A REVIEW OF EFFECTS OF WARM WATER TEMPERATURE ON STEELHEAD/RAINBOW TROUT

Appendix G

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1.0 INTRODUCTION

Coastal rainbow trout, *Oncorhynchus mykiss*, (but called *Salmo gairdneri* in most of the older literature) has both anadromous and non anadromous populations. Steelhead, an anadromous fish, spawns in freshwater and migrates to the ocean to mature and grow. The non-anadromous populations of this species are called resident rainbow trout. Expression of the anadromous life history strategy is flexible: steelhead can give rise to progeny that go to sea or remain in their natal stream, and the same is true of resident rainbow trout. Also, steelhead and resident trout can be found together in a given stream that is open to the ocean, and are indistinguishable as juveniles. Steelhead trapped behind impassable barriers, such as a dam, can revert to a freshwater-resident lifestyle.

Steelhead return to their natal stream to spawn. For example, fish from Oregon rivers tend not to interbreed with fish from more distant California streams. Over time, differences can evolve among populations. The National Marine Fisheries Service (NMFS) has defined 15 population groups of western United States steelhead, called "Evolutionarily Significant Units" (ESUs), on the basis of geographic range, life histories, and genetic studies. In 1997, the NMFS listed many of these ESUs for protection under the Endangered Species Act. The Southern California ESU, which extends from the Santa Maria River south to Malibu Creek and includes the Santa Ynez River, was listed as an endangered species. Southern California steelhead are presumed to be more tolerant of warm water than steelhead from more northerly stocks because they evolved at the southern limit of trout distribution in North America. This has led to suggestions that steelhead/rainbow trout in southern California should be managed differently than fish of more northern stocks, as regards its thermal tolerances.

Studies by the SYRTAC have shown that summer water temperatures in the main-stem Santa Ynez River and portions of the tributaries can reach temperatures close to levels that are thought to be stressful or lethal to rainbow trout/steelhead (SYRTAC 1997). Water quality guidelines, based on general knowledge of the temperature relations of this species, were proposed with upper limits of 20°C average daily temperature and 25°C daily maximum as providing acceptable habitat conditions. Men daily water temperatures of 22 °C were considered stressful. In SYRTAC studies, these guidelines have been used to evaluate habitat suitability and to identify potentially stressful situations. Rainbow trout/steelhead in the Santa Ynez system, however, have been observed at temperatures around 25°C, which has led to suggestions that these fish could thrive and be healthy at temperatures higher than the proposed guidelines.

Understanding the relationship between water temperature and fish health will be important to the successful management of steelhead/rainbow trout in Santa Ynez River.

The purpose of this document is first to describe the relationship between temperature and metabolism in cold-blooded animals such as trout. We then review the scientific literature upon which the thermal guidelines were based, and finally examine the possibility of prudent alternatives. This information will be used as the SYRTAC develops a the fish management plan for the Santa Ynez River which will propose management measures and indicate areas where these would be most effective. Water temperature constraints will play an important role in assessing potential benefits to rainbow trout/steelhead of various management actions.

2.1 METABOLISM OF COLD-BLOODED ORGANISMS

Fully aquatic organisms such as fish cannot make their bodies cooler than the surrounding water. There is generally an intermediate range of temperature at which growth and other functions are optimized, and then as temperature rises further, first sublethal deleterious effects occur, and finally upper limits of temperature beyond which the species cannot exist (see, e.g. Fry 1947, 1971, Brett 1956) (Figure 2-1). Fish have widely ranging upper lethal temperatures. For example, some arctic species are known to die at upper temperatures as low as 5°C, whereas many temperate and tropical fishes can survive at temperatures approaching 40°C (Fry 1971). All salmonids (the family that includes salmons, trouts, charrs, and their close relatives) fall between these extremes of upper lethal temperatures.

Cold-blooded animals adapt to changing temperatures by complex biochemical adjustments to cellular membranes, enzymes, etc. An animal allowed to adjust (acclimate) to a warmer temperature can survive to a higher temperature. Within the limits of temperature tolerated by a given species, there are also non-adaptive changes to systems that simply are controlled by temperature. For example, the work of Fry and others showed that both the resting and active metabolic rates of an animal, as measured by oxygen consumption, would generally increase until the upper incipient lethal temperature was reached (the temperature at which half of a group of animals dies). This means that the animal's food requirements similarly increase, to the point that unnaturally high food rations are required to keep the animal from starving at high ambient temperatures. This introduces the concept of thermal resistance, or resistance to lethal temperature. To quote Fry (1947), "(an) animal can exist, often for substantial periods of time, at a temperature level beyond the zone of tolerance, and may frequently do so, particularly during (daily) fluctuations." So for a number of reasons, casual observations of trout living and feeding at temperatures in the range of 24-25°C do not necessarily mean that fish are thriving at these temperatures. The following sampling of the literature on this subject employs experimental and highly structured observational evidence to define upper limits and daily average temperatures likely to be tolerated by steelhead/rainbow trout in the Santa Ynez system.

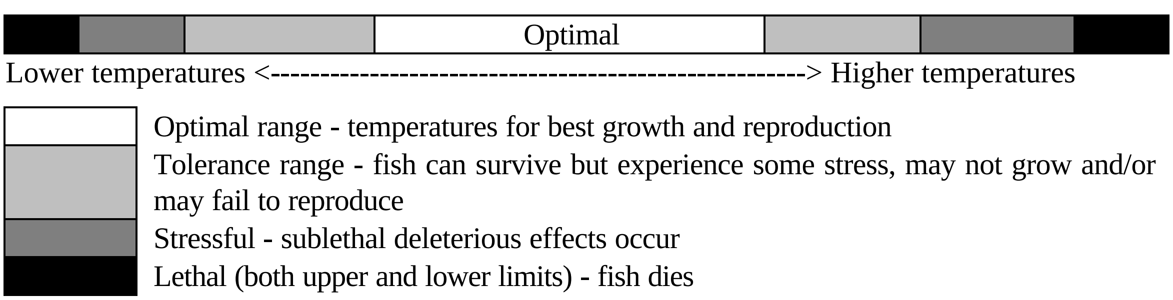

Figure 2-1. Schematic Depiction of the Range of Thermal Tolerance.

Response to high temperature can be measured by criteria that involve the death of the fish, some behavioral or performance parameter, or a biochemical measure. Studies of temperature-related increases in general stress indicators (Strange *et al*. 1977) or more specific heat-induced proteins in fish blood (Thomas 1990) are not well-enough advanced for the present purpose. Therefore, in the following review, various mortality and behavioral/performance indicators will be examined. Emphasis will be on laboratory studies of rainbow trout/steelhead in which oxygen concentration was maintained at high values, and fish of defined size and age were acclimated to well-defined, high temperatures. Field studies will be mentioned where they are most appropriate to our purpose. Studies of other salmonids are mentioned but not emphasized in this brief review.

2.2 MORTALITY

A common mortality-based measure of upper thermal tolerance is the incipient lethal temperature, or ILT, calculated as the temperature at which half of a group of experimental fish will die. Because fish have a limited ability to adapt to gradually increasing temperature, ILT's increase slightly with acclimation temperature up to an upper limit. This measure of high-temperature tolerance has not been found to vary much within a given species. For example, Bidgood and Berst (1969) tested juveniles of four populations of rainbow trout that homed to different streams in the Great Lakes region. Despite their presumed genetic isolation, all four populations, acclimated to 15°C, had ILT's between 25 and 26°C under the experimental conditions.

A similar set of experiments involved juveniles of a warm-water-adapted rainbow trout and two hatchery strains (Kaya 1978). The warm-water strain were the descendants of rainbow trout planted in the Firehole River in Yellowstone Park, were isolated from other populations, and were known to inhabit reaches of the river where temperatures in summer exceeded 25°C for a few days each summer. Although the Firehole fish tolerated elevated temperatures longer than the two hatchery strains at intermediate acclimation temperatures, the ILT's of all fish acclimated to 21 and 24.5°C were identical at 26.2°C.

2.3 BEHAVIOR AND PERFORMANCE

Fish can be stressed or impaired by a number of factors, including temperature, at levels that do not actually kill the fish but that are outside the envelope of normal performance and positive growth. Given the chance, fish will select a combination of conditions of temperature, oxygen concentration, food availability, depth, etc., that is the best available compromise for survival and growth (Baltz *et al*. 1987).

A west-coast complement to the observations of Kaya is the work of Nielsen *et al*. (1994), who studied juvenile steelhead in streams where warm summer temperatures reached levels normally considered to exceed healthy conditions for this species. In Rancheria Creek (tributary to the Navarro River), where deep stratified pools offered cooler water with high oxygen content, foraging in the main stem decreased and aggressive behavior increased as temperatures rose to 22°C. At that point, fish of all sizes would take refuge in the cooler pool habitat for the warmest part of the day, returning to the main stream when ambient temperature there fell back below 23°C. However, in the Middle Fork Eel River, where stratified pools existed but had low oxygen content, juvenile steelhead were observed actively feeding in 24°C water rather than taking refuge in the cooler pools. These observations are in accord with the results of Cech *et al*. (1990), who showed that hypoxia depressed rainbow trout metabolism at 15°C, but killed the trout at 20°C.

In a classic study, Fry (1948, re-presented in Brett 1956) showed that oxygen consumption in rainbow trout increased up to an ILT of 26°C. The higher oxygen consumption implies greater energy requirements, which must be met by increased food consumption if the fish are to continue to grow. More recently, Myrick and Cech (1996) tested two strains of rainbow trout as well as Kern River golden trout (*Oncorhynchus aguabonita*). These studies, using modern equipment, found lower oxygen consumption in resting fish at 25°C than at 19 or 22°C, perhaps indicating the onset of physiological dysfunction. Follow-up work (Myrick, personal communication) showed that these same fish, when held at 25°C and fed to satiation, did not grow over a 30-day period.

Myrick and Cech (1996) did not measure ILT, but did find that all three strains of trout had identical critical temperature maxima (CTM). The CTM is a useful measure of thermal tolerance in circumstances where large numbers of fish are not available to be sacrificed. Rather than gradually approaching a lethal endpoint, the temperature is raised more rapidly, and the temperature at which half the fish lose equilibrium is noted. In another study employing CTM, Lee and Rinne (1980) found that thermal tolerances of five trout species (rainbow, brown *Salmo trutta*, brook *Salvelinus fontinalis*, Arizona *Oncorhynchus apache*, and Gila *O. gilae*) were all essentially the same. Lee and Rinne also tested these five trout species in fluctuating temperature regimes, wherein the temperature cycled by 6°C over a 24-hr period, and both minima and maxima were raised by 1°C every 48 hrs until all fish lost equilibrium. The rainbow, brown, Arizona, and Gila trout all tolerated a maximum fluctuating regime of 21-27°C, the brook trout, 22-28°C. So in both these studies, where trout species from southern geographic locations might have been expected to be more tolerant of high temperatures, they were found not to differ from other salmonids as regards CMT.

Cherry *et al*. (1975, 1977) performed experiments in which several species of fish, including rainbow trout and two other salmonids (brown trout and brook trout), were acclimated to various temperatures and then introduced into an apparatus where the fish were allowed to choose a temperature. Like ILT, the preferred temperatures of all species tended to rise as acclimation temperature increased. However, all three of the salmonids, when acclimated to temperatures above 20°C, preferred temperatures below the acclimation temperature. The highest non-lethal acclimation temperature for salmonids was 24°C (the next highest acclimation temperature used, 27°C, killed all three species).

Short-term experiments of thermal tolerance and thermal preference all leave out important aspects of ecology and physiology that are essential to real-world trout stream management. To contribute to the maintenance of a population, young fish must not only survive, but also grow and mature. A measure of performance that is most applicable to fisheries management is yield of a population, defined as the net balance between growth and mortality. Hokanson *et al*. (1977), in a series of 50-day experiments with juvenile rainbow trout, concluded that the highest constant temperature at which growth and mortality effects would just cancel was 23°C. They also performed tests in which temperature was caused to fluctuate daily ±3.8°C about a mean. At an average fluctuating temperature of 22°C, growth was not significantly different from zero, and all fish died within ten days. The authors further noted that reports of increased trout mortality at above-optimum (for growth) temperatures were common in the literature.

Some of the increased mortality of rainbow trout exposed to high temperatures is manifested as delayed mortality after brief exposures. For example, Coutant (1973) demonstrated increased susceptibility to predation in rainbows that had been exposed to high temperatures for only 20% of the time necessary to cause observable disorientation and at only 10% of the exposure time that resulted in 50% mortality in the range from 26 to 30 °C. Predation was not a factor in the experiments of Hokanson *et al*. (1977), so presumably other deleterious effects of temperature, such as susceptibility to pathogens or stress-related illness, lead directly or indirectly to death over expended exposure periods.

This sampling of the extensive literature on salmonid thermal biology can be summarized this way:

1. Steelhead/rainbow trout, regardless of acclimation temperature, will not select water warmer than 22°C when given the choice of suitable forage and oxygen content at lower temperature.

2. This species, including those stocks from warm environments, has not attained an incipient lethal temperature (ILT) greater than 26.2°C.

3. The metabolic rate of active rainbow trout (as well as other fish) increases at high temperature, invoking high energy demands that may not be sustained in field situations.

4. There is no evidence that a steelhead/rainbow trout population can experience a net yield (positive growth minus mortality) at daily average temperatures > 22°C.

Southern steelhead live, almost by definition, at the southern extreme of the range of the species along the west coast of North America. It has been suggested by Bennett (1987, cited in Nielsen *et al*. 1994) that high summer temperatures limit the range of all salmonids in California. Similarly, Cech *et al*. (1990) speculated that rainbow trout would not occur where stream temperature exceeded 25°C. In this review we searched for evidence that southern steelhead, or any other genetic isolate, might possibly have evolved greater thermal resistance than other strains of the species. Kaya (1978) did show that at intermediate acclimation temperatures, the Firehole River rainbows had increased resistance times to elevated temperatures compared to hatchery fish. However, the difference vanished at higher acclimation temperatures. In other words, the Firehole fish, when held at temperatures of 17°C or higher, had no advantage over the hatchery fish when exposed to temperatures ≥ 26°C. Southwestern trout species, Kern River golden trout (Myrick and Cech 1996) and Arizona and Gila trout (Lee and Rinne 1980), were not found to have increased resistance to high temperature.

Based on evidence from controlled experiments, it seems reasonable to suggest that steelhead/rainbow trout observed actively feeding at temperatures ≥ 23°C are fish living at the outer edge of their survival envelope. These fish are probably not growing, and in fact are likely experiencing higher rates of mortality from direct and indirect effects of elevated temperature.

SYRTAC have shown that summer water temperatures in the mainstem Santa Ynez River and portions of the tributaries can reach temperatures close to levels that are thought to be stressful or lethal to rainbow trout/steelhead (SYRTAC 1997). Southern California steelhead are often presumed to be more tolerant of warm water than steelhead from more northerly stocks because they evolved at the southern limit of trout distribution in North America. Rainbow trout/steelhead have been observed feeding at temperatures above 25°C in the Santa Ynez system (SYRTAC 1998 and Carpanzano 1996). These observations suggest that steelhead/rainbow trout in southern California have different temperature tolerances than fish of more northern stocks, however, these observations have not been confirmed with laboratory studies. In the physiological studies of temperature tolerance and CTM for trout, increased resistance to high temperatures was not evident in rainbow trout even those living in very warm environments (Lee and Rinne 1980; Myrick and Cech 1996; and Kaya 1978). These studies strongly suggest that the upper lethal temperature for southern California rainbow trout/steelhead may not be greater than that of other steelhead stocks (26.2°C), although southern fish may be better able to tolerate temperatures slightly lower than these lethal limits.

To contribute to the maintenance of a population, young fish must not only survive, but also grow and mature. A fish's metabolic rate increases in warmer water, resulting in increased energetic demands for oxygen and food until the upper incipient lethal temperature is reached (Fry 1948 in Brett 1956, Brett 1971, Fausch 1984). In studies of juvenile rainbow trout, Hokanson *et al*. (1977) concluded that the highest constant temperature at which the effects of growth and mortality balance out was 23°C. They also performed tests in which temperature was caused to fluctuate daily ±3.8°C about a mean. At an average fluctuating temperature of 22°C, growth was not significantly different from zero, and all fish died within ten days.

Water temperature guidelines, based on general knowledge of the temperature relations of this species (e.g. Hokanson *et al*. 1977, Raleigh *et al*. 1984), have been proposed as 20°C mean daily and 25°C daily maximum as acceptable habitat conditions. Based on Hokanson *et al*. (1977), a mean daily temperature of 22°C may be a threshold between acceptable and unsuitable from a long-term metabolic perspective. In the SYRTAC studies, these guidelines have been used to evaluate habitat suitability and to identify potentially stressful situations, such as in the mainstem several miles below Bradbury Dam (SYRTAC 1997).

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