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Temperature Effects on Chinook Salmon and Steelhead:
a Review Focusing on California's Central Valley Populations

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The Bay-Delta Modeling Forum is pleased to present this literature review of the effects of water temperature on chinook salmon and steelhead, with particular emphasis on populations in the Central Valley of California. The review is one of two products of an effort that began with a workshop on temperature modeling, held by the Forum in October, 1998. During the workshop, it became clear that there was a need for a review of water temperature models, and also a need for a review of what was known about the effects of water temperature on chinook salmon and steelhead, since much of the concern for managing water temperatures in the Central Valley is related to those species. The Forum solicited proposals for the reviews from well qualified young professionals, authorized partial funding for the reviews, and then secured matching funds from the Bureau of Reclamation and the Department of Water Resources. Because there was an existing contract between the Department and the University of California at Davis, it was expedient to use that funding mechanism for the "temperature effects" review, although the Forum provided the practical oversight of the project.

As is the case with all Forum reports, this one does not necessarily represent the views of the governing bodies of organizational members, or of the individual members.

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EXECUTIVE SUMMARY

California's Central Valley rivers are home to two species of anadromous salmonids, chinook salmon (*Oncorhynchus tshawytscha*) and steelhead, or anadromous rainbow trout (*O. mykiss*). The Central Valley chinook salmon are divided into 4 distinct runs, or races; the Central Valley fall-run, the Central Valley late-fall run, the Central Valley spring-run, and the Sacramento River winter-run. Central Valley streams and rivers represent the southernmost distribution of chinook salmon today. Steelhead in the Central Valley are all classified as winter-run fish, though separate drainages have distinct runs (e.g., Yuba River, Battle Creek). Unlike chinook salmon, which do not occur south of the Central Valley, there are a few steelhead populations further south, though the Central Valley is close to their southernmost distributional limit.

All anadromous salmonid populations in the Central Valley have experienced drastic reductions in size, in some cases to extinction, in the past 100 years. Causes for these declines include introduced species, changes in nutrient dynamics, overharvest, and disease. The most pervasive cause, however, is the presence of impoundments and water diversions on most Central Valley rivers and their tributaries. These structures have a number of deleterious effects on anadromous fish populations, including restricting or preventing access to spawning and rearing habitat, changing historical flow regimes, and the one this report is concerned with, changing the thermal regime or temperature of the remaining flows.

Water temperature is perhaps the physical factor with the greatest influence on Central Valley salmonids, short of a complete absence of water. Temperature directly affects survival, growth rates, distribution, and developmental rates. Temperature also indirectly affects growth rates, disease incidence, predation, and long-term survival. The changes made to Central Valley rivers have had, and will continue to have far-reaching effects on chinook salmon and steelhead populations. All life-history stages of both chinook salmon and steelhead are affected by temperature; this report focuses primarily on the effects of temperature on the survival and physiology of eggs, alevins, juveniles, and smolts.

Chinook salmon and steelhead egg-hatching times are temperature-dependent, with shorter hatching times at higher temperatures. However, there is increased mortality at the higher temperatures, and the fry that survive are small and prone to developmental abnormalities. Chinook salmon eggs can survive temperatures between 1.7 and 16.7°C, with highest survival rates between 4 and 12°C. Steelhead eggs can survive temperatures between 2 and 15°C, with highest survival rates between 7 and 10°C.

Juvenile chinook salmon and steelhead thermal tolerances are a function of acclimation temperature and exposure time. Fish acclimated to high temperatures tend to show greater heat tolerance than those acclimated to cooler temperatures. Once temperatures reach a chronically lethal level (approximately 25°C), the time to death decreases with increasing temperature. The chronic upper lethal limit for Central Valley chinook salmon is approximately 25°C, with higher temperatures (up to 29°C) tolerated for short periods of time. Central Valley steelhead can be expected to show significant mortality at chronic temperatures exceeding 25°C, although they can tolerate temperatures as high as 29.6°C for short periods of time. It is important to note that both species begin to experience serious sub-lethal effects at temperatures below their chronic lethal limits.

Temperatures preferred, or selected, by fish in thermal gradients have been correlated with their optimal temperatures for growth. Hatchery-reared Central Valley steelhead consistently selected temperatures of 18 to 19°C, while wild-caught fish selected temperatures around 17°C. Interestingly, research on Great Lakes rainbow trout found that selected temperatures increased with acclimation temperature from about 15°C to 20°C. However, limited research conducted on chinook salmon thermal preference (none from the Central Valley) suggests that no acclimation effect exists and that selected temperatures do not correlate well with optimal growth temperatures. More research is clearly needed in this area.

Growth is perhaps the most powerful and complete integrator of environmental, behavioral, and physiological influences on a fish's fitness. Temperature affects growth directly through its effect on metabolic processes, and indirectly, through its effects on food availability and activity. Juvenile chinook salmon grow at temperatures of 8°C to 25°C, under otherwise optimal conditions. Maximum growth rates occur when salmon are fed to satiation at 19°C. Studies on Central Valley salmon have conflicting results. One study reported maximum growth between 13.2 and 15.3°C, while two other studies reported maximum growth at 19°C and 17-20°C. Central Valley salmon can apparently grow at temperatures approaching 24°C, but are more sensitive to changes in water quality and the presence of pathogens at higher temperatures. Juvenile steelhead grow at temperatures 6.9°C to at least 22.5°C. Growth rates of N. Santiam River (OR) steelhead reached a maximum at 16.4°C when fed satiation rations; maximum growth occurred at lower temperatures when ration levels were reduced. The highest growth rates reported to date for Central Valley steelhead occurred at 19°C, but higher temperatures have not been tested. Like chinook salmon, it is likely that steelhead can grow at higher temperatures, but they become more sensitive to water quality and more susceptible to pathogens and predators at these temperatures.

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 saltwater), lower temperatures are required. Chinook salmon can smolt at temperatures ranging from 6 – 20°C. Salmon that smolt at higher temperatures (> 16°C) tend to display impaired smoltification patterns and reduced saltwater survival. Additionally, salmon which rear within the 10 – 17.5°C temperature range are optimally prepared for saltwater survival. Steelhead successfully undergo the parr-smolt transformation at temperatures between 6.5 and 11.3°C, and show little seawater adaptation at temperatures above 15°C. Cooler temperatures (< 10°C) tend to increase their seawater adaptation.

Temperature indirectly affects anadromous Central Valley salmonids through its effect on pathogen infectivity and virulence. Unfortunately, the effects of water temperature on pathogens are not well known, but the limited studies completed to date associate elevated water temperatures with higher rates of infection and increased mortality for both juvenile chinook salmon and steelhead. Salmon or steelhead that are caught-and-released during sport fisheries are susceptible to infection. Given the increased physiological stresses experienced during captures at higher water temperatures, it is likely that their susceptibility to pathogens is enhanced.

Predation on juvenile chinook salmon and steelhead is both directly and indirectly affected by temperature. Direct effects are those where temperature increases or decreases the vulnerability to predation through behavioral or physiological pathways. Indirect effects are

manifested through temperatures' influence on some other causative factor, such as disease or predator metabolism. Few studies of indirect effects have been conducted in this area; the single study on Central Valley chinook salmon demonstrated that juveniles reared at temperatures between 21 and 24°C were more vulnerable to striped bass (*Morone saxatilis*) predation than juveniles reared at lower temperatures. Maximum daily consumption of juvenile salmon by fish predators like pikeminnow (*Ptychocheilus spp.*) and bass (*Micropterus spp.*) also increases with temperature. Known indirect effects include the increased vulnerability of juvenile salmon to fish predators following infection with *R. salmoninarum*. More research is clearly needed in this area, given the ongoing losses of juvenile salmon to fish and avian predators.

In summary, optimal temperature ranges for Central Valley chinook salmon and steelhead vary depending on life stage. Eggs and alevins are extremely stenothermal, requiring temperatures between 4 and 12°C for the highest survival rates. Juveniles are more stenothermal, requiring temperatures between 15 and 19°C for maximum growth under optimal conditions. In order to complete the parr-smolt transformation, however, cooler temperatures (10 – 17°C for chinook salmon; 6 – 10°C for steelhead) are needed to maximize saltwater survival. Cooler temperatures also reduce the risk of predation and disease, both of which are enhanced at higher temperatures. 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 pre-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. We identify specific research needs in the final section of this report.

INTRODUCTION

California is home to 4 major species of anadromous salmonids, steelhead or anadromous rainbow trout (*Oncorhynchus mykiss*), chinook salmon (*O. tshawytscha),* coho salmon (*O. kisutch*), and coastal cutthroat trout (*O. clarki clarki*) (Moyle 2000)[5]. Of these four species, only the steelhead and chinook salmon were found in significant numbers in the Sacramento-San Joaquin drainage. This watershed drains California's Central Valley, providing a wide range of habitat types to endemic and introduced fish species. Central Valley rivers and streams represent the southernmost limit for chinook salmon, and are close to the southernmost limit for steelhead (Moyle 2000). The variable climate, geology, and sheer size of the drainage led to the evolution of several distinct races or runs of chinook salmon and steelhead (USFWS 1998; Moyle 2000). Some of the differences between steelhead and chinook salmon populations were readily
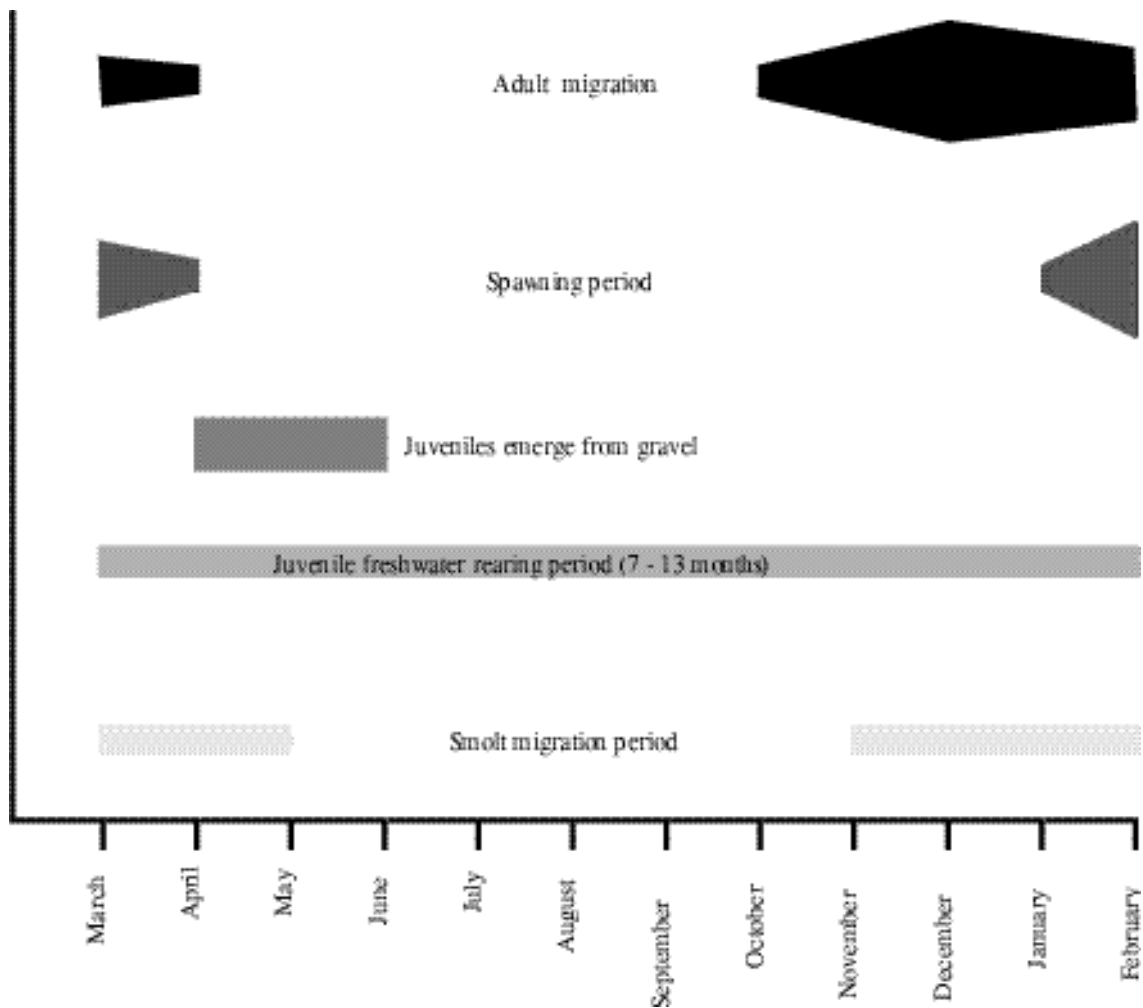

Figure I.1. Sacramento River late-fall run chinook salmon life history timing. Modified from Moyle (2000).

[5] Other species of anadromous salmonid occasionally seen in California include pink salmon (*O. gorbuscha*), chum ssalmon (*O. keta*), and sockeye salmon (*O. nerka*) Moyle (2000).
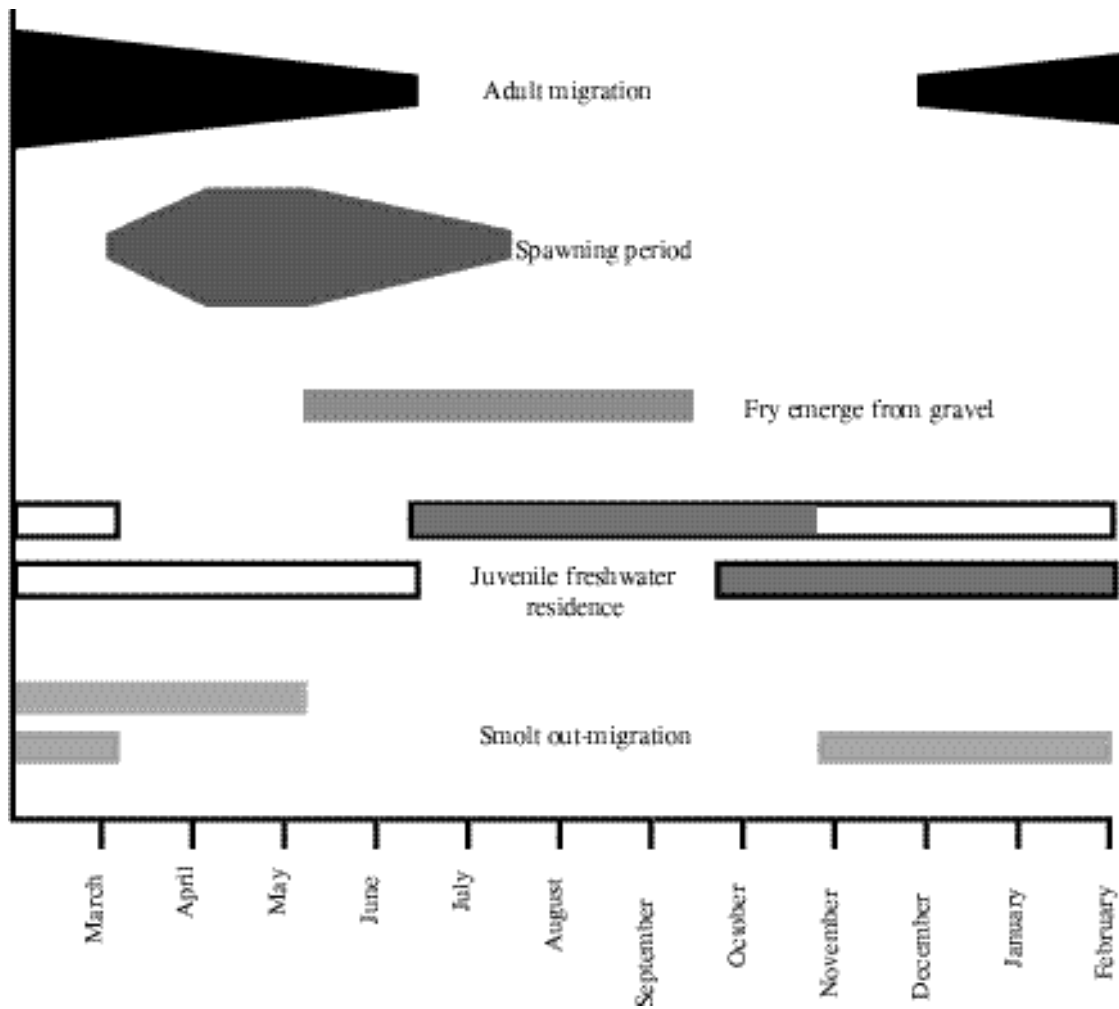
Figure I.2. Sacramento River winter-run chinook salmon life history timing. Modified from Moyle (2000).

apparent because of different morphologies or run timing. More recently, genetic analyses have led to more fine-scaled stock identification (Nielsen, et al. 1994b).

California's Central Valley is unique in that it supports 4 distinct runs of chinook salmon, one of which, the Sacramento winter-run chinook salmon, is found nowhere else. The other 3 runs, the Central Valley fall-run, late-fall run, and spring-run, have analogous runs in other systems. From a legislative standpoint, the Central Valley fall- and late-fall runs are grouped together into the Central Valley fall-run Evolutionarily Significant Unit (ESU); the Central Valley spring-run and the Sacramento River winter-run have their own ESUs.

Chinook salmon can be classified as either stream-type or ocean-type (Love 1996). Stream-type juveniles typically spend more than a year in freshwater; adults enter freshwater before completing sexual maturation. Ocean-type juveniles spend a short amount of time in freshwater (< 1 year); adults are sexually mature when they return to freshwater (Clarke, et al. 1992). Central Valley fall-run salmon are ocean-type, late-fall run are mostly stream-type, Sacramento River winter-run are intermediate (adults are immature when they enter the river,
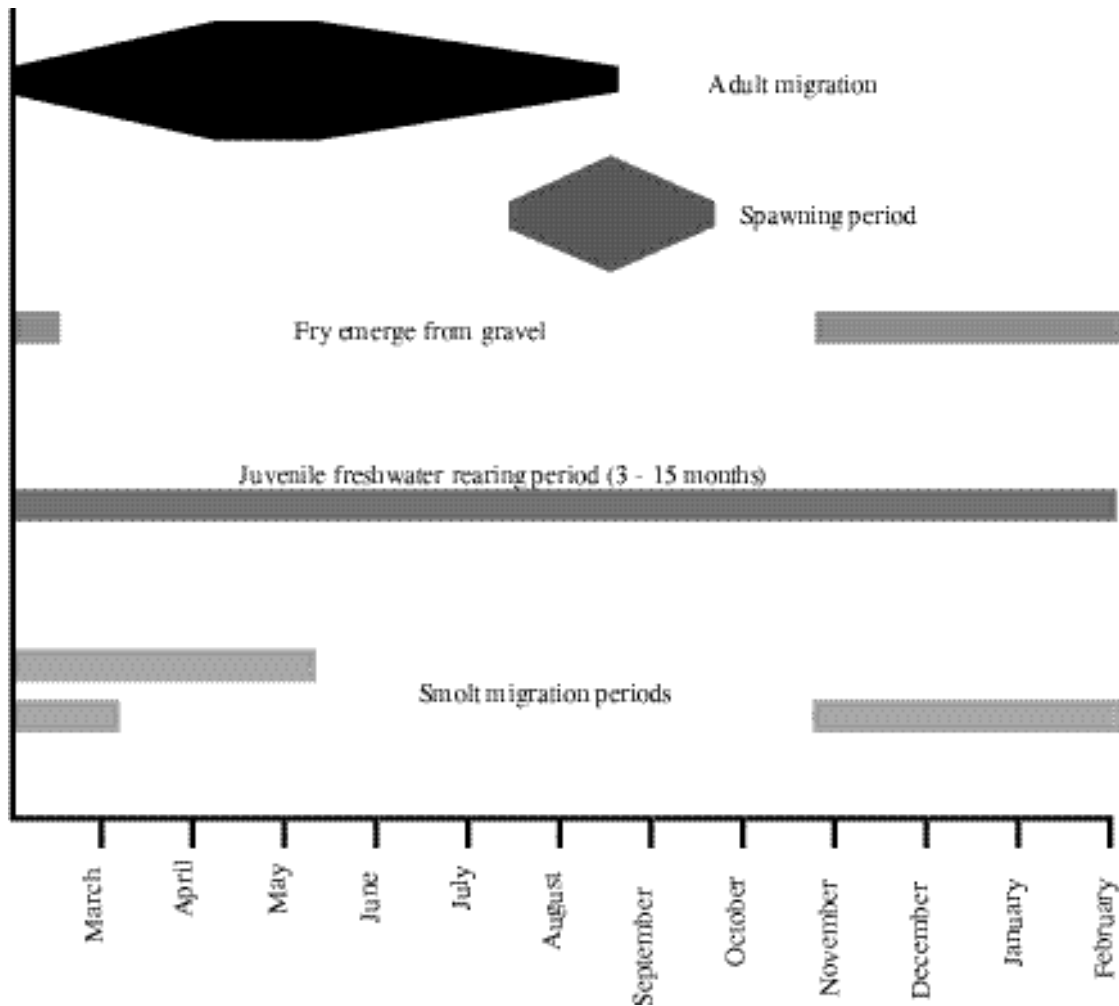
Figure I.3. Spring-run chinook salmon life history timing. Modified from Moyle (2000).

like stream-type salmon, but the juveniles behave more like ocean-type), and Central Valley spring-run are stream type (Yoshiyama, et al. 1998; Moyle 2000). The life-history strategy shown by a particular race is important because it determines the temperature range juveniles will be exposed to during their freshwater rearing period. Stream-type salmon will experience high summer temperatures and low winter temperatures before they emigrate to saltwater, while ocean-type salmon generally do not experience high summer water temperatures. The life-history timing of Central Valley chinook salmon races are summarized in Figures I.1 – I.4.

Rainbow trout and steelhead are the most widely distributed salmonid on the Pacific coast of North America (Love 1996; Moyle 2000). Historically, two subgroups of rainbow trout were found in California—the Sacramento-San Joaquin drainage redband trout and the coastal rainbow trout (this group includes steelhead and most resident rainbow trout in lower reaches of rivers within the drainage) (Behnke 1992). Extensive hatchery plants over the past two centuries have somewhat muddied this picture, although the diversity of California's rainbow trout populations remains high (Moyle 2000). The federally threatened steelhead native to the Central Valley belong to the Central Valley steelhead ESU (USFWS 1998), which also includes resident
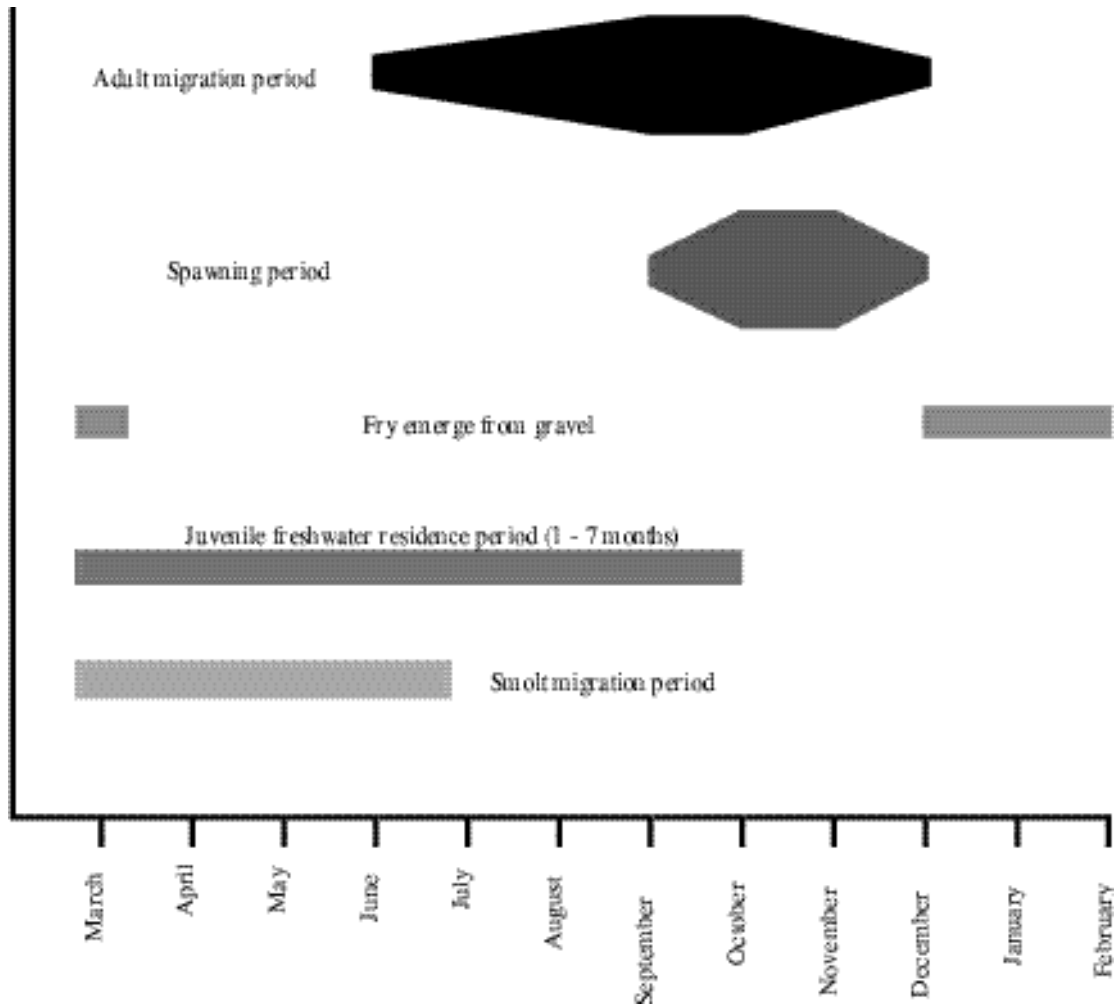
Figure I.4. Sacramento River fall-run chinook salmon life history timing. Modified from Moyle (2000)

non-hatchery rainbow trout. Central Valley drainages also contain hatchery steelhead derived from Eel River stock that are currently listed under the Northern California steelhead ESU (USFWS 1998; Moyle 2000).

Unlike Central Valley chinook salmon races, which show a wide range of life-history strategies, Central Valley steelhead are classified as winter-run fish, although they may enter freshwater as early as August (McEwan and Jackson 1996; Moyle 2000). The majority of adults enter freshwater during the high flows associated with fall and winter rains, and take advantage of these flows and low temperatures for spawning. Juvenile hatching and emergence times are a function of water temperature. Once they emerge from the gravel, steelhead parr remain in freshwater for 1 – 3 years before smolting and migrating to saltwater. Because of their extended freshwater residence time (compared to chinook salmon), steelhead may be more vulnerable to alterations of the natural thermal regime.

Native salmon and steelhead populations throughout the Pacific Northwest have undergone serious declines, resulting in the extinction of numerous runs (Yoshiyama, et al. 1998; Moyle 2000). Moyle (2000) lists 12 general reasons for the decline of salmon and steelhead

populations. The primary cause for the declines is the widespread construction of dams on rivers and streams used for spawning and freshwater rearing. These dams (1) are barriers to upstream and downstream migration (Giorgi, et al. 1997), (2) restrict salmon and steelhead in the Central Valley to   20% of their historical freshwater habitat (Moyle 2000), (3) alter flow and thermal regimes in the remnant portions of rivers below the dams, and, (4) alter the nutrient dynamics of the riverine ecosystems. Other reasons for the declines include overharvest in fresh- and saltwater fisheries, entrainment of juveniles in water diversions, loss of habitat, enhanced predation, increased incidence of disease, pollution, competition from hatchery fish and introduced species, and, habitat degradation (Moyle 2000).

The purpose of this review is to summarize the body of knowledge on the effects of water temperature on chinook salmon and steelhead biology, with an emphasis on physiological processes. A number of the factors listed above, including dam construction, thermal pollution, and habitat degradation, can directly alter instream water temperatures, thereby directly affecting native salmonids. Other factors, such as predation, disease, and competition are themselves affected by temperature. We attempt to summarize the body of knowledge of temperature effects on chinook salmon and steelhead, with an emphasis on Central Valley stocks. Where there are few data, information on other stocks has been used. S.I. units have been used throughout this review, but a conversion table for degrees Celsius to degrees Fahrenheit is included below (Table I.1).

Temperature			
Degrees Celcius (°C)	Degrees Fahrenheit (°F)	Degrees Celcius (°C)	Degrees Fahrenheit (°F)
0.0	32.0	18.0	64.4
1.0	33.8	19.0	66.2
2.0	35.6	20.0	68.0
3.0	37.4	21.0	69.8
4.0	39.2	22.0	71.6
5.0	41.0	23.0	73.4
6.0	42.8	24.0	75.2
7.0	44.6	25.0	77.0
8.0	46.4	26.0	78.8
9.0	48.2	27.0	80.6
10.0	50.0	28.0	82.4
11.0	51.8	29.0	84.2
12.0	53.6	30.0	86.0
13.0	55.4	31.0	87.8
14.0	57.2	32.0	89.6
15.0	59.0	33.0	91.4
16.0	60.8	34.0	93.2
17.0	62.6	35.0	95.0

Table I.1. Temperature conversion table.

THERMAL TOLERANCE

Introduction

California's Central Valley is located at the extreme southern limit of chinook salmon distribution and near the steelhead trout's southern limit, so temperature regimes experienced by resident populations may be dissimilar to those of more northern drainages. In particular, low water temperatures ($< 5°C$) are rarely of concern in the Sacramento – San Joaquin system because of the low frequency of periods of extreme cold in areas used by salmonids. However, because of the regular occurrence of temperatures exceeding $20°C$ in parts of the system, warm water temperatures are a critical management issue. Water temperatures in the lower Sacramento R. mainstem regularly exceed $20°C$ by late spring (City of Sacramento water treatment plant, unpublished data); and statistical studies of coded-wire-tagged juvenile chinook show that high temperatures are an important factor in mortality (Baker et al. 1995).

Direct evaluations of thermal tolerance in fishes use death or loss of equilibrium as the endpoint (Becker and Genoway 1979). These studies fall into one of two broad classes—those that place fish in water of changing temperature that continues to increase or decrease until the endpoint is reached and those that hold the fish at a constant temperature. In the former case, further subdivision is possible on the basis of the duration of exposure to each temperature. Rapid rates of change ($\Delta T > 1°C\ h^{-1}$) are used in critical thermal maximum (CT_{Max}) or minimum (CT_{Min}) tolerance studies (Becker and Genoway 1979). Rates of temperature change used in these studies (ca. $0.33°C\ min^{-1}$) are rarely encountered in field situations with the notable exception of cooling water discharges (Orsi 1971). Critical thermal tolerance studies are useful for detecting differences in thermal tolerance caused by a number of factors including species, or race (Grande and Andersen 1991), stress (Strange, et al. 1993), acclimation temperature (Konecki, et al. 1995a), water quality (Gunn 1986), and pollutants (Roch and Maly 1979).

Studies that use slower rates of change ($\Delta T \leq 1°C\ h^{-1}$) are used to determine the incipient lethal temperatures (ILT) (Kaya 1978). Rates of thermal flux in these studies (ca. $\Delta T = 1°C\ d^{-1}$) are more ecologically relevant as they closely match rates observed in field situations.

Thermal tolerance may also be evaluated in studies where the fish are held under a fixed thermal regime (either a constant or cyclically fluctuating temperatures) (Hokanson, et al. 1977; Myrick and Cech 2000a). These studies are useful for: (1) determining survival times at a given temperature; (2) determining the effects of temperature on eggs and embryos that cannot be used in CTM- or ILT-type studies, and; (3) for observing chronic lethal or sublethal thermal effects. In the latter case, thermal tolerance observations are often made concurrently with other experiments, such as a feeding trial or growth study (Rich 1987; Myrick and Cech 2000a). Studies of all three types have been conducted on chinook salmon and steelhead (or rainbow trout) at life stages from eggs to adults.

Regardless of protocol, data collected in all thermal tolerance studies are affected by thermal acclimation effects. Thermal acclimation is a short-term physiological adaptation to a chronic change in environmental temperature. Fish that are acclimated to higher temperatures typically exhibit higher thermal tolerances than fish acclimated to cooler temperatures (Becker and Genoway 1979; Threader and Houston 1983). Thermal acclimation is not an instantaneous

process—estimates of the minimum time required for acclimation to occur range from days to weeks. The physiological and biochemical principles underlying thermal acclimation are not well understood, but may include the production of heat shock proteins. Heat shock proteins (HSPs) are produced by most organisms that experience stress (e.g., thermal, chemical, etc.), and serve to prevent and/or repair damage to cellular proteins.

Egg and Alevin Thermal Tolerance

Egg and alevin thermal tolerances are normally tested using a modification of the third method described above. Eggs and/or alevins are held at constant temperatures or thermal regimes to determine the effects of temperature on hatching success (eggs) (Healey 1979) and the transition from alevins to swim-up fry (Olson and Foster 1957; USFWS 1999)].

Chinook salmon

Chinook salmon eggs can survive constant temperatures between 1.7°C (Combs and Burrows 1957) and 16.7°C (USFWS 1999) with significant mortality at either extreme (Figure TT.1). Embryo development time is a function of water temperature, with faster development (shorter times to hatch) seen at elevated temperatures (Figure TT.2). The average time to
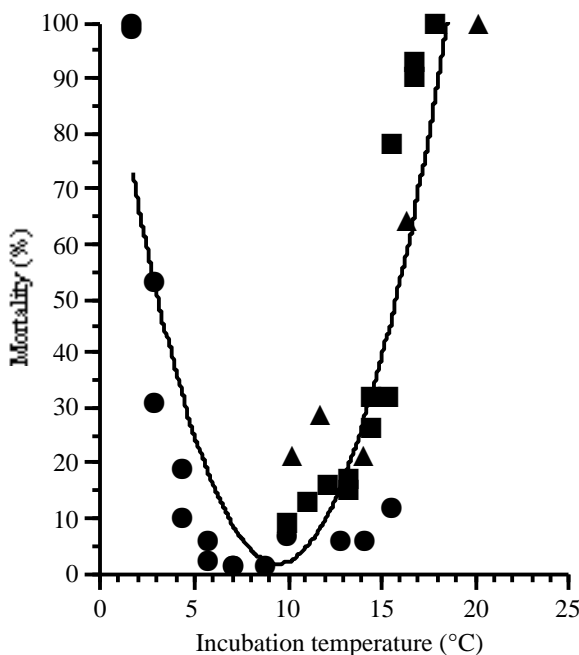
Figure TT.1. Effects of incubation temperature on mortality of chinook salmon eggs. Data are from Combs and Burrows (1957) (solid circles), USFWS (1999) (solid squares), and Jensen and Groot (1991) (solid triangles).

Figure TT.2. Models of hatching times of chinook salmon eggs at different temperatures (model 1b = open squares; model 3 = open circles). Data are from Crisp (1981).

hatching for chinook salmon eggs can be predicted (97% accuracy or better) using simple models (Crisp 1981; Beacham and Murray 1990).

Slater (1963) reported that Sacramento R. winter–run eggs are limited to 5.6 to 14°C. Although extremely cold (< 5°C) water temperatures are rarely recorded in the Sacramento R. mainstem, it is possible that eggs located in shallow redds or in tributari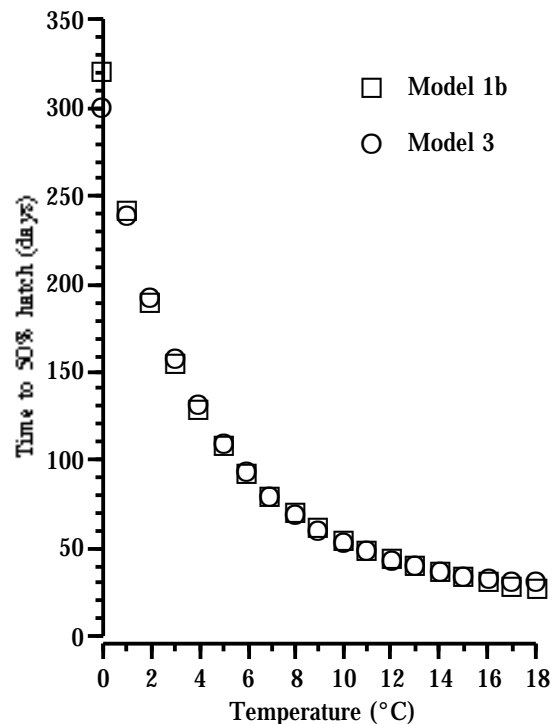es may experience such temperatures under unusual conditions. Combs and Burrows (1957) found that eggs taken from Entiat and Skagit River (OR) chinook salmon suffered 100% mortality when incubated at a constant 1.7°C but that mortality rapidly decreased as the incubation temperature was increased (Figure TT.1). Between 5.8°C and 14.2°C, mortality was minimal.

Sacramento-San Joaquin R. temperatures may approach lethal levels during the incubation of chinook salmon eggs, especially those of the winter and spring runs and, to a lesser extent, the late–fall run (Vogel and Marine 1991). Fall-run eggs incubating between October and March are less likely to encounter water temperatures above 14°C, except at the start of the spawning season, when temperatures may still be above this point. American River (CA) chinook salmon eggs incubated in water above 16.7°C experienced 100% mortality before the eyed stage but that mortality decreased with decreasing incubation temperature (Hinze 1959). Healey (1979) found that Sacramento R. fall run eggs had greater than 82% mortality at temperatures higher than 13.9°C. In addition to the high egg mortality seen, Healey also found that post-hatching mortality was higher at warmer temperatures. Healey concluded that Sacramento R. fall-run eggs are no more tolerant of high water temperatures than more northern chinook races.

The US Fish and Wildlife Service (USFWS) conducted the most recent study on Sacramento R. fall and winter-run chinook salmon egg thermal tolerance. Fall-run mortality in the 11.1 to 13.3°C range was not significant, but increased over the 12.2 to 15.6°C range and increased again at 16.7°C (USFWS 1999). Sacramento R. winter-run eggs experienced increased mortality as water temperature increased from 13.3 to 17.8°C. In concurrence with Healey (1979), higher post-hatching mortality was also observed in this study for both fall- and winter-run races (USFWS 1999). The study recommends that water temperatures between the Bend Bridge and Keswick Dam (Sacramento R.) not exceed 13.3°C during the incubation period to prevent excessive mortality among developing winter-run eggs. Interestingly, the study suggests that winter-run eggs and fry may be slightly more tolerant of elevated temperatures than fall-run. Because data from studies on northern chinook salmon races generally agree with those from California, it appears unlikely that there is much variation among races with regards to egg thermal tolerance.
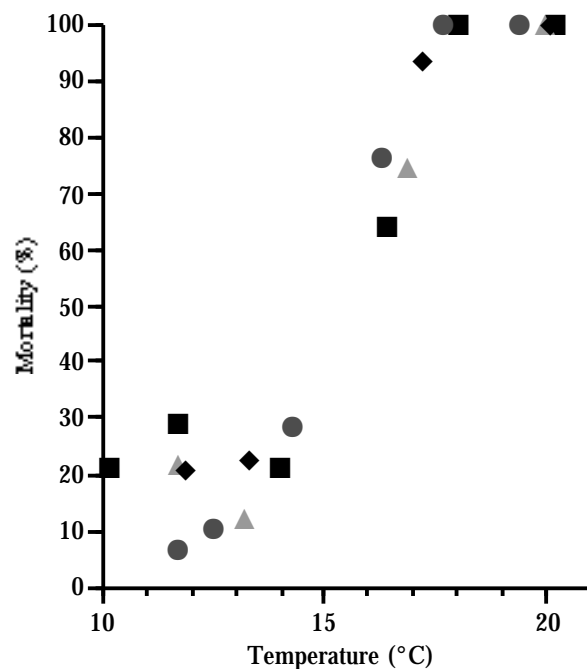

Figure TT.3. Effects of temperature and length of dewatering periods (100% immersed = solid squares; 8.3% immersed = solid circles; 4.2% immersed = solid triangles; 2.1% immersed = solid diamonds) on chinook salmon egg mortality. Data are from Jensen and Groot (1991).

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River temperatures are rarely constant during the incubation period, therefore it is important to consider the effects of increases or decreases in water temperature. Combs (1965) found that Entiat River (OR) chinook salmon eggs incubated at 5.8°C could withstand subsequent rearing at 1.7°C provided they had reached the 128-cell stage at 5.8°C. Shorter incubation times at 5.8°C led to increased mortality, with 92% mortality for eggs that were incubated at 5.8°C for 0 days. Sacramento R. fall- and winter-run eggs exposed to increased temperatures during the incubation period also showed increased mortality compared to eggs held at constant temperatures (USFWS 1999).
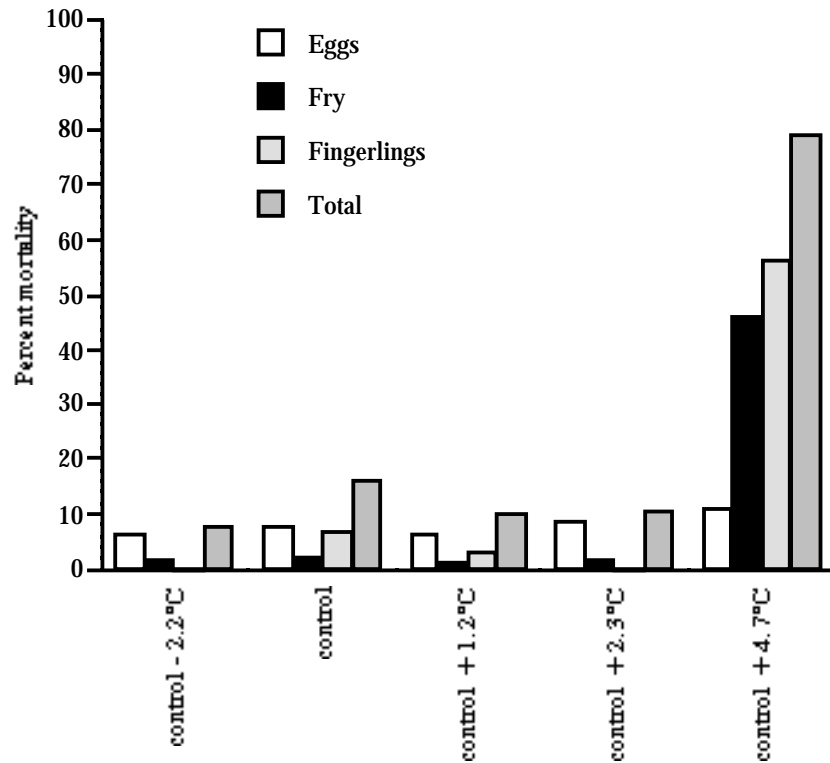

Figure TT.4. Mortalities of Columbia river chinook salmon exposed to different temperature conditions. Data are from Olson and Foster 1957.

Olson and Foster (1957) studied the effects of declining temperatures on the survival of egg and larval chinook from the Columbia River. They exposed the eggs to initial temperatures of 11.6, 13.8 (control), 15, 16.1, and 18.5°C and maintained the temperature differences as control water temperatures dropped to 3°C during the winter. Olson and Foster reported no significant difference in mortality except in the control + 4.7°C treatment (Figure TT.4). Although egg mortality in this treatment was low, high fry and fingerling mortality (45.9 and 56.4%, respectively) contributed to the overall 79% mortality. This study is relevant to Sacramento R. chinook salmon, especially fall- and spring-run races that may spawn before water temperatures decrease.

An aspect of egg thermal tolerance that may have application to the Sacramento-San Joaquin system is that of eggs in dewatered redds. Redd dewatering may occur during demand- or weather-driven flow alterations. Chinook salmon eggs can withstand being dewatered for periods up to 24-h provided the eggs remain moist (Jensen and Groot 1991). Jensen and Groot (1991) studied the effects of incubation temperature and dewatering interval on eggs from Big Qualicum R. chinook salmon. They reported significant egg mortality at temperatures higher than 14.3°C, with complete mortality at temperatures above 17.4°C (Figure TT.3). Surprisingly, temperatures below 14°C and length of air exposure did not affect egg mortality.
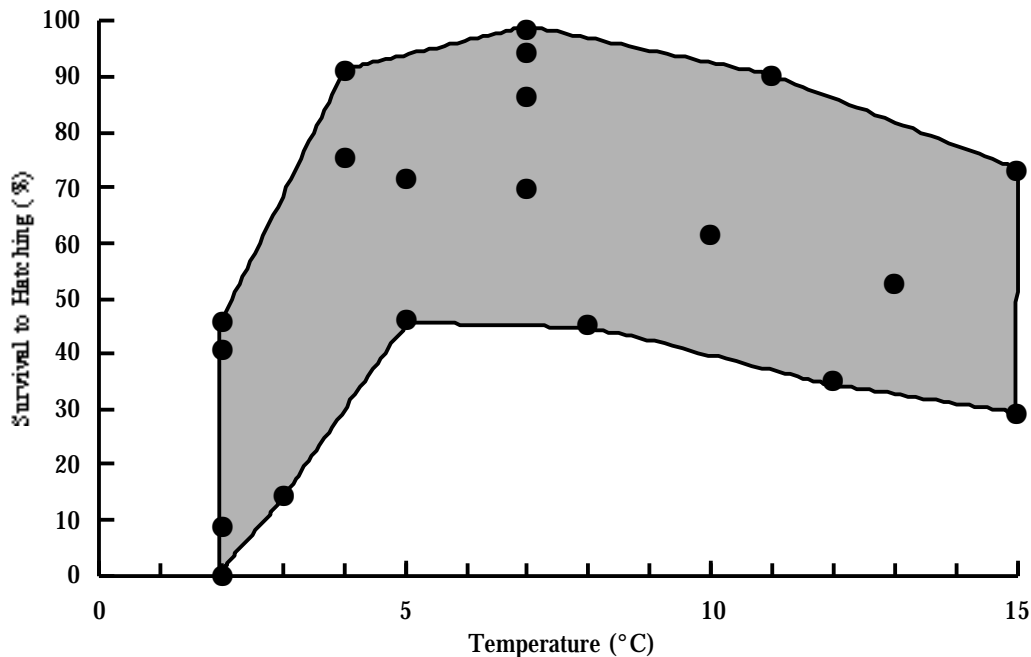
Figure TT.5. Effect of incubation temperature on the survival to hatching of steelhead and rainbow trout eggs and embryos.

Steelhead

As with chinook salmon, steelhead eggs and embryos are more vulnerable to temperature than later life stages. The initial egg incubation temperature is a function of the spawning temperature. Orcutt et al. (1968) reported that steelhead spawning in late spring in the Clearwater and Salmon Rivers (Idaho) did so at temperatures between 2 and 8°C.

Until recently, surprisingly little was published on the effects of temperature on steelhead (or rainbow trout) egg survival and development rates. Embody's (1934) pioneering research established guidelines for artificial rearing that are still used today. Subsequent studies have increased our knowledge of temperature effects on both survival and egg hatching times. Steelhead and rainbow trout egg survival is low at low temperatures (< 5°C) and increases rapidly to a maximum around 7 – 10°C before declining as the temperature increases past 10°C.

The wide variation seen in Figure TT.5 is a function of strain-level variation in egg temperature tolerance. If the data are shown as individual studies (Figure TT.6), it is apparent that different strains show different levels of tolerance for both low and high temperatures. Timoshina (1972), working on Asian rainbow trout (likely derived from Kamchatka steelhead), reported 55% mortality for eggs reared at 2°C. Mortality fell to a low of 29 – 31% between 5 and 7°C and then increased. (Figure TT.6).

Stonecypher et al. (1994) compared survival and development rates of Eagle Lake (spring spawning) and Hot Creek (fall spawning) strains of rainbow trout. Eagle Lake strain were more tolerant of low temperatures than the Hot Creek strain. This finding may have far-reaching implications, as it clearly shows that steelhead and rainbow trout with different life-history
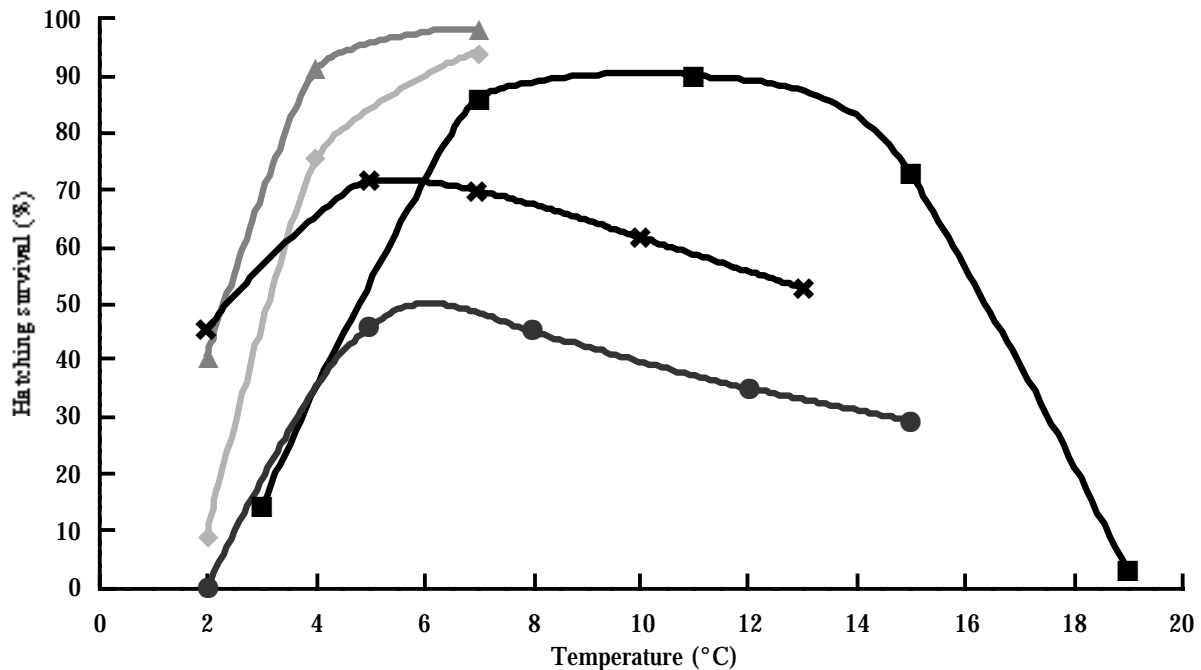
Figure TT.6. Strain-level differences in the effect of incubation temperature on steelhead and rainbow trout egg survival to hatching. 1983 (squares) and 1984 (circles) data are from Humpesch (1985); Eagle Lake (triangles) and Hot Creek (diamonds) data are from Stonecypher et al. (1994), and Asian (crosses) data are from Timoshina (1972).

strategies (or from different drainages) are likely to show different levels of thermal tolerance at the egg and embryo stages.

Water temperature determines steelhead egg and embryo development rates (McLean, et al. 1991). Again, surprisingly few published studies on the effects of temperature on the development rate of steelhead and rainbow trout eggs exist. The observed pattern is that as water temperature increases, time to hatching (incubation or development time) decreases (Figure TT.7). The increased development rate is due to the increased metabolism of the embryo at higher temperatures. The average time to hatching for steelhead and rainbow trout eggs can be predicted reliably (97% accuracy or better) using simple models (Crisp 1981; Humpesch 1985; Crisp 1988; McLean, et al. 1991). Crisp (1981) used data from five salmonid species, including chinook salmon and rainbow trout, to develop 2 models for predicting the relationship between temperature and hatching time.
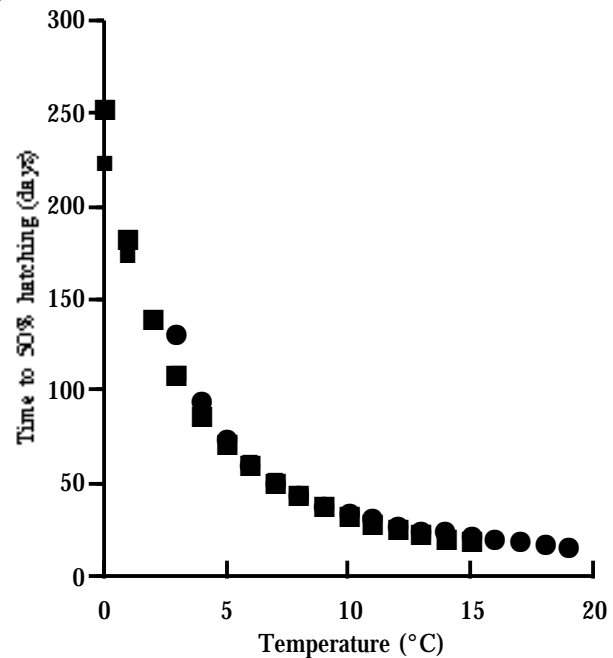

Figure TT.7. Effect of constant incubation temperature on rainbow trout and steelhead egg hatching times. Data are from Crisp (1981) (squares) and Humpesch (1985) (circles).

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Model 1b: $\log_{10}D = \log_{10}a + b\log_{10}(T - \text{ })$ (power law with temperature correction model)

Model 3b: $\log_{10}D = \log_{10}a + bT + b_1T^2$ (quadratic model)

where D = the number of days to 50% hatching, T = the temperature in degrees Celsius, = temperature correction in degrees Celsius, and a, b, and b_1 are constants. Both of Crisp's models account for 97% of the observed variation, though Model 1b is favored for its simplicity. Humpesch's (1985) model: $D = aT^b$ accounts for 98% of the observed variation. Both Humpesch and Crisp point out that their models lose accuracy at very low temperatures (< 5°C). Additionally, in agreement with Embody (1934), they noted that significant variation in hatching times can be introduced by differences among eggs from the same individual (up to 20 days difference at low temperatures), and by differences between adults from the same strain (2.3 – 4.3%).

Acute lethal effects of temperature on salmonid eggs are well known from a handful of studies, but sub-lethal effects are not as well known. Timoshina (1972) noted that sac-fry hatching from eggs incubated at 5 and 7°C were larger and more active than those hatched at 2°C and at temperatures > 7°C. This temperature effect has been reported for other salmonids, including Atlantic salmon (*Salmo salar*) (Peterson, et al. 1977) and Pacific salmon (*Oncorhynchus spp.*) (Murray and McPhail 1988). Faster development rates do result from higher temperatures, but the higher metabolic rates (Rombough 1988) lead to a more rapid exhaustion of energy stores and reduced partitioning of available energy to growth.

Additionally, there is an increase in deformities (e.g. lordosis) at the higher temperatures (Myrick and Cech, unpublished data). The ecological result of this is that eggs that develop at higher temperatures will produce fry that are smaller and therefore more susceptible to gape-limited predation and displacement during inter- and intraspecific territorial interactions (Pettersson, et al. 1996; Cutts, et al. 1998).

Juvenile thermal tolerance

Unlike salmonid eggs and larvae, which are extremely stenothermal (narrow thermal range), juvenile salmonids (fry, parr, smolts) are only moderately stenothermal. Acute and chronic elevated temperatures are more of a concern for chinook salmon and steelhead in the Sacramento-San Joaquin system than are low water temperatures. Temperatures in some of the small tributaries used by juvenile salmonids are unregulated (Moore 1997), but temperatures in the mainstems (lower Sacramento, Feather,
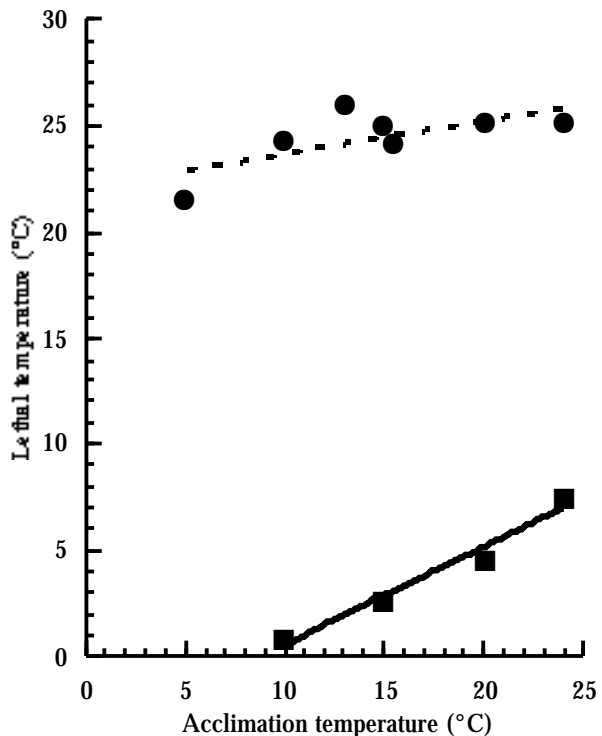

Figure TT.8. Upper (dashed line) and lower (solid line) incipient lethal temperatures for juvenile chinook salmon. Data are from Brett (1952), Hanson (1991) and Orsi 1971).

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American, and San Joaquin R.) can be regulated to some degree through reservoir releases (NBS 1995; McEwan and Jackson 1996). It is crucial to know what the maximum and minimum allowable temperatures are for survival of juvenile salmonids to properly manage water temperatures in these reaches. This information is also needed in order to determine the spatial and temporal boundaries of juvenile rearing habitats.

Juvenile chinook salmon are moderately stenothermal (Brett 1952). Chinook salmon from the Dungeness hatchery (WA) tolerated temperatures as low as 0.8°C (ILLT) when acclimated to 10°C (Figure TT.8). The ILLT increased to a maximum of 7.4°C for salmon acclimated to 24°C (Brett 1952), showing the effects of thermal acclimation. Brett (1952) found that the smaller juvenile salmon were less tolerant of low temperatures than larger juveniles. No data on the incipient lower lethal limit for California races of chinook salmon are available, though it is likely that they exhibit similar tolerance levels.

Upper incipient lethal limits for chinook salmon range from 21.5°C for a WA race acclimated to 5°C (Brett 1952) to 26°C for Feather River (CA) salmon acclimated to 13°C at the Mokelumne R. Fish Facility (Hanson 1991) (Figure TT.8). Brett (1952) reported that a positive thermal acclimation effect was present as the acclimation temperature increased from 5 to 15°C. At acclimation temperatures above 15°C, no further increase in IULT was observed. Hanson (1991) found that an increase in acclimation temperature from 12 to 18°C resulted in a 2.7–fold increase in median resistance time. These studies demonstrated that there was a physiological maximum temperature that further increases in acclimation temperature will not alter, and that those acclimation temperature increases may confer increased temporal resistance.

Chinook salmon subjected to acute temperature changes can tolerate temperatures as high as 28.8°C when acclimated to 19°C (Cech and Myrick 1999). Their ability to tolerate temperatures higher than the IULT is a function of exposure time, with an inverse relationship between exposure time and tolerated temperature. Chinook salmon chronic (> 7 days) upper thermal tolerance limits are remarkably similar to the IULT values discussed above (Table TT.1). Brett (1952) and Brett et al. (1982) found that the chronic upper thermal limit fell between 24.7 and 25.1°C for northern (WA and BC) chinook salmon races.

In experiments by Rich (1987), American R. (CA) chinook salmon died after being held at 24°C for more than 8 days in river water. This temperature is lower than that tolerated by some northern stocks. Rich's result may stem from the effects of near–lethal temperatures, water chemistry/quality, and/or disease. Marine (1997) was able to rear Sacramento R. fall-run

Strain (Source)	Acclimation temperature (°C)	Duration (days)	Thermal limits (°C)		Source
			Lower	Upper	
Dungeness Hatchery (WA)	24	7	–	25.1	Brett 1952
Dungeness Hatchery (WA)	20	7	–	25	Brett 1952
Big Qualicum R. (BC)	20	7	–	24.7	Brett et al. 1982
American R. (CA)	?	8	–	24	Rich 1987

Table TT.1. Chronically lethal temperatures for juvenile chinook salmon.

chinook salmon in well water at 21 - 24°C without significant mortality.

Steelhead

The ability to resist or tolerate elevated temperatures is a function of exposure time . Bidgood (1969) conclusively demonstrated this effect with juvenile rainbow trout from 4 anadromous Great Lakes populations (Figure TT.9). This relationship is also evident when one studies the CTM and ILT data available for various strains of steelhead and rainbow trout (Table TT.2).

Under acute conditions, steelhead CT_{Max} range from 27.7°C for American R. steelhead acclimated to 11°C to a maximum of 29.6°C for American R. steelhead acclimated to 19°C (Table TT.2). Because of the similarity between steelhead and resident rainbow trout thermal tolerances, data for various strains of resident rainbow trout are also included in Table TT.2. The CT_{Max} was 32°C for Eagle Lake rainbow trout acclimated to 25°(Myrick and Cech 2000b). Myrick and Cech (2000a) reported an interesting finding on wild steelhead from the Feather R. (CA). Although recorded temperatures in the river rarely exceeded 20°C, these steelhead displayed a critical thermal maxima approaching that of 22°C-acclimated Mt. Shasta and Eagle Lake rainbow trout Myrick (2000b). This suggests that wild fish may tolerate higher temperatures than hatchery fish, even when acclimated to lower temperatures. Few data have been published on the lower lethal limits for steelhead and rainbow trout. Rainbow trout acclimated to temperatures of 10°C tolerated temperatures of 0°C (Becker and Genoway 1979; Currie and Tufts 1997), while those acclimated to 15 and 20°C had CT_{Min} that were slightly higher.
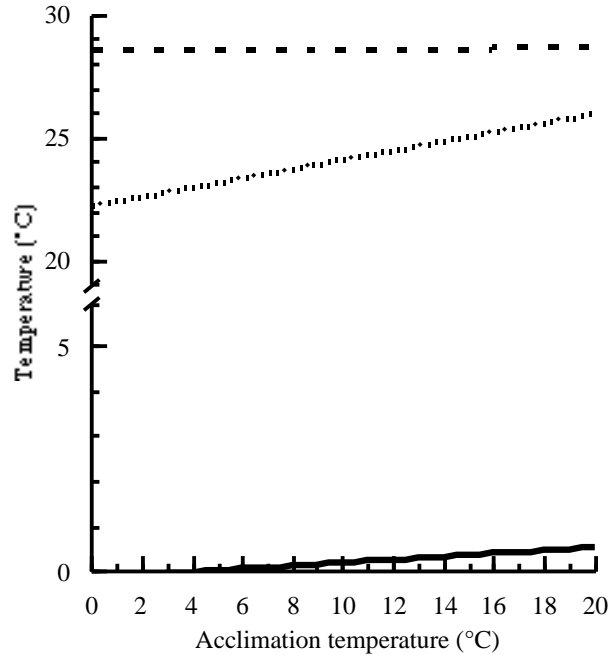

Figure TT.9. Lower (CT_{Min} = solid line) and upper (IULT = dotted line; CT_{Max} = dashed line) thermal tolerance of juvenile steelhead at different acclimation temperatures.

Strain	Acclimation temperature (°C)	Thermal limits (°C)		Source
(Source)		Lower	Upper	
Crystal Lake Fish Hatchery (MO)	10	0	28	Currie et al. (1998)
Hatchery	10	–	28.5	Lee and Rinne (1980)
Eagle Lake rainbow trout (Mt. Shasta hatchery)	10	–	27.6	Myrick and Cech (2000)
Mt. Shasta rainbow trout (Mt. Shasta Hatchery)	10	–	27.7	Myrick and Cech (2000)
American R. Nimbus Hatchery (CA)	11	–	27.5	Cech and Myrick (1999)
Eagle Lake rainbow trout (Mt. Shasta hatchery)	14	–	28.6	Myrick and Cech (2000)
Mt. Shasta rainbow trout (Mt. Shasta Hatchery)	14	–	28.4	Myrick and Cech (2000)
American R. Nimbus Hatchery (CA)	15	–	28.4	Cech and Myrick (1999)
Crystal Lake Fish Hatchery (MO)	15	0.2	29.1	Currie et al. (1998)
Hatchery	15	–	29.4	Strange et al. (1993)
American R. Nimbus Hatchery (CA)	19	–	29.6	Cech and Myrick (1999)
Eagle Lake rainbow trout (Mt. Shasta hatchery)	19	–	30.1	Myrick and Cech (2000)
Mt. Shasta rainbow trout (Mt. Shasta Hatchery)	19	–	29.7	Myrick and Cech (2000)
Crystal Lake Fish Hatchery (MO)	20	2	29.8	Currie et al. (1998)
Hatchery	20	–	29.4	Lee and Rinne (1980)
Eagle Lake rainbow trout (Mt. Shasta hatchery)	22	–	31	Myrick and Cech (2000)
Mt. Shasta rainbow trout (Mt. Shasta Hatchery)	22	–	30.7	Myrick and Cech (2000)
Eagle Lake rainbow trout (Mt. Shasta hatchery)	25	–	32	Myrick and Cech (2000)
Mt. Shasta rainbow trout (Mt. Shasta Hatchery)	25	–	31.5	Myrick and Cech (2000)
Feather R. Hatchery (CA)	16 ± 0.1	–	29.4	Myrick and Cech (2000)
Feather R. Hatchery (CA)	16 ± 2.0	–	29.4	Myrick and Cech (2000)
Feather R. (CA)	natural	–	30.8	Myrick and Cech (2000)

Table TT.2. Critical thermal maxima and minima of rainbow trout and steelhead acclimated to various temperatures.

Steelhead chronic lethal limits are lower than their critical thermal limits. Rainbow trout IULTs range between 22.8 and 25.9°C, depending on the acclimation temperature (Threader and Houston 1983) (Table TT.3). Figure TT.9, based on Bidgood's (1969) data, shows the effect of exposure time on the ability of rainbow trout to tolerate elevated temperatures. At the

approximate cutoff for chronic values (24 h or greater), the four populations Bidgood examined tolerated temperatures between 24 and 26°C for a 24 h period.

Summary

Eggs from Sacramento-San Joaquin R. chinook salmon races do not appear to be more tolerant of high temperatures than more northern races. Although data on their tolerance of low water temperatures are unavailable, it is likely that these would be similar to those of northern races. Water temperatures between 4 and 12°C produce the lowest levels of mortality; eggs survive temperatures between 1.7 and 16.7°C, but mortality is greatly increased at the temperature extremes. Significant post-hatching mortality resulting from increases in water temperature during incubation is possible. Finally, eggs in redds that are dewatered for   24 h are equally susceptible to temperature as those that remain fully submerged.

Figure TT.10. Thermal resistance times for 4 runs of Great Lakes rainbow trout (solid = North Ck.; dotted = Wilmot Ck.; dot-dashed = Nottawasaga R.; dashed = Speckled Trout Ck.). Data are from Bidgood (1969).

Steelhead and rainbow trout eggs are stenothermal, with highest survival rates between 5 and 10°C, but published data show considerable variation among strains They can tolerate temperatures as low as 2°C or as high as 15°C but are subject to increased mortality. Time to hatching is inversely related to temperature, but as the temperature increases past the optimal range, there is a reduction in alevin size. Because of the presence of strain- and individual-level variation in thermal tolerance and development rate, we strongly suggest that the use of strain-specific data be emphasized to increase management success.

The available data suggest that the chronic upper lethal limit for juvenile Central Valley chinook salmon is approximately 25°C, with higher temperatures (up to approximately 29°C) as the acute lethal limits, in high-quality (e.g., air-saturated dissolved oxygen levels) water. Central Valley chinook salmon, despite their southern distribution, do not appear to display greater tolerance of elevated temperatures than more northern races, with the possible exception of San Joaquin spring-run (Clark 1943) and Butte Creek populations.

There are two major factors to consider with regards to thermal tolerance. First, chinook salmon, like steelhead (Nielsen, et al. 1994a), coho salmon (Konecki, et al. 1995b) and other salmonids will actively try to avoid unsuitable temperatures through behavioral thermoregulation (movement to more suitable temperatures). This behavior allows them to exploit seasonally suitable habitats, such as small tributaries that exceed 23°C during the summer (Maslin, et al. 1997). Second, numerous authors have pointed out that temperatures above the optimum yet
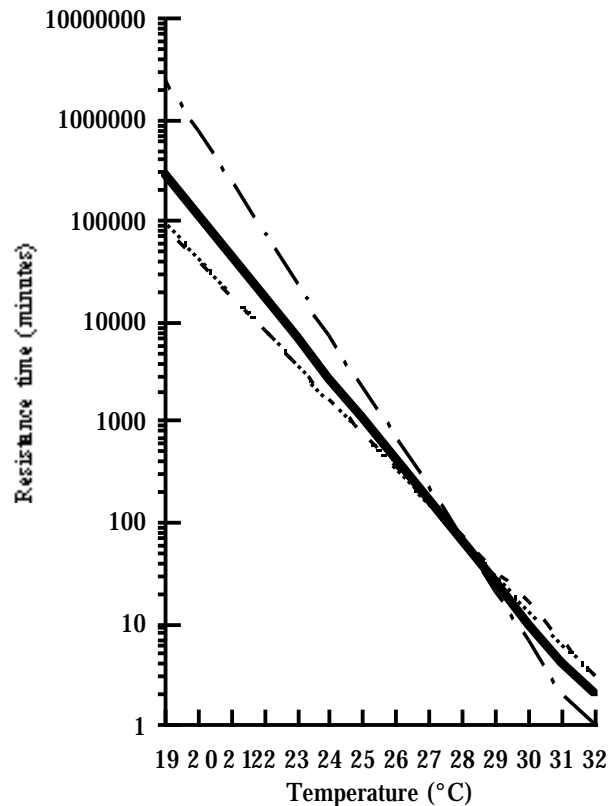
below lethal levels can have detrimental effects on juvenile salmon physiology, ecology, and behavior. Sublethal temperatures are known to reduce growth rates (Brett, et al. 1982; Marine 1997), increase vulnerability to predation (Coutant 1973; Marine 1997) and increase the risk of disease. These topics are discussed in other sections.

THERMAL PREFERENCE

Introduction

Most fish cannot physiologically regulate their internal temperature as a direct result of their circulatory, respiratory and muscular structure (Dewar, et al. 1994). However, fish can regulate their internal temperature through behavioral thermoregulation. Behavioral thermoregulation takes advantage of thermally heterogeneous environments (Nevermann and Wurtsbaugh 1994; Brio 1998).

Many behavioral thermoregulation studies have been conducted in lentic (lake) systems, especially those that thermally stratify (Brio 1998). Behavioral thermoregulation allows fish like brook charr (*Salvelinus fontinalis*) and Bear Lake sculpin (*Cottus extensus*) to realize bioenergetic advantages and survive periods of stressful temperatures (Nevermann and Wurtsbaugh 1994; Brio 1998).

Fish in lotic systems (streams and rivers) also use behavioral thermoregulation (Konecki, et al. 1995b). Though lotic systems may appear thermally homogenous, this is rarely the case. More typically, they are thermally heterogeneous, with temperature gradients created by groundwater inflows (Torgersen, et al. 1999), thermal stratification in deep pools (Nielsen, et al. 1994a), surface water inflows (Baltz, et al. 1987), and shading by streamside vegetation (Mundahl 1990). Fish are capable of detecting minute temperature differences and can locate thermal refuges in these systems [Matthews, 1997 #1774].

Salmonid thermal preference can be measured in laboratory or field studies. Both are valuable tools for management and modeling purposes. Laboratory thermal preference studies allow the isolation of the thermal preference response to variables like feeding state (Javaid and Anderson 1967), ontogeny (Shrode, et al. 1983), and acclimation temperature (Konecki, et al. 1995b). Results from such studies may not have direct application to field situations, but are needed for bioenergetic models to allow accurate predictions of a fish's thermal preference under certain conditions. Field observations of thermal preference are an integrative measure of the effects of both abiotic (e.g., temperature, water depth) and biotic (e.g., feeding state, predation risk, etc.) variables. Although there are often large differences between laboratory and field measurements of thermal preference (Myrick and Cech 2000a), simultaneous measurements are invaluable for identifying
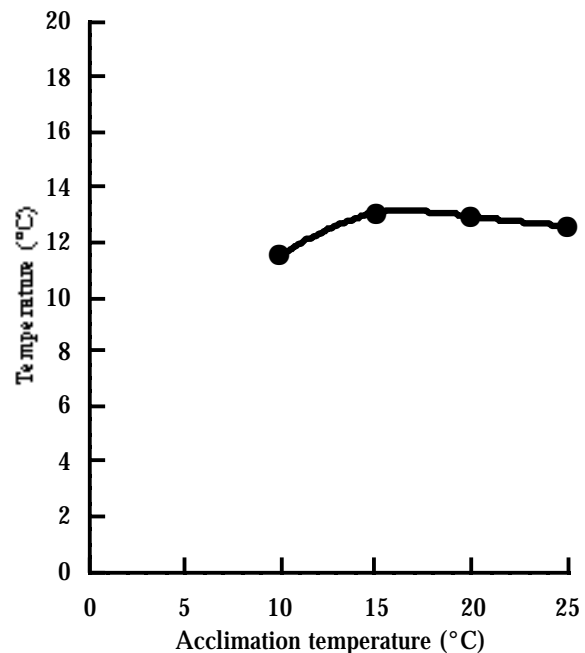

Figure TP.1. Thermal preference of juvenile spring-run chinook salmon. Data are from Brett (1952).

cause-and-effect relationships between observed fish distributions and other variables (e.g., predation risk).

Accurately measuring thermal preference under laboratory conditions involves the use of either a shuttlebox mechanism (Konecki, et al. 1995b) or thermal gradient tanks (Magee, et al. 1999). Early thermal preference studies used vertical gradient tanks (Garside, et al. 1977; Roed 1979) that took advantage of water's tendency to stratify into thermally distinct layers. The disadvantage of these tanks is the introduction of water depth as another variable, though careful experimental procedures can minimize this effect. More recent studies have used horizontal gradient tanks (Magee, et al. 1999) that eliminate depth as a variable. Most horizontal tanks are rectangular, and fish may select the ends of the tank because of the presence of greater amounts of apparent cover (Magee, et al. 1999). A recent innovation is the toroidal (donut-shaped) gradient tank (Myrick and Cech 2000a) that evenly distributes the apparent cover throughout the tank.

Chinook salmon

Chinook salmon thermal preferences have been the subject of very few laboratory studies. Brett (1952) evaluated the thermal tolerance and preference of juvenile spring-run chinook salmon from the Dungeness, Washington hatchery. Juvenile salmon were acclimated to temperatures of 10 – 25°C, in 5°C increments. A substantial acclimation effect was not observed (Figure TP.1), and the juvenile spring-run salmon appear to prefer temperatures in the 11 – 13°C range, significantly cooler than those preferred by juvenile steelhead. While one might be tempted to use the relationship between optimal growth temperature and preferred temperature (Beitinger and Fitzpatrick 1979), Brett's results indicate that in spring-run chinook salmon at least, this correlation might not hold true. Again, this is an area of chinook salmon thermal biology that needs more attention.

Steelhead and rainbow trouts

Thermal preference studies on steelhead and rainbow trout are surprisingly few in number. Cherry et al. (1975; 1977) conducted the most exhaustive studies to date on anadromous Great Lakes rainbow trout, while more recently Myrick and Cech (1998; 2000a) conducted limited studies on California steelhead populations.

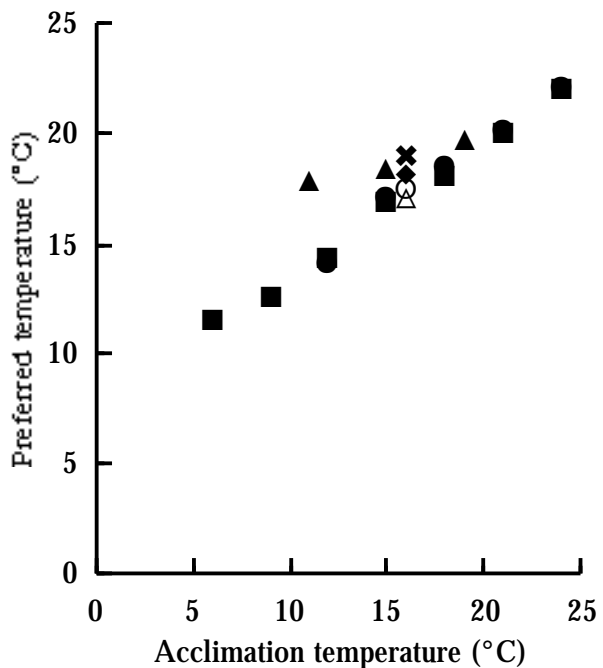Figure TP.2 Preferred (selected) temperatures for Great Lakes rainbow trout (solid squares, Cherry et al.1975); solid circles (Cherry et al. 1977), Nimbus hatchery steelhead (solid triangles, Myrick, 1998), hatchery Feather R. steelhead held at constant (solid diamonds) and cyclic (solid x) temperatures (Myrick and Cech 2000b), and fasted (hollow circles) and fed (hollow triangles) wild Feather R. steelhead Myrick and Cech 2000b).

Cherry et al. acclimated rainbow trout to temperatures of 6 to 24°C (Cherry, et al. 1975) and 12 to 24°C (Cherry, et al. 1977) in 3°C increments. They reported that the preferred or selected temperature changed with acclimation temperature in both studies (Figure TP.2). As acclimation temperatures increased from 6 to 18°C, selected temperatures were higher than the acclimation temperature, but fish acclimated to temperatures higher than 18°C selected cooler temperatures. The overall mean preferred temperatures for the fish in the 6 – 24°C and 12 – 24°C experiments were 16.5 and 18.4°C, respectively.

Myrick (1998) measured American River (Nimbus strain) steelhead thermal preference over the 11 – 19°C range. He reported a similar increase in thermal preference with acclimation temperature, but did not reach an acclimation temperature where juvenile steelhead began to select cooler temperatures. Myrick's (1998) results are interesting because (1) the steelhead selected higher temperatures than one might expect for a cold-water fish (Moyle 1976), and (2) because the selected temperatures closely match the temperature at which Myrick observed the highest growth rates (Table G.2). Myrick and Cech (2000a) measured the thermal preference of hatchery Feather River steelhead acclimated to constant (16°C) and diel cycling temperature regimes (16 ± 2°C) and that of wild-caught Feather R. steelhead that were fasted   24 h before testing and fed   24 h before testing. Hatchery fish acclimated to constant and cyclical thermal regimes had similar thermal preferences (Figure TP.2), selecting temperatures in the 18 – 19°C range. Wild fish, which probably were exposed to cooler temperatures in the Feather R. (Myrick and Cech 2000a), selected slightly cooler temperatures (17°C) under both fed and food-deprived conditions. Interestingly, the wild fish were collected from much cooler temperatures (< 15°C), yet selected warmer temperatures, as one might expect from the trends seen in Cherry et al.'s (1975; 1977) studies.

An interesting facet of Cherry et al.'s (1975; 1977) work on rainbow trout temperature

Figure TP.3. Tolerated temperatures for anadromous Great Lakes rainbow trout acclimated to temperatures of 6 – 24°C. Data are from Cherry et al. (1975).

selection was their determination of the upper and lower limits of the temperatures tolerated by trout acclimated to 6 – 24°C. These data, shown in Figures TP.3 and TP.4 are useful for establishing the limits of rainbow trout thermal niches at a given acclimation temperature. Naturally, because of the observed variability in rainbow trout thermal biology, it is important that these data are used conservatively until population-specific data sets are available. Such data are probably more applicable to modeling and management scenarios than thermal tolerance data (either CTM or ILT) because they delineate the realized thermal niche.
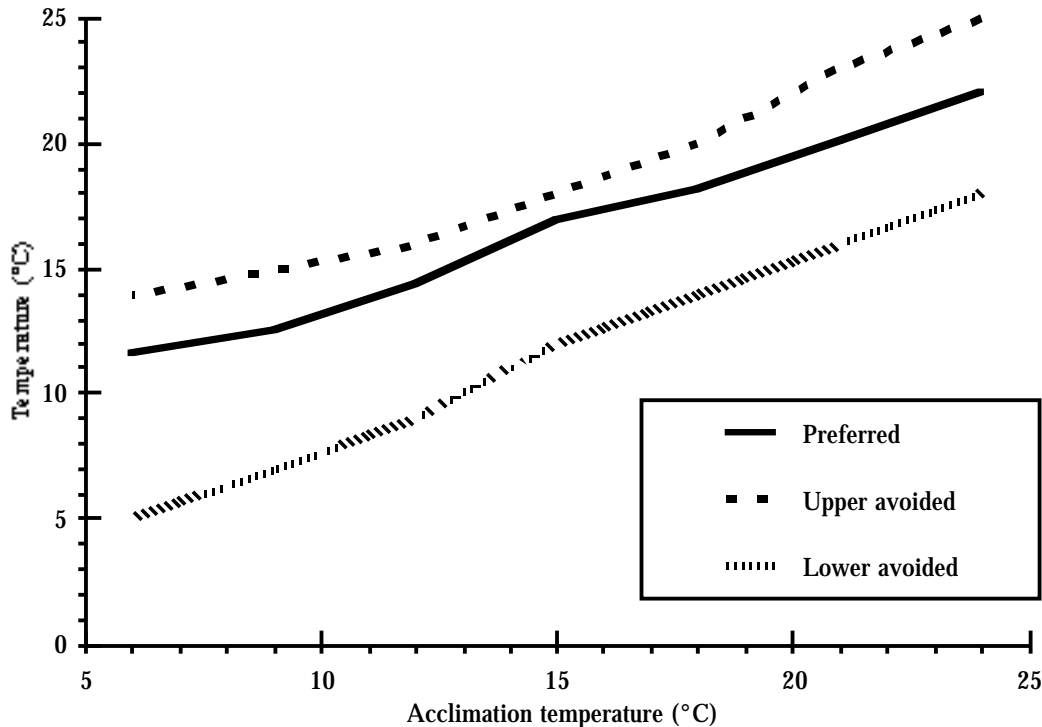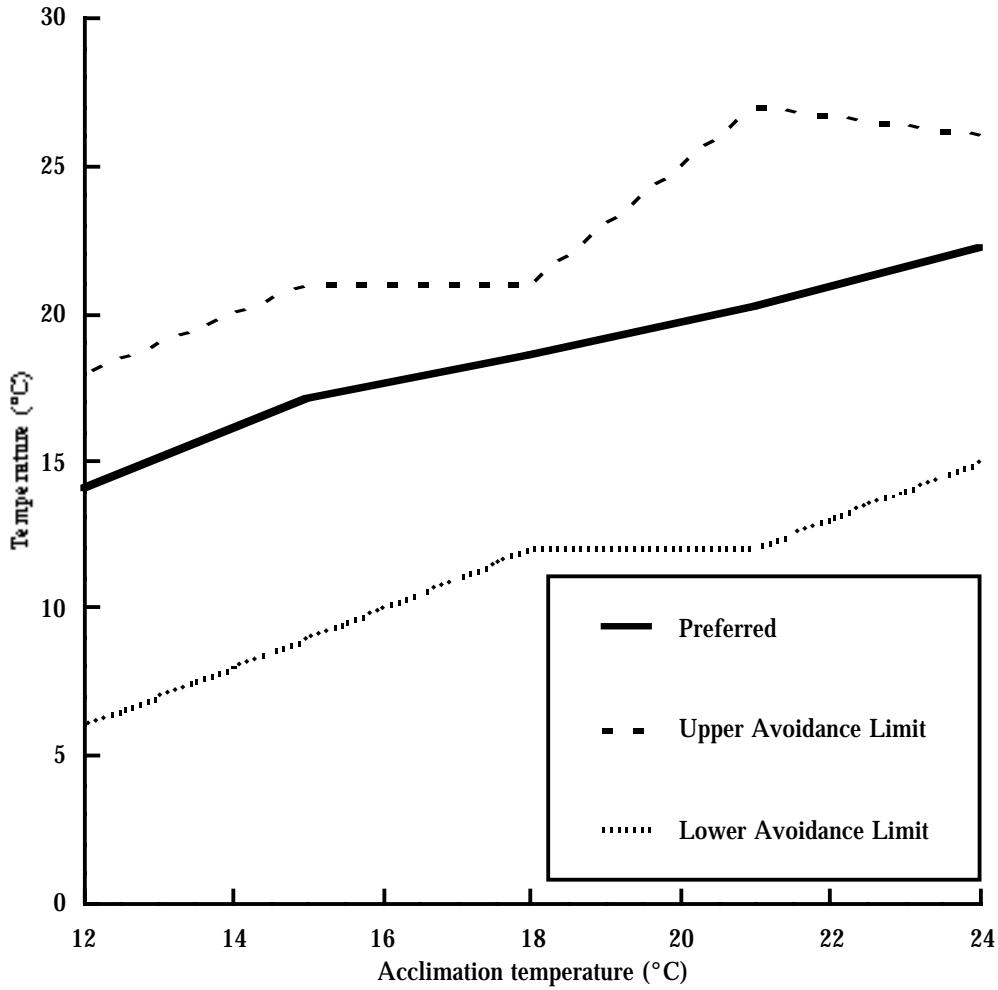

Figure TP.4. Tolerated temperatures for anadromous Great Lakes rainbow trout acclimated to temperatures of 12 – 24°C. Data are from Cherry et al. (1977).

GROWTH

Introduction

      Growth is perhaps the most powerful and complete integrator of environmental, behavioral, 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 (Myrick and Cech 2000a), race (Cheng, et al. 1987), ration size (Shelbourn, et al. 1995), ration quality (Fynn-Aikins, et al. 1992), disease (Jensen 1988), fish size (Wurtsbaugh and Davis 1977a), habitat (Ewing, et al. 1998), social interactions (McDonald, et al. 1998), photoperiod (Clarke, et al. 1992), and water quality (Ross, et al. 1995). 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. Carefully controlled laboratory experiments have given us a significant understanding of the effects of water temperature on growth, yet there are still a number of areas that warrant further investigation.

Juveniles

      Most chinook salmon and steelhead growth studies have focused on hatchery and wild-reared juveniles. The large size and pelagic marine habitat of adult salmon and steelhead make direct measurements of growth difficult. The freshwater phase of juvenile growth is the most important because of the dramatic physiological, behavioral, 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 tolerance (smoltification) in chinook salmon and steelhead is partially a function of size (Clarke and Shelbourn 1985; Johnsson and Clarke 1988), making it important that these fishes reach an appropriate size for smolting before they reach saltwater (see smoltification section for more information). 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
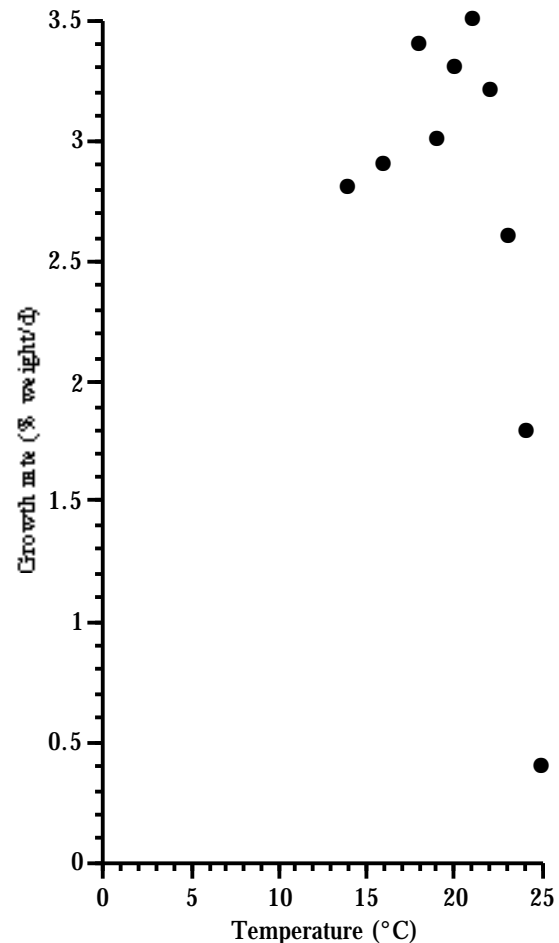

Figure G.1. Effect of temperature on chinook salmon growth.

(Alanärä and Brännäs 1997). From a management standpoint, chinook salmon and steelhead released from hatcheries as larger juveniles contribute more to the adult fisheries than those released at smaller sizes (Sholes and Hallock 1979; Reisenbichler, et al. 1982).

Salmonids respond to temperature in the classical fish manner (Figure G.1), 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 (Brett, et al. 1969; Brett and Groves 1979; Brett, et al. 1982). 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).

Growth is one of the components of the standard energy budget equation shown here in the form described by Adams and Breck (1990): $C = \left(M_r + M_a + SDA\right) + \left(F + U\right) + \left(G_s + G_r\right)$. Energy consumed (C) must balance the energy used for maintenance ("respiratory") and activity metabolism (M_r and M_a, respectively), specific dynamic action (SDA), fecal (F) and urinary (U) losses, and somatic and reproductive growth (G_s and G_r, respectively). Somatic growth is affected by any changes in the relative amounts of energy allocated to the other components of this equation. If the temperature increases, then the energy required for both activity and maintenance metabolism typically increases, making less energy available for growth if food consumption remains constant. If the food consumption rate is reduced, growth can respond in
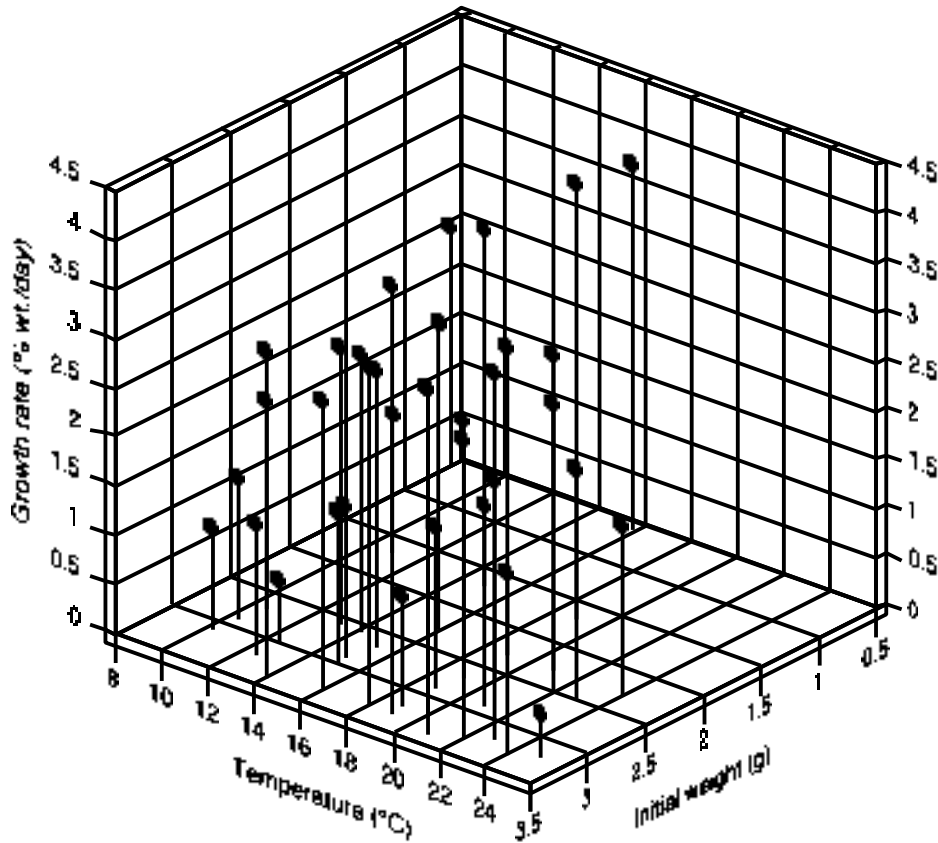

Figure G.2. Effects of temperature and initial weight on the growth of juvenile chinook salmon fed 100% rations. Data are from Clarke and Shelbourn (1985) and Brett et al. (1982).

two ways. If the ration is slightly reduced, the fish may be able to increase its conversion efficiency (the amount of food converted into body tissue) (Kreiberg 1991), thereby extracting the same amount of energy and maintaining energy homeostasis. 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. Growth in salmonids is also sensitive to changes in the size of the fish. Larger fish grow relatively slower than smaller fish (Wurtsbaugh and Davis 1977a) when fed at the same ration level.

Chinook salmon

Juvenile chinook salmon show positive growth at temperatures ranging from 8°C (Clarke and Shelbourn 1985) to 25°C (Brett, et al. 1982) with optimal growth under maximal rations at approximately 19°C (Figure G.2). Brett et al. (1982) fed hatchery Big Qualicum R. (BC) chinook salmon maximal rations at temperatures ranging from 14 to 25°C and found that growth rates increased with temperature to a maximum of 3.32 % d^{-1} at 20.5°C. Brett et al.'s (1982) comparative study of a hatchery salmon (Big Qualicum R.) with wild-caught chinook salmon

Temperature (°C)	Ration (% Rmax)	Source	Initial weight (g)	Growth rate (% wt./d)
10.2	60	Irvine's Lodge, Nechako R. (BC)	2.6	0.6
10.3	60	Diamond Isl., Nechako R. (BC)	2.7	0.5
12.4	60	Diamond Isl., Nechako R. (BC)	3	0.4
12.6	60	Irvine's Lodge, Nechako R. (BC)	2.6	0.6
15.1	60	Irvine's Lodge, Nechako R. (BC)	2.9	0.5
15.1	60	Diamond Isl., Nechako R. (BC)	2.8	0.2
18.8	60	Irvine's Lodge, Nechako R. (BC)	2.4	0.4
18.9	60	Diamond Isl., Nechako R. (BC)	2.9	0.4
10.1	80	Diamond Isl., Nechako R. (BC)	3.1	0.6
10.2	80	Irvine's Lodge, Nechako R. (BC)	2.8	1.1
12.4	80	Diamond Isl., Nechako R. (BC)	2.8	0.9
12.5	80	Irvine's Lodge, Nechako R. (BC)	3.1	1
15	80	Diamond Isl., Nechako R. (BC)	2.8	1.1
15.2	80	Irvine's Lodge, Nechako R. (BC)	2.6	0.9
18.2	80	Diamond Isl., Nechako R. (BC)	2.8	0.6
18.8	80	Irvine's Lodge, Nechako R. (BC)	2.9	1.1
10.2	100	Diamond Isl., Nechako R. (BC)	3.1	1
10.3	100	Irvine's Lodge, Nechako R. (BC)	2.9	1.4
12.6	100	Irvine's Lodge, Nechako R. (BC)	3.2	1.3
12.6	100	Diamond Isl., Nechako R. (BC)	3	0.6
15	100	Irvine's Lodge, Nechako R. (BC)	2.9	1.5
15	100	Diamond Isl., Nechako R. (BC)	3	1.5
18.8	100	Irvine's Lodge, Nechako R. (BC)	2.9	1.6
18.9	100	Diamond Isl., Nechako R. (BC)	3.2	1.1

Table G.1. Comparison of temperature and ration effects on the growth rates of chinook salmon from 2 areas of the Nechako River, BC. Data are from Shelbourn et al. (1995).

from the Nechako R. (BC) found that there was a strain-related difference in growth rate. Nechako R. salmon growth rates peaked at 3.15 % d^{-1} at 18.9°C. Brett et al. (1982) also reported that food conversion efficiencies increased with temperature to a maximum at 19.7°C, but that the difference in food conversion ratios at temperatures between 16 and 21°C were not biologically significant.

Using a model developed for sockeye salmon (*O. nerka*), Brett et al. (1982) determined that temperatures of 18.9 to 20.5°C were optimal for fish fed at R$_{max}$, but salmon fed at 60% of the maximum (R$_{0.6}$) reached their optimum at 15°C. The R$_{0.6}$ was based on field studies that suggested that wild fish fed at roughly 60% of the measured R$_{max}$. The study emphasizes the importance of investigating the combined effects of temperature and ration under laboratory conditions to allow inferences to be made about conditions in the field.

The effects of relatively low temperatures (less than 15°C) were evaluated in wild-caught Nechako R. chinook salmon (Shelbourn, et al. 1995) (Table G.1). Shelbourn et al. (1995) reported that chinook salmon from two collection sites showed reduced growth rates as water temperatures declined (Table G.1). They also recorded reduced growth rates as ration levels were reduced to either 80 or 60% of satiation.

Temperature effects on Central Valley salmon growth have also been studied. Rich's (1987) study on fall-run salmon from the Nimbus State Fish Hatchery (American R., CA) covered the widest temperature range (10.5 to 24°C). Salmon reared at 24°C died before the end of the experiment, so only the data for salmon reared at 10.5 to 21°C are presented in Figure G.3. Rich (1987) reported a maximum growth rate of 2.8 % wt. d^{-1} at 13.2, 14.1 and 15.3°C, with reduced growth rates at temperatures higher than 15.3°C (2.4 % wt. d^{-1} at 19°C and 2.0% wt. d^{-1} at 21°C). Because of the use of surface water from the American R., the fish were exposed to fluctuations in water quality (especially dissolved oxygen levels) and pathogens, particularly at the higher temperatures, which may have been responsible for the reduced growth rates at those temperatures.

Castleberry et al. (1991; 1993) published the preliminary results and conclusions of a study on American River salmon and steelhead growth rates in 1991 and 1992. Growth rates of 449 salmon ranging from 26 - 86 mm salmon captured in the American River were estimated using otolith back-calculation. Growth rate varied somewhat with length, and averaged 0.38 mm per day at 50 mm. The assumption that otolith rings are laid down daily was validated by Castleberry et al. (1994). These growth rates correspond to a specific growth rate of 0.76%
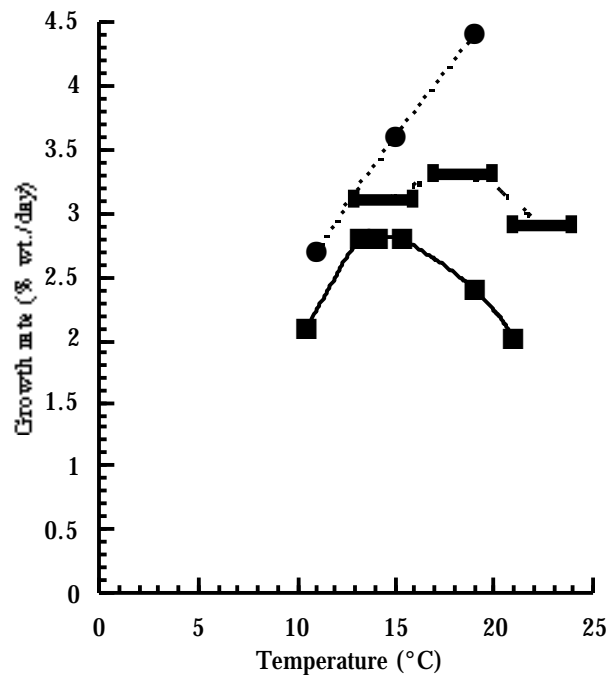

Figure G.3. Growth rates of American (dotted line, dashed line) and Sacramento R. chinook salmon (solid line) at different temperatures. Data are from Rich (1987) (solid line), Marine (1997) (dashed line), and Cech and Myrick (1999) (dotted line).

length·d^{-1}; however, neither data on weights or specific growth rates based on weights are present in the reports. The American R. fish increased in length slightly faster than tagged Sacramento R. chinook salmon (0.33 mm d^{-1}), and somewhat slower than salmon in the Sacramento -San Joaquin delta that reportedly have growth rates of 0.53 - 0.86 mm d^{-1}. Castleberry et al. (1991; 1993) conclude that (1) growth rates were lowest for newly emerged fish, and; (2) growth rates increased with temperature. This study is significant because it used wild-reared fish under natural temperature regimes—unfortunately, these factors also prevent direct comparisons with laboratory studies.

Salmon from the Nimbus Hatchery (American R.), reared in pathogen-free air-saturated well water had maximum growth rates of 4.4 % d^{-1} at 19°C, and lower growth rates at 15 and 11°C (Figure G.3; Cech and Myrick 1999). Cech and Myrick (1999) used smaller fish than Rich (1987), which may explain the consistent 1.3-fold difference in growth rates between salmon in Cech and Myrick's (1999) 15 and 11°C and Rich's (1987) 10.5 and 15.3°C treatments. However, the 1.8-fold difference in growth rate at 19°C is clearly not wholly attributable to the 37% smaller size of Cech and Myrick's salmon. The relationship between temperature and growth rate seen in Cech and Myrick's (1999) data parallels that observed in northern salmon that exhibit maximum growth at 19°C when fed satiation rations.

Marine (1997) reared Sacramento R. fall-run chinook salmon from the Coleman National Fish Hatchery at temperatures of 13–16, 17–20, and 21–24°C (Figure G.3). Maximum growth rates of 3.3 % wt. d^{-1} were observed in salmon reared at 17–20°C, with lower growth rates in salmon reared at 21–24°C (Marine 1997). Marine reported lower growth rates (by 33%) for the 17–20°C salmon than Cech and Myrick's 19°C salmon, despite their 47% smaller size. Smaller salmon should have higher growth rates, so it is possible that some race-related differences exist between Sacramento and American R. fall-run chinook salmon. Alternatively, it is possible that temperature or water chemistry/quality differences in Marine's study were sufficient to depress the growth rate below that of Cech and Myrick's study. The 1.2–fold increase in Big Qualicum R. salmon growth between 16 and 18°C reported by Brett et al. (1982) supports this hypothesis.

Steelhead

Steelhead growth at different temperatures has not been as extensively studied as that of chinook salmon. Numerous studies on resident rainbow trout growth have been published, but because of the different life history strategies it is important that such data be carefully evaluated before being substituted for anadromous trout data.

Research into and management of steelhead temperature requirements in California have been secondary to research and management of temperature for chinook salmon (McEwan and Nelson 1991). The status of Central Valley steelhead is uncertain, but there are still runs (especially in the smaller tributaries) that are supported by wild reproduction (McEwan and Jackson 1996). Juvenile steelhead typically spend at least one summer in fresh water, and so are more likely to be exposed to adverse temperature effects than juvenile fall-run chinook salmon (McEwan and Nelson 1991). Field observations on California coastal steelhead suggest that at least some races may have greater thermal tolerance than races from more northern latitudes (Matthews and Berg 1997). Nielsen (1994a) observed juvenile steelhead actively feeding at temperatures of 25°C on Rancheria Creek and the Middle Fork of the Eel River, a temperature held to be chronically lethal for juvenile steelhead (Hokanson, et al. 1977). Nielsen also reported

that the juvenile steelhead used thermal refugia when stream surface temperatures reached 23 - 28°C. Observations like these provide evidence for a greater thermal tolerance among California steelhead races and illustrate the need for additional research on their thermal limits and preferences.

Wurtsbaugh and Davis' (1977a; 1977b) studies of North Santiam River (OR) studies are the most extensive yet published. They studied the effects of temperature, ration level, and fish size on juvenile steelhead growth. As temperature increased, growth rate increased from a minimum of 1 % wt. d^{-1} at 6.9°C to a maximum of 3.5 % wt. d^{-1} at 16.4°C (Table G.2).

At temperatures higher than 16.4°C, steelhead growth rates declined rapidly, though the steelhead still grew at 1.7 % wt. d^{-1} at 22°C. Wurtsbaugh and Davis also investigated the effects of ration on steelhead growth rates. As ration decreased from 100% to 60 - 70% satiation, the optimum growth temperature also decreased (Table G.3, Figure G.4).

Temp. (°C)	Ration level	Initial weight (g)	Growth rate (% wt./d)	Source
6.9	12	2	-1.1	Wurtsbaugh and Davis (1977)
6.9	36	2.3	-0.6	Wurtsbaugh and Davis (1977)
6.9	60	2	0.3	Wurtsbaugh and Davis (1977)
9.4	25	2.3	-0.4	Wurtsbaugh and Davis (1977)
9.4	48	2.3	0.6	Wurtsbaugh and Davis (1977)
9.4	69	1.2	1.3	Wurtsbaugh and Davis (1977)
10	16	1	-0.3	Wurtsbaugh and Davis (1977)
10	31	2	0.9	Wurtsbaugh and Davis (1977)
10	56	1.1	2.1	Wurtsbaugh and Davis (1977)
10.1	12	1	-1.3	Wurtsbaugh and Davis (1977)
10.1	31	2.3	-0.6	Wurtsbaugh and Davis (1977)
10.1	55	2	0.2	Wurtsbaugh and Davis (1977)
11	82	3.1	1.5	Cech and Myrick (1999)
12.6	30	1	-0.3	Wurtsbaugh and Davis (1977)
12.6	48	1	0.5	Wurtsbaugh and Davis (1977)
12.6	72	2.2	1.4	Wurtsbaugh and Davis (1977)
13	35	1.9	-1.3	Wurtsbaugh and Davis (1977)
13	53	1	-0.8	Wurtsbaugh and Davis (1977)
13.3	13	2	-0.7	Wurtsbaugh and Davis (1977)
13.3	28	2.4	0.5	Wurtsbaugh and Davis (1977)
13.3	47	2.2	1.7	Wurtsbaugh and Davis (1977)
15	92	2.6	1.2	Cech and Myrick (1999)
15.2	36	1.1	-0.4	Wurtsbaugh and Davis (1977)
15.2	66	2.4	1.6	Wurtsbaugh and Davis (1977)
16	25	1	-0.14	Myrick and Cech (2000)
16	50	2.6	0.9	Myrick and Cech (2000)
16.2	34	2	0	Wurtsbaugh and Davis (1977)
16.2	50	1.2	1.2	Wurtsbaugh and Davis (1977)
16.2	66	2.3	1.5	Wurtsbaugh and Davis (1977)
16.4	41	0.9	1.3	Wurtsbaugh and Davis (1977)
19	88	2.2	1.7	Cech and Myrick (1999)
19.5	38	1.2	0.1	Wurtsbaugh and Davis (1977)
19.5	50	1.2	1.1	Wurtsbaugh and Davis (1977)
19.5	66	1.1	1.6	Wurtsbaugh and Davis (1977)
22.5	55	1.8	0	Wurtsbaugh and Davis (1977)
22.5	69	1.1	0.5	Wurtsbaugh and Davis (1977)

Table G.3. Effects of reduced ration level and temperature on juvenile steelhead growth.

Another important aspect of Wurtsbaugh and Davis' work related fish size to growth rates. They found that as steelhead increased in size, their growth rates at a given temperature decreased (Wurtsbaugh and Davis 1977a). Therefore, if growth is being modeled, it is important to take the change in fish size into account. California steelhead have been little studied. A landmark study on steelhead ecology (Shapovalov and Taft 1954) and studies on American River steelhead and chinook salmon (Castleberry, et al. 1991; Castleberry, et al. 1993) are available , but few other detailed studies on the effects of temperature are available. The recent listing of California steelhead populations as threatened or endangered (USFWS 1998) has prompted increased interest in steelhead physiology, especially with regards to environmental tolerances, preferences, and requirements.
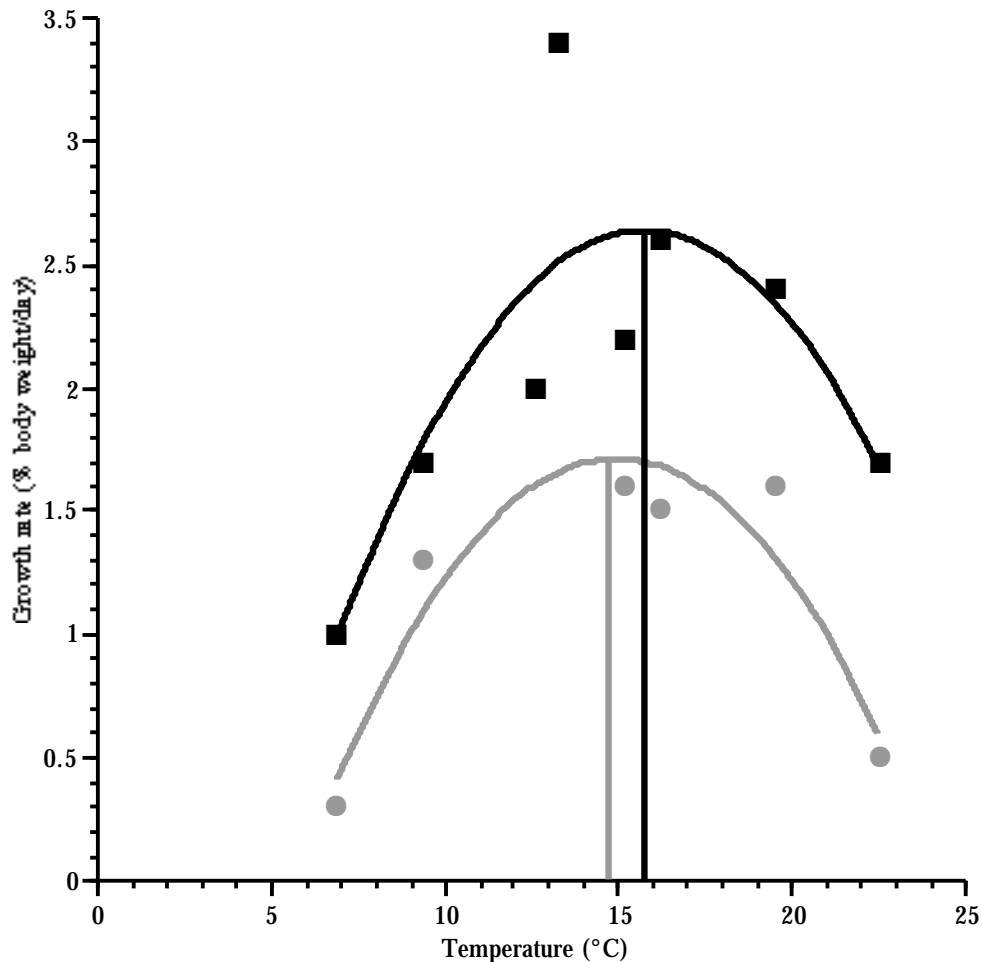

Figure G.4. Effects of temperature and ration level (100% = squares; 60-70% = circles) on the growth of juvenile N. Santiam River (OR) steelhead. Data are from Wurtsbaugh and Davis (1977a, 1977b).

Myrick (1998) investigated the combined effects of temperature (11, 15, and 19°C) and ration level (100% satiation and 82–92% satiation) on Nimbus strain steelhead (American R., CA) growth rates. Following the extirpation of native American R. steelhead runs by the dam construction, a run of Eel River steelhead was established in the lower American River, and is now the "American R. steelhead" (McEwan and Nelson 1991). Myrick reported an increase in

growth rate from 1.3 % wt. d^{-1} at 11°C to 2.6 % wt. d^{-1} at 19°C (Table G.2). Growth rates at ration levels 8 - 18% lower than satiation were generally the same as those at 100% satiation. This similarity was attributed to a higher conversion efficiency at the lower ration levels, which parallels the conclusion reached by Wurtsbaugh and Davis (1977b).

Myrick and Cech (2000a) evaluated the effects of ration (25, 50, and 100% satiation) and 'constant' or cyclic temperature (16 ± 0.1°C and 16 ± 2.0° on a 24 h cycle, respectively) on the growth and thermal biology of juvenile steelhead from the Feather River (CA). Growth rate increased with ration level. A consistent, though not statistically significant, trend was observed where fish on the cyclic thermal regime (14 - 18°C) grew slower than those reared under the constant regime.

Results from studies on resident rainbow trout are varied. Myrick and Cech (2000b) compared the growth rates of two strains of resident California rainbow trout (Eagle Lake and Mt. Shasta) at temperatures of 10 to 25°C (Figure G.5). Growth rates increased with temperature to a maximum near 19°C and declined rapidly at temperatures higher than 19°C. Although similar methods and fish sizes were used, resident rainbow trout growth rates were consistently higher than those of either American or Feather River steelhead. It is possible that the Eagle Lake and Mt. Shasta races are more adapted to captive rearing than steelhead because they are raised from captive broodstock that may not be subject to natural selective pressures (Busack and Gall 1980).

Figure G.5. Growth rates of resident Eagle Lake (solid squares) and Mt. Shasta (solid circles) strain rainbow trout. Data are from Myrick and Cech (2000).

Summary

Fall-run Central Valley and northern chinook salmon growth rates are similarly affected by temperature. One should note, however, that comprehensive data on the effects of temperature on the growth of Sacramento R. spring and winter-run salmon, the runs most likely to encounter elevated rearing temperatures, are not readily available, if at all. Until more comprehensive studies on the different runs and races of Central Valley chinook salmon are undertaken, we recommend that managers err on the side of caution and use conservative estimates. Additionally, while Rich's (1987) study may have been influenced by disease or water quality issues, it does reemphasize that temperature effects on disease and water quality cannot be ignored under natural conditions. Finally, because optimal growth temperatures are ration-dependent, careful field assessments of wild salmon feeding states and growth rates should be undertaken prior to establishing temperature criteria. The studies conducted by Castleberry et al. (1991; 1993) were a step in the right direction, but more detailed, long-term studies are recommended. Temperatures that maximize growth with satiation
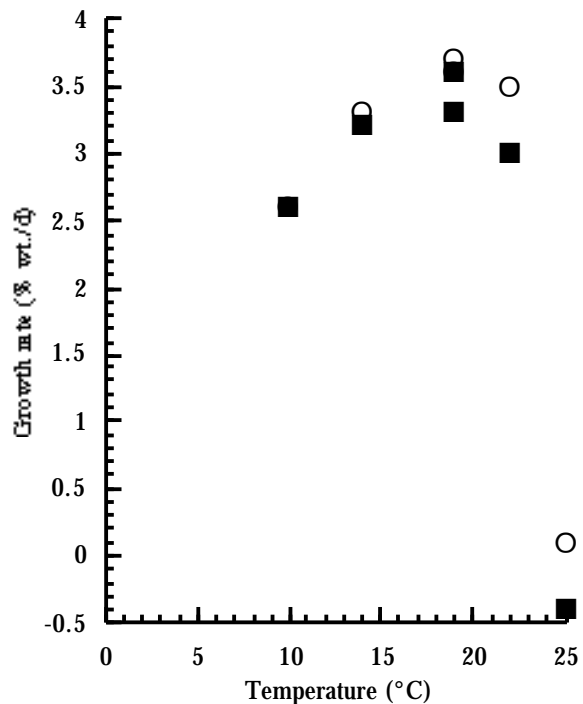
feeding under laboratory conditions may be conducive to disease outbreaks (see disease section) and may also increase vulnerability to predators (see predation section).

Some growth rate differences appear to exist between California steelhead and those from more northern latitudes (Table G.2, G.3). The limited data collected by Myrick and Cech hint at physiological differences in their responses to temperature, but until large-scale experiments are conducted, clear conclusions will not be possible.

SMOLTIFICATION

Introduction

The adaptation to living in saltwater, a process known as smoltification (parr-smolt transformation) (Wedemeyer, et al. 1980) is a crucial phase in the life history of any anadromous fish. Freshwater fish are hypertonic to their environment and must actively excrete water and acquire ions (primarily Na^+ and Cl^-) (Moyle and Cech 2000). Marine fish are hypotonic (less salty than environment) and must drink copious quantities of sea water (Moyle and Cech 2000) and actively excrete salt. The cells used to excrete salt are known as saltwater chloride cells. They achieve this task through the use of Na^+-K^+-ATPase in conjunction with other mechanisms (Pisam, et al. 1987).

Saltwater chloride cells activation, and the corresponding increase in Na^+-K^+-ATPase activity, are brought about by a number of factors. These include changes in circulating hormone concentrations (Iwata 1995), increasing photoperiod (Hoffnagle and Fivizzani 1998), increasing temperature (Zaugg 1981), and increasing body size (Zaugg 1981; Johnsson and Clarke 1988). The degree to which these factors affect smoltification is species-specific (Clarke, et al. 1981). Smoltification is a reversible process—if smolts remain in freshwater too long or if conditions are not suitable for continued maintenance of hormone and chloride cell levels, they revert to a freshwater or parr state (Hoar 1988). The duration of the smolt period is temperature-dependent, with shorter periods of high Na^+-K^+-ATPase activity at warmer temperatures (Wagner 1974).

Chinook Salmon

Chinook salmon can smolt at temperatures as low as $6 – 7°C$ (Zaugg and McLain 1972) and as high as $20°C$ (Marine 1997). They do so at a relatively small size (> 70 mm) (Kjelson, et al. 1981; Ewing and Birks 1982).

Marine (1997) evaluated the smoltification patterns of juvenile Sacramento R. fall-run chinook salmon reared at low ($13 – 16°C$), moderate ($17 – 20°C$), and high ($21 – 24°C$) temperatures. Salmon reared under the high temperature regime demonstrated altered and impaired smoltification patterns relative to those in the low temperature treatment. Salmon in the moderate treatment displayed some alteration and variable impairment of smoltification patterns.

Although chinook salmon can smolt at temperatures as high as $20°C$, their saltwater survival is improved at lower temperatures. Clarke et al. (1981) reported that chinook salmon reared at $10°C$ survived seawater challenges better than those reared at $15°C$. Subsequent studies (Clarke and Shelbourn 1985; Clarke, et al. 1992) provide more evidence that chinook salmon that complete juvenile and smolt phases in the $10 – 17.5°C$ range are optimally prepared for saltwater survival.

Chinook salmon smolts have variable migration timing (Achord, et al. 1996), which is indicative of variable periods of saltwater tolerance. In a study evaluating the combined effects of a 3-month accelerated photoperiod and elevated temperature ($10 –11°C$) on yearling spring

chinook salmon from Dworshak National Fish Hatchery, Idaho, Muir et al. (1994) found that photoperiod had more of an effect on migration speed than temperature. The fastest downstream movement and highest Na^+-K^+-ATPase activities were seen in the photoperiod + temperature treatment, with lower Na^+-K^+-ATPase activities and slower migration speeds with photoperiod alone and the lowest Na^+-K^+-ATPase activities and migration speeds with temperature alone (Muir, et al. 1994).

It is important that modelers and managers consider the ontogenetic changes in chinook salmon thermal requirements. While temperatures in the 15 – 19°C range lead to high juvenile growth rates, cooler temperatures are optimal for smoltification. Managing system temperatures to benefit one life stage at the detriment of others will only lead to failure, as will managing temperatures to benefit one species at the expense of others. Obviously, the best management strategy is to replicate the natural (pre-disturbance) thermal regime, provided sufficient suitable habitat is available. Without suitable habitat, even the most ideal thermal conditions will not be enough to sustain populations of either steelhead or chinook salmon.

Steelhead

The importance of temperature, photoperiod, and size on smoltification is quite variable, despite broad similarities in life-history patterns of anadromous salmonids (Shapovalov and Taft 1954; Taylor 1990; Thorpe 1994). Steelhead smolt in a very narrow temperature range. Adams et al. (1973) measured Skamania (WA) summer-run steelhead gill Na^+-K^+-ATPase activity at 6.5, 10, 15, and 20°C. At both 6.5 and 10°C, Na^+-K^+-ATPase activity was higher than control values and condition factor (another indicator of smolting) declined. No increase in Na^+-K^+-ATPase activity was observed at 15 and 20°C. Adams et al. (1975) increased the resolution in a subsequent study using the same strain of steelhead held at 10, 11.3, 12.7, and 14°C, and winter-run steelhead from the Eagle Creek National Fish Hatchery held at 6 and 15°C. In this study, increased Na^+-K^+-ATPase activity was detected at 6, 10, and 11.3°C. Steelhead in the 10 and 11.3°C treatments showed elevated activities, but their saltwater survival period was shorter than that of the 6°C treatment. A later study by Johnsson and Clarke (1988) on winter-run steelhead from the Chilliwack hatchery, BC, Canada, corroborates these results.

When steelhead smolting and optimal growth temperatures are considered within the framework of steelhead life histories, the biological rationale for the observed differences is apparent. 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 temperatures are kept below those optimal for growth during non-smolt periods, there is a risk that the steelhead will be to small to smolt, forcing them 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.

DISEASE

Introduction

Pathogens affect chinook salmon and steelhead in the Sacramento-San Joaquin River system, yet are often overlooked during temperature studies. Salmon and steelhead infection and mortality rates vary with pathogen and temperature. Most chinook salmon and steelhead disease studies have focused on juvenile life stages (e.g. eggs, alevins, parr, and smolts). However, adult salmonids can be, and often are, infected with pathogens, but do not readily succumb to these infections as do smaller fish. Because numerous pathogens can be transmitted vertically (from parents to offspring) as well as horizontally, (Baxa-Antonio, et al. 1992) the mere presence of the pathogens is cause for concern.

Figure D.1. Infective/virulent ranges (solid lines) for 8 chinook salmon diseases. Dashed lines indicate the range of tested temperatures. Data are from 1) Oláh and Farkas (1978); 2) Bell (1996); 3) Antonio and Hedrick (1995); 4) Holt et al. (1975), and; 5) Groberg et al. (1978).

Salmon and steelhead

Studies on the effects of temperature on pathogens have predominantly been conducted in Oregon and Washington, with a few studies conducted in California. Results from chinook salmon studies are shown in Figure D.1; results for steelhead and rainbow trout studies are shown in Figure D.2. Some pathogens are infective at temperatures as low as 5°C, but the general trend observed is that infectivity and mortality increase as water temperature increases above 12°C. At temperatures of 15°C and above, there is often heavy mortality (Figure D.3).

Pathogens also have indirect effects on salmonids—they don't have to kill the fish to have a significant effect on their long term survival and contribution to the stock. Different salmonid species have different resistances to pathogens at different temperatures (Groberg, et al. 1978; O'Grodnick 1979) that may result in a competitive advantage for the more resistant species (Wald and Wilzbach 1992). Sublethally infected fish may experience reduced growth rates and be more susceptible to predation. Mesa et al. (1998) compared the vulnerability of juvenile chinook salmon infected with *R. salmoninarum* to that of uninfected salmon and demonstrated that infected salmon were 1.9 times more likely to be eaten by predators (northern pikeminnow, *Ptychocheilus oregonensis*). It has been suggested that some of the mortality observed in chinook salmon smolts migrating through the Sacramento-San Joaquin Delta may be due to
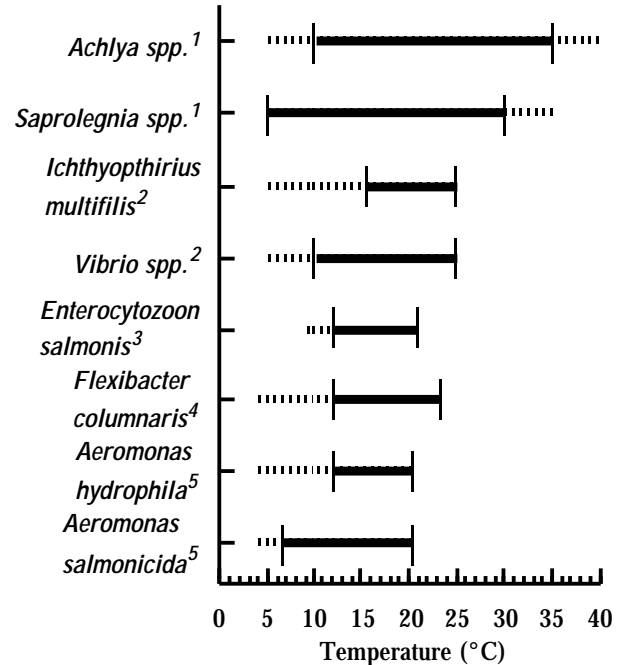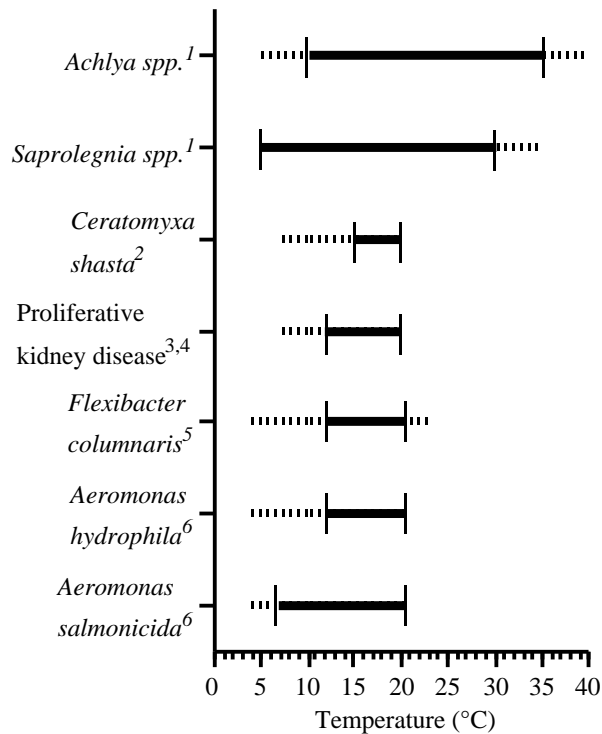
Figure D.2. Infective/virulent ranges (solid lines) for 7 steelhead pathogens. Dashed lines indicate the range of tested temperatures. Data are from 1) Oláh and Farkas (1978); 2) Hendrickson et al. (1989); 3) Clifton-Hadley et al. (1986); 4) Foott and Hendrick(1987); 5) Holt et al. (1975), and; 6) Groberg et al. (1978).
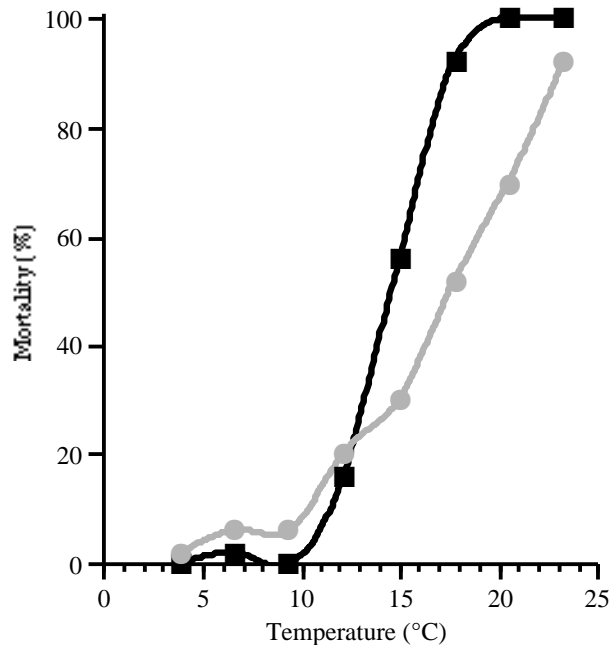
Figure D.3. Example of the typical temperature effects on mortality of steelhead (solid squares) and chinook salmon (solid circles) infected with a pathogen (*F. columnaris* in this case). Data are from Holt et al. (1975).

predation (Gritz 1971; Baker, et al. 1995); possibly these are fish that are sublethally infected with one of the pathogens listed below.

Chinook salmon and steelhead in California's Central Valley are exposed to a variety of pathogens, including *Aeromonas salmonicida* and *A. hydrophila* (Groberg, et al. 1978), *Ceratomyxa shasta* (Hendrickson, et al. 1989), *Enterocytozoon salmonis* (Baxa-Antonio, et al. 1992), the "rosette agent" (Arkush, et al. 1998), infectious hematopoietic necrosis virus (IHNV) (LaPatra, et al. 1989), proliferative kidney disease (Foott and Hedrick 1987), *Saprolegnia* (Oláh and Farkas 1978), *Flexibacter columnaris* (Holt, et al. 1975), *Myxosoma cerebralis* (O'Grodnick 1979), *Renibacterium salmoninarum* (bacterial kidney disease; BKD) (Mesa, et al. 1998), *Vibrio spp.* (Bell 1986), and *Ichthyopthirius multifilis* (Bell 1986). Despite the presence of valuable commercial and sport fisheries for both chinook salmon and steelhead, the effects of temperature on the lethal and sublethal aspects of these pathogens in the Sacramento R. system have been the subject of comparatively few studies. There have been a few studies investigating the effects of water temperature on mortality rates of chinook salmon and steelhead exposed to a handful of pathogens. There does not appear to be standardized methodology for conducting these studies, so the types of exposure, length of exposure, and post–exposure times vary greatly.

Summary

The effects of water temperature on the pathogens that infect steelhead and chinook salmon in the Sacramento-San Joaquin system are not well known. Based on a limited number of studies, it is apparent that elevated water temperatures are associated with higher rates of infection and mortality for both juvenile chinook salmon and steelhead.

PREDATION

Introduction

Pacific salmonids are exposed to predation throughout their lives. Eggs are preyed on by birds, fish and invertebrates. Juveniles fall prey to vertebrate predators, and adults are preyed upon by large fish and mammals. Given the pervasive nature of temperature effects on salmonid physiology, it is not surprising that their vulnerability to predators is partially temperature-dependent. Temperature has both direct and indirect effects on juvenile salmonids.   Direct effects are those where temperature increases or decreases the vulnerability to predation through behavioral or physiological pathways. Indirect effects are manifested through temperature's effect on some other causative factor, such as disease or the predator metabolic rates.

Direct Effects

Predation on juvenile salmonids has been a major concern throughout the Pacific Northwest (Mesa and Olson 1993; Mesa 1994; Parker, et al. 1995; Gregory and Levings 1998), yet surprisingly little research has focused on the direct effects of temperature. Marine (1997) studied the vulnerability of juvenile Sacramento River fall-run chinook salmon to striped bass (*Morone saxatilis*) predation following chronic exposure to elevated water temperatures. Salmon reared at high temperatures (21 – 24°C) were eaten more often than those reared at moderate (17 – 20°C) or low (13 – 16°C) temperatures (Figure P.1).   The mechanism underlying the increased vulnerability is unknown, though it may involve a combination of reduced swimming performance, condition, and neurological damage. Temperature effects on swimming performance have been well documented (see Videler 1993 for a comprehensive review and Castleberry et al. 1991; 1993 for American R. data). More research is clearly needed in this area, given the ongoing losses of juvenile salmonids (especially out-migrating smolts) to fish and avian predators (Vigg and Burley 1991; Smith, et al. 1997).
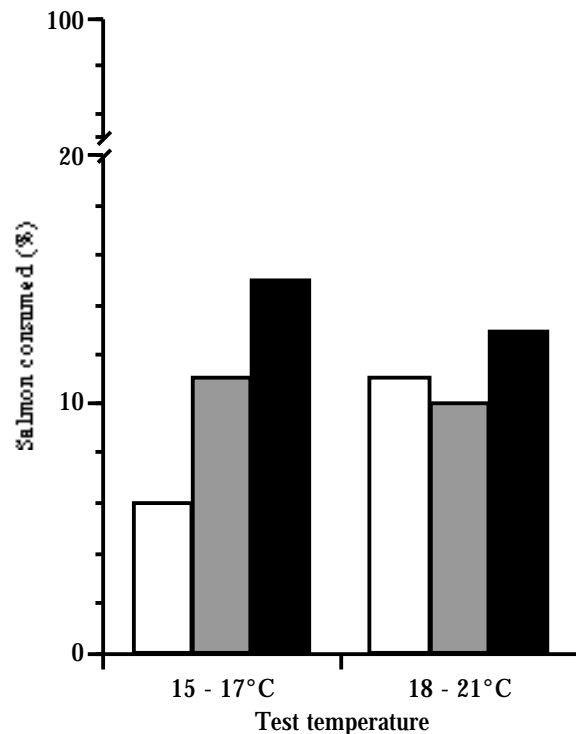

Figure P.1. Striped bass predation rates on juvenile chinook salmon chronically exposed to elevated water temperatures (white = 13 - 16°C, gray = 17 - 20°C, black = 21 – 24°C). Data are from Marine (1997).

Indirect Effects

The indirect effects of temperature vulnerability to predation can be difficult to study. If the physiological state of a juvenile

salmonid is compromised or weakened by a temperature-related stressor, such as disease or stress, it is likely to show greater vulnerability to predation. Mesa et al. (1998) measured the susceptibility of juvenile Entiat R. (WA) spring-run chinook to northern pikeminnow and smallmouth bass (*Micropterus dolomieui*) predation after different levels of *R. salmoninarum* infection. Fish infected at moderate to high levels were 1.9-times more vulnerable to predation. Other stressors known to degrade predator avoidance ability include hatchery practices and dam passage (Mesa 1994). Neither of these were studied with temperature as an interacting variable, but in both cases predator avoidance ability was restored to pre-stress levels after 1 hour. The length of the recovery period may be temperature related.

Temperature indirectly affects predation rates on juvenile salmonids through its effects on predators. Beyer et al. (1988) reported that the gastric evacuation time of northern pikeminnow at 20°C was two-thirds that of pikeminnow at 10°C. Temperature-dependent maximum daily consumption of juvenile salmon by northern pikeminnow increased 10-fold and the number of salmon eaten per day increased 14-fold when water temperatures increased from 8 to 21.5°C (Figure P.2) (Vigg and Burley 1991). These results demonstrate that temperature effects on predators can have profound consequences for prey populations.
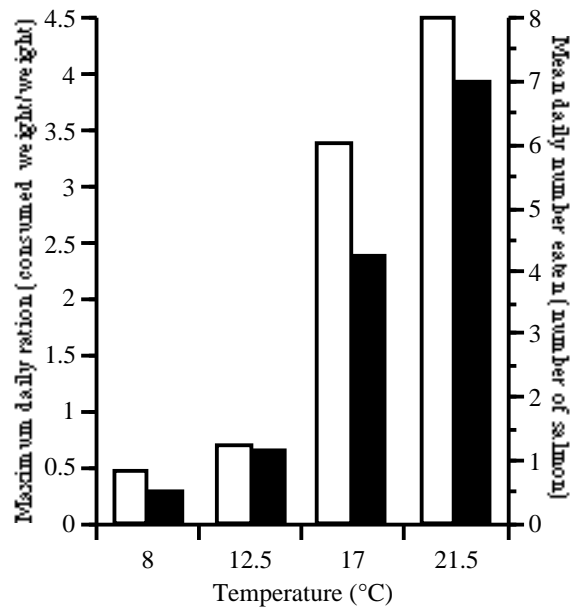

Figure P.2. Temperature–dependent maximum daily consumption of juvenile salmon by northern pikeminnow. White bars indicate maximum daily consumption in g salmon consumed per g pikeminnow; black bars indicate mean number of salmon consumed per predator per day. Data are from Vigg and Burley (1991).

HOOKING MORTALITY

<u>Introduction</u>

Hooking mortality may be a significant source of mortality for adult salmon and steelhead migrating in freshwater. Both chinook salmon and steelhead are subject to variable catch-and-release fisheries in the Sacramento-San Joaquin system. Complex regulations governing steelhead, rainbow trout, and chinook salmon sport fisheries in the system create a spatially and temporally heterogeneous release matrix.

Hooking, playing, landing, and releasing any fish is stressful and can be influenced by the water temperature. Higher activity levels at higher water temperatures will lead to longer hooked periods and greater energy expenditures, resulting in more extensive build-up of lactic acid and stress hormone levels. Additionally, the indirect effects of hook wounds and/or reduced immune function following the stresses of being hooked may result in infection by a number of pathogens. As explained in the disease section, most of pathogens display temperature-dependent levels of virulence, with increased virulence at higher temperatures.

The effects of hooking on the mortality of chinook salmon and rainbow trout have been investigated in a number of studies, though none were conducted in the Central Valley. Wertheimer et al. (1989) quantified the hooking mortality of ocean troll-caught chinook salmon at temperatures between 7.9 and 9.2°C. Bendock and Alexandersdottir (1993) used radiotelemetry to quantify hooking mortality of sport-caught chinook salmon in the Kenai River, Alaska. Schisler and Bergersen (1996) studied hooking mortality in rainbow trout.

<u>Chinook Salmon</u>

The river fishery for chinook salmon relies heavily on drifting salmon roe or multiple-hook lures through holding areas. Hooking mortality of both ocean troll-caught salmon (Wertheimer, et al. 1989) and sport-caught salmon (Bendock and Alexandersdottir 1993) was determined to depend primarily on hooking location, rather than temperature, or lure type. Troll-caught chinook salmon had low mortality when hooked in the snout, maxillary, or corner of the mouth. Mortality increased to moderate levels when hooked in the lower jaw, isthmus, cheek, and eye. Highest mortality levels were observed among fish were hooked in the gills (Wertheimer, et al. 1989). Wertheimer et al. (1989) found that larger fish had higher survival rates than smaller (sublegal: < 66 cm FL) salmon, and reported overall mortality rates of 18.5 – 22.1% for troll-caught salmon in relatively cold (7.9 – 9.2°C) water.

Bendock and Alexandersdottir (1993) reported similar results for sport-caught Kenai River salmon. Of fish caught and released in the Kenai R. estuary, 63% survived and 19% were harvested farther upriver. The average post-release mortality was 7.6%, and both size and hooking location were the primary factors affecting mortality. Large (> 750 mm TL) females had the highest survival (93.5%), followed by the large males (> 750 mm TL; 90.1%), and the small males (< 750 mm TL; 82.5% survival). Fish hooked in vital areas (gill, "tongue", eye) had a high chance of death; fish that were bleeding upon capture were 4 – 5 times more likely to die than non-bleeders. An interesting difference between the fish caught and released in this study

and those in the Sacramento-San Joaquin system is that these salmon cannot be removed from the water when they are being unhooked, whereas those in the Sacramento-San Joaquin system are commonly removed from the water. The additional stresses (netting, handling, air-exposure with consequent hypoxia and hypercapnia, etc.) undoubtedly affect on their ability to survive the catch-and-release experience and suggests that mortality rates in the Sacramento and San Joaquin rivers may be somewhat higher than in the Kenai River.

Rainbow Trout & Steelhead

Schisler and Bergersen (1996) studied the effects of different types of artificial baits on the hooking mortality of rainbow trout. As was the case with the chinook salmon, hooking location and fish size were the most important determinants of mortality. Fish hooked in or near the gills were more likely to succumb than those hooked in the corner of the mouth or the peripheral part of the jaw (i.e., the outer jaw).

Summary

The effects of temperature on the hooking mortality of salmonids have not been adequately documented. Studies with other species (e.g. largemouth bass) and anecdotal evidence from studies of temperature effects on salmonid physiology suggest that temperature may indeed play an important role in determining the susceptibility of Sacramento-San Joaquin system anadromous salmonids to acute or delayed mortality from catch-and-release events. Given the thermally heterogeneous nature of the system, especially in the lower reaches, it is likely that a significant fraction of released fish experience higher mortality rates through direct (e.g. hemorrhaging) and indirect (e.g., pathogens) effects of hooking mortality.

RECOMMENDATIONS FOR FUTURE RESEARCH

The following are a set of questions that attempt to summarize the greatest needs of water managers (J. Williams, pers. comm.). Research answering these questions 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 on 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?

Thermal tolerance

More data sets similar to Bidgood's (1969) that examine resistance time at a range of temperatures are needed to better model the responses of chinook salmon, steelhead and rainbow trout to chronic elevated temperature conditions.

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

Despite the considerable data available on juvenile chinook salmon growth in freshwater, it is apparent that more research is critically needed. 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. Such a study (proposed by Cech and Myrick in 1999 but not funded) would produce the data needed to develop models similar to those of Brett (1969) for Central Valley chinook salmon. Field data on the condition and feeding–states of wild salmon (e.g. (Castleberry, et al. 1993; Moore 1997)) could then be used in the model to begin to determine the year–by–year or season–by–season temperature requirements for optimal juvenile growth. 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. In addition to the basic studies outlined for salmon, 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.

Finally, data sets provided in Castleberry et al. (1991; 1993) hint at significant differences among growth rates of both salmon and steelhead from different tributaries of the Sacramento system. Further investigation of these differences are warranted to determine the extent to which basin-specific temperature criteria may be needed.

Disease

Because direct and indirect mortality due to pathogens may be major factors in determining recruitment rates, more studies are needed. Specifically, temperature effect studies on the following topics would greatly improve the current state of knowledge: 1) horizontal and vertical transmission rates for dominant pathogens in the Sacramento-San Joaquin system; 2) sublethal effects of low levels of infection on juvenile and adult salmonids, especially in relation to growth, osmoregulation, and reproduction, and 3) wild and hatchery salmonid recruitment rates in the presence of the dominant Sacramento-San Joaquin pathogens.

Predation

Predation on juvenile steelhead and salmon may represent a significant fraction of early mortality in the Sacramento-San Joaquin system. Data on predator population sizes and predation rates would greatly improve the predictive power of population models. Such models should incorporate temperature-related changes in predation and gastric evacuation rates. Such data are relatively easy to collect. Additionally, the indirect pathways by which temperature degrades the predator avoidance behavior of juvenile salmon and steelhead (e.g., disease, loss of condition) need to be further investigated in large-scale, carefully controlled experiments.

One area of "predation" that is beginning to receive more attention are the losses of salmon to screened and unscreened diversion (mechanical predators). The Cech lab at UC Davis is conducting an extensive series of experiments using a simulated water diversion that may provide valuable insights on rates of loss to these diversions. Modelers would be well advised to examine these data once the experiments are completed.

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