Reviews in Fish Biology and Fisheries (2004) 14: 113–123 © Springer 2005

Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know?

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Accepted 5 August 2004

Contents

Key words: disease, growth, predation, salmonid, smoltification, temperature

Abstract

The anadromous Chinook salmon (*Oncorhynchus tshawytscha*) (4 runs) and steelhead (rainbow trout, *O. mykiss*), are both native to California's Sacramento-San Joaquin River (SSJR) system, whose watershed encompasses the central valley of California. The SSJR system holds the southernmost extant Chinook salmon populations in the Eastern Pacific Ocean, whereas coastal anadromous steelhead populations are found at more southerly latitudes. Populations of both species of anadromous salmonid have experienced dramatic declines during the past 100 years, at least partly from water impoundments and diversions on most central valley rivers and their tributaries. These changes restricted the longitudinal distribution of these salmonids, often forcing the superimposition of steelhead populations and Chinook salmon populations in the same reaches. This superimposition is problematic in part because the alterations to the river systems have not only changed the historic flow regimes, but have also changed the thermal regimes, resulting in thermally-coupled changes in fish development, growth, health, distribution, and survival. Given the highly regulated nature of the system, resource managers are constantly trying to strike a balance between maintaining or increasing the population size of anadromous fish runs and with other demands for the water, such as irrigation and water quality. To do so, in this review, we summarize the published information on the temperature tolerance and growth of the stream-associated life stages of these two valuable species, which are so central to the natural heritage of the State and its cultures. We show that many of these limits and growth-related effects are specific regarding life stage and that some may be specific to distinct strains or races of Chinook salmon and steelhead within the system. Because the number of published studies on the

physiology of central valley salmonids was surprisingly low, we also use this review to highlight critical areas where further research is needed. Overall, this review should assist biologists and resource decision-makers with improved understanding for the protection and enhancement of these native fishes.

Introduction

Four species of anadromous salmonids are regularly found in California, coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*), steelhead (anadromous rainbow trout, *O. mykiss*), and coastal cutthroat trout (*O. clarki clarki*). All four species occur in the rivers along California's northern coast, but only the Chinook salmon and steelhead are found in appreciable numbers in the Sacramento-San Joaquin River (SSJR) system, whose drainage basin encompasses California's central valley. The status, biology, and distribution of these central valley stocks have been the subject of intense debate and scrutiny in recent years for a number of reasons, including those listed below.

The variable climate, geology, and sheer size of the drainage system contributed to the evolution of several distinct races of Chinook salmon and steelhead, including one form, the Sacramento River winter-run Chinook salmon, that has no equivalents in other river systems (USFWS, 1998; Moyle, 2002). Other races found in the system are the fall-run, late fall-run, and spring run Chinook salmon. In the case of Chinook salmon, both stream-type and ocean-type life histories are present (Clarke et al., 1992; Love, 1996). The life-history strategy shown by a particular race is important because it determines the temperature regime the juveniles will be exposed to during their freshwater rearing period.

Rivers within the Sacramento-San Joaquin system support the southernmost stocks of Chinook salmon (Moyle, 2002), a distinction that has led some researchers to hypothesize that these populations are better adapted to warmer Mediterranean climates than stocks from cooler, more northerly regions. Conditions in the drainage basin are arguably warmer than those found in Oregon, Washington, or British Columbia, so water temperatures are more likely to approach critically warm levels in the SSJR system than in other regions.

Perhaps the strongest catalyst for the intense interest in these fish populations was generated by the protection, or proposed protection of some of the stocks under both state and federal endangered species regulations. The majority of the rivers comprising the Sacramento-San Joaquin system are highly modified, regulated, and are actively managed for multiple purposes including water development for agricultural, industrial and municipal uses, flood control, fisheries, and recreation. Any listing of a particular Chinook salmon or steelhead stock was, and still is likely to have cascading effects on the various stakeholders, so the demand for accurate information on the stocks is high.

The proximity of the SSJR system to large population centres like Sacramento, Stockton, and the San Francisco Bay Area subjects the steelhead and Chinook salmon populations to an extensive sport fishery. The Chinook salmon populations, particularly those in the Sacramento, Feather, and American Rivers, have long been managed with this sport fishery in mind.

Unlike the Chinook salmon, which are no longer found in rivers south of the Sacramento-San Joaquin system, coastal *O. mykiss* populations can still be found in rivers and streams as far South as northern Baja California (Moyle, 2002). Presumably, these southern stocks show even greater adaptation to elevated temperatures than those in the central valley. Nevertheless, steelhead are of interest in central valley rivers for most of the reasons listed above for Chinook salmon, and also because they now have overlapping distributions with Chinook salmon in those rivers. Steelhead native to rivers in the Sacramento-San Joaquin system are members of the coastal rainbow trout group (Behnke, 1992; Moyle, 2002), and are regarded as members of the central valley steelhead evolutionarily significant unit (ESU) by the US Fish and Wildlife Service (1998). However, central valley steelhead stocks have been supplemented with hatchery transfers, including fish from the Eel River, on the northern California coast, that are listed in the Northern California steelhead ESU.

Central valley steelhead are classified as winter-run fish, although they may enter freshwater as early as August (Moyle, 2002). 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 steelhead 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 or to managed thermal regimes designed to protect juvenile fall-run Chinook salmon that have a relatively short freshwater residence time.

The effects of water temperature on Chinook salmon and steelhead have been the subject of a large number of published studies; the findings of many of these were comprehensively reviewed by McCullough (1999). However, the majority of the published studies on the responses of Chinook salmon and steelhead to water temperature have been conducted on fish from stocks in Oregon, Washington, and British Columbia. Because of the presumed northerly bias of these studies, stakeholders interested in the management of central valley rivers and their Chinook salmon and steelhead stocks often request regional, or even drainage-specific information to support their management decisions. A common complaint of such stakeholders is that despite the large volume of research that has been conducted, the information they desire remains unknown or unavailable. A significant amount of research at the regional and drainage-specific levels has been conducted by state and federal agencies, private consulting firms, non-profit organizations, and academic institutions, but a surprisingly small proportion of this information has appeared in peer-reviewed scientific journals. The objective of this review is to summarize the peer-reviewed literature generated from regional or drainage-specific studies of Chinook salmon and steelhead physiology and behaviour in California's SSJR system in an effort to identify topics where additional research is warranted, or, if suitable studies have already been conducted, where an effort to submit the results to the scientific peer-review process should be made. This review is not an attempt to comprehensively summarize our knowledge about the effects of temperature on Chinook salmon and steelhead in general, as such work has already been done (e.g., see McCullough 1999). The review will focus on four topic areas where data are available: thermal tolerance, thermal preference, growth, and smoltification. The authors recognize that other, temperature-related topics, including behaviour (including thermal preference), disease, smoltification, migratory patterns, and interspecific interactions, are of interest. However, the paucity of data preclude their inclusion.

Thermal tolerance and thermal preference

Introduction

California's SSJR system represent the southern limit of Chinook salmon distribution and includes some of the more southerly populations of anadromous steelhead, so temperature regimes experienced by endemic 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 and duration of periods of near-freezing water temperatures in areas used by salmonids. However, because of the regular occurrence of water temperatures exceeding 20 °C in parts of the system, warm water temperatures are an important management issue. Water temperatures in the lower Sacramento River mainstem regularly exceed 20 °C by late spring, and studies of coded-wire tagged juvenile Chinook salmon show that high temperatures are an important factor in mortality (Baker et al., 1995). Because of the prevalence of spatially and temporally distinct regions with high water temperatures, studies of Chinook salmon and steelhead thermal tolerance have been of significant interest to California fisheries managers.

Direct evaluations of thermal tolerance in fishes use death or loss of equilibrium as the experimental endpoints (Becker and Genoway, 1979). Such studies fall into two broad classes – those that place fish in water whose temperature continues to increase or decrease until the endpoint is reached, and those that hold the fish at a constant temperature until the endpoint is reached or no effect is seen. Critical thermal tolerance (CTM) studies use rapid rates of temperature change (ca. 0.33 °C min^{-1}), and 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., 1995; Myrick and Cech, 2003), water quality (Gunn, 1986), and pollutants (Roch and Maly, 1979). Studies that use slower rates of change (ca. 1 °C d^{-1}) than CTM-type studies are used to determine the incipient lethal temperatures (ILT) (Kaya, 1978). The latter studies typically provide more useful information regarding a species' ability to tolerate elevated temperatures under field conditions.

Thermal tolerance may also be evaluated in studies where fish are held under a fixed thermal regime (Hokanson et al., 1977). Such studies are useful for determining survival times at a known temperature, determining the effects of temperature on a specific life stage, or observing chronic lethal or sublethal thermal effects. Studies of all three types have been conducted on Chinook salmon and steelhead at life stages from eggs to adults. Regardless of experimental methodology, all thermal tolerance data are affected by acclimation temperature, wherein fish acclimated to higher temperatures typically have higher upper thermal tolerances than fish acclimated to cooler temperatures (Becker and Genoway, 1979; Threader and Houston, 1983). It is important, therefore, to have some knowledge of a fish's thermal history when evaluating thermal tolerance.

Egg and alevin thermal tolerance

Egg and alevins thermal tolerance is most commonly measured in studies where the subjects are held under a fixed temperature until a developmental endpoint is reached or until a fixed percentage of the fish reach a certain endpoint. Data commonly collected from such studies include time to hatching, survival at hatching or swim-up (Combs and Burrows, 1957), size at hatching, and survival during the sac-fry to swim-up fry transition (Murray and McPhail, 1988).

Chinook salmon eggs and larvae can survive temperatures as low as 1.7 °C (Combs and Burrows, 1957) and approaching 16.7 °C (Hinze, 1959) but mortality at both extremes is high. Slater (1963) reported that Sacramento River winter-run Chinook salmon eggs could develop between 5.6 and 14.0 °C; he also pointed out that temperatures at the lower extremes were not often encountered. Hinze (1959) found that American River Chinook salmon eggs incubated in water warmer than 16.7 °C experienced 100% mortality before reaching the eyed stage; he also noted that mortality decreased as the water temperature decreased. Healey (1979) reported that Sacramento River fall-run Chinook salmon egg mortality rates exceeded 82% at temperatures over 13.9 °C and that post-hatching mortality was also higher at the elevated temperatures. Healey also stated that Sacramento River fall-run Chinook salmon eggs did not appear to be any more tolerant of elevated water temperatures than eggs from more northern races. A recent unpublished study on Sacramento River Chinook salmon by the US Fish and Wildlife Service (1999) concurred that fall-run egg mortality increased at temperatures greater than 12 °C and winter-run egg mortality increased at temperatures over 13.3 °C. Based on these studies, and on studies of temperature requirements for northern races of Chinook salmon, temperatures between 6 and 12 °C appear best suited to Chinook salmon egg and larval development.

There are no published peer-reviewed studies on the effects of temperature on the development and survival of Sacramento-San Joaquin steelhead eggs and sac-fry. Most of the data on steelhead are circumstantial, such as the report by Orcutt et al. (1968) that steelhead in Idaho's Clearwater River spawned at temperatures between 2 and 8 °C. There are also data on the effects of temperature on non-anadromous rainbow trout egg and larval survival and development, including Embody's (1934) pioneering work, and Stonecypher and Hubert's (1994) comprehensive survey of Eagle Lake and Hot Creek strain rainbow trout. This latter study demonstrated that the Eagle Lake strain was more tolerant of low temperatures than the Hot Creek strain. Given the continuum of rainbow trout and steelhead life histories, the Stonecypher and Hubert (1994) study hints at the possibility that some gross strain-level differences may exist. Unpublished data on central valley steelhead egg thermal requirements and tolerances undoubtedly exist, as the species has been cultured in hatcheries for decades. Ideal temperature ranges for steelhead can only be looked at in a broad sense; egg survival is low at temperatures below 5 °C, increases to a maximum around 7–10 °C, and declines at temperatures above 10 °C.

If you compare the data that are available for central valley Chinook salmon and steelhead egg and alevins, it is apparent that while there is some overlap of optimal temperature ranges, steelhead probably do better in slightly cooler water than do Chinook salmon. In most central valley rivers that still support runs of both steelhead and Chinook salmon, the amount of spawning habitat available is limited and Chinook salmon and steelhead may be forced to use the same reaches, whereas they were likely spatially separated under pre-impoundment conditions. This superimposition of spawning habitat means that managers need to take care not to set temperature criteria that are biased towards the upper end of Chinook salmon optima that are outside of the optimal range for steelhead.

The acute lack of central valley – specific published data on Chinook salmon and steelhead egg and larval temperature requirements is problematic. The Chinook salmon do not appear to show strain-level differences in thermal requirements and limits, but it is possible that the steelhead might. Based on our review of the available literature, the authors recommend that studies in the following categories be conducted.

First, comprehensive studies of how incubation temperatures between 5 and 17 °C (in 2–2.5 °C increments) affect the development, mortality, and recruitment of the various races of Chinook salmon and steelhead. If possible, such a study would compare races both within and between the various central valley rivers to answer, once and for all, the question of whether certain races are more cold- or warm-tolerant than others. Such a study should look at survival, size at swim-up, and hatching time, with the intent of producing predictive models similar to those developed by Crisp (1981, 1988) and Humpesch (1985). If the model results can link development and survival to the number of degree-days, then they will be more applicable to field conditions where fluctuating temperatures are encountered.

Secondly, a comparative study between representative races of central valley Chinook salmon and steelhead and northern races should also be conducted to check for the presence of latitudinal variation in thermal tolerance, because such variation does occur in other aspects of Pacific salmon physiology, such as egg size and egg number (Fleming and Gross, 1990; Beacham and Murray, 1993). The objective of such a study would be to determine whether central valley fisheries managers can confidently use data collected on northern strains of Chinook salmon and steelhead. Once studies along these lines are completed, fisheries managers will have a much greater understanding of the effects of temperature on the most stenothermal lifestages of these two species, and will be better equipped to tackle the challenging management situation posed by their superimposed spawning areas.

Juvenile thermal tolerance

Juvenile salmonids are moderately stenothermal, compared to the more stenothermal eggs and larvae. In the Sacramento-San Joaquin system, acute and chronic episodes of elevated temperatures (above the optimal range for salmonids) are of major concern, while episodes of temperatures below the optimal range are rare and of little concern. Water temperatures in the SSJR mainstems and the major tributaries (e.g., Stanislaus River, Feather River, American River) can be regulated to some degree by reservoir releases, though these releases require the use of water that may be earmarked for other uses such as irrigation or power generation. Biologists in the central valley are particularly interested in the maximum and minimum temperatures that occur within a waterway because those will define the spatial and temporal boundaries of juvenile rearing habitats.

Juvenile Chinook salmon are stenothermal (Brett, 1952) and can survive up to 7 days in temperatures as low as 0.8 °C when acclimated to 10 °C water. In the same study, Brett (1952) showed that the incipient lower lethal temperature (ILLT) for the Dungeness Hatchery strain (WA) Chinook salmon increased to 7.4 °C for fish acclimated to 24 °C water. There are no published data on the lower acute or chronic lethal temperatures for the various races of Chinook salmon within the SSJR. It is likely, however, that SSJR Chinook salmon lower thermal limits are similar to those of more northern strains, though biologists should pay close attention to the fishes' thermal history, if known, because of the large effect acclimation temperature has on thermal tolerance.

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

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

While IULTs are generally of the most interest to managers, there are a few situations where data on acutely lethal temperatures may be needed. Under low flow conditions, it is possible for water temperatures to exceed the IULT for short periods; in these cases, critical thermal maxima (CTM) data would be useful, particularly if the study correlated water temperature with resistance time. No published data of this type are available for central valley Chinook salmon; an unpublished report by Cech and Myrick (1999) based on critical thermal tolerance trials conducted on American River fall-run Chinook salmon that had been previously reared for a related growth study (Myrick and Cech, 2002) states that the CTM for 19 °C – acclimated Chinook salmon was 28.8 °C. It is clear that a study looking at the relationship between elevated water temperature and tolerance time is needed for central valley Chinook salmon strains, because exposure to water that is less than a degree warmer than the IULT for a few minutes is obviously less critical than a more prolonged exposure to the same temperature, or a short exposure to a temperature that approaches, or exceeds the CTM.

Data on the thermal tolerances of central valley steelhead strains are even rarer than those for Chinook salmon. Rainbow trout (and presumably steelhead) ILLTs approach 0 °C when the fish have been acclimated to 10 °C, and are slightly higher as the acclimation temperature is increased (Becker and Genoway, 1979; Currie and Tufts, 1997). Studies on rainbow trout report IULTs of 22.8 to around 26 °C (Bidgood and Berst, 1969; Threader and Houston, 1983), but none of these studies were conducted on California rainbow trout strains. Myrick's (1998) dissertation reports CTM of 27.5, 28.4, and 29.6 °C for juvenile American River steelhead that were acclimated to 11, 15, and 19 °C, while a technical report by Myrick and Cech (2000a) states that juvenile steelhead from the Feather River had a CTM of 30.8 °C, a higher value than the CTM of 29.4 °C that they measured on hatchery-reared juvenile Feather River steelhead acclimated to 16 °C.

Clearly, more research is required on the thermal tolerances of central valley strains of Chinook salmon and steelhead, as these are some of the values most often requested by resource managers. Because of the strong influence of acclimation temperatures, future studies should look at a range of specific acclimation temperatures, but should also look at natural thermal regimes and at warming scenarios superimposed on natural thermal regimes. Ideally, a model could be developed with data from such studies that would predict the percent survival of the species of interest given a specific thermal profile. It is also important to realize that because juvenile steelhead and Chinook salmon can take advantage of spatially heterogeneous temperature profiles, often at a finer resolution than is normally measured or modelled (Nielsen et al., 1994; Matthews and Berg, 1997), it is important that we gain some understanding of the thermal histories of fish within central valley systems. Additionally, though death is the most common endpoint for most studies of acute and chronic thermal tolerance, detrimental effects to a fish's physiology and behaviour start to occur at lower temperatures, and studies that can quantify these sublethal effects are perhaps even more important, in the long run, than studies that merely determine the absolute thermal limits.

Growth and smoltification

Introduction

Growth is perhaps the most powerful and complete integrator of environmental, behavioural, and physiological influences on a fish's fitness. Growth is the storage of excess energy; positive growth indicates an energy surplus. Fish growth rates are influenced by a number of factors including temperature (Myrick and Cech, 2000b), 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., 1981), 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.

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, behavioural, and environmental changes they experience. Both Chinook salmon and steelhead are subject to gape-limited predation and are themselves gape-limited predators (Sholes and Hallock, 1979). If these juvenile salmonids can rapidly increase in size, their vulnerability to predation decreases while their ability as predators increases.

The development of seawater 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. 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 (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, 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):

$$C = (M_r + M_a + SDA) + (F + U) + (G_s + G_r).$$

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 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

There have been two studies published on the effects of temperature on the growth of SSJR Chinook salmon races; one by Marine and Cech (2004) on Sacramento River fall-run fish, and the second by Myrick and Cech (2002) on American River fall-run fish. Marine and Cech (2004) reared fall-run Chinook salmon at 13–16 °C, 17–20 °C, and 21–24 °C and reported a maximal growth rate of 3.3% wt/d at 17–20 °C. An interesting side note from this study was that fish reared at 21–24 °C still grew, but were more vulnerable to predation (under laboratory conditions) by striped bass (*Morone saxatilis*). Myrick and Cech (2002) reported a maximal growth rate of 4.4% wt/d for American River fall-run Chinook salmon fed satiation rations at a constant 19 °C; fish reared at 15 and 11 °C grew at slower rates, as did those fed a 25% satiation ration at all three temperatures. The results of these two studies compare favourably with those conducted on two northern Chinook salmon races by Clarke and Shelbourn (1985) and Brett et al. (1982), where the Big Qualicum River strain grew at 3.3% wt/d at 20.5 °C, and the Nechako River strain grew at 3.2 % wt/d at 18.9 °C.

The studies referenced above suggest that the optimal temperature for Chinook salmon growth lies within the 17–20 °C range, provided that food is not limiting, and other factors, such as disease, predation, and competition have a minimal effect. However, it is unlikely that Chinook salmon in field conditions will feed at 100% satiation, and the effects of disease, competition, and predation should also be taken into account. Therefore, growth rates observed under field conditions are likely to be lower. Using a model developed for sockeye salmon (*O. nerka*), Brett et al. (1982) determined that temperatures of 18.9–20.5 °C were optimal for juvenile Chinook salmon fed to satiation, but salmon that fed at 60% of satiation reached their optimal growth temperature at ≈15°C. Brett et al. (1982) based the feeding level (60% of satiation) on field studies that suggested that wild fish fed at roughly 60% of their physiological maximum. This study underscores the importance of taking field conditions into account when trying to apply results from a laboratory study.

The effects of water temperature on Chinook salmon growth are extremely important, perhaps only second to the direct effects of water temperature on Chinook salmon survival. As was noted above, larger juveniles have a greater probability of survival during the parr – smolt transformation (Wedemeyer et al., 1980) and of returning as mature adults (Unwin, 1997), therefore resource managers should try to provide conditions that allow juvenile anadromous salmonids to maximize their freshwater growth rates. Given the small number of published studies available, it is apparent that more research is needed, particularly on the combined effects of temperature with ration levels and ration types comparable to those seen under field conditions. A useful model for such studies are the comprehensive investigations conducted by (Elliott, 1975a, b and 1976) on brown trout (*Salmo trutta*) that examined the effects of temperatures from the ILLT to the IULT and ration levels from sub-maintenance levels to 100% satiation. A study of this scale should be conducted for the major central valley Chinook salmon races, and would lead to the development of more accurate models of the effects of temperature and ration level on central valley salmon growth. Such studies need to be conducted concurrently with studies of field growth rates, food availability, and thermal profiles.

Steelhead

Whereas most juvenile central valley Chinook salmon spend less than a year in freshwater, and rarely over-summer, juvenile steelhead in the SSJR system spend at least one full summer in freshwater, and therefore have a greater likelihood of being exposed to chronically elevated water temperatures. The California Department of Fish and Game has recognized this problem, but until fairly recently, research into, and management of central valley steelhead populations has been secondary to research and management of Chinook salmon populations (McEwan and Nelson, 1991; McEwan and Jackson, 1996). Because of the loss of access to upstream rearing habitats, juvenile steelhead in most central valley rivers now rear in the same areas as juvenile Chinook salmon, and have thus been subjected to thermal regimes that were tailored primarily for Chinook salmon rearing.

Unfortunately, research on central valley steelhead has been rare, and no studies of the effects of temperature on central valley steelhead growth have yet been published in the primary literature. Myrick (1998) reports that when American River steelhead were fed to satiation at temperatures of 11, 15, and 19 °C, growth rates increased from a low of 1.3% wt/d at 11 °C to a maximum of 2.6% wt/d at 19 °C. This study only looked at three temperatures in a relatively narrow range, and did not explore the effects of sub-optimal temperatures (i.e., those above 19 °C). Therefore, one cannot conclude that 19 °C is the best temperature for juvenile steelhead growth, or if it was just the best temperature among those tested. In defence of Myrick's (1998) information, the results do show the same patterns as those reported by Wurtsbaugh and Davis (1977a, b) who conducted the most extensive studies yet published on the effects of temperature and ration level on juvenile steelhead, albeit a northern strain from the North Santiam River in Oregon. Key findings from their studies include that maximal growth (3.5% wt/d) occurred at 16.4 °C and that steelhead were capable of growing at temperatures as high as 22 °C. Wurtsbaugh and Davis (1977b) also reported that the optimal growth temperature declined as the ration level was reduced from satiation to 60–50% of satiation.

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

Conclusion

Environmental temperature exerts profound effects on stream-associated life stages of Chinook salmon and steelhead. Egg and alevin temperature tolerance limits for Chinook salmon (approximately 6–12 °C) and steelhead (approximately 7–10 °C) are more narrow than those for these species' juveniles (approximately 1–24 °C, and approximately 1–25 °C, respectively). Both species grow more slowly at temperatures above and below approximately 17–20 °C for Chinook salmon juveniles and approximately 19 °C for steelhead juveniles. Some differences among strains (within species) appear to exist, but more comparative-strain studies are needed using fish with identical thermal acclimatory histories (for temperature tolerance limits), rations (for growth rates), and water qualities (for both types of experiments). Overall, field conditions of particular watersheds should be incorporated into the design of future laboratory experiments. Finally, habitat temperature characteristics should be strongly considered in future ecosystem management efforts, to reverse decreasing population trends (e.g., associated with stream modifications and predicted global warming effects) of these valuable species in California's central valley streams.

Acknowledgements

We thank the US Bureau of Reclamation, the California Department of Water Resources, the Bay-Delta Modeling Forum, and the Department of Fishery and Wildlife Biology at Colorado State University for financial support; J. Williams, and three anonymous reviewers for reviewing a prior version of the manuscript, and J. Roessig for editorial assistance.

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