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August 17, 2012

Kimberly D. Bose
Secretary
Federal Energy Regulatory Commission
888 First Street, NE
Washington, DC 20426

Re: *Turlock Irrigation District and Modesto Irrigation District*, Project No. 2299-075
(Don Pedro Hydroelectric Project)

Dear Ms. Bose:

On behalf of the City and County of San Francisco, please find enclosed for filing in the above-referenced matter: (1) Ronald M. Yoshiyama and Peter B. Moyle, Memorandum on Factors that Influence the Expression of Anadromy in Steelhead-Rainbow Trout (*Oncorhynchus mykiss*) and Other Salmonids (July 3, 2012); and (2) Ronald M. Yoshiyama, Commentary on Evaluating the Temperature-Related Flow Requirements of Steelhead-Rainbow Trout (*Oncorhynchus mykiss*) in the Lower Tuolumne River (July 5, 2012).

These documents relate to the following studies required by the study plan determination in the above-captioned proceeding:

W&AR-5	Salmonid Populations Information Integration and Synthesis
W&AR-10	<i>O. mykiss</i> Population Study
W&AR-12	<i>O. mykiss</i> Habitat Survey
W&AR-14	Temperature Criteria Assessment

San Francisco believes these documents will be useful in the ongoing discussion between Turlock Irrigation District and Modesto Irrigation District, relicensing participants, and the Commission regarding *O. mykiss* management in the lower Tuolumne River.

Kimberly D. Bose
August 17, 2012
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I certify that a copy of this letter is being served on all parties included on the Commission's official service list for this proceeding, by electronic mail or such other means as a party may have requested.

Sincerely,

/s/ William S. Huang

William S. Huang
Attorney for the
City and County of San Francisco

WSH:fh
Enclosures

**FACTORS THAT INFLUENCE THE EXPRESSION OF
ANADROMY IN STEELHEAD-RAINBOW TROUT
(ONCORHYNCHUS MYKISS) AND OTHER SALMONIDS**

**RONALD M. YOSHIYAMA AND PETER B. MOYLE
JULY 3, 2012**

MEMORANDUM

FACTORS THAT INFLUENCE THE EXPRESSION OF ANADROMY IN STEELHEAD-RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) AND OTHER SALMONIDS

Ronald M. Yoshiyama and Peter B. Moyle

July 3, 2012

Summary

- The **developmental “decision”** by individual fish to follow an anadromous or a non-anadromous (resident) life-history pathway is set early in life and is affected by both environmental and genetic factors. The environmental factors probably operate throughout the early lifetimes of individuals but appear to be especially important during two times: (1) very early (perhaps during or soon after fry emergence from the gravel) at which time the developmental pathway is determined, and (2) later in juvenile growth when specific environmental factors (e.g., photoperiod) trigger the smoltification process in those individuals that are following the anadromous pathway.
- **Growth rate** is a key attribute of individual steelhead that is correlated with both the early “decision point” (i.e., for committing to anadromy versus residency) and the later “trigger point” (i.e., when to initiate smoltification). However, there evidently is an interactive effect of growth rate with genetics and probably other factors such that some individuals that have high growth rates remain as residents and mature quickly in fresh water while in other cases the faster growing individuals become smolts and migrate to sea.

Growth rate in itself is not necessarily the determining factor but is affected by, or at least is correlated with, other biological aspects—particularly the **energetic state** (i.e., standard metabolic rate) and **energy balance** (i.e., metabolic, growth and activity costs versus food intake) of the fish. One key insight from bioenergetic studies is that if individuals have a surplus of energy, they will tend to remain at their location and continue to grow and mature (i.e., residency), but if they have a deficit of energy, they will migrate to seek better feeding and growing areas (i.e., migratory-anadromy).

- At the **population level**, the environmental conditions at localities occupied by *O. mykiss* populations appear to strongly affect the life-history composition of those populations—i.e., whether they contain predominantly resident rainbow trout or anadromous steelhead. Generally, if conditions are highly conducive and relatively constant then rainbow trout tend to predominate; in contrast, steelhead evidently are favored at the more challenging, variable localities—i.e., localities with periodically reduced streamflows and stressful higher temperatures (Payne et al. 2005, citing Pearsons et al. 1998 and Cramer et al. 2003).
- It appears that probably all ***O. mykiss* populations**--whether composed of entirely resident types (i.e., rainbow trout) or of both anadromous and resident types—are capable of producing at least a few anadromous/migratory individuals that were spawned by resident-type mothers. It is not clear whether this is just an atavistic trait that produces some anadromous progeny that have little chance of surviving and reproducing or, alternatively, those progeny have sufficient fitness to continue to transmit the anadromous trait over successive generations. **The question here** is whether or not populations that are purely or

primarily composed of resident phenotypes **can ever be induced to produce large numbers of anadromous (steelhead) individuals.**

- Given the possibility that largely resident-type populations of *O. mykiss* may be able to produce significant numbers of steelhead, the **major question is: “What (1) historical or genetic preconditions and (2) present-future environmental conditions were/are necessary to induce *O. mykiss* populations to produce more steelhead?** It is clear from studies that certain environmental conditions have key roles in inducing smoltification and, hence, successful anadromy. However, it is uncertain how much genetic “reconstitution” would be needed to cause presently residential populations (including those that formerly contained larger fractions of anadromous individuals) to once again start producing substantial numbers of steelhead. The fact that hatcheries can and do select for the anadromous phenotype/genotype suggests that the shift can occur fairly rapidly, given the appropriate conditions.
- From an **evolutionary perspective, the balance of benefits versus costs is expected to determine** whether a population evolves (i.e., adapts itself) toward a **primarily anadromous or primarily non-anadromous “resident” life-history.** If growth and survival conditions are highly favorable in the freshwater environment compared with those in marine and estuarine environments, then *O. mykiss* populations are expected to be more heavily composed of the selectively advantageous freshwater-resident (rainbow trout) phenotypes. In the extreme case, it is possible that a population existing where prevailing conditions have long favored a resident life-history may have evolved in its genetic architecture such that it can no longer produce viable individuals of the anadromous life-history, even if that population were to subsequently experience a change in environmental conditions that generally favor the expression of anadromy.
- **Experimental manipulations of streamflows** and, concomitantly, stream temperatures should be attempted in order to explore potential flow-management options for increasing the expression of anadromy in Central Valley *O. mykiss* populations. For that purpose, an “adaptive” approach to flow management is necessary because the environmental regulation of anadromy in *O. mykiss* is still not clearly understood. Such experimental, flow-regulated management of *O. mykiss* populations would require an intensive monitoring program over a relatively long time-frame (e.g., at least 5-10 years).

1 Introduction

Steelhead-rainbow trout, *Oncorhynchus mykiss* (hereafter, “*O. mykiss*”), are widely recognized as occurring in two distinct life-history forms – viz., the anadromous steelhead and freshwater resident rainbow trout. Yet, those two forms are actually endpoints of a spectrum of life-history expressions in this species (cf., Narum et al. 2004, Quinn and Myers 2005, Riva-Rossi et al. 2007). The factors and mechanisms that determine whether individuals within a population follow anadromous, residential or some intermediate life-history pathways are only partially understood, but it is known that both environmental and genetic factors are involved.

A better understanding of the causes underlying anadromy in *O. mykiss* populations can be achieved by viewing the issue on two levels—i.e., the individual and the population. These two levels correspond to the following questions, respectively:

- (1) Within a given population comprising potentially anadromous individuals, what factors trigger the expression of anadromy in those individuals at the appropriate times of their lives?

- (2) Why do certain *O. mykiss* populations contain more anadromous individuals (relative to residents) than do other populations?

We address these two questions sequentially (here and in Section 2) but it is important to remember that they are actually inseparable aspects of life-history determination in salmonids. For example, higher temperature, food supply and individual growth rates may favor the transition of certain individuals to an anadromous life-pathway, but those factors also appear to influence the proportions of the population that become anadromous versus remaining in fresh water as life-long residents (e.g., Jonsson 1985, Beakes et al. 2010).

In general terms, Thorpe (1994: p.608) described the most basic developmental alternatives available to anadromous salmonids as follows.

“The two most striking choices that face anadromous salmonids are, in time sequence, smolting and sexual maturation. It has been shown that these choices are taken in response to specific seasonal signals...but that the direction of choice depends on some internal process of assessment of performance at that time, performance that is almost certainly associated with energy status...”

The issue of greatest interest here is to identify the main underlying factors that affect the developmental “decisions” of individual fish to diverge onto either the anadromy or residency pathways. Those factors include environmental conditions and the genetic composition of the population (e.g., Jonsson 1985, Narum et al. 2004).

Generally, the key factor associated with determining the life-history developmental pathway of individuals (e.g., anadromy versus residency) appears to be growth rate which, in turn, depends on environmental factors such as food supply, temperature and any other variables that affect the ability of individuals to acquire food and transform it into body growth (e.g., Bohlin et al. 1994). Hence, various physiological stressors – including unfavorable temperatures, flows and dissolved oxygen levels – that reduce body growth and increase maintenance metabolism are expected to ultimately affect the success rate of smoltification and the frequency of anadromy.

The role of temperature, and probably of other factors, is complex and not entirely clear but it is evident that temperature operates over a range of organismal levels (i.e., individuals to populations) and timeframes. At the individual level, increased temperatures serve to accelerate the time-course of smolting for those individuals that already have been committed to an anadromous pathway (as summarized by Clarke and Hirano 1995). At the population level, certain ranges of increased temperature favor greater individual growth rates and thereby can increase the tendency for freshwater residency in salmon and probably steelhead.

Many studies have examined the details of environmental cues and biological responses of salmonids during smolting (references given in Thorpe 1994); however, we view this aspect as secondary in the broader discussion because the decision to smoltify or not appears to have been made by the time of, and in some cases preceding, the initiation of the smolting process. It is nevertheless important to understand the proximate (i.e., immediate) effects of particular environmental cues as shown, for example, by studies on temperature and smolting. Therefore, additional details on proximate effects of temperature and photoperiod on the smoltification schedule of anadromous individuals are presented in subsequent subsections and in the Appendix.

2 Proximate Factors that Determine the Individual Expression of Anadromy

Numerous studies have addressed the role of environmental factors in eliciting the expression of anadromy in various salmonids (e.g., brown trout, arctic char, rainbow trout, Atlantic salmon). Jonsson (1985) briefly reviewed the work up to that time and identified temperature and “feeding

intensity" (which depends on food levels) as key variables because they both strongly influence individual growth rate during early life and, therefore, subsequent life-history pathways of those individuals. Early growth rate appears to be a primary determinant, or correlate, of whether or not individuals become anadromous or remain as residents in fresh water. Furthermore, as Jonsson (1985: p.189) noted (for brown trout):

"The 'decision' whether parr develop to residents or migrants is closely connected with age at smolting and age at sexual maturity. Both these traits are themselves influenced by genetics and environment. Growth rates and survival rates differ among brown trout living in different rivers; thus, life histories of adapted fish will differ. Within one stock, growth rates also will vary among individuals. This partly may be due to genetics...but also occurs mainly because different individuals happen to find different amounts of food..."

2.1 Temperature Effects on Smolting

The effects of temperature on the control of smolting in various salmonid species were reviewed and summarized by Clarke and Hirano (1995). They generally found that relatively higher temperature usually accelerated the onset of smolting (Clarke and Hirano (1995: p.339-340):

"Water temperature has several important effects on smolting. First, it controls the rate of growth and thus can influence the attainment of the necessary body size for smolting... It has been known for some time that elevated water temperatures can be used to produce zero-age smolts in coho...and masu salmon... Clarke and Shelbourn (1985) demonstrated the influence of temperature on growth and seawater adaptation of ocean-type chinook salmon. Fry reared at 17°C reached maximal seawater adaptability about two months earlier than those reared at 9°C. Clarke and Shelbourn (1989) showed a similar response in zero-age coho salmon reared under delayed photoperiod... In both studies, the effect of temperature on the timing of smolting was not strictly a function of its effect on body size, because fish exhibited maximal seawater adaptability at different sizes when reared at high and low temperatures."

"Thus, apart from its effect on growth, temperature can control the development of hypoosmoregulatory activity in juvenile salmon that are large enough to become smolts. Zaugg and McLain (1976) illustrated this effect in juvenile coho salmon... Periodic samples [of laboratory-reared coho salmon] demonstrated that the activity of sodium, potassium-stimulated Na⁺K⁺-ATPase, an enzyme involved in ion transport across the gill, reached a maximum one month earlier in fish reared at 10°C than in those reared at 6°C; activity rose earlier still in those reared at 15°C and exhibited only a transitory elevation in coho salmon held at 20°C."

It is notable that several studies cited by Clarke and Hirano (1995) demonstrated the importance of temperature fluctuations during rearing in affecting the onset of smolting and migration--aside from the effects of absolute temperature levels or accumulated thermal units (i.e., the latter defined as temperature multiplied by the duration at that temperature, summed over time). Quoting Clarke and Hirano (1995: p.339),

"It has been suggested that diurnal and seasonal temperature cycles may alter the timing of smolting, either directly by acting as cues or indirectly by sensitizing fish to other factors (Wagner 1974). This is supported by the observation that juvenile coho salmon released from hatcheries with a relatively constant temperature during spring have lower rates of survival to adulthood than those released from hatcheries with more pronounced temperature fluctuations (Olson 1978). Juvenile steelhead reared in a simulated seasonal temperature cycle (6.9°-18.6°C) exhibited greater migratory behaviour and a more pronounced elevation of gill sodium, potassium-activated Na⁺K⁺-ATPase than those reared at constant 12.3°C (Zaugg and Wagner 1973; Wagner 1974)."

2.2 Photoperiod Effects on Smolting

The roles of photoperiod and temperature in affecting the smolting process have been long recognized, or at least suspected. For example, Zaug and Wagner (1973) experimentally exposed *O. mykiss* parr to various photoperiod schedules and rearing temperatures to determine the effects on the parr-smolt transformation, as indexed by the levels of Na⁺, K⁺-stimulated adenosinetriphosphatase (ATPase) activity in the gills. The ATPase activity increased in response to appropriate temperatures (e.g., 6.5° or 10°C) but was inhibited or even depressed at temperatures higher than ~13°C. Increased ATPase activity was associated with active downstream migration of wild *O. mykiss* smolts. Photoperiod duration also influenced ATPase activity and, therefore, smoltification. Increased ATPase activity was observed when the experimental *O. mykiss* parr had been exposed to photoperiods matching the natural photoperiod during April-May (unless temperatures were excessively high, which inhibited smolting). Conversely, ATPase activity decreased (i.e., the smolting process was reversed) when photoperiods approached the natural photoperiod duration of late-June (i.e., the summer solstice), which corresponded to the normal reversion time of fish in the natural environment. However, some parr successfully completed the smolting process even when they were experimentally reared in total darkness, thus illustrating the complicated nature of the parr-smolt transformation.

The extensive studies on the effects of photoperiod on the smolting process were reviewed by Groot et al. (1995). It is clear that photoperiod has variable effects among different salmonid species and even among different life-history types within species. To illustrate, Groot et al. (1995: p.337) noted:

“Juvenile chinook salmon exhibit a variable sensitivity to photoperiod, depending upon their life history type. From the few comparative studies, it appears that stocks having a stream-type juvenile life history respond to photoperiod cues in much the same way as coho salmon, whereas stocks of the ocean type are insensitive to photoperiod...”

“More recently, Clarke et al. (1989) exposed juvenile chum, coho, ocean-type chinook, and stream-type chinook salmon to either a short (9.5 h) or long (14.5 h) daylength for 2 months from the time of first feeding . . . Both the coho and stream-type chinook salmon given the long daylength treatment at swim-up exhibited reduced growth and seawater adaptability compared with their conspecifics given the short-day treatment. In contrast, the chum and ocean-type chinook salmon exhibited good growth and seawater adaptability under both daylength regimes. The ocean-type pattern of growth and smolting exhibits dominance in crosses between ocean-type and stream-type chinook salmon (Clarke et al. 1992).”

2.3 A Specific Experimental Study of the Environmental and Genetic Factors Affecting *O. mykiss* Anadromy

The most pertinent recent study showing the influence of environmental factors on expression of anadromy in *O. mykiss* is that of Beakes et al. (2010). Their laboratory study clearly demonstrated that higher temperatures and food levels contributed to higher growth rates and greater survival rates through smolting, but there also was a definite genetic basis for differences in smolting success among fish from different regions. A more detailed summary of their results is presented in the Appendix.

The results of Beakes et al. (2010) additionally highlight the paradox of Central Valley *O. mykiss*. If higher temperatures and greater food supply (i.e., feeding intensity) facilitate individual survival during smolting, then why aren't there greater numbers of steelhead in the Central Valley *O. mykiss* populations which experience such favorable environmental conditions compared with the coastal *O. mykiss* populations that are dominated by steelhead?

There does not appear to be a fully adequate explanation at the present time. However, part of the answer probably entails a broader perspective that includes the long-term population-level

advantages of greater residency versus anadromy in the Central Valley environment. There possibly are ecological and evolutionary pressures that favor freshwater residency through most or all of the life-history of Central Valley *O. mykiss*, and so the associated genetic structure of Central Valley *O. mykiss* might account for their different responses from those of coastal fish (Beakes et al. 2010). Specifically, the relative constancy of flow and temperature conditions below the major dams may provide a more stable, productive environment and thus promulgate a largely residential life-history—e.g., as seems to have occurred for *O. mykiss* in the upper mainstem Sacramento River below Keswick Dam (McEwan 2001).

2.4 The Interaction of Growth Rates, Smolting and Early Sexual Maturation of Salmonids in Freshwater

Another confounding aspect of the anadromy issue is that studies on salmonids have shown that very high growth rates of individuals generally tend to be associated with early sexual maturation in fresh water which may preempt the smolting process (e.g., Bohlin et al. 1990, Dolloff et al. 1994) – i.e., “smolting and early maturation are mutually inhibitory processes” (Thorpe 1987: p.246). Thus, perhaps the generally warmer and food-rich environments of Central Valley rivers favor faster individual growth and concurrently interact with the mechanism(s) determining smolting-versus-maturation – the current manifestation of which is increased freshwater residency and reduced anadromy at the population level.

Thorpe (1987: p.24) presented a succinct perspective on this issue:

“The developmental programme is genetically defined, but runs under environmental instruction. Smolting and maturation are developmental conversions...[which] require seasonal environmental signals for their initiation. The rate and direction of photoperiod change has been shown to influence the onset of both smolting and maturation in many salmonids... The contention, then, is that the developmental route taken by the fish—either to smolt or to mature—depends on the trophic opportunities available to them at seasonally critical times.”

Therefore, following Thorpe’s (1987) framework, the Central Valley (NCCV) and central coastal California (CCC) *O. mykiss* populations studied by Beakes et al. (2010) are under different “developmental programmes” (sensu “blueprints”) so that each responds somewhat differently to proximate stimuli such as temperature and food supply, which in turn probably interact with photoperiod. It is important to distinguish proximate (i.e., immediate) stimuli that act to trigger the smolting process – which, in a sense, already has been “predetermined” by the combination of an individual’s genetic makeup and its response to external factors– as opposed to the underlying factors that cause individuals to take that particular pathway (e.g., anadromy) rather than another parthway (residency).

More recently, Thorpe (1994) proposed a way of viewing the smoltification phenomenon in salmonids within a developmental, and ultimately evolutionary, context. Specifically, smolting and sexual maturation are conflicting physiological pathways whereby sexual maturation generally takes primacy. If the individual can attain fast growth and early sexual maturation in freshwater, then that pathway preempts smolting and anadromy. Therefore, smolting (i.e., anadromy) is the default alternative outcome if the primary option of freshwater maturation is not taken. As Thorpe (1994) pointed out, there is an enormous volume of published studies covering the detailed biochemical, physiological, morphological and behavioral aspects of smolting and anadromous migration, but viewing the whole issue within this generalized developmental context makes it easier to understand why (and not just how) individuals become anadromous.

Thorpe’s general reasoning was as follows (Thorpe 1994: p.105-106):

“The first priority in the development of fishes is to reproduce, and fish do so at their earliest possible opportunity... There is much evidence that smolting and sexual maturation are

conflicting physiological processes... However, while sexual maturation is obligatory for the continuation of the species, it seems that the smolting migration is optional and not all salmon populations migrate to sea or even to lakes... Migration is a general biological response to adversity... If an animal's needs are being met, it stays where it is: if they are not, it moves until they are. So, it is appropriate to ask what is lacking in the riverine habitat which causes salmon to smolt and migrate from that environment?"

Thorpe's general explanatory framework provides a mechanistic basis for why various salmonid species that are normally anadromous become more "residualized" under certain circumstances or even completely adapted as landlocked populations (examples in Thorpe 1987). The key factor appears to be growth opportunity. As Thorpe (1987: p.247-248) explained:

"Rates of growth are dependent on the rate of acquisition of surplus energy. Conditions which favour very rapid growth, especially at times when the fish are sensitive to triggering of the maturation switch, favour early maturation and particularly maturation before smolting... When food is abundantly available and, simultaneously, photoperiod is increasing and temperature is optimal, growth rate should be rapid. Culturists attempt to create such conditions, and salmonids developing in hatcheries normally grow faster than their counterparts in the wild; here parr maturation is commonplace. Trophic conditions may also be improved for individuals if population densities decrease, thereby reducing competition for food. Populations then respond by increasing individual growth and maturity rates..."

Although much of Thorpe's (1987, 1994) discussion focused on parr sexual maturation in salmon populations (e.g., Atlantic salmon, sockeye salmon, and the Japanese amago and masu salmon), it is clearly also applicable to steelhead-rainbow trout (*O. mykiss*). Based on Thorpe's conceptual, mechanistic framework, situations with ample food supply and favorable conditions for growth should reinforce the tendency of individuals to adopt freshwater residency (as rainbow trout), thus preempting the "default" anadromous (steelhead) life-history.

3 The Differential Expression of Anadromy Among Populations of *O. mykiss* and Other Salmonids

3.1 Environmental and Genetic Factors Both Affect the Expression of Anadromy

Payne et al. (2005) presented a concise, detailed review of information pertaining to life-history determination and expression in *O. mykiss* populations. Numerous studies have shown that the determination of anadromy versus residency is strongly determined by both genetic and environmental factors. Generally, there appears to be a clear correspondence between the level of environmental harshness and the degree of anadromy expressed in local *O. mykiss* populations. Highly favorable environments (i.e., lower temperatures and stable streamflows) tend to support residency (i.e., rainbow trout) whereas more stressful environments (i.e., higher temperatures and less dependable streamflows) tend to induce the production of proportionately more anadromous steelhead.

That general pattern was illustrated by studies of *O. mykiss* populations in the Yakima River and other rivers in Oregon-Washington, as summarized by Payne et al. (2005: p.4-5):

"Cramer et al. (2003) examined data on watershed features and stream temperature in the Yakima, Deschutes, and Willamette river basins which each have separate distributions of resident and anadromous rainbow trout, all within the zone accessible to ocean migration. Temperature regimes were the most consistent feature that distinguished the main production areas for anadromous or resident *O. mykiss*. Data indicate that streams with temperatures below 16°C during summer and capable of producing 12-14 inch trout at first

maturity offer a selective advantage for residency. Streams where growth opportunities during summer are constrained either by temperature or space likely provide a selective advantage for anadromy (Cramer et al. 2003). Cramer et al. (2003) found resident *O. mykiss* were predominant in upper areas of large streams with cool, dependable flow through the summer, while anadromous steelhead were predominant lower in the watershed, especially in streams where flow was reduced and temperatures became stressful during summer.”

“Studies of spawning in the upper Yakima River system by WDFW researchers have shown that the few steelhead spawning there overlap spatially and temporally with resident rainbow spawning. Mating between the two life history forms has been observed (Pearsons et al. 1998). The predominance of resident *O. mykiss* in the upper basin and of anadromous *O. mykiss* in the lower basin, in spite of interbreeding between the forms, provides strong evidence that the difference in environmental conditions strongly influence selection or expression of anadromy and residency. The healthy population of resident rainbow trout in the upper basin appears to be a key constraint (via competition) on expansion of the steelhead population. Both mainstem and tributary rainbow trout populations have been stable in abundance and size over a 13-year period...”

Similar circumstances may be now operating in the lower San Joaquin River tributaries such as the Stanislaus and Tuolumne rivers where resident rainbow trout greatly outnumber steelhead in tailwater reaches below the major dams. This is also likely the case in the Sacramento River below Keswick Dam, where resident life history types predominate despite presence of steelhead of both natural and hatchery origin (Zimmerman et al. 2009). Cases involving other trout species and river systems are given by Jonsson (1985), Thorpe (1987) and Jonsson and Jonsson (1993).

A further example in sockeye salmon (*Oncorhynchus nerka*) illustrates the generality of the interplay between density-dependent growth rates and increased freshwater residualism. During the 1930s-1970s, spawning runs of sea-run sockeye salmon in Siberia and Kamchatka fell precipitously (Thorpe 1987). The resultant low fish densities allowed for greater food resources and growth potential within the lakes for the remnants of the populations, which showed dramatic increases in the frequencies of residency and sexual maturation in freshwater (Thorpe 1987, 1994).

The variable production of anadromous and resident phenotypes in mixed (i.e., partially anadromous) *O. mykiss* populations in the Central Valley and in other California rivers is now fairly well documented. Payne et al. (2005: p.5-6) summarized:

“Even in Central Valley streams, where access to the ocean is always available, the mixing of resident and anadromous forms is common. Hallock et al. (1961) reported difficulty in separating anadromous and resident *O. mykiss* spawners at the Coleman National Fish Hatchery due to the large size of some resident trout. As reported in Cramer and Associates (1994), “The USFWS found a length nadir at 22.8” with about 15% length overlap of resident and anadromous fish on each side. Mark-recapture studies indicate that many progeny from these fish, both male and female, are still maturing as resident fish (personal communication, J. Smith, USFWS, Red Bluff).” Hallock (1989) showed that 31% of returns from CWT steelhead released in February 1985 in Battle Creek and 11% of fish returning from releases at Princeton had reared to maturity in freshwater.”

“Studies conducted by Donohoe et al. (2004) (NOAA Fisheries) with steelhead and rainbow populations in the Central Valley California show that transmission of residency and anadromy from one generation to the next is flexible. This was determined from Sr/Ca analysis of otoliths collected from 375 adult and 425 juvenile progeny of *O. mykiss* broodstock at anadromous (A) and non-anadromous (NA) hatcheries (Donohoe et al. 2004). Donohoe et al. (2004) found that two populations of *O. mykiss* most distant from the ocean produced both ecotypes from parents of either type, while populations at five other hatcheries produced nearly all A progeny from A females. Donohoe et al. (2004) estimated

that 0-17% of A adults were progeny of NA females, and the percentage tended to be higher at hatcheries farther from the ocean. At Coleman National Fish Hatchery, ~40% of adults were NA progeny of A females. At Iron Gate hatchery, 11% of adults were NA progeny of A females, 16% were A progeny of NA females and 13% had Sr/Ca ratios too intermediate to determine ecotype. These findings demonstrate that A parents can produce NA progeny, and that NA parents can produce A progeny.”

Although favorable environmental conditions may have increased freshwater residency rates or at least helped sustain large populations of resident trout in the upper Sacramento River basin, it is also highly likely that countervailing environmental factors concomitantly have disfavored the expression of anadromy in Central *O. mykiss* populations. Inimical circumstances resulting from the massive environmental alterations in the Sacramento-San Joaquin Delta and San Francisco Bay-Estuary--including wholesale replacement of native fishes and flora by invasive species--cannot be viewed as anything but detrimental to the survival of out-migrating smolts and in-migrating spawners. A substantial body of studies provides compelling evidence that the Sacramento-San Joaquin Delta has been and will continue to be increasingly unfavorable to the health and survival of most native fish species, including salmonids (Brown 2000, Feyrer and Healey 2003, Brown and Moyle 2005, Rosenfield and Baxter 2007, Sommer et al. 2007, Grimaldo et al. 2009). Hence, natural selection against steelhead during their freshwater and estuarine migrating phases inarguably has made the anadromous life-history phenotype less successful relative to the resident phenotype. Within that context, the steady decline of steelhead numbers in the Central Valley rivers is not surprising.

Stated in simplified terms, our overall thesis is that Central Valley steelhead appear to be declining because freshwater conditions in the major tributaries generally favor the adoption of the residential life-history while environmental conditions downstream of the tributaries--including those in the rivers flowing into the central and south Delta--have negatively affected the fitness of anadromous individuals (steelhead), most likely by increasing levels of stress during migration and presumably leading to increased mortality..

3.2 The Early Determination of Life-History Mode in Individuals

It is significant that the factors and timing that determine the life-history pathway of juvenile *O. mykiss*—i.e., the “decision window”—come into play early in life. Similar early determination of life-history modes has been observed in other anadromous salmonids (e.g., brook trout, brown trout, Atlantic salmon; McCormick et al. 1985, Bohlin et al. 1994, Dolloff et al. 1994). In their study of anadromous and resident brook trout populations in Quebec (Canada), Morinville and Rasmussen (2006: p.701) concluded:

“The observed differences in both habitat use (this study) and energy allocation (Morinville and Rasmussen 2003) are detectable as early as in the first year of life and persist throughout the juvenile stages, indicating that the life-history variation is expressed early in life and is not simply adopted in the year in which migration occurs.”

The early determination of life-history modes indicates that genetic factors also are involved, but the genetic interactions with environmental factors undoubtedly are complicated. As summarized by Jonsson and Jonsson (1993: p.357-358):

“There is no simple answer to this question: there are elements of both environment and genetics. The environmental influences through feeding have been demonstrated in a number of field and laboratory studies, . . . Improved juvenile feeding tends to increase the proportion of resident fish. Furthermore, both resident and migratory parents from partially migratory populations produce the two types of offspring. Moreover, when reared artificially under the same conditions, the offspring of the two morphs become almost identical... The close link between these two life history types is also evident from releases of resident brown trout in New Zealand which have given rise to anadromous populations

(Frost and Brown, 1967), and releases of offspring of sea-run migratory brown trout in North America which have given rise to resident fish (Rounsefell, 1958)."

"Partial migration [i.e., partial anadromy, whereby a population comprises both anadromous and resident phenotypes] is also partly determined by inheritance. Rearing experiments have revealed that resident parents produced a somewhat lower proportion of migrants and more residents than did anadromous parents . . . Furthermore, field experiments have shown large differences in the tendency to migrate among populations . . . Based on a series of studies with brown trout in the English Lake District, Elliott (1989) concluded that there was strong evidence for genotypic differences between stocks controlling the migratory behaviour of brown trout."

Nevertheless, the operation of environmental factors later during the growth period of salmonids also can be important for at least triggering anadromy. For example, in experiments on landlocked Atlantic salmon that varied the light regimen and food-rations of juveniles, food-deprived juveniles still eventually became smolts after they were later allowed to feed (Kiiskinen et al. 2003).

3.3 Influence of Food Supply on the Tendency for Smolting

The influence of food supply on smolting and migration--or, alternatively, on maturation in freshwater of juvenile salmonids--is now well recognized (e.g., Morinville and Rassmussen 2003) and has been demonstrated for several species (e.g., arctic char (Nordeng 1983) and *O. mykiss* (Tipping and Byrne 1996). The immediate deciding factor appears to be the "energetic state" (i.e., metabolic rates) of the juveniles, which depends on the food levels available to the growing fish. Studies on arctic char and brown trout indicated that juveniles with higher metabolic rates also appeared to grow faster and tended to shift their ecological roles sooner by migrating to different freshwater areas--e.g., from stream to lake or from shallow to deeper lake habitats (Forseth et al. 1994, 1999).

Generally, the literature seems to indicate that lower local food supply results in a greater proportion of individuals with a migratory life-history in a population while higher food supply increases the proportion of resident phenotypes. Such an increase in frequency of residency and concomitant decrease in anadromy (migration) in response to higher local food levels has been demonstrated in arctic char (Nordeng 1983). Conversely, the experimental reduction in food levels for hatchery-raised *O. mykiss* smolts resulted in smaller fish that evidently were more prone to migrate, as reflected by the higher recapture rate of the food-reduced groups of smolts compared with the control group (Tipping and Byrne 1996).

Both the feeding history and energetic state of potential and actual smolts are reflected by their "condition factor"—i.e., basically an index ("K-value") of a fish's weight relative to its length. Studies generally have shown that individual steelhead smolts with lower condition factor (reflecting lower feedings levels and energetic states) were more prone to emigrate downstream than smolts that had higher food levels and higher condition factor (Tipping and Byrne 1996 and references therein). While previous studies had passively observed the relationship between condition factor (K-values) and emigration rate, Tipping and Byrne (1996) demonstrated that artificial manipulation of feeding rates could directly affect the condition factor and, thereby, the rate and timing of emigration by steelhead smolts.

Based on their studies on a freshwater brown trout population, Forseth et al. (1999) presented an energetically based rationale for why some individuals migrate earlier than others while some individuals may not migrate at all. The conceptual mechanism was described as follows (Forseth et al. 1999: p.791):

"Juvenile brown trout thus appear to migrate from one habitat to another as a phenotypically plastic response to declining growth performance as they reach an environmental threshold in their present habitat. This accords with the general assumption

that migration is a biological response to adversity (Taylor & Taylor 1977). Individuals may reach this threshold at different ages and sizes depending on their metabolic status. Fast-growing individuals migrate earlier and at a smaller body size than slower-growing individuals, because their metabolic rates are higher, and consequently experience a larger drop in their allocation of energy to growth. By migrating, the fish are probably able to retain a higher growth rate than possible under the feeding opportunities in the original habitat.”

“For fast-growing individuals, an alternative to migration is to mature sexually in the stream. The size advantage attained in the stream, relative to slower-growing individuals, may then be converted into a fitness advantage by earlier reproduction and the possibility of participating in more spawning events during life. Among brown trout in Litjää, this tactic was followed by a small proportion of the males only. These males were among the largest within their cohorts...”

Furthermore, Forseth et al. (1999) pointed out that the reasons for why individuals within a population differ in their metabolic rates to begin with (i.e., fast growing versus slow growing) may depend on both the environmental influences on early developmental stages and genetic factors.

3.4 Genetic Influence on Growth and Life-History

The strong genetic basis of anadromy in *O. mykiss* has been clearly demonstrated in rearing experiments of progeny that were produced from experimental crosses between steelhead and resident trout (Thrower et al. 2004a). In that study, wild anadromous steelhead from Sashin Creek and Sashin Lake in southeastern Alaska were bred with wild resident rainbow trout from a lake that had previously been artificially established with founders from that same steelhead stock. The study determined the heritability values for three interrelated life-history variables—viz., individual growth, precocious male maturation in freshwater, and smolting. Moderate or high heritability values were found for precocious male maturation, smolting and growth. There was low genetic correlation between growth and smolting, but smolting and freshwater maturation were negatively correlated.

The results of the rearing experiments by Thrower et al. (2004a) indicated a strong genetic basis for the expression of growth and size traits in *O. mykiss* family-lines and also strongly negative phenotypic and genetic relationships between smolting rate and male maturation rate (at age-2). However, year-to-year environmental variation will affect the expression of growth, size, smolting and maturation rates in freshwater. Hence, Thrower et al. (2004: p.303) inferred that “conditions that fluctuate and favour smoltification or maturation to different degrees in different years will tend to maintain genetic and phenotypic variability for these traits in the population.”

Furthermore, it was shown that significant genetic variation in growth, smolting, and male maturation rates among family-lines continues to exist in the Sashin Lake population. That observation “suggests some form of balancing selection in the lake population, one that maintains a selective advantage for fish possessing the genes associated with smolting (e.g., high spring growth rates) while the phenotypic expression of smolting and the associated downstream migration is rarely manifested” (Thrower et al. 2004: p.303).

The persistence of smolting even at low levels in the Sashin Lake population—which has existed as a completely freshwater population that is inaccessible to up-migrating steelhead for over 70 years—indicates that the genetic potential for anadromy can lie essentially dormant for a long time. Any smolts that are produced from resident trout in the lake may be able to down-migrate to the ocean but they cannot return to reproduce in the lake. Hence, the smolts are “spontaneously” produced by resident trout in the lake rather than by anadromous steelhead parents.

However, despite the long-term retention of smolting and perhaps other traits associated with anadromy in the Lake Sashin *O. mykiss* population, Thrower et al. (2004a) noted that the lake-derived smolts appear to experience poor survival in the marine environment compared to smolts produced from fully anadromous steelhead parents. Therefore, some key genetic factors that are related to successful marine survival and migration back to freshwater natal areas appear to have been lost or suppressed in the Sashin Lake population. This apparent deficiency in marine-related fitness of the lake population may have been due to either, or both: (1) a genetic founder effect in the initial introduced population (i.e., very low numbers of founders composed the introduced stock and, hence, a limited gene pool), or (2) the lack of full access to and from the ocean resulted in the loss of adaptive characteristics for marine survival because reinforcing selection for such characteristics had been essentially terminated.

Yet, statistical analysis of genetic data for the Sashin Lake and Sashin Creek *O. mykiss* populations indicated “that 25% of the anadromous adults at the Sashin Creek weir in 1996 and 1997 had originated in the upper watershed” (Thrower et al. 2004b citing Pella and Masuda 2001). Such long-term persistence of the anadromous tendency in Sashin Lake *O. mykiss* indicates that the genetic basis for anadromy remains deeply engrained in the genetic architecture of that population. From a broad perspective, the persistence and pervasiveness of anadromy in *O. mykiss* and other salmonid species have demonstrable benefits in terms of “spreading of risk” of extinction, maintaining demographic resilience and longevity, and having the ability to exploit new habitats (e.g., such as recently deglaciated rivers) (Milner et al. 2000, Quinn 2005).

Another indication of the importance of genetics for anadromy is the ability of hatcheries in the Central Valley--mainly American (Nimbus) and Feather River hatcheries--to maintain steelhead runs, despite apparent strong selection against production of “natural” steelhead in the watersheds. Those hatcheries have long selected for definite sea-run fish for spawning, primarily fish of distinct hatchery strains (e.g., Eel River origin) (McEwan and Jackson 1996).

Thrower et al. (2004a) also point out that environmental conditions that stimulate expression of anadromy in the Sashin Lake population—and by implication in other quasi-isolated populations of *O. mykiss* in which upstream migration from the sea is blocked—may facilitate the continual loss of genotypes associated with anadromy from the population because the down-migrating individuals are permanently lost. If a management goal is to use such populations as refuges and as potential donor sources for reintroduction or augmentation of anadromous stocks, then a prudent strategy may be to minimize the expression of anadromy and consequent loss of smolts from those potential source stocks, perhaps by influencing environmental conditions in the rearing areas (e.g., higher springtime temperatures might inhibit smolt production).

The preceding points have potential management implications for the lower San Joaquin River basin’s *O. mykiss* populations. On the one hand, it would be highly useful to produce large numbers of steelhead smolts to rear in the ocean and return to spawn in the San Joaquin basin tributaries. In such a scenario, there would be reinforcing selection on adaptive characteristics for marine survival, thus maintaining the fitness of the population’s steelhead component. On the other hand, if virtually all the smolts die—which may be currently happening as the smolts migrate through the Sacramento-San Joaquin Delta and San Francisco Estuary—then natural selection is operating to reduce or eliminate the anadromous genotypes from the *O. mykiss* population(s). This latter scenario is similar to the situation of the Sashin Lake *O. mykiss* population. Hence, a prudent strategy for preserving life-history diversity may be to minimize the expression of anadromous phenotypes in these San Joaquin basin populations until the environmental conditions downstream of the natal tributaries are more favorable for survival of down-migrating steelhead smolts. On the other hand, if the primary purpose of *O. mykiss* management is to maintain large, fishable resident trout populations in the rivers, then the continual incidental loss of low numbers of smolts may be inconsequential.

Therefore, whether management measures should aim to facilitate or to inhibit the expression of anadromous phenotypes in *O. mykiss* populations (e.g., by flow or temperature manipulations) depends on the relative magnitudes of growth and survival rates in the ocean and in the estuary and river environments. We currently do not appear to have such information on *O. mykiss* populations of the San Joaquin River basin.

4 Additional Evolutionary Aspects of Anadromy

Hendry et al. (2004) presented an evolutionary perspective on the variable expression of anadromy among different salmonid species and among populations within species. In their review and synthesis of the literature, Hendry et al. (2004) noted that the balance of costs and benefits of anadromy was a major determinant of whether populations expressed high levels of anadromy or were primary non-anadromous. Although that review viewed the issue of anadromy over a broad spatial and temporal scale, it provides a highly relevant and useful context in which to ask why anadromy currently is not as commonly manifested in Central Valley *O. mykiss* populations as it apparently was in the past.

Some pertinent conclusions by Hendry et al. (2004: p.124-125) follow:

“We examined evidence that variation in anadromy/non-anadromy is the result of variation in the benefits and costs of these alternative life histories. We find strong evidence that anadromy has both benefits and costs. Benefits come in the form of increased body size and energy stores, which may then increase reproductive success. These benefits tend to be concrete and absolute for females but variable and relative for males. Costs come in the form of increased mortality and increased energy expenditure during migration. These costs and benefits apply in an opposite manner to non-anadromy. Although these general conclusions seem robust, additional work is needed. For example, comparisons of stage-specific rates of mortality between the two life histories would provide a clearer picture of the actual fitness costs associated with migration per se.”

“Variation in anadromy/non-anadromy should evolve as a function of variation in costs and benefits. For example, the benefits of anadromy are greater for females than for males and, accordingly, males are more likely to forgo anadromy. Among populations, anadromy should decrease with increasing migratory difficulty and with increasing freshwater productivity. These predictions enjoy support from distribution patterns (Rounsefell 1958), direct correlative tests (Kristoffersen 1994; Bohlin et al. 2001), and experimental manipulations (Morita et al. 2000; Altukhov et al. 2000). What remains entirely unknown, is the extent to which variation in anadromy/non-anadromy is the result of phenotypic plasticity or genetic variation...”

The quoted passages above are significant because the evidence indicates that current and continued future conditions in the Central Valley, particularly in the lower San Joaquin River tributaries, should favor the expression of more residency (i.e., non-anadromy) and less anadromy in the *O. mykiss* populations. The major factor in the Central Valley is potentially “migratory difficulty”—viz., through the Sacramento-San Joaquin Delta—which has significantly increased for migrating salmonids in recent decades while “freshwater productivity” has increased (at least in some cases) within tributary stream reaches below the major dams—i.e., in the areas where the salmonid populations are more concentrated. Hence, from an evolutionary perspective, “wild” or “natural” Central Valley *O. mykiss* populations should be expected to continue to be predominated by resident phenotypes and to produce relatively fewer anadromous (steelhead) phenotypes despite the focus by major hatcheries on the production of steelhead. Such an evolutionary trajectory will continue as long as freshwater habitat conditions provide more net benefits than incurred costs for survival and growth, in contrast with an anadromous life-history in which the balance of benefits-to-costs currently seems

more weighted toward costs (e.g., lower migratory survival) than to benefits (e.g., higher growth potential in the ocean).

Hendry et al. (2004: p.125) further concluded:

“Anadromy/non-anadromy should be influenced by density, frequency, and condition dependence. Research on these topics is as yet fragmentary but some preliminary generalizations are possible. First, density-dependent survival and growth is common, and can influence emigration from a local area. Moreover, several studies have shown that anadromy may indeed be density-dependent Second, studies in experimental arenas have suggested that the mating success of anadromous and non-anadromous males may be frequency-dependent, but these have yet to remove potentially confounding effects of density dependence. Third, individual condition may influence migratory tendency in different ways. In some systems, the largest juveniles become anadromous, whereas in other systems, the largest juveniles remain non-anadromous. In any given system, the average fitness of the two life histories may not be equal and instead may be maintained within populations through a conditional strategy (Gross and Repka 1998). Full testing these hypotheses will require studies of lifetime reproductive success in natural systems.”

Hence, our current understanding of the forces and mechanisms underlying the expression of anadromy is incomplete but nonetheless sufficient to explain most of the complex patterns observed. Whether populations express anadromy or non-anadromy depends on population sizes and densities (“density dependence”), on the relative frequencies of anadromous and non-anadromous individuals in the populations (“frequency dependence”) and on how healthy or vigorous the individuals are in those populations (“condition dependence”). The implications are that the relative abundance of anadromous steelhead within the San Joaquin basin and elsewhere in the Central Valley may fluctuate significantly over time according to how the overall *O. mykiss* population levels change. It is evident that selection pressures on naturally spawned fish in the regulated rivers of the Central Valley favor resident rainbow trout, although a small steelhead component is always likely to be present. However, production of steelhead for fisheries is and will continue to be largely the domain of hatcheries.

5 Management Coda

Despite studies showing that environmental factors can strongly influence the expression of anadromy in *O. mykiss* populations in ways that are not always predictable, there are conceivable management actions that could be explored for increasing the frequency of anadromous *O. mykiss* in Central Valley rivers.

Specifically, environmental manipulations of flows and stream temperatures could be conducted during the early spring to early summer months when salmon and steelhead normally rear and smoltify. For example, flow levels that produce and maintain higher temperatures in rearing areas (e.g., in-channel back-water areas) during the early spring may be expected to improve juvenile growth rates, while higher stream temperatures in late spring (i.e., as flow-releases are progressively reduced) may impel the juveniles to move further downriver or to cooler estuarine areas which are more conducive for smoltification.

The putative objectives of such a study would be to show that environmental conditions that maximize body-growth rates can lead to increased smoltification rates for both salmon and steelhead while also maintaining a viable resident population of *O. mykiss* in the rivers. Such experiments would require multiple years to conduct but eventually may provide a more accurate idea of what flow and temperature schedules are better suited for increasing anadromy in *O. mykiss*. Yet, such experimental flow manipulations pose difficult conceptual and logistical challenges because they are not replicable in a scientific or statistical sense—i.e., each river is physically and biologically distinct

(in terms of topography, spatial extent, biological composition) and so their respective *O. mykiss* populations might respond differently to changing flow regimes.

Additionally, studies are needed to provide more quantitative, comparative data on freshwater versus ocean growth and survival of *O. mykiss*, particularly for the San Joaquin basin tributaries where differential selective forces on the life-history types (i.e., anadromous and resident) may be pronounced. Such studies would include: (1) otolith microchemical analyses to reconstruct the life-history schedules of individuals that return as spawners to the streams; (2) tagging and tracking studies (i.e., with radio- or acoustic-transmitters and/or thermal recorders that reveal the spatial movements and their associations with environmental conditions (e.g., temperature) during the freshwater life-stages. The resultant information would demonstrate the relative fitness (i.e., survival rates) of individuals that followed specific life-history and migratory pathways.

To the extent that human-managed environmental control of the expression of anadromy in *O. mykiss* is possible, the strategic goal ideally would be to re-create conditions in regulated Central Valley rivers that mimic conditions in streams where the steelhead phenotype is relatively strongly represented—e.g., as in some central and northern California coastal streams (Russian, Mattole and Mad rivers; Moyle et al. 2008) or in Deer Creek, a small unregulated tributary in the Sacramento River basin (Zimmerman et al. 2009).

However, because the present environmental conditions in the Central Valley drainage generally disfavor the expression of anadromy and strongly favor residency in *O. mykiss* populations, even vigorous experimental management efforts may achieve only limited success in eventually producing significantly higher numbers of “natural” steelhead—particularly in the San Joaquin River basin where migratory challenges through the Delta are substantial and even in the Sacramento River basin despite (or because of) continued hatchery production of steelhead. Presently, it seems the best management strategy is accept the reality that naturally produced steelhead cannot be produced in any appreciable numbers in Central Valley streams where flows are regulated by dams. The Central Valley *O. mykiss* populations will continue to be of mixed hatchery-wild origin (i.e., with detectable hatchery/Eel River genetic influence; Garza and Pearse, undated report) with almost all anadromous fish originating from hatcheries. Existing populations, if any, of “true” native Central Valley steelhead should be identified (e.g., by genetic studies) and management efforts should focus on maintaining conditions that support their life-history requirements.

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APPENDIX. Synopses of Selected Papers

This appendix summarizes selected results from several recent papers that represent the types of research that are significantly increasing our understanding of *O. mykiss* population biology and evolution. These summaries are abbreviated and incomplete; the original papers should be consulted for a fuller appreciation of the findings and their implications. The studies encompass *O. mykiss* populations within California as well as from more northern regions. The topics include:

- (1) The effects of environmental factors and timing on smolting versus non-smolting life-history pathways of individuals within different populations (Beakes et al. 2010).
- (2) The extent to which the anadromous versus non-anadromous composition of populations is related to environmental factors—e.g., water chemistry and other rearing conditions in rivers and hatcheries; migration distances to spawning areas (Donohoe et al. 2008).
- (3) The degrees to which anadromous (steelhead) and non-anadromous (resident trout) parental phenotypes interbreed in various mixed populations of *O. mykiss* (e.g., Seamons et al. 2004, Kulogowski et al. 2005, Olsen et al. (2006), Christie et al. 2011).
- (4) The relationship between “migratory”-anadromous steelhead and resident rainbow trout within local populations (i.e., fine-scale spatial pattern) compared with the relationship between steelhead and resident trout over larger geographical areas (i.e., broad-scale spatial pattern) (Olsen et al. 2006).

Beakes, M.P., W.H. Satterthwaite, E.M. Collins, D.R. Swank, J.E. Merz, R.G. Titus, S.M. Sogard and M. Mangel. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Transactions of the American Fisheries Society 139:1263-1275.

In a laboratory study using a common-garden experimental design, Beakes et al. (2010) examined the effects of temperature regime and food supply on the relationship between growth rates and smoltification success of steelhead juveniles from two distinct source populations (“strains”) in California—Scott Creek (i.e., the Monterey Bay Salmon and Trout Project hatchery) on the central California coast (CCC) and Battle Creek (i.e., Coleman National Fish Hatchery) in the northern California Central Valley (NCCV). The study used experimental temperature regimes (warmer in year 2006, cooler in 2007) that mimicked the natural seasonal temperature cycle in California streams. Food rations were experimentally controlled at designated low and high levels.

Juveniles of the NCCV strain generally had higher growth rates than did CCC juveniles, and the NCCV juveniles also showed more pronounced enhancement of growth rates in response to a warmer temperature regime. A higher temperature regime during the laboratory rearing period resulted in increased growth rates for both the NCCV and CCC strains, and higher food rations also resulted in increased growth rates for both groups. In both strains, the individuals that had higher growth rates and that attained larger body size were eventually more successful in surviving the smolting process, as assayed by seawater challenges. This result suggests that environments that favor fast growth should also favor successful smolting and, hence, the production of steelhead—at least for those individuals with genotypes that are destined or inclined toward an anadromous life-history. Furthermore, there were differences between the strains in survival likelihood. Specifically, CCC steelhead were more likely to survive seawater challenges than NCCV steelhead of the same size which means that the CCC steelhead tended to smoltify at smaller sizes (and younger ages) than did NCCV steelhead.

Beakes et al. (2010) also found that the putative smolts and putative non-smolts had started to diverge in both size and growth rate early in the experiment even before the feeding treatments began—possibly indicating that there were inherent genetic differences between fish that were to

become anadromous within the year (i.e., smolts) and those that would remain in freshwater for at least another year (i.e., the non-smolts). Alternatively, the early growth differences between putative smolts and non-smolts could have resulted from aggressive interactions—especially since both strains of juvenile steelhead were of hatchery origin which may select for aggressive behavior—although the CCC juveniles were only one-generation hatchery fish that were derived from Scott Creek wild adults (Beakes et al. 2010).

Regardless of the mechanism(s) that determine the different growth-rate trajectories, the results from this study showed that the adoption of a life-history pathway (anadromous versus resident) is set well before the actual emigration time of those two source populations (March or later). Evidently, the “decision window” occurs sometime before the winter (although the exact time could not be determined) and the fish become committed to the smolting or non-smolting pathways “no later than November” (Beakes et al. 2010: p.1273). Therefore, the eventual smolts and non-smolts became fixed on their respective developmental pathways even before the natural season of growth opportunity (i.e., winter or early spring). The authors suggested that the early commitment timing for life-history divergence and observed differences in their responses to growth opportunity between the CCC and NCCV strains may indicate some inherent difference reflecting local adaptations to their respective environments, although some of the differences might additionally be due to the different hatchery backgrounds of the strains.

Donohoe, C.J., P.B. Adams and C.F. Royer. 2008. Influence of water chemistry and migratory distance on ability to distinguish progeny of sympatric resident and anadromous rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 65:1060-1075.

Donohoe et al. (2008) analyzed the otolith microchemistry—i.e., strontium to calcium (Sr:Ca) ratios—of *O. mykiss* juveniles produced at eight northern California steelhead hatcheries, plus two inland and one central coastal hatcheries. Their study found that a relatively high number of individuals produced at two hatcheries (Iron Gate Hatchery and Coleman National Fish Hatchery) become resident trout rather than steelhead despite having been derived from anadromous steelhead mothers.

For example, 14 (87%) of resident adults sampled from the Coleman National Fish Hatchery and 18 (50%) of resident adults from Iron Gate Hatchery had otolith Sr:Ca characteristics identifying them as the progeny of steelhead mothers. The maternal origin of the remaining adults at those two hatcheries could not be clearly determined from their otoliths. In contrast, only anadromous progeny were produced from known (based on otolith microchemistry) or inferred (based on large body size) steelhead females at six of the other hatcheries.

The reasons for the increased production of resident progeny (i.e., for “residualism”) at the Iron Gate and Coleman hatcheries may include either (or both) the rearing conditions at those particular hatcheries or natural in-river conditions at their respective locations. The riverine environment near Coleman National Fish Hatchery (on lower Battle Creek) likely offers the same type of conditions that favor adoption of the resident life-history as seen for the highly productive resident rainbow trout population in the uppermost mainstem Sacramento river below Keswick Dam (McEwan 2001).

Donohoe et al. (2008) also investigated the influence of two environmental factors—viz., stream water chemistry (strontium:calcium ratio) and distance of the spawning stream from the ocean (i.e., “migratory distance”)—on the otolith microchemical characteristics of the juvenile *O. mykiss* produced by anadromous and freshwater-resident female spawners. The purpose was to determine how those two factors—in addition to the life-history type of the mothers (anadromous or resident)—affected the otolith Sr:Ca ratios of their progeny.

The study found that for resident-type females, the mean Sr:Ca ratio of their progeny’s otolith core increased as the ambient Sr:Ca ratio of the spawning (natal) stream increased. For anadromous

females, the mean Sr:Ca ratio of their progeny's otolith core was higher than that of the progeny of resident females. Also, the otolith-core mean Sr:Ca ratio in progeny of anadromous females increased as the Sr:Ca ratio of the mother's spawning stream increased but the progeny's Sr:Ca ratio decreased in relation to increased migratory distance and spawning-stream elevation experienced by the mothers. The analysis by Donohoe et al. (2008) quantified (i.e., modeled) the relative effects of those three actors affecting the progeny's otolith-core Sr:Ca ratios—viz., maternal type (anadromous versus resident mothers), ambient Sr:Ca ratio of the natal stream, and migratory difficulty (i.e., distance and elevation, both of which are related to time in freshwater spent by females prior to spawning).

Based on their otolith analysis of adults and juveniles from the northern California hatcheries that produced anadromous fish, Donohoe et al. (2008:1073) concluded that “these results do not provide evidence that resident [*O. mykiss*] females make a substantial contributions to populations of anadromous adults.”

Additional recent studies continue to show that the degree to which resident phenotypes contribute to the production of anadromous progeny can vary markedly among populations, reportedly ranging from zero to as much as 33% of the progeny year-class (studies cited by Donohoe et al. 2008). Generally, the studies indicate that anadromous females produce resident-phenotype progeny at substantially higher rates than resident females produce anadromous progeny, but the limiting factors and mechanisms which control life-history expression in the progeny of anadromous and resident parents remain poorly understood (Donohoe et al. 2008).

As Donohoe et al. (2008: p.1072) noted:

“Genetic analyses also suggest that exchange between life history forms is limited in some systems but may be higher in others (Docker and Heath 2003; Narum et al. 2004). While these studies suggest that the degree of segregation between the two forms can vary greatly among sites, the mechanism for these differences may be complex and varied.”

Christie, M.R., M.L. Marine and M.S. Blouin. 2011. Who are the missing parents? Grandparentage analysis identifies multiple sources of gene flow into a wild population. Molecular Ecology. Blackwell Publishing Ltd. Doi: 10.1111/j.1365-294X.2010.04994.x

In addition to determining the proximate factors that cause individual juvenile *O. mykiss* to follow and anadromous life-history pathway, it is important to determine the extent to which both anadromous and resident parents contribute to the production of anadromous progeny. Christie et al. (2011) analyzed steelhead pedigrees over three generations (6 broodyears) in the Hood River (Oregon) population. Their major findings based on eight microsatellite-DNA loci were as follows.

Among the steelhead progeny that were genetically identified as having only one anadromous parent (i.e., either the mother or father), 83% of those progeny had a resident father and 17% had a resident mother. Hence, matings between a steelhead mother and resident father produced more steelhead progeny than did matings between a steelhead father and resident mother.

Among the juvenile steelhead males that were produced at a hatchery (from steelhead parents) but that subsequently adopted a resident life-history (i.e., became residualized), those that mated with wild steelhead females produced more offspring than did those that mated with hatchery-produced steelhead females. It was suggested that this observed disparity in reproductive success was possibly due to the “high fitness costs” (i.e., reduction in fitness) borne by progeny from matings between two hatchery parents. [Other possible explanations may be (1) that the “residualized” hatchery females are smaller than wild steelhead females and so produce fewer eggs and eventual progeny, or (2) that the offspring from matings between hatchery females and hatchery males had lower survival than did offspring from matings between wild steelhead females and hatchery males.]

Among the progeny of all possible matings in the population involving one or more steelhead parents, only 1% of the genes were inherited from residualized hatchery steelhead that spawned with anadromous steelhead and 20% were from matings between anadromous steelhead and wild resident parents. Up to another 23% of the population's gene pool was determined to have resulted from matings between two resident parents. Therefore, approximately 40% of the genes in the steelhead population each generation came from wild resident parents.

The authors concluded that "These results suggest that wild resident fish contribute substantially to endangered steelhead 'populations' and highlight the need for conservation and management efforts to fully account for interconnected *Oncorhynchus mykiss* life histories" (Christie et al. 2011: p.1). They further stated (Christie et al.: p.12): "More generally, this study underscores the need to adequately protect and appropriately manage all aspects of salmonid life history."

The authors' call for an integrated approach to managing the anadromous and resident components of *O. mykiss* populations reiterates the conclusions and recommendations from similar recent studies (McPhee et al. 2007, Riva-Rossi et al. 2007, Williams et al. 2007). It is increasingly clear that anadromous and resident individuals represent only two phenotypes within a spectrum of genetically interconnected life-history types within *O. mykiss* populations.

Seamons, T.R., P. Bentzen and T.P. Quinn. 2004. The mating system of steelhead *Oncorhynchus mykiss*, inferred by molecular analysis of parent and progeny. Environmental Biology of Fishes 69:333-344.

Seamons et al. (2004) utilized molecular genetic markers (at 12 microsatellite-DNA loci) to analyze the mating system of winter steelhead and resident (rainbow) trout in a natural population. The parental-offspring genetic patterns revealed that both males and females spawned with multiple partners although some single-pair matings also were inferred.

In the case of juveniles for which only one parent could be genetically identified, the great majority (88%) had a known mother and unknown father compared to the juveniles (11%) that had an unknown mother and known father. Because virtually all the returning adult steelhead (both males and females) were captured during the four consecutive years of this study, the genetically unknown parents were inferred to have been resident-phenotype fish. Therefore, the cases involving a high proportion of unknown fathers were interpreted as evidence for spawning by resident males (including precociously mature male parr) with adult steelhead females. After considering several alternative explanations regarding the unknown fathers, Seamons et al. inferred that most of those unidentified resident males were precociously mature male parr that managed to spawn with steelhead females.

There was no evidence of size-assortative mating; i.e., spawning occurred randomly between fish of various body sizes.

Kuligowski, D.R., M.J. Ford and B.A. Berejikian. 2005. Breeding structure of steelhead inferred from patterns of genetic relatedness among nests. Transactions of the American Fisheries Society 134:1202-1212.

Kuligowski et al. (2005) analyzed the breeding structure of a steelhead population in the Hamma Hamma River (Washington) using microsatellite-DNA loci. Their results were similar to the findings by Seamons et al. (2004)—viz., that both male and female steelhead engaged in spawning with multiple mates. Kuligowski et al. appeared to observe a highly biased sex-ratio in the inferred spawners—i.e., 5 females to 16 males in their genetic analysis. They also inferred an overall mating pattern (from the sample) of 6 males having fertilized 83% of all the eggs and 10 additional males

each having fertilized very few (i.e., 7 or less) eggs. On that basis, Kuligowski et al. suggested that the mating pattern was consistent with matings by all 5 female steelhead with 6 male steelhead and 10 other males comprising either resident rainbow trout or precocial male steelhead parr, or both.

Therefore, this study indicated a substantial reproductive contribution by resident fish (rainbow trout or precocial steelhead parr) to the spawnings in this steelhead population, as has been similarly observed in other studies (e.g., Seamons et al. 2004, Christie et al. 2011).

Olsen, J.B., K. Wuttig, D. Fleming, E.J. Kretschmer and J.K. Wenburg. 2006. Evidence of partial anadromy and resident-form dispersal bias on a fine scale in populations of *Oncorhynchus mykiss*. Conservation Genetics 7:613-619.

A genetic analysis of sympatric steelhead and resident rainbow trout in the Copper River (southern Alaska) drainage by Olsen et al. (2004) showed that the two life-history forms were genetically intermixed within local populations but that spatially separated populations were genetically differentiated. Furthermore, it was found that resident rainbow trout were more prone to disperse over short distances (i.e., “fine-scale” gene flow among localities) compared to steelhead that showed broad-scale dispersal and gene flow across more distant tributaries and to the ocean.

Based on their own and other published studies, Olsen et al. (2006: p.617) concluded that “management strategies should aim to maintain both migratory forms” because they may provide gene flow at different spatial scales.

The following excerpts enunciate the two major insights from Olsen et al. (2006: p.617):

“Accumulating evidence indicates that the range of partial anadromy in coastal North American populations of *O. mykiss* extends from Alaska to the Pacific Northwest (this study, Docker and Heath 2003; Narum et al. 2004). Selective forces and natural and man-made migration barriers may not always favor partial anadromy (e.g., Zimmerman and Reaves 2000), but this study and others indicate the degree of relatedness among *O. mykiss* populations is generally associated with geographic proximity, not migratory type, suggesting polyphyly similar to that observed for sympatric pairs of anadromous and nonanadromous sockeye salmon (*O. nerka*, Foote et al. 1989). Also, the potential for anadromy may persist in isolated nonanadromous populations for many generations (Pascual et al. 2001; Thrower et al. 2004b). Evidence of partial anadromy, polyphyly, and the resilience of anadromy, suggest geographic proximity and genetic history, more than migratory type, should be considered when identifying populations for use in restoration of local genetic diversity in *O. mykiss*.”

“Although it is possible that steelhead and resident *O. mykiss* may be restored from each other, management strategies should aim to maintain both migratory forms. The resident form appears to play a large role in gene flow at a small spatial scale in freshwater, but it likely plays a small role in broad-scale gene flow. Migration across distant tributaries and through saltwater will only result from the anadromous form. Therefore it seems prudent to acknowledge the two migratory forms may facilitate gene flow at different spatial scales in *O. mykiss* populations.”

**COMMENTARY ON EVALUATING THE TEMPERATURE-RELATED
FLOW REQUIREMENTS OF STEELHEAD-RAINBOW TROUT
(*ONCORHYNCHUS MYKISS*) IN THE LOWER TUOLUMNE RIVER:
A LITERATURE REVIEW AND SYNTHESIS**

**RONALD M. YOSHIYAMA
JULY 5, 2012**

MEMORANDUM

COMMENTARY ON EVALUATING THE TEMPERATURE-RELATED FLOW REQUIREMENTS OF STEELHEAD-RAINBOW TROUT (*Oncorhynchus mykiss*) IN THE LOWER TUOLUMNE RIVER: A LITERATURE REVIEW AND SYNTHESIS

JULY 5, 2012

Ronald M. Yoshiyama, Consultant to San Francisco

OVERVIEW OF ISSUES

The present commentary consists of a literature review and synthesis of information pertaining to the temperature limitations on salmonids, particularly steelhead-rainbow trout (*Oncorhynchus mykiss*). The specific purpose is to address the issue of streamflows and temperature requirements that must be met to sustain a minimal viable population of steelhead-rainbow trout (*O. mykiss*, or “trout”) in the lower Tuolumne River, a major tributary of the San Joaquin River in the California Central Valley. The following questions in reference to the summer rearing period of the juvenile trout serve as an initial focal point for evaluating this issue.

The Questions:

Are the minimum seasonal streamflows—particularly the 50-75 cfs minimum summer flows specified by the FERC Settlement Agreement ("FSA")--sufficient for the protection of over-summering juvenile trout? In view of the adequacy, or inadequacy, of the minimum summer 50-75 cfs flows, what must be done to ensure that the environmental requirements of steelhead and rainbow trout are maintained in the Tuolumne River?

Outline for Evaluating the Questions

Complete answers to these questions require considering the environmental needs of steelhead-rainbow trout (*O. mykiss*) over a range of spatial and time scales. The questions also require that the trout population of the Tuolumne River be more clearly defined as a biologically valid demographic unit in terms of its relationship to the upriver, above-dam stock(s) and to steelhead-rainbow trout in other Central Valley streams.

In the immediate sense, the question of the adequacy of the 50-75 cfs summer flow can be answered in parts corresponding to different aspects of the issue. Those aspects and the kinds of information needed to address them are as follows.

- (1) What are appropriate temperature cut-off criteria? Review and synthesis of the temperature literature to determine the extent to which various temperature criteria are appropriate for defining hospitable versus inhospitable conditions for trout.

- (2) What are the existing amounts of suitable habitat and flows/temperatures in relation to trout distribution? The Stillwater Sciences SNTMP modeling analysis gives a preliminary picture of how much of the lower Tuolumne River is suitable or unsuitable to trout in terms of these temperature criteria. Additional detailed temperature modeling has been conducted by CDFG's consultant, A.Dotan.
- (3) To what extent do flows and temperatures act as determining factors for trout population size? Specifically assess the demographic consequences of certain flow and temperature configurations for the trout population in the lower Tuolumne River. Components of this question are:
- (a) Population abundance or density of trout in the uppermost reaches. The actual numbers of adult and juvenile trout in the lower Tuolumne River were not accurately known until recently. Routine fish monitoring by the Districts indicates relatively low numbers of trout have been present over the past 1-2 decades--i.e., far below the numbers occurring in the Sacramento River mainstem and tributaries.
- Presently, the informational need is to determine how many juvenile trout persistently occur, or should occur, in the uppermost reaches of the lower Tuolumne River during a given summer under a specified flow regime, and whether that number is sufficient for long-term population viability.
- (b) Population structure of steelhead-rainbow trout within the context of the San Joaquin basin or entire Central Valley region. As a potential management approach, it is plausible that the Tuolumne River trout may be most effectively managed as part of a larger steelhead-rainbow trout meta-population that collectively occupies the lower San Joaquin basin tributaries.

The key to addressing the preceding questions lies in determining the amount of physical habitat (i.e., gravel areas with holding pools) that exists or can be restored in the near future within the reaches below La Grange Dam--i.e., the uppermost ~5-10 miles where flows and temperatures are usually suitable through the summer.

Over the longer time-frame of multiple decades, it will be necessary to implement a monitoring program to determine the total trout population size through a series of years or decades that encompasses the full range of water-year conditions.

Points (1) and (2) above relating to the thermal limitations of steelhead-rainbow trout in the lower Tuolumne River, and more generally to the thermal biology of salmonids, are addressed in the present commentary. Discussion of Point (3) relating to population-level management issues is presented in the accompanying document submitted by the City and County of San Francisco: "Commentary on Steelhead-Rainbow Trout (*Oncorhynchus mykiss*) Population Management in the Lower Tuolumne River."

Addressing the Flow-Temperature Issue

The questions above pertaining to the adequacy of specified minimum summer streamflows, as well as related aspects, can be clarified by drawing from pertinent studies and reviews on temperature requirements of Chinook salmon and steelhead-rainbow trout. Of immediate relevance are results from a recent temperature-modeling analysis conducted by Stillwater Sciences consultants that evaluated how various flow levels combined with specified temperature criteria for suitability are expected to affect habitable areas for *O. mykiss* in the lower Tuolumne River. That analysis demonstrated the flow levels that are needed to provide cool over-summering conditions for varying streamlengths extending downstream from La Grange Dam.

General conclusions from the Stillwater Sciences analysis and a literature review are presented in the following **Section 1** regarding the flow and temperature needs for maintaining trout at minimal levels in the lower Tuolumne River. Those conclusions are essentially tentative inferences that may change as additional information and insights are gained from future studies on salmonid thermal physiology and ecology.

More detailed results from the Stillwater Sciences modeling analysis are presented in **Section 2** below. The Stillwater Sciences analysis provides an informative picture of the expected consequences of specified flow-temperature levels on habitable areas for trout during the summer months.

Section 3 of this commentary collates and summarizes information from published literature and reports on temperature-related effects and temperature criteria in relation to salmonid life-history aspects (e.g., survival, growth), particularly for Chinook salmon and steelhead-rainbow trout. Some information on Chinook salmon is included because it can give additional insight for trout requirements, especially when information on trout is lacking. Altogether, the information summary from the literature review provides a basis for choosing various temperature levels as management targets that represent biologically appropriate conditions for trout survival.

SECTION 1. OVERALL CONCLUSIONS FROM THE MODELING ANALYSIS AND LITERATURE REVIEW

Temperature and Flow Requirements to Maintain Trout Habitat

- Water temperatures of 64.5-68°F appear to represent an adequate target-range for practicable flow management in maintaining steelhead-rainbow trout (*O. mykiss*) during the warmer seasons. Those temperatures are not optimal, but they are not expected to be so highly stressful to the trout as to cause substantial mortalities and significantly impair population viability.
- The best trout habitat in the lower Tuolumne River occurs in the uppermost 5-10 miles below La Grange Dam. At flows of 75 cfs, several miles of river below La Grange Dam can be maintained at suitably cool temperatures.
- During summer 2002, La Grange flows were 75 cfs during June-August and near 60 cfs in September, and temperature monitoring showed the following temperature distribution pattern (based on a data-plot provided by Dr. Carl Mesick, USFWS).
 - A highly suitable temperature range (about 60-65°F) is maintained at the J59 Bridge (river mile 50) through the entire summer.
 - A fairly suitable to marginally stressful range (63-70°F) is maintained at the Basso Bridge area (rm 47.5) throughout the summer.
 - A thermally challenging or highly stressful range (mostly about 70-75°F)--but not necessarily completely lethal--occurs near Turlock Lake State Park (rm 42).
- Information from published literature indicates an upper thermal limit near 75°F for *O. mykiss*. That upper limit suggests that if mostly 72°F water temperatures can be maintained at Turlock Lake State Park, even with occasional spikes above 75°F, then trout may persist there especially if the temperature frequently drops below 70-72°F (e.g., nightly).

Necessary flows

Stillwater Sciences consultants conducted a modeling analysis (Stillwater Sciences memorandum, March 14, 2003; Figures 5b, 5c, 5e, 5f, 5h, 5i) to ascertain amounts of juvenile trout habitat that fall within designated thermal criteria (i.e., upper limits of either 65°F or 70°F were used in the model). The analysis showed that juvenile habitat is maximized by flows of 100-150 cfs during the model-simulation dates (August 2-6, September 1-5, and October 1-5). Flows of 150 cfs provide greater amounts of juvenile habitat than do 100 cfs because higher flows extend the suitable habitat conditions further downstream. However, the relative amounts of suitable juvenile habitat at 100 cfs and 150 cfs are not markedly different, especially when compared to most other flow levels (except for 200 cfs which provide similar amounts of habitat as 150 cfs).

Management Implications. Protecting adults versus juvenile *O. mykiss*

Adult *O. mykiss* that occur in the Tuolumne River during summer and early fall are presumably resident rainbow trout and are not listed (protected). Hence, flow-related efforts to accommodate those adults should be subordinate to any flow measures needed to protect juvenile *O. mykiss*. Those juveniles

may include individuals of the anadromous (steelhead) life-history type and, furthermore, represent the future spawning stock that potentially may produce anadromous individuals.

Additional Aspects

An important point indicated from the literature reviews summarized below is that steelhead that are undergoing smoltification definitely require cooler temperatures--i.e., ~54°F (12°C) or lower--compared with the water temperatures they can tolerate during the preceding freshwater rearing period. Failure to provide necessary cool conditions during this sensitive period will impair the smoltification process and may cause direct mortality, disruption of physiological and behavioral adaptations leading to reduced marine survival, and other negative consequences.

Smoltification for steelhead in the Tuolumne River is expected to occur primarily in the spring months (March-May) as it generally does in other California streams (Barnhart 1986, Hallock 1989, Demko et al. 2000). The smoltification and outmigration phase coincides with high streamflows of the spring snowmelt and reservoir release-period which facilitates providing the necessary cooler water temperatures.

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SECTION 2. STILLWATER SCIENCES MODELING ANALYSIS

Stillwater Sciences Temperature Modeling Analysis

The Stillwater Sciences analysis (memorandum, March 14, 2002) applied a temperature and flow model to show that at least some minimal amounts of suitable habitat can be maintained at temperatures below specified levels for juvenile and adult trout in the uppermost several miles below La Grange Dam. The amount of actual or potential physical habitat for trout (e.g., holding pools or riffles) is concentrated in the uppermost 10-15 miles. The trout habitat is indicated by the maps in the McBain & Trush Coarse Sediment Management Plan (McBain and Trush 2004) and also reflected by observations or captures of adult trout during January-February 2005 throughout those areas down to near Roberts Ferry Bridge (rm 40) (California Rivers Restoration Fund Report 2004).

The analysis showed that sufficiently cool water (i.e., 65°F or lower) can be maintained in at least the uppermost 1.5 miles (from La Grange Dam to below Old La Grange Bridge) by 50 cfs flows throughout May-September (Stillwater Sciences memo, Figure 2a). At 75 cfs, roughly the same amount of cool-water refuge (65°F or less) is maintained during June-August as with 50 cfs flows, but the cool water extends a few miles further downstream during May and September (Figure 2b). Even flows of 150 cfs will provide no more than about 5-6 miles of cool water below La Grange Dam during most of June-August and somewhat less than 10 miles of cool water during the warmer halves of May and September (Figure 2c).

If both the temperature (<65°F) and water velocity requirements of juvenile trout are considered simultaneously, most of the suitable habitat for juveniles during August-October occurs within the uppermost 10 miles of the river at flows less than 300 cfs (Figures 5b, 5e, 5h). Furthermore, if it is true that juvenile trout tolerate water temperatures up to 70°F, then 150 cfs flows can provide suitable habitat for them down to about river mile 43 in early-August (Figure 5c), to about river mile 39 in early-September (Figure 5f), and down to river mile 24 during early October (Figure 5i).

The amount of available habitat for either juvenile or adult trout depends on a balance between suitable water temperatures (as determined from behavioral and physiological studies) and water depth and velocity criteria. Those criteria are inferred for the Tuolumne River fish from studies conducted on rainbow trout in other river systems. Higher flows may provide cooler water over longer stretches of the river but the concomitantly greater depths and velocities can be less suitable for juvenile trout. For example, the Stillwater Sciences report noted that "for a 65F temperature criterion, Figure 2c shows that 150 cfs would extend suitably cool habitat to near Basso Bridge (RM 47.5), whereas Figure 5b shows that EWUA [effective usable habitat area] rapidly falls off above these flows for juveniles."

Another key result from the analysis is that adult and juvenile trout have somewhat conflicting habitat requirements in regard to flows although both life-stages require cold water. The Stillwater Sciences report stated (p.4):

"For adult *O. mykiss*, habitat suitability with flow follows different patterns than juveniles and reflects increased pool habitat use as well as higher velocity thresholds. For

example, using 70F and 250 cfs would extend the temperature criteria boundary to near Turlock State Recreation Area (RM 2) in early August (Figure 2e), very near the optimal EWUA at 300 cfs for this time period (Figure 6b). However, at still higher flows the downstream temperature boundary begins to encompass significant pool habitat and Figure 6b suggests a second local optimum [i.e., further downstream at RM 24-RM 30] at flows in excess of 500-700 cfs."

In regard to the preceding point, the Stillwater Sciences report concluded (p. 4):

"Perhaps the most important consideration for discussion by the TRTAC is the tradeoff between habitat maximizing conditions for adults and juveniles. In general, the results here show that optimal conditions (i.e., higher flows) for adult *O. mykiss* are unsuitable for juveniles, and optimal juvenile conditions may exclude cool water from downstream pool habitat for adults."

A caveat that should be noted is that the Stillwater Sciences analysis did not consider flows greater than 500 cfs, although such high flows probably would not be relevant or feasible during the summer months. Nonetheless, this aspect and other assumptions require further consideration. Specifically, additional work is needed on the following.

- (a) Field surveys of the amount of trout habitat present at flows higher than 500 cfs.
- (b) Determination of "habitat suitability curves" that reflect trout habitat preferences and tolerances based on data for Tuolumne River fish rather than on data from other rivers.
- (c) Evaluate potential differences in habitat needs of steelhead versus those of resident trout.

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SECTION 3. LITERATURE REVIEW OF TEMPERATURE EFFECTS ON SALMONIDS

Some Proposed Temperature Criteria for Steelhead-Rainbow Trout

FERC 1993: Final Environmental Impact Statement. Proposed Modifications to the Lower Mokelumne River Project, California. November 1993.

Page 3-67.

"Temperature requirements of steelhead and rainbow trout have been studies extensively. Staff review of this literature indicates the following:"

spawning: optimum 45-50°F (7.2-10°C); stressful 68°F (20°C); lethal >72°F (22°C),
incubation: optimum 48-52°F (8.9-11.1°C); stressful >55°F (12.8°C); lethal 60°F (15.6°C), and
juvenile rearing: optimum 55-65°F (12.8-18.3°C); stressful 68°F (20°C); lethal 77°F (25°C).

Richter and Kolmes (2005, from their Table 1). Upper optimal temperature criteria

Life stage	7-Day-average of maximum daily temperatures	Weekly mean temperatures
Spawning and incubation	13°C (55°F)	10°C (50°F)
Juvenile rearing	16°C (61°F)	15°C (59°F)
Smoltification salmon	16°C (61°F)	15°C (59°F)
Smoltification steelhead	14°C (57°F)	12°C (54°F)
(at fourth-level hydrologic unit watershed)		
Adult migration	18°C (64°F)	16°C (61°F)

AD Consultants 2004. Peer Review of Water Temperature Objectives Used as Evaluation Criteria for the Stanislaus-Lower San Joaquin River Water Temperature Modeling and Analysis. Peer Review Panel: John Bartholow, Chuck Hanson and Chris Myrick. Prepared for AD Consultants, Moraga, California. July 29, 2004.

Page 24, Table 12. Temperature criteria/goal for identified species and lifestages in the Stanislaus River (after EPA 2003). [This table is slightly modified from the AD Consultants table]

Stanislaus River Terminology	EPA-based Recommended Temperature Criteria/Goals to Protect Salmon and Trout (Criteria based on the 7-day average of the Daily maximum values).
Adult migration	<64°F (<18°C) for salmon and trout migration <68°F (<20°C) for salmon and trout migration--generally in the lower part of river basins that likely reach this temperature naturally, if there are cold-water refugia available
Incubation	<55°F (<13°C) for salmon and trout spawning, egg incubation, and fry emergence
Juvenile rearing (early-year)	<61°F (<16°C) for salmon "core" juvenile rearing--generally in the mid-to upper part of river basins
Smoltification	<59°F (<15°C) for salmon smoltification <57°F (<14°C) for steelhead smoltification (for composite criteria the steelhead conditions are applied)
Juvenile rearing (late-year)	<64°F (<18°C) for salmon and steelhead migration plus non-core juvenile rearing--generally in the lower part of river basins

DISCUSSION

Interpretive Synthesis of Temperature Effects on Chinook Salmon and Steelhead

The many studies and reviews on temperature-related issues of anadromous salmonids collectively indicate at least the following major points.

- (1) There are ranges of temperatures--as defined by various averaging methods--that represent so-called optimal and sub-optimal conditions (also termed non-stressful and stressful) for salmonids, but there is no single, definite cut-off temperature that universally demarcates those two sets of conditions for a given life-stage. Such a rigid demarcation would be an artificial construct that does not truly represent the underlying biological processes. A primary reason is that fish generally show gradated physiological and biochemical responses to environmental stressors such as temperature, salinity and dissolved oxygen levels, among others.
- (2) Another reason for the somewhat different optimal versus sub-optimal temperatures shown by different studies is that temperature interacts in complex ways with other factors to affect the fish—e.g., internal factors such as size, age, and body condition of the individual and external factors such as food supply. Thus, salmon or steelhead-rainbow trout are able to withstand higher temperatures if there is an adequate food supply to offset the increased metabolic demands while allowing enough energy to be allotted to growth.
- (3) The thermal responses of individual fish will change through time as the fish grow through different life-stages (i.e., ontogenetic change). Hence, the thermal requirements or sensitivities of a fry will differ from those of an older juvenile, which will in turn differ from those of a smolt. This point was noted by Dr. Peter B. Moyle in testimony to the Federal Energy Regulatory Commission (Moyle Testimony 2009):

“The temperature requirements of both Chinook salmon (Exhibit 1) and steelhead (Exhibit 2) vary considerably with life stage. Both also show considerable ability to withstand periods of unfavorable temperatures but have a fairly narrow preferred range for most activities. The extent of deleterious biological effects of suboptimal or sub-lethal temperatures upon the two salmonids depends upon various factors such as the length of exposure, extent of acclimation to warm conditions prior to the actual thermal challenge, availability of thermal refuges in deep pools, groundwater inputs, amount of food available to the fish, and perhaps genetic background. The complex interplay of various environmental and physiological factors with thermal tolerances of Chinook salmon and steelhead-rainbow trout result in statements such as the following: “Central Valley steelhead can be expected to show significant mortality at chronic temperatures exceeding 25°C [77°F] although they can tolerate temperatures as high as 29.6°C [85.3°F] for short periods of time. It is important to note that both Chinook salmon and steelhead begin to experience serious sub-lethal effects at temperatures below their chronic limits (Myrick and Cech 20001).” Trout and salmon in the lower Tuolumne River can also respond behaviorally to changing water temperatures and to the spatial pattern of thermal microhabitats, such as cool-water sources along the river below La Grange Dam, by seeking out areas with more preferred conditions (if they exist).”

- (4) This ontogenetic change in thermal requirements of individuals ramifies through the entire cohort of young fish that were produced in that preceding spawning season, but it does so in a complicated way because individuals differ in the dates when they hatched and in their developmental rates. Thus,

various segments of the cohort will have somewhat different and even opposing thermal optima and constraints—viz., younger juveniles would do better at warmer temperatures that enhance growth rates but older juveniles and smolts require cooler temperatures that allow successful smolting.

Flow management, in turn, must balance the sometimes divergent needs of the population segments (i.e., age-groups within species) as they move through the lower San Joaquin River basin and Delta. Furthermore, temperature criteria may have to be set contingent on the prevailing environmental conditions, such as the availability of low-elevation floodplain areas for juvenile rearing. The proper application of thermal tolerance information on the salmonids will require an adaptive and realistic management approach as emphasized by Richter and Kolmes (2005: p.40):

“Definitive criteria for salmonid recovery should eventually define ways to incorporate spatio-temporal variability into them in a realistically complex fashion and have as their eventual goal a process that realigns the distribution of current environmental variables so that they overlay historic conditions rather than simply act as a floor or ceiling.”

Adaptive and realistic flow management to maintain anadromous salmonids and other native fauna in the lower San Joaquin River basin and Delta also must consider the environmental ramifications of regional climate change, as Richter and Kolmes (2005: p.40) noted for the Columbia River basin:

“... Projections for regional climate changes suggest summer flows will be decreased and water temperatures increasing (Mote et al., 2003). The complexity of any solution to the problem of salmonid survival will need to balance all of these considerations while achieving temperature regimes suitable for the persistence of salmon.”

- (5) While specific temperature standards are generally necessary and useful as guidelines for protecting salmonid and other aquatic resources, such standards by themselves are simplistic solutions to very challenging problems. The spatial and temporal variability of both the fish and the environment should be considered in an integrated fashion to maximize population production and survival while minimizing the attendant costs. It is the manner of application of such standards that will determine the degree of success or failure of salmonid resource management in California and elsewhere. This crucial point has been previously expounded by multiple authorities; e.g., (Moyle Testimony 2009: p.14):

“The complex temperature requirements of Chinook salmon and steelhead have been extensively reviewed and form the basis for the exhibit tables. They indicate that setting simple temperature standards for these fish may or may not help the species persist. As McCullough et al. (2009) state: “Standards of the past were based largely on incipient lethal and optimum growth rate temperatures for fish species, while future standards should consider all integrated thermal impacts to the organism and ecosystem.”

Life-History Migration Timing

The salmonid life-stages that are most likely to be affected by San Joaquin River flows during the April-May period are juveniles and smolts of fall-run Chinook salmon and steelhead-rainbow trout (*O. mykiss*) and up-migrating adult steelhead—and eventually spring-run Chinook salmon (i.e., down-migrating juveniles/smolts and up-migrating adults) if that run is successfully introduced into the upper San Joaquin River.

The life-history timings for different stages of Central Valley fall-run Chinook salmon and steelhead are as follows (based on Moyle 2002 and Moyle et al. 2008).

Fall-run Chinook Salmon	
Adult up-migration:	Peak in September-October
Spawning:	Peak in October-November; sometimes through December
Juvenile rearing:	December-March
Juvenile-smolt down-migration:	Peak in March-April
Steelhead	
Adult up-migration:	Peak in late-September to late-October
Spawning:	February-June
Juvenile rearing:	Year-round
Juvenile-smolt down-migration:	Late-December to beginning of May (peak mid-March); A second much smaller peak in the fall (Hallock et al. 1961)

These peak periods will require water temperatures that are conducive to the successful completion of the respective life-stages.

In regard to down-migrating juvenile life-stages, it is likely that at the present time only smolts and older juveniles that are near smolting will benefit from the April-May San Joaquin River flows. The younger stages that are transported downstream from the San Joaquin basin tributaries during that spring period do not appear to have adequate rearing areas in the lower San Joaquin River and Delta that would allow them to survive up to the smolting stage.

Differences Between Populations in Local Adaptation to Warm Temperature

Although the anadromous salmonids as a group are coldwater-adapted and generally restricted by warm conditions (McCullough et al. 2001), there is reason to expect differences in the thermal tolerances of populations that inhabit areas with substantially different environmental conditions. There are two main reasons for this expectation: (1) different acclimation histories and (2) probably different heritable adaptations to local thermal stresses.

(1) **Acclimation history.** It is well documented from numerous studies in the aforementioned reviews that the acclimation history of individual fish strongly affects their ability to withstand thermal stresses. Different localities or regions often have characteristic environmental conditions—i.e., thermal regimes that vary on multiple time scales (daily, weekly, seasonal, etc.). Hence, the individuals that inhabit those areas will have been gradually acclimated to the corresponding thermal regimes and probably would differ in their sensitivities at least to certain additional thermal challenges—e.g., seasonal or episodic heat waves. The implication is that southerly-located populations, for example, may be more able to withstand frequent temperature fluctuations that approach their upper limit of physiological tolerances than would more northerly populations. Hence, there may be some rationale for allowing more flexible temperature standards for protecting salmonids at more southern locations.

(2) **Heritable local adaptations.** Locally adapted populations are a major feature of biological diversity. There is no reason to believe that anadromous salmonids differ in this regard from other taxonomic groups of organisms. In fact, it would be very surprising if all Chinook salmon, or steelhead-rainbow trout, populations within the species had identical or highly similar thermal tolerances.

The existence of genetically based differences in high-temperature tolerances has been firmly established for steelhead-rainbow trout (*O. mykiss*) and they almost certainly exist as well for the various salmon species in the same genus (*Oncorhynchus*). As noted by McCullough et al. (2009: p.93),

“The genetic architecture that underlies temperature tolerance is better understood for rainbow trout than for other fishes. Genetic variation explains roughly half of the phenotypic variability in the upper temperature tolerance (UTT) of individual rainbow trout (Danzmann et al., 1999).”

Examples of within-species variation in thermal tolerances were cited by McCullough et al. (2009: p.99):

“... For example, Beacham and Withler (1991) carefully interbred several generations of individuals from northern and southern British Columbia Chinook salmon (*O. tshawytscha*) stocks. Juveniles from the southern stock proved better adapted to survive high temperatures than the northern stock but seemed to reach a limit beyond which they could no longer achieve additional tolerance. Redding and Schreck (1979) observed that inland steelhead (anadromous rainbow trout, *O. mykiss*) populations, which experience higher average temperatures, tended to have a higher temperature tolerance but slower growth than coastal steelhead populations.”

Some examples of relatively high thermal tolerances of anadromous salmonid populations in California are the following.

(a) **Northern California coastal steelhead.** Adult and juvenile summer-run steelhead used coldwater refuges (stratified pools) during the summers in the Middle Fork Eel River and

(juveniles only) in Rancheria Creek, a tributary of the Navarro River (Nielsen et al. 1994). The steelhead used the coldwater pools when ambient stream temperatures exceeded 23°C [73.4°F]. The coldwater refuges were generally 3.5°C [6.3°F] cooler than the ambient stream temperatures—i.e., 22.5°C [72.5°F] and higher in coldwater pools.

“During this study, however, juvenile steelhead were seen actively feeding in surface waters with ambient temperatures up to 24°C” [in the Middle Fork Eel River] (Nielsen et al. 1994: p.621)

In Rancheria Creek, juvenile steelhead moved into cool stratified pools when ambient stream temperatures reached 23°C or more. However, on days when ambient stream temperatures remained at or below 22°C, the juveniles did not seek the cooler pool refuges.

- (b) **Klamath River Chinook salmon.** Adult Chinook salmon were tagged with transmitters and archival tags in the Klamath River and their up-migration was monitored along with river temperatures (in 2004 and 2005). Strange (2010: p.1091, 1105) reported:

“Mean daily river temperatures upon initiation of upriver migration by adult Chinook salmon after a period of thermally induced migration inhibition ranged from 21.8°C to 24.0°C (mean = 22.9°C) [71.2-75.2°F (mean=73.2°F)]. During the first week (168 h) of migration, mean average body temperature was 21.9°C, mean average minimum daily body temperature was 20.6°C, and mean average maximum daily body temperature was 23.1°C [73.6°F]. Temperatures above these levels appeared to completely block migration in almost all circumstances.”

“The temperatures at which adult Chinook salmon in the Klamath River basin were observed actively migrating approached or exceeded the highest ultimate upper incipient lethal values determined for any life stage of this species (Brett 1952). This finding demonstrates that Chinook salmon adults are capable of enduring, at least for a limited time period, potentially lethal instantaneous temperatures while continuing to migrate. While there is certainly a limit to the duration of exposure that can be endured, it is significant that although temperatures during the first week of migration equaled or exceeded the upper incipient lethal temperature for adult Chinook salmon (Coutant 1970), tagged Klamath River basin adults still had high rates of success in reaching spawning grounds. Cumulative exposure to deleterious temperatures, however, can lead to delayed mortality after arrival on spawning grounds; therefore, when comparing results from the Klamath River basin to numeric water quality criteria, it is important to distinguish between tolerable versus optimal thermal conditions for migration.”

- (c) **Upper San Joaquin River Chinook salmon** (historical population). The Chinook salmon (presumably fall-run) that formerly utilized the upper San Joaquin River, near Friant Dam, were considered by the California Fish Commission to be extraordinarily adapted to relatively warm conditions (Yoshiyama et al. 2001: p.94):

“Large numbers pass up the San Joaquin River for the purpose of spawning in July and August, swimming for one hundred and fifty miles though the hottest valley in the State, where the temperature of the air at noon is rarely less than eighty degrees, and often as high as one hundred and five degrees Fahrenheit, and where the average temperature of the river at the bottom is seventy-nine degrees and at the surface eighty degrees (CFC 1875, p 10; USFC 1876b, p xxv).”

“The Commissioners noted that during August-September of 1875-1877, the average monthly water temperatures for the San Joaquin River where two bridges of the Central Pacific Railroad crossed (at 37°50'N, 121°22'W and 36°52'N, 119°54'W) were within 72.1 to 80.7°F (considering

both surface and bottom water) and maximal temperatures were 82 to 84°F (CFC 1877). The high temperature tolerance of the San Joaquin River fall-run salmon inspired interest in introducing those salmon into the warm rivers of the eastern and southern United States . . .”

It is important to note that in the preceding examples, the fish were observed in their natural environment under the prevailing temperature conditions rather than in laboratory situations—i.e., living proof of their abilities to exist at least at those times and places. These examples appear to represent exceptional levels of tolerance to relatively warm environmental temperatures. It would not seem credible to assume that all other Chinook salmon and steelhead populations have, or had, the same (genetic) capabilities to tolerate such temperatures—and probably few, if any, salmonid biologists would draw such an inference. Yet, that inference is merely the obverse side of assuming that all salmonid populations are essentially equally intolerant of elevated temperatures—i.e., that there is no significant local adaptation to different regional or temperature conditions.

Finally, Richter and Kolmes (2005: p. 40) have noted:

“A rich data set (e.g., Brannon et al., 2004) shows that in terms of thermal tolerances, disease resistance and physiological adaptation in general, salmonid stocks native to specific bodies of water may be better adapted to local conditions than are members of stocks originating in substantially different spawning habitats.”

“Brannon et al. (2004) provide compelling arguments that temperature has been the dominant environmental influence responsible for the evolution of historical chinook and steelhead population structure in the Columbia River basin; if dominant in their evolution, temperature will surely be a dominant factor in their survival or extirpation.”

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SYNOPSIS OF KEY REVIEWS AND REPORTS

Previous workers have reviewed and synthesized a considerable volume of literature on the effects of environmental temperature on Chinook salmon and steelhead-rainbow trout. The objective of those reviews was to periodically update the understanding of temperature effects on various biological aspects of those salmonids.

The present section summarizes the most relevant aspects of previous reviews. Generally for ease of reference, a separate synopsis is given for each review or analysis. An exception is the last synopsis which considers several reports together.

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

Richter and Kolmes (2005) reviewed and summarized the temperature requirements for "sensitive life stages" of several Pacific salmon species and steelhead with the goal to identify "specific numeric maximum temperature criteria" that can be directly applied in species recovery planning in the Pacific Northwest region. Richter and Kolmes cover much of the same material that is summarized elsewhere in our memorandum-report. The following summary omits most of the information on salmon species and focuses on the material pertaining to steelhead.

Richter and Kolmes upper optimal temperature criteria

Drawing from their review, Richter and Kolmes presented a generalized table of optimal temperature criteria for salmon species (i.e. Chinook, coho, and chum salmon) and steelhead as follows. Besides the 7-day-average maximum daily temperatures, their table includes weekly mean temperature criteria to "provide an additional layer of insurance against global and regional environmental challenges including altered flow regimes and water temperatures associated with human activities and projected regional population growth."

Richter and Kolmes (2005, from their Table 1). Upper optimal temperature criteria

Life stage	7-Day-average of maximum daily temperatures	Weekly mean temperatures
Spawning and incubation	13°C (55°F)	10°C (50°F)
Juvenile rearing	16°C (61°F)	15°C (59°F)
Smoltification salmon	16°C (61°F)	15°C (59°F)
Smoltification steelhead	14°C (57°F)	12°C (54°F)
(at fourth-level hydrologic unit watershed)		
Adult migration	18°C (64°F)	16°C (61°F)

To support their proposed criteria, Richter and Kolmes provided the following synoptic comments in relation to the respective steelhead life stages.

"Steelhead spawning occurs at temperatures within the range protected by the 10°C (weekly mean temperature criterion), as does their early fry development . . ."

"Optimal growth temperatures for juvenile steelhead are in the vicinity of 13°C to 15°C . . . although in a laboratory setting slightly higher temperatures were associated with a food supply in excess of that characteristically available in nature."

"The extreme variability of habitat use by steelhead makes established a temperature criterion for their smoltification challenging. The 12°C criterion for a weekly mean temperature at the fourth-level hydrologic unit (HUC) watershed is consistent with Zaug and Wagner's (1973) gill ATPase activity data. Weekly mean temperature values of 15°C proposed as criteria for other salmonids are well above the values having excessive physiological consequences for steelhead . . . The results of Adams et al. (1975) and Hoar (1988), who reported impairment of smoltification at 12.7°C and 13°C, respectively, support the lower criterion for steelhead."

"Adult steelhead migration is not blocked until 21°C . . . Steelhead have been reported to make use of deep stratified pools as thermal refugia when midday ambient stream levels ranged above 22°C . . . or to congregate in cool tributaries when the mainstem reached 21.7-22.8°C . . ."

Alternative inferred temperature criteria.

We present here slightly different temperature criteria inferred from the information compiled by Richter and Kolmes (2005). These criteria are temperature limits that probably are necessary to maintain steelhead at healthy population status. Our inferred criteria may be somewhat conservative by leaning toward "safe" temperature limits but are not necessarily optimal temperatures, in contrast to the Richter and Kolmes "upper optimal temperature criteria." Quoted passages from Richter and Kolmes (2005) are given to show that our inferred criteria and the Richter and Kolmes proposed criteria are consonant with the breadth of steelhead temperature tolerances indicated by past studies.

Upper temperature levels conducive to steelhead health during different life stages

Spawning. Daily average temperature of 10-12.8°C [~50-55°F].

Incubation/early fry development. Constant temperature up to 11-12°C [~52-54°F]; fluctuating temperatures with a single daily maximum of 13.5-14.5°C [~56-58°F].

Juvenile growth. Constant temperatures up to 16-17°C [~61-63°F], possibly up to 18-19°C [~64-66°F] for limited periods and with adequate food rations.

Smoltification. Constant temperatures no greater than 14°C [~57°F].

Adult migration. Temperatures less than 21°C [~70°F] on a single day, or 7-day average of maximum daily temperature up to 16-17°C [~61-63°F].

Lethal temperatures reportedly are 21-22°C [~70-72°F] for adults and 24°C [~75°F] for juvenile steelhead. Recommended daily maximum temperatures are below 19-20°C [~67-68°F] to avoid mortalities.

Temperature preferences or avoidance. Preferred field temperatures of juveniles-yearlings are reported as 15-17.8°C [~59-64°F] (for Oregon coast steelhead) and avoidance temperatures of 23°C or greater (in California). Hence, recommended stream temperatures are less than 23°C [~73°F].

Quoted Information from Richter and Kolmes (2005: p.35-36) on Steelhead Data

Richter and Kolmes presented an excellent synopsis of the temperature-related effects on steelhead, which are copied verbatim below for the juvenile and smoltification life stages. These quoted

passages show the variability in results of various studies and they indicate that the suggested temperature criteria should be viewed as somewhat inexact guidelines.

Juvenile Growth

"Optimal growth for juvenile steelhead occurs in the range of 14°C to 15°C (Hicks, 2000); although in the laboratory, Wurtsbaugh and Davis (1977) found that steelhead growth could be enhanced by temperatures up to 16.5°C. Cech and Myrick (1999) tested winter-run steelhead at three temperatures (11°, 15° and 19°C) and high ration levels (82%-100% of satiation); they found a reduced but still high growth rate (exceeding 11° and 15°) at 19°C as ration was reduced 12%. Hicks (2000) interpreted their data as suggesting a maximal growth rate between 15° and 19°C at more typical reduced ration levels. Grabowski (1973) tested three constant temperatures (8°, 15°, 18°C) and one varying regime (8°-18°C, mean 13°C) and found best growth at constant 15°C, and second best with varying temperature averaging 13°C.

The recommendation by Hicks (2000) to fully protect juvenile rearing of steelhead was 16° to 17°C. Sullivan et al. (2000) recommended the upper threshold for the 7-DAM temperature of 20.5°C for steelhead, assuming that a 10% reduction in growth is an acceptable risk level. McCullough et al. (2001) noted that Wurtsbaugh and Davis (1977) found growth enhanced up to 16.5°C and that the growth rate declined with increasing temperature until it was zero at 22.5°C."

Smoltification

"A variety of upper temperature thresholds have been reported for impairment of steelhead smoltification. Hoar (1988) reported temperatures higher than 13°C. Adams et al. (1975) reported higher than 12.7°C, Zaugg and Wagner (1973) reported higher than 13.6°C, and Zaugg (1981) reported 12°C."

The challenge of applying temperature criteria to real situations

Even with specified temperature criteria--such as those proposed by Richter and Kolmes or our inferred criteria given above--the difficulty still remains in determining how to apply them with regard to the temporal (e.g., seasonal timing) and spatial characteristics of specific salmon and steelhead populations. As Richter and Kolmes (2005:38) recognized:

"For all these criteria, the significant challenge of defining the spatio-temporal range over which they should be applied remains. Those spaces occupied by threatened and endangered salmonids need to be regulated at the times of year that sensitive life stages are present, and defining the bodies of water involved and the times to apply the standards requires additional consideration and research. The complex life histories of salmonids, the variety of habitats used by their different life stages, and the spatially and temporally dynamic nature of the habitats involved, make this an enormous scientific undertaking. . . . [Additionally] Laboratory studies cannot fully substitute for field data, because of difficulties in replicating acclimation conditions, food availability social interactions including territoriality, diurnal physiochemical periodicity, and the complexities of microhabitats accessible to fish in nature . . ."

They further emphasized that the proper application of thermal tolerance information will require an adaptive and realistic management approach. Specifically, Richter and Kolmes (2005:40) stated:

"Definitive criteria for salmonid recovery should eventually define ways to incorporate spatio-temporal variability into them in a realistically complex fashion and have as their eventual goal a process that realigns the distribution of current environmental variables so that they overlay

historic conditions rather than simply act as a floor or ceiling. . . . The challenge of this task is exacerbated by the multiple salmonid life stages whose distributions over space and time will need identification and monitoring."

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Review Panel (Peer Review Panel: J. Bartholow, C. Hanson and C. Myrick). 2004. Peer Review of Water Temperature Objectives used as Evaluation Criteria for the Stanislaus--Lower San Joaquin River Water Temperature Modeling and Analysis. Prepared for AD Consultants, Moraga, California. CBDA Project No. ERP-02-P28. 54 p.

A recent review and assessment of temperature criteria was conducted by a panel of experts to evaluate alternative approaches to restoring anadromous salmonids in the Stanislaus River. The stated goal of that evaluation was to identify an approach that favored "the rapid attainment of restoration goals" and the panel suggested a "conservative approach with respect to selected temperature criteria [that should] be adopted"-- i.e., "to hedge toward the lower end of that range [of temperatures tolerated by the salmonid life-stages] to provide the best protection for the resource under the stated desire to double escapement [which is the CVPIA-AFRP salmonid restoration goal]" (Review Panel 2004:5).

The review panel adopted a unique approach by using a temperature model to determine the thermal repercussions of various water-operations scenarios. The review panel sought to determine temperature criteria that could be used to evaluate the different model-generated temperature effects of those scenarios. Such a model-simulation approach stands in contrast to the more traditional approach of using specified temperature levels as criteria for defining favorable versus unfavorable conditions for salmonids.

The review panel evaluated temperature criteria recommendations that were independently proposed by the California Department of Fish and Game (CDFG) and consultants S. P. Cramer and Associates ("S. P. Cramer") with regard to temperature requirements of the different life-stages of fall-run Chinook salmon and steelhead. Those life-stage-specific temperature criteria were also placed in the spatial context of the Stanislaus River because certain life stages were typically associated with specific portions of the river. The panel's objectives were to identify points where the two sets of criteria differed significantly and where potential modifications could be applied. The review panel presented conclusions and recommendations about Chinook salmon and steelhead temperature requirements through the annual cycle (52 weeks) as follows.

Week 1-4 (September). Water temperatures should be decreased through the month (perhaps in decremental steps over two-week periods) but kept within the range of proposed temperatures--i.e., optimally 55°F and no greater than 55-63°F as proposed by CDFG or optimally 60°F and no greater than 60-65°F as proposed by S. P. Cramer.

Week 5-31 (September-April). Although the S. P. Cramer criteria were higher (by 3°F) than the CDFG criteria, computed river temperatures were generally low during this period. Hence, the panel believed that any potential thermal problems imposed upon the fish by the criteria probably would be of short duration if they occurred at all.

Week 33-39 (April-May). The two sets of proposed temperature criteria for this period evidently were based on different research sources, with the S. P. Cramer criteria allowing temperatures up to 68°F for the suboptimal (or sublethal) range. The review panel specifically "felt that the 68°F criterion . . . was too high for this critical life stage" (i.e., the smoltification stage) (Review Panel 2004:p.18).

Week 40-52 (June-August). Both the CDFG and S. P. Cramer proposed temperature criteria for this period identified 61°F as the optimal thermal level, with the suboptimal or sublethal range being 61-73°F. However, the review panel believed that the upper value of 73°F was too high and would pose a detrimental challenge to the fish. The review panel recommended a range of 65°F or lower as the suboptimal temperature range for this period.

The review panel noted the advantage of using fine-scale information on the varying temperature conditions in the river in conjunction with the life-stage-specific thermal needs of the fish. Specifically, (Review Panel 2004:19):

"For example, exploring longitudinal variation in thermal conditions within the river system under various year hydrologic and meteorological conditions and/or operational scenarios (flow rate and storage/cold water volume). Coupling this information with known habitat types and life stages could result in different reach designations, e.g., for juvenile rearing the target temperature may shift up and downstream based on hydrology, temperature, and operations."

In the initial step of their evaluation, the panel utilized the schedule of recommended temperatures developed by the U.S. EPA which was based on an extensive review of the published literature on temperature effects on salmonids. The EPA recommended temperatures for different life stages were compared to the proposed CDFG and S. P. Cramer temperature criteria schedules. The panel found that for the most part, the EPA-recommended temperature criteria fell between the upper (critical-lethal) and lower (optimal) temperature boundaries defining the sub-optimal ranges for either the CDFG proposed criteria or S. P. Cramer proposed criteria throughout the annual period.

The panel adopted the approach used by both the CDFG and S. P. Cramer wherein two temperature criteria or thresholds were identified during each month of the annual cycle which delineated the optimal, sub-optimal (or sub-lethal), and lethal conditions. Those temperature conditions correspond to successively higher temperature ranges and were defined in terms of their biological effects on the fish as follows (Review Panel 2004:21).

"Optimal conditions -- no adverse impacts on anadromous fish,

"Sub-optimal conditions -- generally a stressful condition imposed on the fish. Conditions may not be continuously stressful, but fish cannot put all their energy to successful life function. As water temperatures approach the upper end of this range impacts become more severe,

"Lethal conditions -- at times termed chronic or acute, lead to increasingly stressful conditions that result in various impacts, but not necessarily death. However, long-term exposure to such conditions is assumed to limit survival, reproduction, and or long-term success of the particular life stage."

The EPA recommended temperature criteria are as follows (from Review Panel 2004: Table 12).

Review Panel (2004), Table 12. Temperature criteria/goal for identified species and life stages in the Stanislaus River (after EPA 2003). [This table is slightly modified from the AD Consultants table]

Stanislaus River Terminology	EPA-based Recommended Temperature Criteria/Goals to Protect Salmon and Trout (Criteria based on the 7-day average of the Daily maximum values).
Adult migration	<64°F (<18°C) for salmon and trout migration <68°F (<20°C) for salmon and trout migration--generally in the lower part of river basins that likely reach this temperature naturally, if there are cold-water refugia available
Incubation	<55°F (<13°C) for salmon and trout spawning, egg incubation, and fry emergence
Juvenile rearing (early-year)	<61°F (<16°C) for salmon "core" juvenile rearing--generally in the mid-to upper part of river basins
Smoltification	<59°F (<15°C) for salmon smoltification <57°F (<14°C) for steelhead smoltification (for composite criteria the steelhead conditions are applied)
Juvenile rearing (late-year)	<64°F (<18°C) for salmon and steelhead migration plus non-core juvenile rearing--generally in the lower part of river basins

C. A. Myrick and J. J. Cech, Jr. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know? *Reviews in Fish Biology and Fisheries* 14: 113-123.

Myrick and Cech (2004) reviewed the current knowledge of temperature effects on Central Valley salmon and steelhead juveniles. They concisely described the types of thermal tolerance studies that have been conducted on fishes, as follows (Myrick and Cech 2004:115-116).

"Direct evaluations of thermal tolerance in fishes use death or loss of equilibrium as the experimental endpoints . . . Such studies fall into two broad classes -- those that place fish in water whose temperature continues to increase or decrease until the endpoint is reached, and those that hold the fish at a constant temperature until the endpoint is reached or no effect is seen. Critical thermal tolerance (CTM) studies use rapid rates of temperature change [about 0.33°C per minute]), and are useful for detecting differences in thermal tolerance caused by a number of factors [i.e., species or race, stress, acclimation temperature, water quality, and pollutants] . . ."

"Studies that use slower rates of change [about 1°C per day] than CTM-type studies are used to determine the incipient lethal temperatures (ILT) . . . [and they] typically provide more useful information regarding a species' ability to tolerate elevated temperatures under field conditions."

"Thermal tolerance may also be evaluated in studies where fish are held under a fixed thermal regime (Hokanson et al., 1977). Such studies are useful for determining survival times at a known temperature, determining the effects of temperature on a specific life stage, or observing chronic lethal or sublethal thermal effects."

"Regardless of experimental methodology, all thermal tolerance data are affected by acclimation temperature, wherein fish acclimated to higher temperatures typically have higher upper thermal tolerances than fish acclimated to cooler temperatures . . . It is important, therefore, to have some knowledge of a fish's thermal history when evaluating thermal tolerance."

Chinook salmon

Myrick and Cech (2004:120) gave the following summary points in regard to temperature effects on Central Valley Chinook salmon.

"There have been two studies published on the effects of temperature on growth of SSJR [Sacramento-San Joaquin River] Chinook salmon races; one by Marine and Cech (2004) on Sacramento River fall-run fish, and the second by Myrick and Cech (2002) on American River fall-run fish. . . . The results of these two studies compare favourably with those conducted on two northern Chinook salmon races . . ."

"The studies referenced above suggest that the optimal temperature for Chinook salmon growth lies within the 17-20°C [62.6-68°F] range, provided that food is not limiting, and other factors, such as disease, predation, and competition have a minimal effect. However, it is unlikely that Chinook salmon in field conditions will feed at 100% satiation, and the effects of disease, competition, and predation should also be taken into account. Therefore, growth rates observed under field conditions are likely to be lower." ". . . Brett et al. (1982) determined that temperatures of 18.9-20.5°C [66.2-68.9°F] were optimal for juvenile Chinook salmon fed to satiation but salmon that fed at 60% satiation reached their optimal growth temperature at ~15°C [~59°F]. . . ."

This study underscores the importance of taking field conditions into account when trying to apply results from laboratory studies."

"The effects of water temperature on Chinook salmon growth are extremely important, perhaps only second to the direct effects of water temperature on Chinook salmon survival. As was noted above, larger juveniles have a greater probability of survival during the parr-smolt transformation (Wedemeyer et al., 1980) and of returning as mature adults (Unwin, 1997), therefore resource manager should try to provide conditions that allow juvenile anadromous salmonids to maximize their freshwater growth rates. Given the small number of published studies available, it is apparent that more research is needed, particularly on the combined effects of temperature with ration levels and ration types comparable to those seen under field conditions."

Myrick and Cech noted the important effect that acclimation temperatures (i.e., the temperatures to which the fish had been previously subjected) had on the temperature tolerances of the fish. They stated (Myrick and Cech 2004:117-118):

"The incipient upper lethal temperature (IULT) for Chinook salmon is also affected by acclimation temperature; Brett (1952) reported an increase in acclimation temperature was closely correlated with an increase in IULT. Hanson (1991) reported that an IULT of 25°C [77°F] for Feather River salmon acclimated to 13°C and saw a 2.7-fold increase in resistance time at 25°C (roughly equivalent to thermal tolerance) when the acclimation temperature was increased from 12 to 18°C [53.6-64.4°F]."

"Studies of IULT are the most biologically relevant form of thermal tolerance study, yet they are surprisingly few in number, especially for central valley Chinook salmon races. Some indirect observations of SSJR Chinook salmon thermal tolerance [exist] that allow us to draw some inference on their IULTs, but specific IULT studies need to be conducted. Marine and Cech (2004) reared Sacramento fall-run Chinook salmon under laboratory conditions at 21-24°C [69.8-75.2°F] without significant mortality, but in an unpublished study on American River strain fall-run Chinook salmon, Rich (1987) reported significant mortality after 8 days of rearing at 24°C. Until a definitive and comprehensive study on the incipient upper thermal tolerance for central valley Chinook salmon races is undertaken, managers may want to use Brett's (1952) and Brett et al. (1982) data from studies on northern Chinook salmon races, where the IULT is determined to be in the 24-25°C [75.2-77°F] range."

The studies on IULT are useful for showing the tolerances of fish during sustained exposures to elevated temperatures, but it also is important to know the effects of short-term episodes of higher temperatures than the IULT levels. Hence, Myrick and Cech (2004:118) stated:

"While IULTs are generally of the most interest to managers, there are a few situations where data on acutely lethal temperatures may be needed. Under low flow conditions, it is possible for water temperatures to exceed the IULT for short periods; in these cases critical thermal maxima (CTM) data would be useful, particularly if the study correlated water temperature with resistance time. No published data of this type are available for central valley Chinook salmon."

Myrick and Cech (2004:118) noted that an unpublished report (Cech and Myrick 1999) "states that the CTM for 19°C-acclimated Chinook salmon was 28.8°C [83.4°F]." Due to the scarcity of information, they emphasized that "a study looking at the relationship between elevated water temperature and tolerance time is needed for central valley Chinook salmon strains," because the fish's

physiological responses depends on both the intensity of thermal exposure (i.e., how high the temperature reaches) and the duration of the exposure.

Steelhead

In regard to the limited information on Central Valley steelhead-rainbow trout, Myrick and Cech (2004:118) summarized as follows.

“Data on the thermal tolerances of central valley steelhead strains are even rarer than those for Chinook salmon . . . Studies on rainbow trout report IULTs of 22.8 to around 26°C [73 to ~78.8°F]. . . but none of those studies were conducted on California rainbow trout strains. Myrick’s (1998) dissertation reports CTM of 27.5, 28.4 and 29.6°C [81.5, 83.1, and 85.3°F] for juvenile American River steelhead that were acclimated to 11, 15, and 19°C [51.8, 59, and 66.2°F], while a technical report by Myrick and Cech (2000a) states that juvenile steelhead from the Feather River had a CTM of 30.8°C [87.4°F], a higher value than the CTM of 29.4°C [84.9°F] that they measured on hatchery-reared juvenile Feather River steelhead acclimated to 16°C.”

In greater detail regarding steelhead, Myrick and Cech (2004:120-121) noted:

“Whereas most juvenile central valley Chinook salmon spend less than a year in freshwater, and rarely over-summer, juvenile steelhead in the SSJR system spend at least one full summer in freshwater, and therefore have a greater likelihood of being exposed to chronically elevated water temperatures.”

“Because of the loss of access to upstream rearing habitats, juvenile steelhead in most central valley rivers now rear in the same areas as juvenile Chinook salmon, and have thus been subjected to thermal regimes that were tailored primarily for Chinook salmon rearing.”

“Unfortunately, research on central valley steelhead has been rare, and no studies of the effects of temperature on central valley steelhead have yet been published in the primary literature.”

"Myrick (1998) reports that when American River steelhead were fed to satiation at temperatures of 11, 15 and 19°C, growth rates increased from a low of 1.3% wt/day at 11°C to a maximum of 2.6% wt/d at 19°C. This study only looked at three temperatures in a relatively narrow range, and did not explore the effects of suboptimal temperatures (i.e., those above 19°C). Therefore, one cannot conclude that 19°C [66.2°F] is the best temperature for juvenile steelhead growth, or if it was just the best temperature among those tested. In defence of Myrick's (1998) information, the results do show the same patterns as those reported by Wurtsbaugh and Davis (1977a,b) who conducted the most extensive studies yet published on the effects of temperature and ration level on juvenile steelhead, albeit a northern strain from the North Santiam River in Oregon. Key findings from their studies include that maximal growth (3.5%wt/d) occurred at 16.4°C [61.5°F] and that steelhead were capable of growing at temperatures as high as 22°C [71.6°F]. Wurtsbaugh and Davis (1977b) also reported that the optimal growth temperature declined as the ration level was reduced from satiation to 60-50% of satiation."

Temperature effects on juvenile growth and smoltification

Temperature has significant effects on both the short-term and long-term survival of salmon and steelhead juveniles. Aside from the immediate effects related to thermal tolerances, environmental

temperatures can affect the growth and smoltification success of salmon and steelhead juveniles and, ultimately, their survival as they leave freshwater habitats for the ocean.

Myrick and Cech (2004:119) noted the importance of maintaining freshwater growth rates:

“Growth is perhaps the most powerful and complete integrator of environmental, behavioural, and physiological influences on a fish’s fitness. Growth is the storage of excess energy; positive growth indicates an energy surplus. Fish growth rates are influenced by a number of factors [including temperature, race, ration size, ration quality, disease, fish size, habitat, social interactions, photoperiod, and water quality]. Most of these factors are directly or indirectly influenced by water temperature, thereby complicating the task of determining the effects of temperature alone on growth rates.”

“The freshwater phase of juvenile growth is the most important because of the dramatic physiological, behavioural, and environmental changes they experience. Both Chinook salmon and steelhead are subject to gape-limited predation and are themselves gape-limited predators (Sholes and Hallock, 1979). If these juvenile salmonids can rapidly increase in size, their vulnerability to predation decreases while their ability as predators increases.”

“The development of seawater tolerances (smoltification) in Chinook salmon and steelhead is partially a function of size . . . making it important that these fishes reach an appropriate size for smolting before they reach saltwater. Larger size also gives juvenile salmonids a competitive advantage over smaller individuals in selecting prime positions (Fausch, 1984) in rearing areas that can lead to increased feeding rates . . . “

Myrick and Cech (2004:119) reiterated the important interactive effects between temperature and food supply on fish growth.

“Salmonids respond to temperature in the classical fish manner, with increasing growth as temperatures increase to an optimum at which growth is maximized, followed by a rapid decline in growth as temperatures increase further . . . The optimum temperature for growth is dependent to some degree on the availability of food. At ration levels lower than the maximum (R_{max}), the optimal temperature for growth is reduced because of the effects of temperature on metabolic rates and the subsequent maintenance metabolic demands for energy inputs (Brett et al., 1969).”

“More drastic reductions in ration level result in a re-partitioning of the available energy from somatic and reproductive growth to more critical components of the energy budget, such as maintenance and activity metabolism.”

Further research needs

Myrick and Cech pointed out the need for more research on Central Valley salmon and steelhead thermal tolerances. Specifically, Myrick and Cech (2004:118) recommended:

“Because of the strong influence of acclimation temperatures, future studies should look at a range of specific acclimation temperatures, but should also look at natural thermal regimes and at warming scenarios superimposed on natural thermal regimes. Ideally, a model could be developed with data from such studies that would predict the percent survival of the species of interest given a specific thermal profile. It is also important to realize that because juvenile steelhead and

Chinook salmon can take advantage of spatially heterogeneous temperature profiles, . . . it is important that we gain some understanding of the thermal histories of fish within central valley systems.”

Myrick and Cech (2004:118) also emphasized the sublethal, chronic effects of stressful water temperatures.

“Additionally, though death is the most common endpoint for most studies of acute and chronic thermal tolerance, detrimental effects to a fish's physiology and behaviour start to occur at lower temperatures, and studies that can quantify these sublethal effects are perhaps even more important, in the long run, than studies that merely determine the absolute thermal limits.”

Conclusions

Myrick and Cech (2004:121) concluded:

“Environmental temperature exerts profound effects on stream-associated life stages of Chinook salmon and steelhead. Egg and alevin temperature tolerance limits for Chinook salmon (approximately 6-12°C) and steelhead (approximately 7-10°C) are more narrow than those for these species' juveniles (approximately 1-24°C, and approximately 1-25°C, respectively). Both species grow more slowly at temperatures above and below approximately 17-20°C [62.6-68°F] for Chinook salmon juveniles and approximately 19°C [66.2°F] for steelhead juveniles. Some differences among strains (within species) appear to exist, but more comparative-strain studies are needed using fish with identical thermal acclimatory histories [and food rations and water qualities] . . . Overall, field conditions of particular watersheds should be incorporated into the design of future laboratory experiments.”

“As was the case with Chinook salmon, the scarcity of information on the effects of temperature on the growth of juvenile steelhead from central valley systems is alarming, and should be rectified as quickly as possible. The same types of studies mentioned for Chinook salmon are also needed for steelhead, along with comprehensive investigations of the distribution and life history of steelhead in central valley rivers.”

“Finally, habitat temperature characteristics should be strongly considered in future ecosystem management efforts, to reverse decreasing population trends . . .”

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Myrick, C. A. and J. J. Cech, Jr. 2005. Effects of temperature on the growth, food consumption, and thermal tolerance of age-0 Nimbus-strain steelhead. North American Journal of Aquaculture 67: 324-330.

Myrick and Cech (2005) examined the effects of temperature on the growth rates, food consumption rates and thermal tolerance of juvenile (age-0) steelhead derived from the non-native Nimbus Hatchery (American River) strain. They found that Nimbus-strain juveniles that had been acclimated to 11°, 15° and 19°C [51.8, 59 and 66.2°F] (for 30 days) showed no statistically significant differences in food consumption rates but did show different temperature effects on growth rates. Specifically, growth rates were higher at 19°C than at 11°C or 15°C, but the growth rates did not differ when compared between 11°C and 15°C. The higher growth rate at 19°C, combined with the similarity of food consumption rates at the three temperatures, indicated that food conversion efficiency was higher at the warmer (19°C) temperature. Fish acclimated at 19°C had growth rates 1.3-1.7 times higher than the rates for fish acclimated at 15°C and 11°C, respectively, based on wet-weight growth and 2-2.3 times higher based on dry-weight growth.

The juvenile (age-0) steelhead showed higher thermal tolerances corresponding to higher acclimation temperatures. Thermal tolerance was measured by using the critical thermal maximum (CTM)--i.e., the temperature at which the exposed individual fish lost equilibrium. The critical thermal maximum increased from 27.5°C (81.5°F) for 11°C-acclimated fish to 29.6°C (85.3°F) for 19°C-acclimated fish.

The study showed that among the three temperatures (11°, 15°, and 19°C), the highest growth rates and highest thermal tolerance (CTM) were demonstrated by fish acclimated to 19°C (66.2°F). However, Myrick and Cech (2005) noted that 19°C does not necessarily represent the physiological optimum for juvenile steelhead and that additional tests at temperatures higher (or lower) than 19°C are needed to pinpoint the optimum temperature. Nonetheless, the main point is that juvenile steelhead are capable of surviving and growing well at temperatures as high as 19°C, at least for a limited period (30 days or more).

Additionally, Myrick and Cech (2005) expressly cautioned that the juvenile steelhead still require much cooler temperatures ("around 11°C") for some period preceding smoltification in order to allow successful osmoregulatory transformation and to enhance survival in salt water. That caveat and suggested temperature (11°C) for smoltification are in accordance with some earlier experimental results. For example, Zaugg et al. (1972) noted that the parr-smolt transformation may not successfully occur if temperatures exceed some level between 10° and 15°C (50-59°F). Zaugg et al. (1972) and Zaugg and Wagner (1973) more specifically indicated 12°C to about 13°C (53.6-55.4°F) to be the upper limiting temperature that would allow juvenile steelhead to complete smoltification and increase their survival during seaward migration.

Furthermore, some level of temperature variability appears to facilitate greater rates of smoltification. Clarke and Hirano (1995:339) noted:

"Juvenile steelhead trout reared on a simulated seasonal temperature cycle (6.9°-18.6°C) [44.4-65.5°F] exhibited greater migratory behaviour and a more pronounced elevation of gill sodium, potassium-activated Na⁺K⁺-ATPase activity than those reared at constant 12.3°C [54.1°F] (Zaugg and Wagner 1973; Wagner 1974)."

Hence an appropriate level of temperature variability--which may reach as high as 65.5°F during the rearing season--seems desirable to produce greater numbers of down-migrating smolts (Wagner 1974).

However, Myrick and Cech (2005:328) cautioned that "it would be important to determine how long the fish can be exposed to the higher temperatures before returning to temperatures that are better suited for smolting."

Myrick and Cech (2005: 328) concluded:

"Overall, our study suggests that hatchery managers on rivers within the Sacramento-San Joaquin system could increase the size and survival potential of age-0 steelhead by rearing them at temperatures approaching 19°C, provided that the fish still experience a prolonged exposure to cooler temperatures so that they can successfully undergo smoltification. Furthermore, if the steelhead are to be released into stream reaches where elevated summer water temperatures are a concern, a period of acclimation to 19°C temperatures could prove beneficial."

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Temperature-related Tolerances and Survival

Myrick and Cech (2001) reviewed and synthesized information on the temperature-related biology of Chinook salmon and steelhead, especially pertaining to Central Valley stocks. In summarizing the temperature requirements of those salmonid stocks, Myrick and Cech (2001:iv) stated:

"Central Valley steelhead can be expected to show significant mortality at chronic temperatures exceeding 25°C [77°F] although they can tolerate temperatures as high as 29.6°C [85.3°F] for short periods of time. It is important to note that both species [i.e., Chinook salmon and steelhead] begin to experience serious sub-lethal effects at temperatures below their chronic lethal limits."

A number of studies have determined that the "critical thermal maximum" (CT_{max}) temperatures for steelhead and rainbow trout (summarized in Table TT.2 in Myrick and Cech 2001:29). The CT_{max} values are the temperatures at which the experimental fish experience death or loss of equilibrium following a rapid rise in temperature. CT_{max} values can be regarded as the upper thermal tolerance limits of the fish but are highly dependent on the temperatures to which the fish were previously acclimated. In general, studies show that CT_{max} temperatures for various steelhead and rainbow trout strains range from 27.6 to 30.8 °C [81.7-87.4°F].

In regard to upper thermal limits of some Central Valley stocks, the CT_{max} values for American River-Nimbus Hatchery steelhead ranged from 27.5°C [81.5°F] (for fish acclimated to 11°C) up to 29.6°C [85.3°F] (for fish acclimated to 19°C). Wild steelhead from the Feather River-- for which the "acclimation" temperature was unknown but Feather River temperature records rarely exceeded 20°C-- showed an even higher upper thermal limit (CT_{max}) of 30.8°C [87.4°F] (Myrick and Cech 2001). That observation suggests that "wild fish may tolerate higher temperatures than hatchery fish, even when [the wild fish are] acclimated to lower temperatures" (Myrick and Cech 2001:28).

Temperature Preferences

Myrick and Cech (2001:iv) noted from previous studies that fish in experimental thermal gradients preferred, or selected, temperatures that were correlated with the optimal temperatures for growth. Myrick's (1998) study on American River (Nimbus Hatchery strain) steelhead examined their thermal preferences over the 11-19°C range and showed that fish previously acclimated to higher temperatures correspondingly preferred higher test temperatures.

Myrick and Cech (2001: p.36) stated:

"Myrick's (1998) results are interesting because (1) the steelhead selected higher temperatures than one might expect for a cold-water fish . . . and (2) because the selected temperatures closely match the temperatures at which Myrick observed the highest growth rates."

Myrick and Cech (2001:36) further noted that "Hatchery fish [that had been] acclimated to constant and cyclical thermal regimes had similar thermal preferences . . . [and] selecting temperatures in the 18-19°C [64.4-66.2°F] range." In contrast, wild-caught Feather River steelhead which had been living

in "much cooler temperatures (15°C) [<59°F]" selected laboratory water temperatures around 17°C [63°F] under both fed and food-deprived conditions."

Summarizing the studies on Great Lakes rainbow trout (by Cherry et al. (1975, 1977), Myrick and Cech (2001:35-36) noted that trout that were acclimated to temperatures within the ranges 6-24° and 12-24°C (in two separate experiments) had "overall mean preferred temperatures" of 16.5°C [61°F] and 18.4°C [64°F], respectively. It was also noteworthy that rainbow trout that had been acclimated to 18-24°C [64.4-75.2°F] showed increasing temperature preferences in the 18-22°C [64.4-71.6°F] range--i.e., preferences generally lower than their acclimation temperatures but nonetheless at relatively warm temperatures (Figures TP3 and TP4 in Myrick and Cech 2001).

Growth

Generally, juvenile steelhead show net growth in the temperature range 6.9-22.5°C (44.4-72.5°F) and possibly also some growth at lower and higher temperatures. Myrick and Cech (2001:v) stated:

"The highest growth rates reported to date for Central Valley steelhead occurred at 19°C [66.2°F], but higher temperatures have not been test. Like chinook salmon, it is likely steelhead can grow at higher temperatures, but they become more sensitive to water quality and more susceptible to pathogens and predators at these temperatures."

Furthermore, Myrick and Cech (2001:v-vi) noted:

"Both Central Valley chinook salmon and steelhead have high growth rates at temperatures approaching 19°C, however, in order for them to complete the parr-smolt transformation (i.e., become adapted to life in salt water), lower temperatures are required. . . . Steelhead successfully undergo the parr-smolt transformation at temperatures between 6.5 and 11.3°C [43.7 and 52.3°F], and show little seawater adaptation at temperatures above 15°C [59°F]. Cooler temperatures (<10°C) tend to increase their seawater adaptation."

Smoltification

Myrick and Cech (2001:53) noted that "Steelhead smolt in a very narrow temperature range, citing studies by Adams et al. (1973, 1975) that showed elevated gill Na^+ - K^+ -ATPase activity at 6, 6.5 10 and 11.3°C [i.e., 42.8-52.3°F]. However, they also emphasized the importance of the interplay of factors such as temperature, photoperiod and fish size on the smoltification process within the highly variable steelhead-rainbow trout life cycle. Specifically, Myrick and Cech (2001:54) concluded:

"Steelhead grow best at temperatures of 15-19°C, yet these temperatures are unsuitable for smolting. However, because steelhead spend at least 1 year in freshwater, high growth rates during warm summer periods help them reach a suitable size (>160 mm TL, Zaugg, 1981) for smolting during the cooler winters. If river temperature are kept below those optimal for growth during non-smolt periods, there is a risk that the steelhead will be small too smolt, forcing them to spend another year in freshwater. Conversely, if the river temperatures are managed year-round at a level that is optimal for growth (i.e., ~15-19°C), smolting rates and success will be reduced. What is needed for steelhead, and indeed for all anadromous fishes, is a flexible management plan that is tailored to their temporally changing needs."

Further Research Needs and Recommendations

Myrick and Cech (2001) identified some aspects and questions needing further research in regard to temperature-related requirements of Central Valley Chinook salmon and steelhead.

Temperature Tolerances

Although thermal tolerance studies provide guidance on temperature ranges that roughly correspond to optimal, suitable, and deleterious conditions, the boundaries of those temperature "zones" can be only broadly specified because they depend on multiple factors--e.g., body condition and size of the fish, acclimation history, and stability or cyclicity of the temperature exposure. There is a need for studies to more thoroughly determine the temperature tolerance ranges of fish exposed to chronic, elevated temperatures. Myrick and Cech (2001:65) stated:

"The greatest weakness of most thermal tolerance studies is that the fish are not given an environment that is both spatially and temporally heterogeneous. The ideal study would investigate the thermal tolerance of both species when they are subjected to temperatures that fluctuate near their incipient lethal limits (~25°C)."

Growth

Likewise, a better understanding of the effects of various thermal ranges on salmonid growth and physiological transformation must be developed. Myrick and Cech (2001:65) concluded:

"A comprehensive study is needed on temperature effects over the 1 to 26°C range (in 1-2°C increments) at 20-100% satiation ration levels for the various races and runs of chinook salmon in the Sacramento-San Joaquin system. . . . Although it may be tempting to establish a single, fixed, temperature criterion for the juvenile salmon, the stochastic nature of hydrologic conditions and food supplies (Merz and Vanicek 1996) demands the use of a more adaptive and responsive management approach."

"Similar arguments can be made for additional studies on juvenile steelhead . . . further investigations of the effects of diel cycling temperatures are needed in order to more accurately model the growth of juvenile steelhead rearing in smaller, thermally heterogeneous (spatially and temporally) tributaries. Additionally, studies comparing the growth and seawater adaptability of resident and anadromous rainbow trout strains are needed to determine the suitability of using resident data to predict anadromous responses."

Physiological differences between populations

Despite the broad similarity in thermal requirements of at least several salmonid species and of populations (strains) within species, the potential existence of different physiological tolerances among salmon and trout stocks may enable, or necessitate, different temperature and flow management measures. Hence, Myrick and Cech (2001:66) suggested that "Further investigation of these differences are warranted to determine the extent to which basin-specific temperature criteria are needed."

Other studies

Although less immediately amenable, other studies that are important to conduct would address the long-term (or sublethal) and indirect effects of elevated temperature regimes on the disease susceptibility of rearing salmonids, competitive interactions among wild and hatchery salmonids and with other fish species, and predation losses of juvenile salmonids to other fishes and terrestrial predators.

High-priority questions

Myrick and Cech (2001:64) posed the following questions that encapsulate the research topics that "should be afforded the highest priority."

1. "What is the relationship between temperature and the growth and condition of juvenile chinook salmon and steelhead?"
2. "What are appropriate measures of condition to use in monitoring studies?"
3. "What is the relationship between temperature and predation on juvenile salmon and steelhead in the Sacramento-San Joaquin system?"
4. "What is the effect of declining water temperatures on the survival of eggs of fall and spring-run chinook, at temperatures typical of those encountered by spawning fish?"
5. "What is the effect of exposure of adults to high temperatures on egg survival and quality?"

Closing Statements

Myrick and Cech (2001:vii) summarized their review with the following statements which will continue to be valid into the foreseeable future.

"Based on this literature review, it is not possible to recommend a single, fixed temperature criterion. Ideally, river temperatures should be managed so that they follow the -re-regulation thermal regime. Because this is unlikely, we strongly recommend that resource managers evaluate the changing temperature needs of juvenile chinook salmon and steelhead and take advantage of modern reservoir design to maintain instream temperatures within those ranges. Finally, more research on the effects of temperature on Central Valley chinook salmon and steelhead physiology, behavior, and survival is clearly needed.

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Lindley, S. T., R. S. Schick, A. Agrawal, M. Goslin, T. E. Pearson, E. Mora, J. J. Anderson, B. May, S. Greene, C. Hanson, A. Low, D. McEwan, R. B. MacFarlane, C. Swanson and J. G. Williams. 2005. Historical population structure of Central Steelhead and its alteration by dams. San Francisco Estuary and Watershed Science 4(1): 1-21.

In a recent study, Lindley et al. (2005) reconstructed the historical steelhead distribution in the greater Central Valley drainage--encompassing the Pit River watershed and Tulare Lake basin at the extreme ends of the drainage. The inferred historical distribution of steelhead was derived from models using information on key environmental features (e.g., mean annual stream discharge, stream gradient and mean August air temperatures) to assess the suitability of stream reaches for steelhead habitation. The thermal criterion for a stream segment considered to be suitable was that the segment's mean August air temperature remained $<24^{\circ}\text{C}$ [$<75.2^{\circ}\text{F}$], as indicated by previous studies. Specifically, Lindley et al. (2005: p.4) stated:

"Stream temperature is linearly related to air temperature between 0 and 24°C (Mohseni and others 1998). Steelhead in southern California are almost never found in areas where mean August air temperatures exceed 24°C (D. Boughton, NOAA Fisheries Santa Cruz Lab, in preparation). Schmidt and others (1979) reviewed available information on thermal tolerance of *O. mykiss*, and found that 24°C was the upper lethal temperature for juvenile steelhead in northern California. In the Eel River, steelhead were not found in streams with maximum weekly average summer temperatures greater than 22°C (Harvey and others 2002)."

Hence, those studies reinforce the perception that the upper thermal limit of steelhead in natural field environments is around $22\text{-}24^{\circ}\text{C}$ ($71.6\text{-}75.2^{\circ}\text{F}$).

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U.S. EPA Issue Papers

EPA Issue Paper 1. Salmonid Behavior and Water Temperature. S. T. Sauter, J. McMillan and J. Dunham. EPA-910-D-01-001. May 2001. 36 p.

EPA Issue Paper 5. Summary of Technical Literature Examining the Physiological Effects of Temperature on Salmonids. D. A. McCullough, S. Spalding D. Sturdevant and M. Hicks. EPA-910-D-01-005. May 2001. 114 p.

Recent technical reports by the U. S. Environmental Protection Agency (EPA Issue Papers) include reviews of thermal effects on salmonids and perspectives on how temperature and other factors affect salmonids at both individual and population levels.

EPA Issue Paper 1

The EPA Issue Paper 1 (EPA Paper #1) reviewed studies on temperature effects upon salmonid behavior. The review affirmed the wide variability in temperature tolerances and preferences of steelhead-rainbow trout, reflecting differences in life-stage (i.e., age), experimental conditions and populations (or genetic strains). For example, the "acute preference temperature[s]" shown by juvenile rainbow trout in one study ranged from 52.9°F to 71.6°F, depending on the acclimation temperatures (and possibly other factors) experienced by individual fish. The acute preference temperature is defined as "[t]he immediate preference temperature of a fish placed in a laboratory gradient" (EPA Paper #1, citing Cherry et al. 1975). Similarly, a study on another strain of juvenile rainbow trout showed variable acute preference temperatures ranging from 47.1°F to 64.2°F that reflected differences among individuals in their age (1 month to 12 months) and acclimation temperatures (50-68°F).

The EPA Paper #1 (p.11-12) also noted the following general points.

"The ecological significance of a species' thermal preference is that it frequently coincides with the species' thermal optimum for physiological functioning. This optimum may shift with age and during various life history stages of an animal . . . Innate thermal preferences displayed by salmonids with age and development reflect genetic adaptation of species or subspecies (stocks) to predictable annual thermal conditions in their environment (Magnuson et al. 1979)."

"Although salmonids tend to be adapted to a narrow temperature range (and thus are stenothermic), they show some capacity to acclimatize to higher daily and seasonal water temperatures . . . Notable differences exist in the degree of their stenothermy and capacity for thermal acclimation. For example, the literature suggests that rainbow trout may have a greater capacity for thermal acclimation than do Pacific salmon or char, . . ."

"It is important to remember that salmonids are physiologically adapted to live in cold-water environments, and their ability to acclimate to higher water temperatures is restricted to the cold-water range of temperatures in which they evolved. Under laboratory conditions, acclimation may extend the thermal limits of salmonids; however, in nature growth, survival, and successful reproduction are a much more rigorous test of thermal tolerances. Fish may be able to physiologically acclimate to some extreme thermal conditions in laboratory settings, but face "ecological death" under natural conditions where ecological factors such as food availability and vulnerability to predation are important components of survival . . . Adaptation to higher environmental water temperatures and altered annual thermal regimes may require many generations . . ."

Some especially pertinent conclusions from the EPA Paper #1 (p.26) were the following.

- [conclusion 5]** "Water temperatures of ($>73.4^{\circ}\text{F}$ [23°C]) for even short periods of time (hours) result in movement into cold water refugia by Pacific salmon and trout (Nielsen et al. 1991)." Colder water temperatures are required for adult migration."
- [conclusion 6]** "Mean daily water temperatures ($>69.8^{\circ}\text{F}$ [21°C]) decrease or eliminate feeding behavior by Pacific salmon and trout (Hokanson et al. 1977)."
- [conclusion 7]** "Larvae and juvenile salmonids require a variety of water temperatures for behavioral thermoregulation to optimize physiological functioning. A certain amount of thermal diversity is important and commonly available in undisturbed naturally occurring rearing habitat. Water temperature criteria can play a central role in the protection and rehabilitation of rearing habitat by protecting and promoting restoration of cold-water refugia, and by setting numeric criteria for water temperature based on the optimal temperatures that drive behavioral thermoregulation."
- [conclusion 8]** "Potamodromous salmonids display a wide array of freshwater migratory strategies that support different life history stages and facilitate genetic exchange between isolated populations, thus forming a metapopulation."
- [conclusion 9]** "Higher seasonal water temperatures and longer periods of warm water in aquatic systems increase the feeding rate of predatory fish species that prey on juvenile salmonids."
- [conclusion 10]** "The preference temperatures of juvenile char, trout, and salmon suggest that interspecific competition plays a role in the distribution and phylogenetically derived thermal preferences of these fish."

Substantial variation is likewise shown by rainbow trout of various ages in regard to avoidance temperatures and "final preference temperature"--the latter defined as "the innate, species-specific temperature preference of an organism dictated by a thermal set point in the brain" (EPA Paper #1, p.11).

EPA Issue Paper 5

The EPA Issue Paper 5 (EPA Paper #5) provides a synopsis of salmonid thermal biology and temperature criteria and delineates the thermal ranges corresponding to optimal or benign conditions versus harmful conditions. Some conclusions and verbatim statements that are most pertinent to steelhead-rainbow trout requirements are selectively listed as follows.

(p.1) "Anadromous salmonids and coastal cutthroat and rainbow trout tend to have similar temperature requirements; . . . For this guild, maximum growth and swimming speed occur at $55.4\text{--}68^{\circ}\text{F}$ ($13\text{--}20^{\circ}\text{C}$) under satiation feeding; reduced ATPase levels are experienced at temperatures as low as $51.8\text{--}55.4^{\circ}\text{F}$ ($11\text{--}13^{\circ}\text{C}$), potentially resulting in delayed or ineffective smoltification; adult migration may be blocked at $69.8\text{--}73.4^{\circ}\text{F}$ ($21\text{--}23^{\circ}\text{C}$); and temperatures of $42.8\text{--}50^{\circ}\text{F}$ ($6\text{--}10^{\circ}\text{C}$) or lower during incubation result in maximum survival and size at emergence."

(p.5) "Growth rate is a function of temperature but also of food availability . . . Food availability in the field is normally thought to be substantially less than that needed to provide satiation feeding. Consequently, if stream productivity restricts salmonid feeding to levels less than satiation, then lower temperatures are required to ensure optimum growth rates."

"Also, in order to provide the greatest population production capacity (contributing to biomass, abundance, and fecundity--all indicators of fitness and population long-term viability, it is important to provide the full range of natural potential temperature longitudinally. This means very cold headwaters, cold midreaches, and cold/cool lower reaches. This will produce, in general, lower than optimum growth in headwaters, optimum growth in midreaches, and lower than optimum growth downstream."

(p.5) "Preferred temperatures, optimum growth temperatures, and high disease resistance from common warm-water diseases . . . tend to be similar (Jobling 1981). Consequently, we are able to survey the literature about optimum growth temperatures, compare these temperatures with optima for other performances such as disease resistance or swimming ability, and find a temperature range that would satisfy growth objectives but also meet other key needs influencing survival."

(p.6) "These contrasting demands [of growing rapidly to attain large size at smolting versus growing at a rate to allow the appropriate timing of smolting] imply that it is important to achieve high growth rates during the growth season . . ."

(p.6) "The general form of the relationship between growth is a hump-shaped (symmetrical or skewed) curve in which an intermediate temperature produces optimum growth, and temperatures both higher and lower result in declines in growth rate to zero. . . . However, growth rates at temperatures above the optimum can plummet rapidly to zero with increasing temperature and reach zero at temperatures less than the UILT (Brett et al. 1982). Growth response can also be fairly broad in the vicinity of the optimum so that an optimum zone might be described. Again, temperatures above the optimum zone can result in sharply declining growth rates, so caution is warranted in setting criteria at the upper end of the optimum zone."

(p.7) "Salmon and steelhead during the smolt phase have various degrees of sensitivity to elevated water temperatures . . . Temperatures that have been reported in the literature as impairing smoltification range from approximately 53.6-59°F (12-15°C) or more . . . Steelhead appear to be most sensitive during this stage, as opposed to their greater resistance to high temperatures during other juvenile stages. . . . Smolt migration during periods of high water temperatures can cause inhibition or reversal of the smoltification process or a termination of migration (i.e., return to freshwater residency for an additional year."

(p.13) "Laboratory results may need to be adjusted downward [for field management applications in order] to account for the influences of reduced food availability, competition, predation, and other environmental variables. Also, laboratory results may not reveal sublethal effects associated with an increased risk of warm-water disease and physiological stresses of smoltification under elevated water temperatures."

"Maximum growth and swimming speed generally occur within the range of 55.4-68°F (13-20°C) for native salmon and trout under laboratory conditions in which fish are fed to satiation."

(p.13-14) "Streams with naturally low productivity or in which food availability is lower [due to altered conditions] than under natural conditions . . . can be expected to produce optimal growth at temperatures that are lower by at least 3.6-7.2°F (2-4°C) and, under certain conditions, as much as 14.4°F (8°C) from temperatures producing optimal growth under satiation feeding."

(p.15-16) "[Disease occurrence and severity] . . . constant temperatures below 53.6-55.4°F (12-13°C) often reduce or eliminate both infection and mortality; temperatures above 59-60.8°F (15-16°C) are often associated with high rates of infection and notable mortality; temperatures above 64.4-68°F (18-20°C) are often associated with serious rates of infection and catastrophic outbreaks of many fish diseases."

(p.17) "The range in UILT [upper incipient lethal temperature] values found in multiple tests of various species of juvenile salmonids is 73.4-75.2°F (23-24°C) when acclimation temperatures are between 50 and 59°F (10 and 15°C). Although UUILT (ultimate upper incipient lethal temperature) values reported in the literature and in this paper are up to 78.8°F (26°C), fish in the field will not necessarily be acclimated to warm temperatures as they are in laboratory tests of UUILT. Therefore, UILT in the field may be 1.8-3.6°F (1-2°C) lower than the UUILT values derived in the laboratory."

(p.17) "The range in UILT values for adult salmonids is 69.8-71.6°F (21-22°C) when acclimation temperatures are approximately 66.2°F (19°C). Adults appear to have lethal tolerances 3.6-5.4°F (2-3°C) lower than the juvenile fish typically used in lethality testing."

"In a fluctuating environment, multiple-day exposure to lethal temperatures may create cumulative effects."

The EPA Paper #5 compiled from various studies the following temperature levels as being conducive to optimum growth of rainbow trout kept under full-food rations (EPA Paper #5, Table 1): 17.2-18.6°C (63-65.5°F); 16.5°C (61.7°F); 15°C (59°F).

To allow normal smoltification to occur, the upper temperature thresholds (EPA Paper #5, Table 2) were listed.

For steelhead, > 12.7°C (>54.9°F) and >13°C (>55.4°F)

For summer steelhead, 12°C (53.6°F) and >13.6°C (56.5°F)

Detailed Information from EPA Paper #5

Additional information on specific aspects are given in the following subsections. The selected passages are meant to represent the more pertinent information from the comprehensive review in EPA Paper #5.

Thermal Preferences

Water temperatures that are preferred (selected) by fish show high correspondence with temperatures that are most conducive to physiological processes. Specifically, the EPA Paper #5 (p.44) noted:

"Hutchinson and Maness (1979) cited numerous physiological processes that achieve optimum performance near the thermal preferendum: growth rate, appetite, food conversion efficiency, digestion, egestion, metabolic scope, oxygen debt load, . . . reproductive function, elimination of anaerobically produced lactate, and enzymatic activity."

"Preferred temperature also is correlated with the temperature providing the maximum metabolic scope. This, in turn, is related to the temperature providing the maximum critical swimming speed . . . Also, fish tend to be more immunologically resistant to pathogens at their preferred temperatures."

Steelhead-rainbow trout, as well as other salmonid species, have been observed in both laboratory and field situations to feed in water temperatures $>70^{\circ}\text{F}$, although feeding rate and propensity decline as temperatures increase above the mid- to high-60s degrees Fahrenheit.

[EPA Paper #5, p.45]

"In CTM (critical thermal maximum) experiments in which the heating rate was 3.6°F (2°C)/d, five species of juvenile salmonids were observed feeding up to temperatures that were $1.8\text{--}3.6^{\circ}\text{F}$ ($1\text{--}2^{\circ}\text{C}$) less than the LT_{50} "; ". . . rainbow trout . . . were observed feeding at temperatures of . . . 79.9°F . . . during CTM experiments."

"In northern California streams, juvenile steelhead were seen actively feeding in water temperatures as high as 75.2°F (24°C) (Nielsen et al. 1994). However, once temperatures reached 71.6°F (22°C), rate of foraging began to decline."

[EPA Paper #5, p.53]

"Hahn (1977) investigated the effects of fluctuating ($46.4\text{--}66.2^{\circ}\text{F}$ [$8\text{--}19^{\circ}\text{C}$]) and constant (47.3 , 56.3 , 65.3°F [8.5 , 13.5 , 18.5°C]) temperatures on steelhead trout fry and yearlings. . . We can conclude from Hahn's work that juveniles had equal preference for constant (56.3°F [13.5°C]) water and fluctuating ($46.4\text{--}66.2^{\circ}\text{F}$ [$8\text{--}19^{\circ}\text{C}$]) water with a mean of 56.3°F (13.5°C)."

It is noteworthy that Hahn's (1977) study showed overall preferences by steelhead juveniles for increasingly cooler water, either fluctuating or constant, and preferred fluctuating conditions over constant temperatures as long as part of the fluctuating cycle encompassed cooler conditions than the constant temperature being tested.

Juvenile Growth

The EPA Paper #5 summarized results from numerous studies of temperature effects on steelhead-rainbow trout growth and showed substantial variation in the range of temperatures considered to be optimal for growth. Some abbreviated results are given here.

[EPA Paper #5, p.29]

"On the basis of studies of growth at constant temperatures within the overall range 50-77°F (10-25°C), Myrick and Cech (2000) inferred an optimal growth rate between 57.2 and 66.2°F (14 and 19°C) . . ."

[EPA Paper #5, p.42]

Wurtsbaugh and Davis (1977) compared three fluctuating temperature regimes. Highest growth for steelhead occurred under the natural regime (mean summer temperature = 61.2°F) compared to the elevated test regimes (mean temperatures of 67.1°F and 72.5°F). Under the highest temperature regime (mean, 72.5°F) and food consumption rate of 7% of body weight per day, the fish showed zero growth rate.

"Final preferred and optimal temperatures for rainbow trout have been reported at 53.6-66.2°F (12-19°C) . . . and scope of activity and growth for juvenile fish are commonly reported to be optimal between 59 and 69.8°F (15-21°C) on a satiation diet . . ."

"Piper et al. (1982) set the optimal at 50-62.1°F (10-16.7°C) . . . McCauley and Huggins (1975) found that large (150-250 g) rainbow trout had a preferred mean temperature of 62.1°F (16.7°C), and that the fish actively traveled at temperatures between 56.8 and 64.4°F (13.8-18°C) in a thermal gradient. Behnke (1992) suggested that the optimum temperature for growth and food assimilation in salmonids occurs between 55.2 and 60.8°F (13-16°C). Ferguson (1958) cites 56.5°F (13.6°C) as the final preferred temperature for rainbow trout"

"Dockray et al. (1996) found that [for rainbow trout] in a fluctuating temperature environment, temperature increases benefited growth up to daily maximum temperatures of 64.4°F (18°C), above which long-term growth was inhibited."

"De Leeuw (1982) found that stream temperature increases that raised the summertime maximum temperature from 53.6 to 61.7°F (12-16.5°C) were associated with an increase in growth rates [of rainbow trout] in three streams in British Columbia, Canada."

"Hokanson et al. (1977) found that a constant exposure of 63°F (17.2°C) produced the greatest growth rates in trout fed to satiation over a 40-d test period. Increased mortality was observed in temperatures above this growth optimum. They also noted that in fluctuating temperature experiments, growth was accelerated when the mean temperature was below the constant temperature optimum (63°F [17.2°C]), and growth was retarded by mean fluctuating temperatures above this optimum. The highest growth rate in the fluctuating temperature environment occurred at a mean of 59.9°F (15.5°C) (range of 53-66.7°F [11.7-19.3°C]). A statistically nonsignificant decrease occurred at a mean of 63.1°F (17.3°C) (range of 56.3-70°F [13.5-21.1°C])."

[EPA Paper #5, p.43]

"Cunjak and Green (1986) found that rainbow trout were able to compete better with brook trout at 66.2°F (19°C) than at either 46.4 or 55.4°F (8 or 13°C)."

"Bisson and Davis (1976) . . . found that streams with daily maximum temperatures of 60.8-73.4°F (16-23°C) had greater standing crops of trout than did streams with warmer maximum temperatures (78.8-87.8°F [26-31°C])."

"Frissell et al. (1992) studied the distribution of rainbow trout and found that although they could be found in water temperatures over 73.4°F (23°C), there was a general threshold response for age 1+ fish above 71.6°F (22°C) and for age 2+ fish above 69.8° (21°C)."

[Li et al. (1993)] ". . . [rainbow trout] actively avoided waters warmer than 73.4-77°F (23-25°C)."

"Linton et al. (1997) noted that rainbow trout fed to satiation continued to feed and grow at a mean temperature of 68.9°F (20.5°C), a 30% reduction in food intake occurred at 71.6°F (22°C), and juvenile fish continued to feed near their thermal maximum."

"Linton et al. (1997) found that increasing the temperature regime by 3.6°F (2°C) over the natural (base) level for Lake Ontario trout resulted in increased spring and early summer growth, which was lost later in the summer due to suppression of appetite and growth. Mortality rates increased from 6% to 13.1% in the warmer test water during the late summer . . . when the mean monthly base temperature in August was 73.4°F (23°C). Mortality was almost nonexistent . . . [during] a mean August base temperature of 64.4°F (18°C)."

"Behnke (1992) cited work . . . trout reduce and finally cease feeding as temperatures rise to between 71.6 and 77°F (22-25°C), often well below the lethal temperature."

[EPA Paper #5, p.52]

"Hokanson and colleagues [1977] studied growth and survival of rainbow trout (*O. mykiss*) juveniles reared on maximum rations under fluctuating temperatures (T°F ±6.8°F [3.8°C]) versus constant temperatures. The physiological optimum (PO) temperature of rainbow trout is 60.8-64.4°F (16-18°C) . . . [The study showed that] specific growth rate at mean temperatures less than PO was lower . . . under a constant (T°F) versus a fluctuating (T°F ±6.8°F [3.8°C]) temperature regime. This indicates a benefit of a fluctuating regime when the mean temperature is less than PO. . . . However, specific growth rates at mean temperatures greater than PO were higher at constant than fluctuating temperatures having the same mean temperature."

Hence, the Hokanson et al. (1977) study cited above indicated that rainbow trout growth evidently is "accelerated under fluctuating temperatures when the mean temperature is below the constant temperature optimum for growth and retarded by fluctuating temperatures when the mean is higher."

"They determined that rainbow trout growth rates under fluctuating regimes do not correspond to those in a constant temperature regime having a mean equal to that for the cycle. Rather, they acclimate to some value between the mean and maximum daily temperatures and consequently their growth rates reflect this "effective" temperature."

[EPA Paper #5, p.53]

Also, Grabowski (1973) compared steelhead growth rate at different test temperatures (constant temperatures at 46.4, 59 and 64.4°F and a fluctuating regime of 46.4-64.4°F (mean, 55.4°F). Grabowski found that "Steelhead grew better at 59°F (15°C) than at other temperatures" and that the fluctuating test regime yielded the "second highest growth rate and actual weight gain." A plot of data (growth rate versus midpoint test temperatures) showed "near linear growth from 46.4 to 59°F (3-15°C), with a steep drop as temperature progresses to 64.4° (18°C)."

In general, the reviewed information clearly demonstrates a wide range of estimated optimal temperatures for rearing rainbow trout, evidently reflecting the adaptations of various stocks or strains to their respective natural habitats. However, the EPA Paper #5 (p.44) concluded: "Because criteria must protect both adult and juvenile forms of rainbow trout, an optimal temperature regime seems to most consistently occur in the range of 55.4-60.8°F (13-16°C)."

Steelhead Smoltification and Downstream Migration [EPA Paper #5, p.61-64]

[p.62] "Smolt transformation in steelhead rearing in water 52.3°F (11.3°C) was inhibited (Adams et al. 1973); rearing temperatures >55.4°F (13°C) prevent increases in ATPase activity (Hoar 1988)." . . . "In

winter steelhead, a temperature of 54.1°F (12.3°C) is nearly the upper limit for smolting (Zaugg and Wagner 1973). Zaugg (1981) found that a temperature of 53.6°F (12°C) could inhibit successful migration to the ocean in winter steelhead."

[p.63] "Some smoltification processes are greatly retarded by water temperatures >55.4°F (13°C), and in some Pacific salmonids smolt stage cannot be attained at 60.8°F (16°C) . . . "

[p.63] "Yearling steelhead held at 43.7°F (6.5°C) and transferred to 59°F (15°C) had a marked reduction in gill ATPase activity, indicating a reversal of some smolting changes (Wedemeyer et al. 1980). When temperatures exceeded 55.4°F (13°C), gill Na-K-ATPase activity declined in fish that had already begun smoltification, and there was a decreased ability to migrate (Zaugg and Wagner 1973). Zaugg and Wagner (1973) considered this effect, operating well below lethal limits, to have serious implications for survival of steelhead because it inhibited migratory ability."

[p.64] "Most steelhead emigration occurs before river temperatures rise above 53.6°F (12°C). Emigration can extend into temperatures as high as 61.7°F (16.5°C). The 53.6°F (12°C) limiting temperature normally does not occur until mid-May, but in low-flow years can occur in late April; this shift in thermal regime may cause a reduction in steelhead survival (Zaugg 1981)."

Lethal Limits

[EPA Paper #5, p.86]

"However, at most acclimation temperatures likely to be encountered during the spring through fall seasons (53.6-68°F [12-20°C]), lethal levels are consistently in the range of 77-78.8°F (25-26°C) . . . With cautious acclimation to temperatures in the range of 73.4-75.2°F (23-24°C), rainbow trout may not experience LT50 effects until a week at 78.8°F (26°C) . . . Even with careful acclimation, 77°F (27°C) results in high or complete mortality in less than 24 hours . . ."

"Under fluctuating temperature test conditions, rainbow trout have experienced 50% mortality in a week of daily cycles from 69.8 to 77°F (21-27°F) . . . [Sonski (1983)] was able to culture rainbow trout in ponds that reached 84°F (28.9°C), . . . [and other researchers] reported that rainbow trout were largely able to survive in rearing ponds with months of daily maximum temperatures of 78.8-84.2°F (26-29°C)."

The EPA Paper #5 (their Figure 3) presents a curve of 50% mortality (over 7 days of constant temperature exposures) plotted against acclimation temperature. That curve is the basis of recommended temperature criteria for all salmonids as a group. Specifically, the EPA Paper #5 (p.87) noted:

"At low acclimation temperatures, constant exposure to just above 72.5°F (22.5°C) would be expected to result in 50% mortality over a week. Reducing this value to a level where no lethality would be expected to any adults or juveniles would result in a daily maximum not to exceed 68.9°F (20.5°C)."

Species have broadly similar thermal tolerances

Based on several data compilations, it appears that the five Pacific salmon species and various trouts (both native and introduced species) in North America generally have similar lethal temperature limits. The EPA Paper #5 gave a range for the UUILT values of 73-78°F of the North American Salmonidae, excluding redband trout (exceptionally warm-tolerant) and bull trout (exceptionally cold-tolerant). A study on rainbow trout and other trout species indicated UUILT values of 73.4-77°F (Cherry

et al. 1977). Likewise, a study of Pacific salmon species showed UUILT values ranging between 74.8-77.2°F (EPA Paper #5 citing Brett 1952).

Another study using a different measure of thermal tolerances of trout up to their lethal limits also showed small differences between species--i.e., CTM values for rainbow (84.9°F), brown (85.8°F), brook (85.6°F), Gila (85.3°F) and Arizona (84.9°F) trout. The EPA Paper #5 (p.25) noted that the "CTM and UUILT [or UUILT] test methodologies are fundamentally different and yield different kinds of information on thermal tolerance."

The EPA Paper #5 also noted that fishes in the families Cyprinidae and Centrarchidae, which are now numerous in Central Valley watersheds, are highly active feeders at temperatures exceeding 68°F and can effectively exclude salmonids from habitats at such higher temperatures. The paper further states that "This [capability] is a partial explanation for the disappearance of salmonids from streams when maximum temperatures are in the range of 71.6-75.2°F [22-24°C]" (EPA Paper #5, p.24)

Within-species variation of thermal tolerances

In comparing different populations within the same salmonid species, the differences in thermal tolerances tend to be minor or statistically non-detectable. Even for some cases where such differences have been reported, they may be partly or wholly due to extraneous environmental factors (e.g., acclimation conditions) rather than to the innate biological characteristics of the stocks or strains of fish tested.

The EPA Paper #5 (p.27) noted that the Myrick and Cech (2000) study on "two rainbow trout strains (Eagle Lake and Mount Shasta) revealed no differences in thermal tolerance as measured by the CTM method" and "no differences in conversion efficiency, oxygen consumption rates, or swimming performance."

Nonetheless, differences in thermal tolerance may occur between some salmonid stocks within the same species--e.g., ocean-type and stream-type Chinook salmon juveniles that show different cumulative mortality patterns in response to sustained exposure to high temperatures (70.7°F and 74.6°F test temperatures) (EPA Paper #5, p.26, citing Beacham and Withler 1991).

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Earlier Literature Reviews of Temperature Effects on Salmon-Steelhead

- (1) McCullough, D. A. 1999. A Review and Synthesis of Effects of Alterations to the Water Temperature Regime on Freshwater Life Stages of Salmonids, with Special Reference to Chinook Salmon. Report to the U. S. Environmental Protection Agency, Region 10, Seattle, Washington. February 22, 1999. 279 p.
- (2) Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34: 639-648.
- (3) Boles, G. L., S. M. Turek, C. D. Maxwell, and D. M. McGill. 1988. Water Temperature Effects on Chinook Salmon (*Oncorhynchus tshawytscha*), with Emphasis on the Sacramento River. A Literature Review. Report by the California Department of Water Resources, Northern District, Sacramento. January 1988. 42 p.

The information from these three reports is presented below in subsections corresponding to different biological processes (e.g., survival, growth) and ecological ramifications (i.e., field distributions, protective temperature criteria).

Survival

The upper thermal limits for survival of juvenile rainbow trout appear to be around 24-29°C (75.2-84.2°F) as indicated by laboratory test procedures (McCullough 1999). For example, the critical thermal limits for rainbow trout and four other trout species--i.e., the temperatures at which test fish show a loss of equilibrium before the onset of death--were 28.5°C [83.3°F] for fish that were initially acclimated to 10°C [50°F] and 29.5°C [85.1°F] for fish acclimated to 20°C (68°F).

In some cases, rainbow trout that are acclimated to fluctuating temperatures may be better able to tolerate higher temperatures than do fish acclimated to a constant temperature. For example, juvenile rainbow trout that were acclimated to a diel cycle of 8-16°C [46.4-60.8°F] survived longer when exposed to a "challenge" temperature of 26° [78.8°F] than did fish acclimated to a constant 12°C [53.6°F] (McCullough 1999 citing Threader and Houston 1983).

Conversely, fluctuating temperatures may be detrimental to juvenile rainbow trout survival if the temperature cycle approaches too closely to the upper lethal limits. Specifically, rainbow trout acclimated at 16°C [60.8°F] showed no growth and experienced an initial mortality rate of 42.8% per day when subjected to a fluctuating thermal regime of 18.4-26°C [65.1-78.8°F]

Growth

An extensive set of studies on Oregon steelhead (North Santiam River) showed that the growth rate of juvenile steelhead increased to a maximum level as temperature increased to 16.4°C [61.5°F] and then dropped as temperature was further increased to 23°C. That relationship applied to fish provided with full food rations (i.e., satiation level) and a similar bell-shaped relationship with peak growth rate at ~15°C [59°F] was shown by juveniles on 60-70% food rations (Myrick and Cech 2001 citing Wurtsbaugh and Davis 1977a, 1977b). Those studies also showed that at any given temperature, larger steelhead juveniles had lower growth rates than did smaller juveniles.

McCullough (1999:61, apparently citing Hokanson et al. 1977) stated, "The physiological optimum (PO) temperature of rainbow trout is 16°C-18°C [60.8-64.4°F]." With regard to upper thermal

limits for juvenile growth, Hokanson et al. (1977) determined that rainbow trout would not grow if temperatures reached a constant 23°C [73.4°F] or a fluctuating level of 21° ± 3.8°C [69.8° ± 6.8°F].

McCullough (1999:95) also stated that Hokanson et al. (1977) "recommended a mean weekly temperature no greater than 17° ± 2°C for [rainbow] trout experiencing fluctuating temperatures in the field" (based on laboratory studies). "Optimal growth conditions under constant temperatures occurred at 17.2°C-18.6°C [63-65.5°F] but in a fluctuating (± 3.8°C) [± 6.8°F] temperature regime, optimum growth conditions occurred at mean temperatures of 15.5°C-17.3°C [59.9-63.1°F]."

Similarly, a laboratory study on (Great Lakes) rainbow trout showed that juvenile growth rates were significantly lower under a warmer diel regime (mean daily temperatures of 15-26°C, or 59-78.8°F) compared with the natural ambient regime (mean daily temperatures of 13-24°C, or 55.4-75.2°F). Furthermore, growth rates were substantially higher in the earlier phase of the study when water temperatures were cooler (13-18°C [55.4-64.4°F]) than later (19-24°C [66.2-75.2°F]) (McCullough 1999:64, citing Dockray et al. 1996). In that study on rainbow trout, where both water temperature and water hardness (i.e., ionic content) were the experimental variables, Reid et al. (1995:241) concluded:

"Between day 60 and day 90, the water temperature in the softwater exposure system peaked at either 24 and 26°C . . . and resulted in dramatic reductions in gill and liver protein synthesis, accretion and degradation . . . These alterations in protein turnover were reflected in other indicators of metabolic activity in these fish (food conversion efficiency, appetite and growth) and implicate that metabolism is dramatically and rapidly reduced at temperatures between 24 and 26°C. . . . These data also suggest that at the very extreme range of their thermal tolerance, between 24 and 26°C, metabolism is dramatically suppressed possibly in an attempt to conserve energy as a last resort prior to heat-induced mortality."

An earlier laboratory study on steelhead growth rates under fluctuating thermal regimes indicated that temperatures less than 16.5°C [61.7°F] would be optimal for the fish, with the upper limit (i.e., at which there is no body growth) occurring at a mean temperature of 22.5°C [72.5°F] (McCullough 1999:63). Another study on steelhead parr showed that the best growth occurred at a constant temperature of 15°C (59°F) and lower growth occurred at a constant 18°C (64.4°F) or under a variable regime of 8-18°C (46.4-64.4°F) (McCullough 1999:64, citing Grabowski 1973).

Myrick (1998) investigated the combined effects of temperature (11°, 15°, 19°C [51.8°, 59°, 66.2°F]) and food ration levels (100% versus 82-92% of saturation levels) on the growth rates of American River (Nimbus Hatchery) steelhead. Growth rates were generally similar between the two food levels at a given temperature, but the highest growth rates occurred at 19°C for both food levels (Myrick and Cech 2001 citing Myrick 1998). A greater range of food rations (25%, 50%, and 100% of saturation) and more varied temperature regimes (i.e., comparing constant temperatures versus cyclical temperatures) were subsequently tested on Feather River steelhead (Myrick and Cech 2001 citing Myrick and Cech 2000). Their study showed that growth rates increased as food levels increased and that the fish grew more slowly (but not statistically significant) in a cyclical thermal regime (14-18°C [57.2-64.4°F]) than under constant temperatures.

Smoltification

Elevated water temperature is an important factor that may decrease the frequency at which steelhead and salmon smolts are produced from juveniles. For example, a review by the California Department of Water Resources (Boles et al. 1988) noted the following.

"Seaward migratory behavior of steelhead trout and coho salmon has been found to be inhibited in juvenile fish at temperatures greater than 54°F." (Boles et al. 1988:10)

"Temperatures greater than 55°F inhibit adenosine triphosphatase activity in steelhead trout (*Salmo gairdneri gairdneri*), . . . Although specific temperature limits have not been determined for chinook salmon, a maximum temperature of 54°F for all species of salmonids has been recommended to maintain migratory response and seawater adaptation in juveniles." (Boles et al. 1988:4)

Earlier experimental studies on salmonid smoltification "indicated that metamorphosis (and, therefore, successful migration) of juvenile steelhead trout is directly controlled by water temperature" (Adams et al. 1975:766). A study by Adams et al. (1975:768) on steelhead from Washington state "suggest[ed] that steelhead trout undergo the smolt transformation when reared in water at temperatures below 11.3[°]C but not at higher water temperatures." That result corroborated a previous study (Zaugg et al. 1972:416) which stated:

"On the basis of the experiments reported herein we show only that the parr-smolt transformation may not occur or persist at some temperature between 10° and 15°C. We have conducted other experiments, however, which indicate the limiting temperature to be near 13°C. Pending further investigation, we suggest 12°C (about 54°F) as an upper limit for waters used by migrating juvenile steelhead."

The sensitivity of steelhead smoltification to higher temperature was, in fact, greater than that of coho salmon, for which the "maximum allowable temperature" was above 15°C. That fact led the authors to conclude "that the steelhead is a colder water fish than the coho salmon" (Adams et al. 1975:768).

McCullough (1999) cited studies that indicated that the smolting process in steelhead is blocked when temperatures approach the 11.3-13.6°C range [52.3-56.5°F]. Specifically, (McCullough 1999:69) stated:

"In smolting steelhead trout, rearing temperatures >13°C [>55.4°F] prevent increase in ATPase activity (Hoar 1988). The smolt transformation in steelhead rearing in water >11.3°C [>52.3°F] was inhibited (Adams et al. 1975). This inhibitory effect on steelhead is stronger than on coho, chinook, or Atlantic salmon (Adams et al. 1975). Temperatures >13.6°C [> 56.5°F] do not permit smoltification in summer steelhead (Zaugg et al. 1972, as cited by Zaugg and Wagner 1973). In winter steelhead a temperature of 12.3° [54.1°F] is nearly the upper limit for smolting (Zaugg and Wagner 1973). When temperatures exceeded 13°C, gill Na-K-ATPase activity declined in fish that had already begun the smoltification process and there was a decreased ability to migrate (Zaugg and Wagner 1973). Zaugg and Wagner (1973) considered this effect, operating well below lethal limits, to have serious implications for survival of steelhead due to inhibition of migratory ability."

Therefore, it is evident from those physiological studies that some type of water management strategy might be used to influence the relative abundance of steelhead and rainbow trout phenotypes in a population by controlling water releases from reservoirs and, hence, stream temperatures. For northern steelhead stocks, the maximum water temperatures that allow normal smoltification appears to be around 11.3-12°C (52.3-53.6°F). It is probably reasonable to assume that the corresponding "limiting" temperatures for Central Valley steelhead smoltification are similar. Myrick and Cech (2005:328) recently noted that juvenile steelhead can be exposed to elevated rearing temperatures to facilitate growth and survival prior to the smoltification stage. However, "it would be important to determine how long the

fish can be exposed to the higher temperatures before returning to temperatures that are better suited for smolting."

In any event, temperatures somewhat exceeding those limits would be inhibitory for the expression of the steelhead (migratory) life-history form but would not preclude the persistence of *O. mykiss* populations in the form of resident (rainbow) trout.

Field Distributions

Field studies in aggregate indicate that the upper temperature levels that determine the presence or absence of steelhead and rainbow trout juveniles lie approximately at 19-21°C [66.2-69.4°F] (McCullough 1999).

In some natural situations, juvenile rainbow trout may occur at maximum temperatures up to 22.5-24°C (72.5-75.2°F) (McCullough 1999), although it seems that their occurrence at such high temperatures most likely would be for limited periods (e.g., periodically for days or perhaps weeks during the warmer season). However, a broad data-base analysis by Eaton et al. (1995) showed that 24°C (75.2°F) was the maximum field temperatures tolerated by rainbow trout, as determined by the study criteria. In defining the study criteria, the highest 5% weekly mean temperatures of the original data pool was pre-selected, from which the 95 percentile of that subset was taken as the "maximum tolerance estimate." By comparison, somewhat similar maximum tolerance estimates were determined for Chinook salmon (24°C), coho salmon (23.4°C) and brown trout (24.1°C).

Additional field studies have shown that densities of rainbow trout decreased as the maximum stream temperatures rose from 17°C (62.6°F) to 20-22°C (68-71.6°F), although a few individuals (age 0+) could persist at temperatures up to 24.5°C (76.1°F) (McCullough 1995 citing Frissell et al. 1992).

Temperature Criteria for Protecting Steelhead-Rainbow Trout

Hokanson et al. (1977:645) stated that the "Temperature criteria recommended for rainbow trout waters by the NAS/NAE [National Academy of Sciences/National Academy of Engineering] (1972)" were a maximum weekly average of 19°C (66.2°F) and a "short-term" maximum temperature of 24°C (75.2°F). The latter temperature criterion corresponded to an adjusted "median tolerance limit (TL50)"--i.e., which was defined as the temperature at which 50% of the fish survived for 24 hours, adjusted downward by a 2°C "safety factor." Furthermore,

"The maximum temperature at which a rainbow trout population can be expected to maintain its weight for 40 days was a constant temperature of 23°C [73.4°F] and a fluctuating mean temperature (± 3.8 deg C) (± 6.8 °F) of 21°C [69°F]. The temperature range from 21 to 23°C [69.8-73.4°F] has also been reported by various authors as representing the upper limits of rainbow trout distribution . . ."

Hokanson et al. (1977:646) noted the important fact that natural environments may differ in the range of temperature cycles. Hence, the temperature criteria indicated from laboratory results should be "retracted towards the optimum [cooler] end point derived from constant temperature studies (i.e., 17°C [62.6°F] for rainbow trout" to ensure their protection. They further recommended that because fish under limited food supply require cooler temperatures to energetically maintain themselves: "These limits should be further retracted towards colder temperatures to safeguard natural populations receiving less than full [food] rations . . ." (Hokanson et al. 1977:647).

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