Organization and Planning

To sufficiently understand protective temperatures for CCC steelhead, we recommend developing a series of focused studies to fill data gaps (summarized in Table 1 and described in detail below). The highest priority studies focus on genetics of the population, regional and reach-scale monitoring, and temperature adaptation and acclimation. We recommend that all studies be conducted within the region and with fish from streams within the CCC DPS or local hatchery fish. Where possible, steelhead from outside the CCC DPS should be included in adaptation and acclimation studies to determine if there are considerable differences with CCC steelhead.

These recommended studies will build a robust scientific understanding of steelhead populations in the CCC DPS and benefit short- and long-term management decisions of this endangered species and its habitat. The coordination of these efforts must be carefully organized and planned because information from each study can inform similar or subsequent studies. There is also a need to accommodate important spatial and temporal scales associated with the biotic and environmental factors in the study area. We suggest beginning with a genetic analysis of steelhead in the region because it will inform all following monitoring, modeling, and

laboratory efforts. Further, we strongly recommend a review of the potential range of habitat models and associated data needs prior to implementing field monitoring programs. We also encourage coupling environmental monitoring and laboratory studies where possible. These combined efforts can inform models addressing flow, temperature, water quality, habitat suitability, mesohabitat dynamics, species distribution, and species survivability under varying conditions. Laboratory and field studies can be coordinated to utilize available resources effectively and efficiently.

Table 1. Summary of recommended focused studies

Study Category	Description	Priority Category
Genetic Survey		High
Monitoring and Modeling Studies	Regional Monitoring	High-Medium
	Synoptic Studies	Medium
	Reach-scale Monitoring	Medium-Low
	Thermal Refuge Assessment	Medium-Low
	Climate Change/Land Use Change Modeling <ul style="list-style-type: none"> WQ, habitat suitability, hydrologic connectivity 	Medium-Low
Laboratory Studies	Thermal Performance	High
	Growth	High
	Metabolic Advantage	Medium
	Oxygen	Medium
	Temperature Oscillation	High

Genetic Survey

Priority Category: High (high impact, low difficulty)

Questions to be addressed: What is the genetic structure of *O. mykiss* populations in the CCC DPS? How does this structure compare to that of populations in California and the PNW? Are there genetic differences among watersheds within the region? To what

extent do wild fish hybridize with hatchery fish? Are rainbow trout above dams residual steelhead that can play a role in conservation or are they genetically resident fish?

Overview: We recommend conducting widespread, nondisruptive tissue sampling via fin clip samples of fish in watersheds across the CCC DPS, which includes naturally spawned fish below barriers to anadromy from the Russian River south to Aptos Creek, including all drainages eastward to Chipps Island. Fin clip samples should also be collected on rainbow trout above barriers to anadromy within the CCC region to assess the proportion of the population with genomic evidence of anadromy using established genetic markers. Hatchery genetic information should also be gathered for comparative analysis to determine the degree of hybridization with wild fish and to help evaluate genetic structure of populations across watersheds. Finally, CCC steelhead trout genetic structure should be compared to other populations in California and across the Pacific Northwest. Comparisons with the South-Central California Coast and Southern California steelhead DPSs would be especially important because they would most likely have greater temperature tolerances than more northern populations.

The genetic analysis will inform all monitoring, modeling, and laboratory efforts recommended below. First and foremost, it will establish the degree to which CCC steelhead populations differ from those in the PNW. It will also help to understand the genetic differences and similarities between wild and hatchery fish. If wild populations show distinct genetic structure, laboratory studies conducted solely on hatchery fish will be insufficient for developing protective temperatures for wild fish. In that case, we suggest including small numbers of wild fish in laboratory studies to ground results. Similarly, populations within the region that show considerable genetic divergence also need to be represented. If genetic differences among CCC steelhead populations are small, then less representation of isolated wild populations is needed. However, some effort should be made to determine if *O. mykiss* in streams above dams are genetically similar to *O. mykiss* below to see if they can be used in place of CCC steelhead in studies.

Monitoring and Modeling Studies

There is a clear need to further assess CCC steelhead habitat and distribution in the region and to conduct a suite of laboratory and in situ experiments to determine how flow and stage, and water temperature and water quality, affect distribution and abundance of steelhead. We recommend developing a study plan that includes both a monitoring program and targeted field investigations. Field monitoring and assessment will require effort over an extended period (e.g., 10 years) to encompass a range of hydrology, meteorology, and fish utilization, while field investigations include, but are not limited to, physical habitat, water quality, fish distribution, and habitat utilization studies. This research should be conducted in a variety of reach types and across managed streams (i.e., streams managed for water supply and flood) and unmanaged streams and degrees of urbanization.

Regional Temperature and Stream Flow Monitoring

Priority Category: High-Medium (high impact, low-to-moderate difficulty)

Questions to be addressed: What are the stream temperatures and flows throughout the year across the DPS region (above and below barriers to anadromy) and how do they vary both daily and seasonally? Where, when, and how often and for how long do temperatures reach levels that negatively impact biological functions?

Overview: A continuous monitoring program should be implemented to collect data on stream temperature, flow, and dissolved oxygen (where possible). Probes collecting temperature and pressure transducers collecting continuous (e.g., 15-minute) data should be deployed throughout stream reaches in the region to characterize spatial and temporal conditions and used in conjunction with data from existing stream gauges. Data from these probes can be accessed and downloaded via field visits or set up to transmit remotely via telemetry. Collection of information throughout the year is important to characterize conditions throughout the various steelhead lifecycles, and additional focus on over-summering habitats can occur in months when elevated stream temperatures are of concern (e.g., April through October). Pressure transducers are used to monitor stage, which can be used in concert with flow measurements to develop stage-discharge relationships that can yield continuous time series of flow. Finally, sufficient spatial representation of meteorological stations to represent climate conditions in the area is necessary to pair with continuous stream temperature and stage data and to support modeling. Developing a data storage system to store temperature, flow, and meteorology data, and their associated metadata, is important to maintain high quality data, create a consistent data sharing process, and for data transparency to support sound and defensible scientific studies.

Synoptic Studies

Priority Category: Medium (moderate impact, high difficulty)

Question(s) to be addressed: Where and when are fish present or absent throughout the year within the CCC DPS region and what is the temperature, water quality, and food availability at each survey time?

Overview: Synoptic studies characterize conditions across the region and help identify trends. Continuous regional monitoring would be bolstered ideally by regular (monthly if possible) sampling of fish presence/absence, dissolved oxygen (DO), sampling of benthic and drifting invertebrates through driftnets, and other water quality indicators at multiple locations (e.g., near the locations of sensors for monitoring temperature and stage). This would involve a coordinated effort among agencies and researchers in the DPS region to collect a large amount of data over a large area in a short period of time. Examples include short duration, detailed studies (e.g., sub-daily information collected over a week), or longer duration studies where monthly surveys collect information

annually at multiple locations. Synoptic surveys should consider, and augment, other monitoring efforts, leveraging multiple efforts to increase characterization and understanding of the system.

Reach-Scale Monitoring

Priority Category: Medium-Low (moderate-to-high impact, moderate-to-high difficulty)

Questions to be addressed: How do temperature and fish distribution and abundance vary throughout a reach? What habitats are most fish selecting? What role does temperature play spatially and temporally (i.e., seasonally) in habitat selection, and are thermal refuges a seasonally important habitat? Are fish able to access cooler water microhabitats (refuges) when macroscale water temperature is high? Do dissolved oxygen or other water quality conditions influence fish distributions?

Overview: Understanding the dynamics of CCC steelhead habitat at the reach-scale and how fish choose to occupy and utilize that space is critical to developing management and recovery approaches. Reach-scale monitoring is intended to complement larger-scale regional temperature and flow monitoring efforts. Monitoring should encompass both wet and dry years and ideally include extreme events (e.g., drought, floods).

We recommend selecting a set of stream reaches across the region to conduct detailed habitat condition assessments. These would ideally be monthly, detailed reach-scale surveys to record flow, temperature, dissolved oxygen, fish abundance, and life stage (juvenile vs adult) throughout a reach. The effort would include evaluating conditions of fish thermal refuges and avoidance areas. Methods for fish observation can include bank observation, snorkeling, seining, and electrofishing.

This type of study informs development of protective temperature metrics by identifying key details related to steelhead behavior, adaptation, and acclimation. Reach-scale studies improve understanding of temperature variations (at the seasonal, short-term, sub-daily range) in streams, which will inform other studies, and potential interactions with other native and non-native aquatic species. These studies will also provide foundational information on the biology of other native fishes such as the Ohlone riffle sculpin (*Cottus ohlone ohlone*) (see Moyle and Campbell 2022).

Thermal Refuge Assessment

Priority Category: Medium-Low (moderate-to-low impact, moderate difficulty)

Questions to be addressed: What best characterizes a thermal refuge? Are thermal refuges important in CCC steelhead streams, especially during dry years? How are thermal refuges utilized by CCC steelhead? When do these refuges become ecological traps?

Overview: Once thermal refuges are identified in the reach-scale monitoring studies, a more detailed assessment can be conducted to quantify refuge habitat features including areal extent, depth, temperature, DO, and physical characteristics. The physical and ecological value of each refuge type should be determined and refugia should be assessed over time to determine the persistence and quality of each feature. This effort should also include the identification of “ecological traps,” where a refuge does not persist through the warmer period of the year. In such cases, fish may seek out a thermal refuge in early summer, become trapped as conditions warm, and ultimately perish later in the season. Characterizing the difference between refugia and potential ecological traps requires that temperature and dissolved oxygen, as well as other conditions (flow, habitat, predators, etc.) be monitored over the late spring through early fall.

Climate Change/Land Use Change Modeling

Priority Category: Moderate-Low (high impact, moderate-to-high difficulty)

Questions to be addressed: How are stream temperatures in steelhead-bearing streams expected to change in the future? Where in the region will impacts of climate change and land use change/urbanization be greatest on stream temperatures?

Overview: Simple numerical models can be used to predict the impacts of climate change and land use change on water temperature. Modeling analysis should include evaluation of changes to precipitation and subsequent base flow during the dry and wet season, dry season air temperature, and other important meteorological conditions; analyses should make inferences to changes to riparian vegetation conditions and seasonal shade. Modeling efforts should focus on understanding how physical conditions are expected to change (e.g., location of reaches with perennial flow that are expected to become intermittent) and the associated potential impact to steelhead habitat distribution and usage.

As a basic rule, habitat model selection follows system characterization, so this is a future phase of work after practitioners have a basic understanding of where fish are throughout the DPS region, during what times of year, and under what flow conditions and temperatures. Both regional and reach-scale monitoring efforts are needed for system characterization, and these should be conducted with specific modeling data needs in mind. A variety of modeling efforts can be implemented to address the range of questions to be addressed, including:

Temperature and water quality modeling: This type of modeling can be informed by reach-scale stream flow and temperature models. An appropriate temperature model would require flow and stage, stream morphology to define surface area and volume, and meteorological conditions to calculate temperature and rate of temperature change in streams. Water quality processes are generally a function of water temperature because many rate reactions and

processes are temperature dependent (Kim & Chapra 1997). Thus, water quality models (e.g., dissolved oxygen, nutrients, primary production) require the same set of information as temperature models, as well as appropriate field data for the represented water quality constituents to calibrate and test these models.

Temperature and water quality models assessing climate change can make use of climate change forecasts based on global circulation models to define the range of potential future meteorological conditions. Modeling can assist in identifying streams that are most vulnerable to climate-related temperature and water quality changes in the region.

Habitat suitability models: Models that predict the suitability of a stream location or reach based on observed relationships between steelhead and habitats can be developed for stream networks in the region. This would require field data such as flow and stage, stream morphology, water temperature, and habitat features (e.g., velocity, depth, substrate, cover, etc.) to be collected to populate, calibrate, and test the model. Some of these data needs overlap with other modeling efforts (e.g., temperature and water quality). Well-characterized thermal refugia can be extrapolated across systems using habitat modeling approaches, and assist in understanding the role of temperature refugia in a stream or watershed and identifying areas in need of protection or restoration.

Hydrologic Connectivity: Hydrologic connectivity refers to maintaining sufficient flow to provide physical, chemical, and biological continuity in a stream system throughout the hydrologic cycle or a critical portion of the hydrologic cycle. Studies have shown that when and where streams go dry can be predicted using hydrologic (Reynolds et al. 2015) and/or statistical modeling (Jaeger et al. 2019). Climate change may increase hydrologic variability, which could create challenges for migrating steelhead – an important consideration for steelhead that are iteroparous (able to spawn, return to the ocean, and later spawn again). Understanding and characterizing stream flow connectivity is important for predicting the potential risk of steelhead being unable to out-migrate. When adult (or juvenile) steelhead are unable to out migrate, identifying if and where sufficient summer habitat exists is necessary for management and restoration of existing stocks.

Laboratory Studies

Thermal Performance

Priority Category: High (high impact, low difficulty)

Questions to be addressed: What are the critical thermal maxima for CCC steelhead and their potential predator species? What is the optimal temperature window (range) for aerobic scope? How is swimming performance influenced by temperature? How do these values differ for migrating adults and juveniles?

Overview: Two primary physiological limitations to be evaluated in a laboratory experiment are the critical thermal maximum (CT_{max}) and the optimal temperature (T_{opt}) window for CCC steelhead. These can be determined by measuring aerobic scope, or respiratory performance, at a range of temperatures. The study should be designed to identify the temperatures that bound the optimal temperature window and evaluate how rapidly aerobic scope declines between the upper T_{opt} and CT_{max} . The resulting performance curve can be compared to other steelhead populations to determine if local adaptations exist. Multiple trials should be conducted to account for inter-individual variability. It would be valuable to also vary the duration of exposure to temperatures near CT_{max} in order to learn about the population's degree of tolerance.

Measurements of aerobic scope are often conducted in swim tunnels and can be an evaluation of swimming performance. We recommend studying swimming performance for both adults and juveniles in order to develop TPCs that could apply to migrating populations. This knowledge could then be used in management of adult and juvenile populations during migration periods.

We also recommend including other key native species that share *O. mykiss* habitat in this study. *O. mykiss* may be able to survive for short periods in extreme temperatures, but other species may not. When determining protective temperatures for steelhead the health of the community and ecosystem they inhabit must also be considered. Suggested species include the Ohlone riffle sculpin (*Cottus ohlone ohlone*) and southern coastal roach (*Hesperoleucus venustus subditus*). Both species are newly described so have not been well studied (Baumsteiger and Moyle 2019, Moyle and Campbell 2022). Amphibians should include both California red-legged frog (*Rana draytonii*) and foothill yellow-legged frog (*R. boylei*), in both tadpole and adult stages.

Metabolic Advantage

Priority Category: Medium (high impact, moderate difficulty)

Question(s) to be addressed: Do predator species have a thermal performance advantage over steelhead that significantly impacts steelhead survival at high temperatures?

Overview: We recommend a thermal metabolic advantage study to evaluate possible physiological advantages of known local predator fish species at warmer temperatures and gauge potential survivorship of juvenile steelhead. CCC steelhead may be able to survive in warmer temperatures, but as stream temperatures warm with climate change, they may experience higher rates of predation. Metabolic advantage experiments would include measures of burst speed and the ability to burst repeatedly, as well as aerobic scope for steelhead and predator fish such as largemouth bass (*Micropterus salmoides*) and striped bass (*Morone saxatilis*). Burst speed varies depending on how much a fish has eaten, so introduce varied feeding regimes into this study.

Growth

Priority Category: High (moderate impact, low difficulty)

Question(s) to be addressed: How does temperature affect growth rates of juvenile steelhead?

Overview: It is also important to conduct a growth trial for juvenile CCC steelhead. Groups of juvenile steelhead can be acclimated to different temperatures and fed at various rates to measure growth as well as aerobic scope. The impact of higher temperatures on growth rates will give an idea of survivability. Warmer temperatures allow for greater metabolic rates, which could increase growth rates. However, this knowledge must be incorporated into the broader context of habitat and oxygen availability as well as predation rates at these higher temperatures.

Oxygen

Priority Category: Medium (moderate impact, moderate difficulty)

Question(s) to be addressed: To what degree do CCC steelhead tolerate or acclimatize to hypoxic conditions at varying temperatures?

Overview: Dissolved oxygen (DO) is a known limiting factor for fish, and high-temperature water has a lower capacity to hold DO. While fish can tolerate low DO levels, they may only be meeting minimum metabolic demands, which can limit growth and increase risk of predation. We recommend a temperature-dependent hypoxia tolerance study that would evaluate how well CCC steelhead are adapted to—or able to acclimate to—hypoxic conditions.

It is also important to know the incipient lethal oxygen saturation (a measure of hypoxia tolerance) for CCC steelhead because this dissolved oxygen concentration is likely to occur more often at higher temperatures. This concentration will also help field researchers determine what constitutes an oxygen refuge. Coupling this information with reach-scale monitoring, we can determine the frequency and extent of hypoxic conditions at varying temperatures.

Temperature Oscillation

Priority Category: High (moderate impact, low difficulty)

Question(s) to be addressed: Do fish perform better with oscillating temperatures around a mean temperature (akin to diurnal variations typically experienced in CCC steelhead) or worse than with a stable temperature?

Overview: Once a baseline thermal tolerance is established for fish in this region, we can study performance under a variety of conditions. Stream temperatures vary over

time and space, and temperature oscillations mimicking those observed in monitoring data should be evaluated in laboratory experiments when possible. All studies listed above (CT_{max} , metabolic advantage, growth, and dissolved oxygen) would benefit from temperature oscillation by adding a layer of complexity that would bring results even closer to natural conditions.

4. Summary and Conclusions

As an outcome of the listing of lower Los Gatos Creek as temperature impaired for steelhead within the CCC DPS, Valley Water and the RWQCB worked with regulatory agency representatives and interested stakeholders to conduct a two-year Regional Temperature Study (RTS). The overall goal of the study was to assess regionally-appropriate temperature evaluation guidelines for CCC steelhead. As part of the RTS, the Technical Review Panel (TRP) reviewed RTS work products, assessed the key considerations for protective temperatures for CCC steelhead, and developed ideas for studies that could help provide useful information for refining protective temperature evaluation guidelines for CCC steelhead. Within this TRP Recommendations Memo, we present our findings and recommendations. Here, we put forth four Guiding Principles that capture our thoughts on the traits of steelhead that need to be considered when developing protective temperature guidelines, and provide details for eleven study concepts that we think would provide useful information for addressing key data gaps and improving our understanding of protective temperatures for CCC steelhead. We think the focus should be on genetics of the population, regional and reach-scale monitoring, and temperature adaptation and acclimation.

We think that collecting the information needed to understand protective temperatures for CCC steelhead will be an endeavor that will require considerable coordination among studies and researchers. We therefore recommend a large-scale research program, taking 5-10 years or more, to effectively capture an appropriate range of hydrology, meteorology, and other conditions to resolve the temperature requirements of CCC steelhead, as well as to determine what these fish need for long-term persistence in regional streams. Research goals and desired outcomes should be developed through a close collaboration among regulatory agencies and regulated entities responsible for managing regional streams for water supply and flood protection. This program should include a mix of habitat conditions assessments, laboratory experiments, and modeling, and all entities would have access to the resulting data and developed analytical tools. In the near-term, the focus could be on high impact/low cost efforts like widespread deployment of water temperature probes. A good first step for initiating this collaborative program would be developing a 3-year work plan (which could be an addendum to this memo). Such a program could ultimately improve management of the streams to benefit not only CCC steelhead but other desirable biota as well, both now and into the future as climate continues to change. Such a research effort would be a model for other agencies to follow to benefit other steelhead populations.

5. References

- Adams, O.A., Zhang, Y., Gilbert, M.H., Lawrence, C.S., Snow, M. and Farrell, A.P. 2022. An unusually high upper thermal acclimation potential for rainbow trout. *Conservation Physiology*, 10(1), p.coab101.
- Baker, M.A., C.N. Dahm, and H.M. Valett. 2000. Anoxia, Anaerobic Metabolism, and Biogeochemistry of the Stream-water—Groundwater Interface. In *Streams and Ground Waters*. Ed. J.B. Jones and P.J. Mulholland. Academic Press. San Diego, CA. USA. Pg 259-283.
- Barrett, D.E. and Bartholomew, J.L. 2021. A tale of two fish: Comparative transcriptomics of resistant and susceptible steelhead following exposure to *Ceratonova shasta* highlights differences in parasite recognition. *PLoS One*, 16(2), p.e0234837.
- Baumsteiger, J. and P. B. Moyle. 2019. A reappraisal of the California Roach/Hitch (Cypriniformes, Cyprinidae, *Hesperoleucus/Lavinia*) species complex. *Zootaxa* 4543 (2): 2221-240. <https://www.mapress.com/j/zt/article/view/zootaxa.4543.2.3> (available as open-access download)
- Carter, K. 2005. The effects of dissolved oxygen on steelhead trout, coho salmon, and chinook salmon biology and function by life stage. California Regional Water Quality Control Board, North Coast Region, 10.
- Carter, K. 2008. Effects of Temperature, Dissolved Oxygen/Total Dissolved Gas, Ammonia, and pH on Salmonids. Implications for California's North Coast TMDLs. North Coast Regional Water Quality Control Board. Santa Rosa, CA.
- Chen, Z., Snow, M., Lawrence, C.S., Church, A.R., Narum, S.R., Devlin, R.H., and Farrell, A.P. 2015. Selection for upper thermal tolerance in rainbow trout (*Oncorhynchus mykiss* Walbaum). *Journal of Experimental Biology*, 218(5), 803–812. <https://doi.org/10.1242/jeb.113993>
- Chen, Z., Farrell, A.P., Matala, A., and Narum, S.R. 2018. Mechanisms of thermal adaptation and evolutionary potential of conspecific populations to changing environments. *Molecular Ecology*, 27, 659– 674. <https://doi.org/10.1111/mec.14475>
- Colt, J., S. Mitchell, G. Tchobanoglous, and A. Knight. 1979. The use and potential for aquatic species for wastewater treatment: Appendix B, the environmental requirements of fish. Publication No. 65, California State Water Resources Control Board, Sacramento, CA.
- Connolly, P.J. and Petersen, J.H. 2003. Bigger is not always better for overwintering young-of-year steelhead. *Transactions of the American Fisheries Society*, 132(2), pp.262-274.
- Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. *Journal of Fisheries Research Board Canada*. 32(12), 2295-2332.
- Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., and Farrell, A.P. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science*, 332(6025), 109–112. <https://doi.org/10.1126/science.1198767>

- Eliason, E.J., Clark, T.D., Hinch, S.G., Farrell, A.P. 2013. Cardiorespiratory collapse at high temperature in swimming adult sockeye salmon. *Conservation Physiology*, 1(1), cot008, <https://doi.org/10.1093/conphys/cot008>
- El-Matbouli, M., McDowell, T.S., Antonio, D.B., Andree, K.B. and Hedrick, R.P. 1999. Effect of water temperature on the development, release and survival of the triactinomyxon stage of *Myxobolus cerebralis* in its oligochaete host. *International Journal for Parasitology*, 29(4), pp.627-641.
- Fangue, N.A., Hofmeister, M., and Schulte, P.M. 2006. Intraspecific variation in thermal tolerance and heat shock protein gene expression in common killifish, *Fundulus heteroclitus*. *Journal of Experimental Biology*. 209(15), 2859–2872. <https://doi.org/10.1242/jeb.02260>
- Fangue, N.A., Mandic, M., Richards, J.G., and Schulte, P.M. 2008. Swimming performance and energetics as a function of temperature in killifish *Fundulus heteroclitus*. *Physiological and Biochemical Zoology*, 81(4), 389-401. <https://doi.org/10.1086/589109>
- Farrell, A.P. 2016. Pragmatic perspective on aerobic scope: peaking, plummeting, pejus and apportioning. *Journal of Fish Biology*, 88(1), pp.322-343.
- Farrell, A.P., Hinch, S.G., Cooke, S.J., Patterson, D.A., Crossin, G.T., Lapointe, M. and Mathes, M.T. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and biochemical zoology*, 81(6), pp.697-708.
- Farrell, A.P., Eliason, E.J., Sandblom, E. and Clark, T.D. 2009. Fish cardiorespiratory physiology in an era of climate change. *Canadian Journal of Zoology*, 87(10), pp.835-851.
- Ferreira, E.O., Anttila, K., and Farrell, A.P. 2014. Thermal optima and tolerance in the Eurythermic Goldfish (*Carassius auratus*): Relationships between whole-animal aerobic capacity and maximum heart rate. *Physiological and Biochemical Zoology*, 87(5), 599-611. <https://doi.org/1086/677317>
- Garza, J.C. and Pearse, D. 2008. Population genetics of *Oncorhynchus mykiss* in the Santa Clara Valley Region. Report to the Santa Clara Valley Water District. National Marine Fisheries Service, Southwest Fisheries Science Center, 110.
- Hinch, S.G, Bett, N.N., Farrell, A.P. 2022. A conservation physiological perspective on dam passage by fishes. Chapter 9 in *Conservation Physiology for the Anthropocene - Issues and Applications*. Editor: Nann A. Fangue, Steven J. Cooke, Anthony P. Farrell, Colin J. Brauner, Erika J. Eliason. *Fish Physiology*, Academic Press, Volume 39, Part B, 2022, Pages 429-487.
- Jaeger, K.L, Sando, R., McShane, R.R., Dunham, J.B., Hockman-Wert, D.P., Kaiser, K.E., Hafen, K., Risley, J.C., and Blasch, K.W. 2019. Probability of streamflow permanence model (PROSPER): A spatially continuous model of annual streamflow permanence throughout the Pacific Northwest. *Journal of Hydrology*, X(2), pp. 2589-9155. <https://doi.org/10.1016/j.hydroa.2018.100005>.
- Jeffries, K.M., Hinch, S.G., Sierocinski, T., Clark, T.D., Eliason, E.J., Donaldson, M.R., Li, S., Pavlidis, P. and Miller, K.M. 2012. Consequences of high temperatures and premature mortality on the transcriptome and blood physiology of wild adult sockeye salmon (*Oncorhynchus nerka*). *Ecology and Evolution*, 2, 1747-1764. <https://doi.org/10.1002/ece3.274>

Keefer, M.L., Clabough, T.S., Jepson, M.A., Johnson, E.L., Peery, C.A. and Caudill, C.C. 2018. Thermal exposure of adult Chinook salmon and steelhead: Diverse behavioral strategies in a large and warming river system. PLoS One, 13(9), p.e0204274.

Kim, K.S., and Chapra, S.C. 1997. Temperature model for highly transient shallow streams. Journal of Hydraulic Engineering, 123(1), 30-40. [https://doi.org/10.1061/\(ASCE\)0733-9429\(1997\)123:1\(30\)](https://doi.org/10.1061/(ASCE)0733-9429(1997)123:1(30))

Kitancharoen, N., Yuasa, K. and Hatai, K. 1996. Effects of pH and temperature on growth of *Saprolegnia diclina* and *S. parasitica* isolated from various sources. Mycoscience, 37(4), pp.385-390.

Kurylyk, B.L., MacQuarrie, K.T., Linnansaari, T., Cunjak, R.A. and Curry, R.A. 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology, 8(6), pp.1095-1108.

Lehman, B.M., Johnson, R.C., Adkison, M., Burgess, O.T., Connon, R.E., Fangue, N.A., et al. 2020. Disease in Central Valley Salmon: Status and Lessons from Other Systems. San Francisco Estuary and Watershed Science, 18(3).
doi:<https://doi.org/10.15447/sfews.2020v18iss3art2> Retrieved from
<https://escholarship.org/uc/item/8259p3t6>

Lee, C.G., Farrell, A.P. Lotto, A., Hinch, S.G., and Healey, M.C. 2003. Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. Journal of Experimental Biology, 206(18), 3253–3260. <https://doi.org/10.1242/jeb.00548>

Little, A.G., Dressler, T., Kraskura, K., Hardison, E., Hendriks, B., Prystay, T., Farrell, A.P., Cooke, S.J., Patterson, D.A., Hinch, S.G., and Eliason, E.J. 2020. Maxed out: Optimizing accuracy, precision, and power for field measures of maximum metabolic rate in fishes. Physiological and Biochemical Zoology, 93(3), 243-254.
<https://doi.org/10.1086/708673>

McInturf, A.G., Zillig, K.W., Cook, K., Fukumoto, J., Jones, A., Patterson, E., Cocherell, D.E., Michel, C.J., Caillaud, D. and Fangue, N.A. 2022. In hot water? Assessing the link between fundamental thermal physiology and predation of juvenile Chinook salmon. Ecosphere, 13(11), p.e4264.

Moyle, P.B. 2002. Inland fishes of California: revised and expanded. Univ of California Press.

Moyle, P. B. and M.A. Campbell. 2022. Cryptic species of freshwater sculpin (Cottidae, Cottus) in California, USA. Zootaxa 5154 (5):501-507

Moyle PB, Lusardi RA, Samuel PJ, Katz JVE. 2017. State of salmonids: status of California's emblematic fishes. Center for Watershed Sci, University of California, Davis and California Trout, San Francisco, CA

Myrick, C. and Cech, J.J. 2004. Temperature effects on juvenile anadromous salmonids in

California's central valley: what don't we know?. *Reviews in Fish Biology and Fisheries*, 14, pp.113-123.

Neubauer, P. and Andersen, K.H. 2019. Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conservation Physiology*, 7(1), p.coz025.

National Marine Fisheries Service (NMFS). 2016. Coastal Multispecies Recovery Plan. California Coastal Chinook Salmon, Northern California Steelhead, Central California Coast Steelhead. National Marine Fisheries Service, West Coast Region, Santa Rosa, California. 2016

Poletto, J.B., Cocherell, D.E., Baird, S.E., Nguyen, T.X., Cabrera-Stagno, V., Farrell, A.P., and Fague, N.A. 2017. Unusual aerobic performance at high temperatures in juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Conservation Physiology*, 5(1), 1–13.
<https://doi.org/10.1093/conphys/cow067>

Quinn, T.P. 2018. The behavior and ecology of Pacific salmon and trout. University of Washington press.

Reeves GH, Everest FH, Hall JD. 1987. Interactions between the redbside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in Western Oregon: the influence of water temperature. *Can J Fish Aquat Sci* 44:1603–1613.

Reese, C.D. and Harvey, B.C. 2002. Temperature-dependent interactions between juvenile steelhead and Sacramento pikeminnow in laboratory streams. *Transactions of the American Fisheries Society*, 131(4), pp.599-606.

RWQCB. 2019. Final California 2018 Integrated Report (303(D) List/305(B) Report). Supporting Information. California Regional Water Quality Control Board, San Francisco Bay Region.
https://www.waterboards.ca.gov/sanfranciscobay/water_issues/programs/TMDLs/2018_303d/03557.shtml

Reynolds, L.V., Shafroth, P.B., and Poff, N.L. 2015. Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change. *Journal of Hydrology*. 523. Pp. 768-780. <http://dx.doi.org/10.1016/j.jhydrol.2015.02.025>

Richter, A. and Kolmes, S.A. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. *Reviews in Fisheries science*, 13(1), pp.23-49.

Schulte, P.M., Healy, T.M., and Fague, N.A. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integrative and Comparative Biology*, 51(5), 691–702. <https://doi.org/10.1093/icb/icr097>

Shapovalov, L. and A.C. Taft. 1954. The Life Histories of The Steelhead Rainbow Trout (*Salmo Gairdneri* Gairdneri) and Silver Salmon (*Oncorhynchus Kisutch*) With Special Reference to Waddell Creek CA and Recommendations Regarding Their Management. State of California Department of Fish and Game Bulletin No. 98.

Smith, J.J. and Li, H.W. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. In *Predators and prey in fishes* (pp. 173-180). Springer, Dordrecht.

Spina, A.P. 2007. Thermal ecology of juvenile steelhead in a warm-water environment.

Environmental Biology of Fishes, 80(1), pp.23-34.

Stillwater Sciences. 2023. In situ Temperature Tolerance of Steelhead at the Southern End of Their Range. Prepared by Stillwater Sciences, Ventura, California for Santa Clara Valley Water District, San Jose, California.

Sullivan K., D.J. Martin, R.D. Cardwell, J.E. Toll, and S. Duke. 2000. An analysis of the effects of temperature on salmonids of the Pacific Northwest with implications for selecting temperature criteria. Sustainable Ecosystems Institute. Portland, OR. 147 pp.

State Water Resources Control Board (SWRCB). 2021. 2018 Integrated Report for Clean Water Act Sections 305(b) and 303(d). Adopted by the SWRCB on October 20, 2020. Released on January 14, 2021.

U.S. Environmental Protection Agency (USEPA). 1977. Temperature criteria for freshwater fish: protocol and procedures. Ecological Research Series. EPA-600/3-77-061 (NTIS PB270032). Prepared by W.A. Brungs and B.R. Jones. U.S. Environmental Protection Agency, Washington, D.C.

U.S. Environmental Protection Agency (USEPA). 2003. EPA Region 10 Guidance for Pacific Northwest State and Tribal Water Quality Standards. Region 10, Seattle, WA. EPA 910-B-03-002. 49pp.

Valley Water. 2020. Comment Letter - 303(d) portion of 2018 California Integrated Report - Listing of Lower Los Gatos Creek for Temperature Pursuant to the San Francisco Regional Water Quality Control Board's Recommendation. Submitted to the State Water Resources Control Board on April 30, 2020.

Verhille, C.E., English, K.K., Cocherell, D.E., Farrell, A.P., and Fangue, N.A. 2016. High thermal tolerance of a rainbow trout population near its southern range limit suggests local thermal adjustment. *Conservation Physiology*, 4(1), 1–12. <https://doi.org/10.1093/conphys/cow057>

Zhang, H-Y., Zhao, Z-X., Xu, J., Xu, P., Bai, Q-L., Yang, S-Y., et al. 2018. Population genetic analysis of aquaculture salmonid populations in China using a 57K rainbow trout SNP array. *PLoS ONE*, 13(8), e0202582. <https://doi.org/10.1371/journal.pone.0202582>

Zillig, K.W., Lusardi, R.A., Moyle, P.B. and Fangue, N.A. 2021. One size does not fit all: variation in thermal eco-physiology among Pacific salmonids. *Reviews in Fish Biology and Fisheries*, 31(1), pp.95-114