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Water temperature thresholds for coho salmon in a spring-fed river, Siskiyou County, California

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Coho salmon (*Oncorhynchus kisutch*) populations in California have declined at an alarming rate in the last 40 to 50 years. Detrimental water temperatures in the Shasta River have contributed to this decline. At one time, the Shasta River was a cool water stream with flows dominated by springs originating from underground flow from Mt. Shasta and snowmelt from the Eddy Mountains. Agricultural practices and water diversions have eliminated much of the historic high-quality aquatic habitat, and only remnants of the once abundant cool water habitat exist. Cool water temperatures are critical for the freshwater phase of the coho salmon life cycle, and are imperative for population recovery. Based on a literature review of the effects on the physiology, behavior, and survival of coho salmon, we break water temperatures into optimal, suboptimal, and detrimental ranges. Identifying water temperature thresholds for coho salmon will support the implementation of monitoring stations and adaptive management practices to assure that suboptimal temperature thresholds are not exceeded. It is well documented that the establishment and use of locally determined thresholds as performance criteria in the monitoring and adaptive management of ecosystems is critical to conducting restoration activities. We conclude that protecting the cool water produced by springs located in the upper Shasta River springs complex will improve the likelihood of coho salmon persistence in this watershed and contribute to coho salmon recovery.

Key words: California, cold water springs, coho salmon, *Oncorhynchus kisutch*, rearing habitat, recovery, temperature, thresholds, Shasta River, Siskiyou County

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A status review of coho salmon (*Oncorhynchus kisutch*) concluded that populations in the Southern Oregon-Northern California (SONCC) Evolutionarily Significant Unit continue to decline (Southwest Fisheries Science Center 2001). In this portion of their range, coho salmon are listed as a threatened species under both the state and federal endangered species acts. The current population status of coho salmon in the Shasta River, a tributary to the Klamath River in northern California (Figure 1), has reached a critical point. Due to the low abundance of returning adults and observed low smolt survival rates, all three cohorts are well below depensation threshold levels (Williams et al. 2008). In 2009, a total

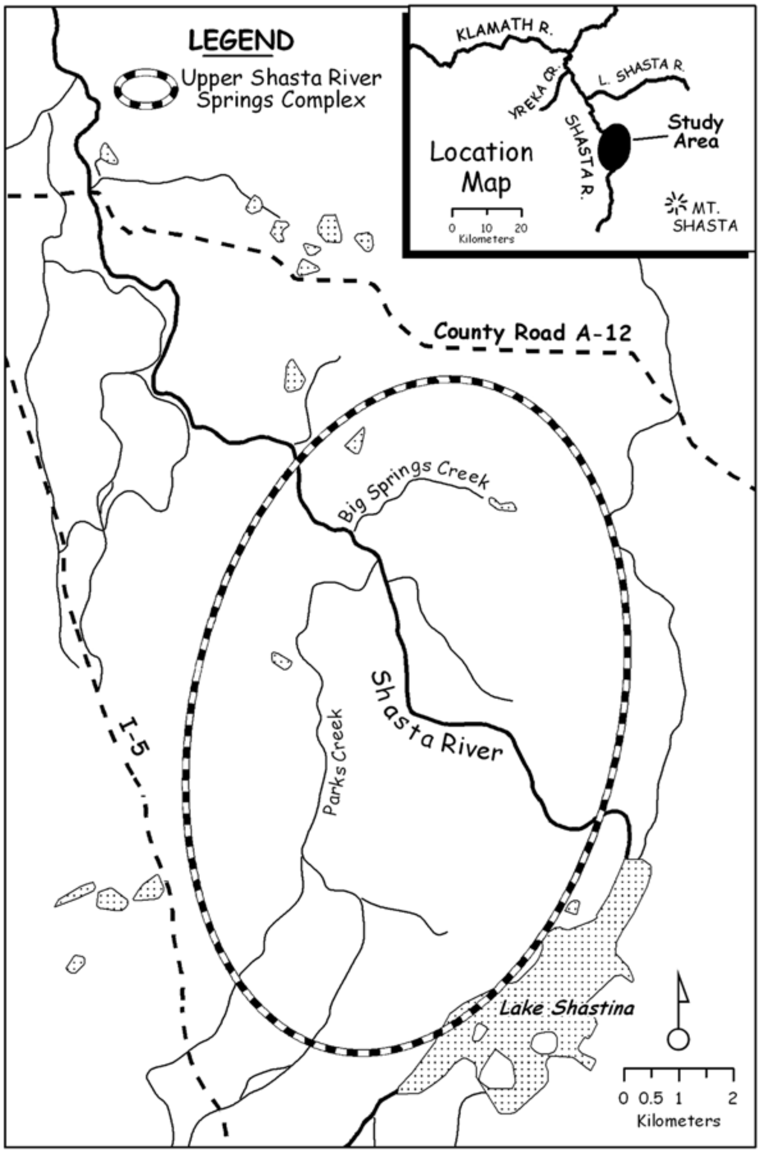

Figure 1.— Location of Shasta Valley and the upper Shasta River springs complex, Siskiyou County, California.

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of nine adult coho were documented returning to the Shasta River to spawn. In 2010, a total of 44 coho returned to spawn; unfortunately, the 2010 cohort was considered the strongest remaining cohort. It is well documented that small populations are particularly vulnerable to extirpation (Shaffer 1981). Specifically, extinction risk is quite high once the effective population size is lower than 50 spawners (Williams et al. 2008).

To improve survival of juvenile coho salmon in the Shasta River and promote recovery, it is important to maintain optimal stream water temperatures all summer. Juvenile coho salmon rearing in the Shasta River move into and utilize remnant cold water springs during the summer months. When air temperatures exceed 38ºC and there is increased demand for irrigation water, juvenile coho salmon may be displaced from cold water habitat into portions of the watershed with suboptimal aquatic habitat conditions. Temperature is one of the most important abiotic factors exerting control over performance and survival (Brett 1971, Beitinger and Fitzpatrick 1979, Hutchison and Maness 1979). Previous studies of juvenile coho salmon rearing in the Shasta River indicate water temperature plays a crucial role in their distribution, behavior, and survival (Chesney et al. 2009). Fish are ectothermic organisms, whose body temperature is regulated by external environmental conditions. Growth, physiology, and behavior of fish are all influenced or modified by water temperature. Temperature requirements are even more acute among salmonids, in which optimum survival conditions are confined within a narrow range of temperatures (McCullough et al. 2001).

Since swimming performance, growth, disease resistance, and other functions all are optimized within a fairly limited temperature range, California Department of Fish and Game (2004) identified general water temperature threshold values for coho salmon. Due to declining coho salmon numbers and the potential to improve habitat conditions and increase productivity by managing for optimal water temperature conditions, this paper re-examines existing literature with the goal of identifying Shasta River-specific water temperature thresholds for coho salmon. The purpose of this paper is to identify freshwater temperature thresholds for coho salmon in the Shasta River, specifically in areas influenced by cold spring inflow, and we identify three distinct water temperature categories in this exercise: optimal, suboptimal, and detrimental.

STUDY AREA

The Shasta River, located in Siskiyou County in northern California, is one of four major tributaries to the Klamath River. The Shasta River enters the Klamath at river kilometer (RK) 285 at an elevation of approximately 607 meters, and drains a watershed of approximately 2,100 km^2. Major tributaries to the 80-km long Shasta River include Parks Creek, Big Springs Creek, the Little Shasta River, and Yreka Creek (Figure 1). The Shasta River watershed is bounded on the north by the Siskiyou Mountains, to the east by the Shasta-Cascade mountains, to the west by the Klamath Mountains, and to the south by Mount Shasta and Black Butte. The geographic coordinates of the center of the study area are 41° 33' 48" N and 122° 25' 36" W.

Annual precipitation ranges from less than 38 cm in parts of the Shasta Valley to over 114 cm in the Eddy and Klamath mountains, while precipitation on Mount Shasta ranges from 216 to 318 cm. As relatively little precipitation falls on the floor of the valley, the Shasta River receives much of its flow from glacial melt, which surfaces as spring flow, and runoff from precipitation on Mount Shasta and the Eddy Mountains.

The Shasta River is an inland drainage with hot dry summers and cold, snowy winters. Summer temperatures at times exceed 38ºC and average temperatures at Yreka range from approximately 20.5ºC in the summer to 2ºC during the winter. Vegetation in the watershed is diverse due to the variability in elevations, precipitation, and soil depths, and includes subalpine conifer, montane hardwood-conifer, rabbit brush, juniper, and montane riparian areas.

For purposes of this paper, the upper Shasta River is defined as the portions of the Shasta River and its tributaries upstream of Siskiyou County Road A-12 (Figure 1). A collection of springs known as the upper Shasta River springs complex provides cold water rearing habitat in this area, and will be referred to throughout the remainder of this paper (Figure 2).

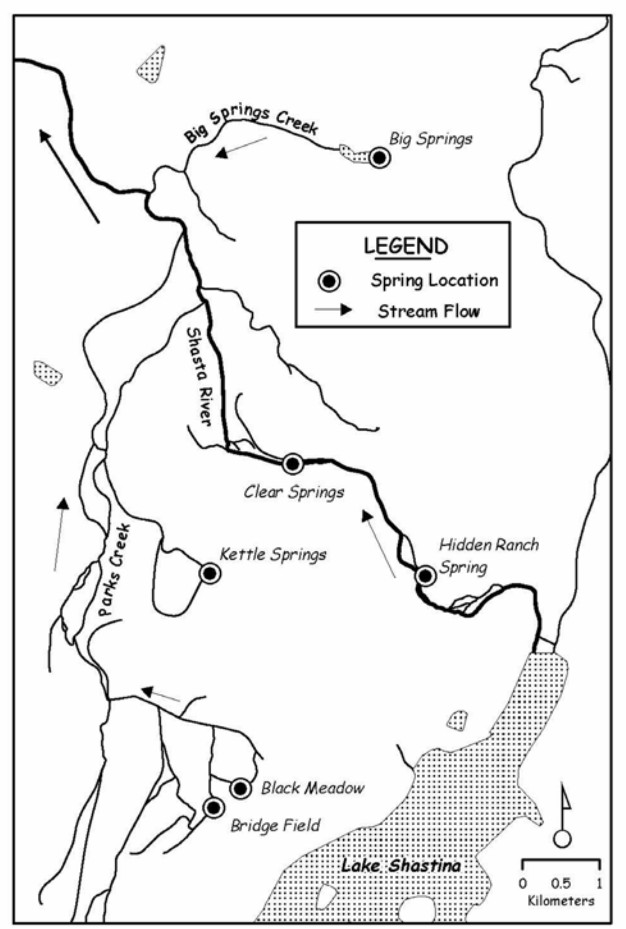

Figure 2.— Locations of cold water springs in the upper Shasta River springs complex, Siskiyou County, California.

Historic conditions.—Shasta River coho salmon abundance was described by Snyder (1931), who noted that salmonids in the Klamath River watershed were already in a state of decline. Snyder (1931) stated that due to "diversion of water for agriculture, mining, and power purposes, spearing fish on the spawning beds, and what not," habitat conditions for salmon in the Shasta River had been severely compromised. Hume (1893) described the devastation of the Klamath River by hydraulic mining and stated that salmon were so abundant in 1850 (prior to mining), "that in fording the stream it was with difficulty that they could induce their horses to make the attempt, on account of the river being alive with the finny tribe." By the time he published his account, Hume (1893) observed that the spring Chinook salmon were practically extinct and the fall Chinook salmon were reduced to very small portions of their historic runs. Written documentation regarding coho salmon in the Klamath Basin, especially in the upper Klamath River, is scarce prior to the early 1900s. Contributing to the lack of information was the apparent difficulty in recognizing that there were different species of salmon inhabiting the rivers of California.

Prior to 1893, accounts of aquatic habitat quality are embedded in the cultural accounts of Native Americans. Merriam (undated) described the existence of a summer salmon fishing camp on the Klamath River at the mouth of the Shasta River that was used by the Shasta tribe prior to the discovery of gold and the resulting European settlement (~1850s). The presence of this camp indicates that spring Chinook salmon were present during the summer. In documenting the customs of the Shasta tribes, Curtis (1924) noted that salmon runs formerly appeared in the Klamath River and its tributaries "in the spring at the time of greening grass." Optimal spring Chinook water temperatures for holding adults are 8°C to 12.5°C (McCullough 1999). Optimal water temperatures for rearing juvenile coho salmon, also present during the summer months, are 8°C to 15.6°C (discussed below). Therefore, we make the assumption that aquatic habitat conditions necessary for both species were present in the Shasta River watershed.

Snyder (1931) and Wales (1952) both noted that spring Chinook salmon historically entered the Shasta River in June and early July. The California Department of Water Resources (CDWR; 1964) reported that spring Chinook salmon entered the Shasta River during May and June and spent the summer in the river, benefiting from the cool, steady flow from upper Shasta River springs. Moyle (2002) postulated that the spring Chinook salmon run in the Shasta River may have been the largest run in the Klamath River watershed. Spring Chinook salmon still enter Klamath River tributaries, such as the Salmon River, during late spring and early summer while not yet gravid. They typically hold in deep cold pools in the upper reaches of tributaries during summer. For spring Chinook salmon to be present, adequate water temperature had to be sustained all summer long.

The elimination of spring run Chinook in the Shasta River has largely been attributed to habitat degradation, altered flow regimes, and elevated water temperatures that were realized after construction of the Dwinnell dam (Moyle et al. 1995). Constructed in 1928, the dam acted as a barrier that eliminated access to approximately 22% of the historic habitat for migratory salmonids (Wales 1952, National Research Council 2004). Wales (1952) remarked that the migratory movement of spring-run Chinook salmon would be impossible with water temperatures frequently rising above 26°C-29°C. He stated that "very probably these high temperatures were not attained until after large scale irrigation was begun in the Shasta Valley." Furthermore, in his description of Big Springs, which, prior to modification, supplied 100 cfs of cold water (11°C), he went on to note that, "if none of this water was removed for irrigation, the volume and temperature would make the river suitable for salmon all the way to the mouth and at all times of the year" (Wales 1952). This view was supported by the National Research Council (2004), which found that historic spring flows and accretions would have maintained flow volumes similar to today's bank-full conditions, even during summer months. Additionally, this cold water may have also cooled the main-stem Klamath near the confluence with the Shasta River (National Research Council 2004). CDWR (1964) reported that a section of river below Big Springs, as well as Big Springs Creek itself, were heavily utilized by spawning steelhead and coho salmon.

Current conditions.—Irrigation demands, tailwater return flow, and the construction of diversions blocking anadromous fish movements are among the factors that have reduced the historic salmonid range and abundance within the Shasta River basin. In addition, unfenced grazing has led to the trampling of banks and removal of vegetation in riparian areas, which has contributed to the acceleration of bank erosion, loss of shading, reduced accumulation of woody debris, loss of channel complexity, and degredation of water quality (National Research Council 2004). The upper Shasta River springs complex comprises the remnant of the historic high-quality habitat; however, most of these springs have been impacted by the construction of dams that facilitate flood-irrigation practices. Moreover, the removal of cold water from the stream channel below the spring source for irrigation purposes affects its utilization by various life stages of salmonids.

The North Coast Regional Water Quality Control Board (NCRWQCB) identified the Shasta River as an "impaired" waterbody due to water temperatures exceeding those temperatures in which native coldwater fish species can thrive. Water temperature data collected by the NCRWQCB in 2002 and 2003 showed that maximum daily water temperatures in the Shasta River (in reaches outside of areas influenced by spring inflow) exceeded 21°C for the entire summer (June through September) during both years (Flint et al. 2005). The threshold of 21°C was selected by NCRWQCB because it is the temperature above which migration of adult spring Chinook salmon is halted and at which the fish may begin to experience reduced survival as a result of increased exposure to adverse conditions while awaiting decreases in temperature necessary for the resumption of migration (Major and Mighell 1967, Armour 1991, Flint et al. 2005).

Field studies conducted in the Shasta River during 2008 and 2009 determined that summer rearing habitat utilized by juvenile coho salmon was limited to three locations in the upper Shasta River where water temperatures were maintained at optimal levels by cold springs (Chesney et al. 2009). Juvenile coho salmon tagged with passive integrated transponders (PIT) migrated over 6 km upstream to these spring reach locations as water temperatures in the river warmed.

In many years, after the onset of the irrigation season (1 April), emigrating coho salmon smolts are deprived of the amount of cold water necessary to allow for survival and migration into the Klamath River. During monitoring of smolt emigration in 2009, regions of the upper Shasta River were identified where high mortality occurred, and low flows and high water temperatures were documented. PIT-tagged coho smolts experienced 43% mortality in a 2.4 km reach (RK 58.7 to 56.3) of the upper Shasta River compared to 20.3% mortality for the remaining 56.3 km to the Klamath River. In addition, rotary screw trap data collected in April 2001, 2002, and 2003, from the lower Shasta River showed that age 0^+ salmonid outmigration is positively correlated with the onset of low flows and increased water temperatures (Chesney et al. 2004). Coho salmon smolts have similar thermal requirements as do rearing juveniles.

The once extensive cold water habitat available in the Shasta River, as illustrated by available historic spring Chinook salmon abundance data, has been reduced to a small percentage of its former extent. The cold water habitat that does remain is located in the area of the upper Shasta River spring complex (Figure 2). Establishing and implementing protective temperature standards and flows within and adjacent to these residual cold water rearing habitat areas will likely increase survival rates of the progeny of each coho salmon cohort, and assist in the recovery of Shasta River salmonid populations in general.

Materials and Methods

To develop criteria for water temperatures that will assure survival of coho salmon and other anadromous fish in the Shasta River, we conducted a careful and thorough literature review. The literature on effects of water temperature on species and communities is voluminous. However, despite the extent of that literature, there is still debate about how this information applies to conditions found in natural streams (McCullough 1999). In this paper we summarize information about this topic, recap the important issues, and synthesize the results to provide guidance that could be used for monitoring and adaptive management purposes. We have attempted to evaluate our sources and advise the reader on the most pertinent or relevant information. Specifically, we evaluated each source to determine if it provided information about the effects of water temperatures on the physiology, behavior, or survival of salmon. We collected experimentally derived temperature data from the literature that illustrated the relationship of water temperature to salmonid growth rate, survival, and physiological optima. This is referred to as "experimental temperature tolerance results" by Armour (1991).

In order to simplify the temperature thresholds we propose for coho salmon in the Shasta River, we focus on identifying temperatures that optimize the growth rate of juveniles. Exceedance of lethal temperatures in the summer in rearing habitat is one of the main limiting factors for juvenile coho salmon in the Shasta River. With peak summertime ambient temperatures and peak irrigation needs occurring at the same time, juvenile survival is a primary concern. Another approach to setting temperature thresholds would be to identify a temperature regime that would allow us to identify different temperature ranges for each life stage (Armour 1991). Due to the immediacy of the need to minimize lethal temperatures in summer rearing habitat, we focused our efforts on achieving temperatures that will maximize juvenile rearing and growth.

Results

Based on the documented effects on the physiology, behavior, and survival of juvenile coho salmon, water temperatures can be broken into optimal, suboptimal, and detrimental ranges.

Optimal temperature range for rearing and growth.— McCullough (1999) defined "the optimal temperature range" as the temperatures in which fish demonstrate "normal physiological responses and normal behavior (i.e., without thermal stress symptoms)." Several authors have reported that the optimum temperature range for many juvenile salmonids, including coho salmon, is generally between 10.0°C and 15.5°C. For example, Bell (1991) identified optimal temperatures for coho salmon between 11.7°C and 14.5°C.

Reiser and Bjornn (1979) reported similar values as the optima for juveniles. Moyle (2002) indicated that coho salmon juveniles favored temperatures between 12°C and 14°C. Similar values for optimum thermal ranges for juvenile salmonids have been noted by a number of authors (Jobling 1981, Konecki et al. 1995, McCullough 1999, Sullivan et al. 2000, Carter 2008). McCullough et al. (2001) conducted an extensive survey of available literature and identified an optimal growth temperature of 15°C for coho salmon feeding on full rations. The optimum growth temperature for juvenile coho salmon, as listed by Brungs and Jones (1977), is 15°C assuming an unlimited food supply (i.e., lab conditions). Sullivan et al. (2000) recommended an upper threshold for the seven day maximum temperature at 16.5°C in order to minimize growth loss in coho salmon; the lower threshold was listed as 13.0°C.

With respect to freshwater diseases, temperatures in the range 12.8°C-15°C appear to be least problematic for salmonids in resisting broad classes of disease (McCullough 1999). Coho infected with *Ceratomyxa shasta* exhibited low survival in water temperatures above 20.6°C, high survival at 9.4°C-15°C, and very high survival at 3.9°C-9.4°C (McCullough 1999). Generally, temperatures below 15.5°C are considered beneficial in allowing salmonids to maximize growth and swimming ability, while also conferring higher resistance against many diseases.

Most of the studies cited above occurred in laboratory settings. Even though field observations may be considered more meaningful because they are not influenced by the artifices of experimental equipment, much of the information on salmonid temperature requirements comes from laboratory studies. Laboratory experiments have been indispensable in determining fish survival and preference under various temperatures (McCullough 1999). In many of the laboratory experiments, fish are exposed to a temperature gradient until individuals ultimately congregate in the preferred temperature. Jobling (1981) noted that the final temperature preference of a fish species is a good indicator of the optimum temperature for growth.

Summary of optimal temperature range characteristics.—Juvenile salmonid growth, swimming performance, and disease resistance are best optimized at temperatures ranging from 10°C-15.5°C. Growth rates are positive and not directly affected by temperature. Many important pathogens have reduced virulence within this thermal range (McCullough 1999).

Suboptimal temperature range for rearing and growth.— Within the range of 15.6°C-20.3°C, juvenile salmonids still experience positive growth, but at a reduced rate. Even if food quality is maintained at a high level with increasing temperature, feeding rate and growth decline beyond the optimum temperature (McCullough 1999). Bell (1991) asserted that, in general, all cold water fish cease growth at temperatures above 20.3°C. This is due to increasing metabolic activity made necessary to maintain equilibrium at higher temperatures, but generally precluding the partitioning of resources for somatic development. Salmonids also experience a sharp rise in respiratory rates at temperatures above 15°C (Materna 2001). Generally speaking, temperatures above 15.6°C induce a number of compensatory behavioral and physiological responses in the salmonid meant to mitigate the effects of cumulative sublethal stressors, directly or indirectly attributable to thermal increase. The ability of the animal to tolerate or mitigate these stressors can be compromised if temperatures continue to rise.

Swimming ability may not be affected if factors such as food availability and dissolved oxygen levels are not limiting. Davis et al. (1963) found the maximum sustained swimming speed in under-yearling coho salmon to be highest at 20°C, compared to those fish held at 10° or 15°C. Brett (1995) identified the optimum temperature for maximizing metabolic scope in coho juveniles to be about 20°C.

The temperature value (20°C) derived by Brett (1952) is repeated in the literature and sometimes stated as an "optimum" temperature. However, this is a lab-derived value based on the behavior of fish that were fed, "in sufficient quantity to ensure abundance" (Brett 1952). Under field conditions, it is more likely that food is available at 60% of maximum laboratory rations (Brett et al.1982). Using juvenile Chinook salmon, Brett et al. (1982) found that optimum growth occurred at 19°C, but with the food levels assumed under normal field conditions; optimal growth is realistically achieved at 14.8°C. Willey (2004) stated that growth rates of juvenile coho salmon may decrease as water temperatures rise above 15.7°C if food availability is limiting.

The suboptimal temperature range can support growth and can be tolerated for relatively long periods. However, rearing salmonids including coho salmon may be displaced from existing habitat sites as temperatures increase to less than optimal levels. Tolerance of a particular high temperature does not imply that the fish will continue to persist under those conditions for any extended period of time. Behavioral thermoregulation is an important response to temperature changes. In fish, this is limited to seeking appropriate water temperatures. In comparison with terrestrial ectotherms (reptiles), fish require more space to behaviorally thermoregulate because of the differences in temperature gradients in water as compared to those of air temperatures (Beitinger and Fitzpatrick 1979). Lestelle (2007) noted that excessively high water temperatures or diminished flows could cause juvenile coho salmon to embark on extensive movements during summer. Sutton and Soto (2010) reported that juvenile coho salmon in the Klamath River entered cold water habitats when main-stem water temperatures surpassed 19°C. Konecki et al. (1995) observed that coho salmon generally avoided temperatures >15°C.

With rising temperatures, disease susceptibility (as measured by increasing incidence) tends to rise proportionally. Juvenile salmon show greater sensitivity to certain diseases at higher temperatures. Studies conducted on juvenile coho salmon and other salmonids have shown that individuals exposed to pathogens at higher temperatures experienced higher mortality and a decrease in mean-time to death. Ordal and Pacha (1963) described a study in which juvenile salmon exposed to a particular strain of *Flavobacterium columnare*, the causative agent of Columnaris disease, experienced a mortality rate of 30% at 16.1°C, which increased to 100% at 22.2°C. Above 21°C, the pathogen easily penetrated the protective mucus layer of uninjured fish. Fryer and Pilcher (1974) demonstrated a similar temperature-dependent rise in mortality among juvenile coho salmon exposed to *F. columnare*.

High water temperatures not only increase the incidence of bacterial disease, but may also increase susceptibility of salmonids to parasitic diseases. *Ichthyophthirius* (Ich) is a ubiquitious freshwater parasite that shows no host specificity and is difficult to treat (Herman 1990). Bell (1991) noted that this disease often affects juvenile salmon at water temperatures above 15.5°C. Temperature plays a role in susceptibility of salmonids to Ceratomyxosis (a disease that is caused by the parasite, *Ceratomyxa shasta*). In coho salmon exposed to *Ceratomyxa shasta*, mortalities increased progressively as water temperatures increased, from 2% at 9.4°C to 22% at 15.0°C to 84% at 20.5°C (Udey et al. (1975). It is important to note that virulence of a particular pathogen varies among different strains and is influenced by a number of factors. Infection, as well as any resultant morbidity or mortality, is not solely dependent upon temperature.

As water temperatures begin to exceed the optimum range, the availability of cold water habitat to individual salmonids may begin to contract, or disappear altogether. Feeding may also increase to maintain higher metabolic rates. Such increased demand for food, coupled with the decreasing availability of suitable cold water habitat, may increase competition among salmonids. Temperature regime is a key determinant of competitive interactions in a fish community (McCullough 1999). Juveniles that are smaller in size or those already experiencing various stresses may not be able to successfully compete for available habitat and may thus be forced into suboptimal habitats.

Fish operating within their optimum temperature range have an improved capability of performing, especially in relation to other species not within their optimum regime. Competition with warm water species may increase as temperatures rise. Many of the introduced species in the Shasta River system are warm water species whose physiological optima are at temperatures higher than those of the local salmonids. A number of introduced centrarchids and native and non-native cyprinid species, including those found in the Shasta River, have optimum growth rates at temperatures above the thermal preferences of juvenile salmonids (Brungs and Jones 1977). Increased temperatures depress the competitive advantage of salmonids and their ability to avoid predation, while simultaneously increasing the competitive advantage of warm water species (Sauter et al. 2001). This increases predation by piscivorous fish, while also increasing competition among other species for foraging space and food items. Sauter et al. (2001) described a study in which redside shiners (*Richardsonius balteatus*) affected juvenile Chinook salmon distribution at temperatures >18°C, but not at the optimum range of 12°C -15°C. Similarly, Reeves et al. (1987) noted that at temperatures >19°C, redside shiners affected the growth of juvenile steelhead trout (*Oncorhynchus mykiss*) and were able to exploit a wider variety of habitats. Those authors concluded that water temperature influenced the outcome of competitive interactions for habitat between the two species (Reeves et al. 1987). There is a paucity of studies on the interactions between introduced centrarchids and native salmonids. Moreover, similar studies on the nature of competitive interactions between juvenile coho salmon and various non-salmonids inhabiting the Shasta River have yet to be performed.

Summary of suboptimal temperature range characteristics.—Juvenile salmonids still experience positive growth rates in the suboptimal temperature range of 15.6°C-20.3°C, although such rates rapidly decrease with rising temperature. Metabolism and respiration increase dramatically above 15.6°C. Pathogen virulence and disease susceptibility begin to increase. Infected fish may experience increased mortality. As water temperature increases above 15.5°C, conditions become suboptimal for salmonids, but tend towards the optimal range of a number of introduced warm water fish. This increases competition between salmonids and non-salmonids, and can lead to greater predation on juvenile salmonids; thus far, this situation has not been documented in the Shasta River watershed.

Detrimental temperatures.— When water temperatures exceed 20.3°C, not only do the aforementioned factors increase in importance, but salmonids also experience detrimental effects directly attributable to temperature, and sublethal stresses begin to accumulate. Temperatures > 21°C can decrease or eliminate feeding behavior of salmonids (Hokanson et al. 1977). Since high temperatures depress feeding rates, prolonged exposure would eventually lead to deaths of fish simply because of malnourishment, if for no other reason (Brett 1952). Juvenile coho salmon exposed to temperatures in excess of 25°C, or subjected to a quick rise in temperature from 20°C to 25°C, experienced high rates of mortality (Sandercock 1991). Becker and Genoway (1979) determined the critical thermal maximum for coho salmon. Coho salmon acclimated to 15°C water, and then subjected to a 6°C rise in temperature per hour, experienced loss of equilibrium (i.e., locomotor activity became disorganized) at 28.2°C. At that stage the animal loses the ability to escape from conditions that will promptly lead to death. The upper lethal temperature reached was 28.8°C (Becker and Genoway 1979). Brungs and Jones (1977) indicated that juvenile coho salmon acclimated to 15°C have an upper lethal threshold of 24°C, while those acclimated to temperatures of 20°C or 23°C experienced an upper lethal threshold temperature of 25°C. Similarly, Brett (1952) reported that 25°C was the ultimate upper lethal temperature for juvenile coho salmon. Bell (1991) reported that the upper lethal temperature of juvenile coho salmon was 25.8°C, which is the highest temperature that can be achieved by acclimation. It must be noted, however, that death from extreme temperatures is not solely dependent upon exceeding a particular threshold, but also depends on exposure time.

Duration of exposure is an important factor to consider when considering lethal temperature effects. When discussing detrimental temperatures for fish, both the duration of high temperature as well as the ability of fish to recover from periods of heat stress must be considered. The latter can be accomplished either by thermoregulatory behaviors such as moving into available cold water habitat, or by taking advantage of the nightly drop in temperature. Bjornn and Reiser (1991) described a study performed in an Idaho stream that experienced a maximum daily temperature of up to 24°C that lasted for less than an hour. At night, water temperatures dropped to between 8°C and 12°C. Despite the high temperatures during the day, juvenile Chinook salmon and rainbow trout maintained high densities and grew normally, likely due to low temperatures at night. Hokanson et al. (1977) noted that the growth of rainbow trout was increased under fluctuating temperature conditions if the mean temperature was below a constant temperature optimum (≤17.3°C). However, large diel fluctuations have been positively correlated with increased mortality of juvenile coho salmon during summer months (Martin et al. 1986). Martin et al. (1986) reported that streams affected by a debris avalanche after the eruption of Mount Saint Helens had broad and shallow channels devoid of riparian vegetation and, thus, experienced excessive diel fluctuations and maximum temperatures exceeding lethal limits for juvenile coho salmon (25°C). Similar stream channel conditions can be produced by unfenced grazing, which can lead to the elimination of riparian cover, as well as bank trampling and erosion resulting in channel widening that allows for increased exposure to solar radiation.

On the other end of the temperature spectrum, water temperatures ideally should remain above 4.4°C for coho salmon, particularly during egg incubation and early rearing (Spence et al. 1996). Below that point, feeding will cease and fish may attempt to move to refugia (Sullivan et al. 2000). The lower lethal temperature for rearing coho salmon is listed at 1.7°C (50% mortality within 5,500 minutes for fish acclimated at 10°C) (Brett 1952).

Summary of detrimental temperature range characteristics.—Temperatures <4.4°C and >20.3°C have direct effects on juvenile salmonid survival. Mortality rates increase, growth rates are no longer positive, feeding ceases, and fish will attempt to seek other habitat if available. Cumulative stressors are magnified and exert further strain on any salmonid. Metabolic demands can no longer be met, and the animal will eventually lose equilibrium if high temperatures are sustained. In general, as water temperatures increase, time to death decreases (Brett 1952).

Discussion

The water temperatures of the cold water springs south of Highway A-12 in the Shasta Valley, in the upper Shasta River springs complex (Figure 2), are between 11°C and 13.6°C (Table 1). Water produced at these springs is constant at these temperatures throughout the year. The springs have characteristics which create favorable habitat conditions for juvenile salmonids. The stable temperature, nutrient content, discharge characteristics, and resulting dense macroinvertebrate prey base produced by springs in the upper Shasta River naturally create ideal rearing habitat for juvenile coho salmon (Jeffres et al. 2009).

Table 1.—Estimated flows (in cubic feet per second) and average temperatures of springs in the Big Springs complex in Shasta Valley, Siskiyou County, California.

Name of spring	Flow range	Temperature
Big Springs	~70 cfs[a]	11- 12.8ºC[a]
Clear Springs	1.1 – 3.6 cfs [b]	13.6ºC[c]
Kettle Springs	4.0 – 5.6 cfs [b]	13.0ºC [b]
Bridge Field	1.4 – 5.7 cfs [b]	13.0ºC [b]
Black Meadow	0.4 – 1.3 cfs [b]	12.1ºC [b]
Hidden Ranch Spring	1.2 cfs[d]	13.9ºC[d]

[a] Null et al (2010)

[b] Grant Davids, Davids Engineering Inc., personal communication

[c] Chesney et al. (2009)

[d] Nathenson et al. (2002)

The unique nature of these springs was described by Waring (1915). He reported that Big Springs "yields a large flow of water that is noticeably above the normal temperature." Although Waring did not define what constitutes conditions "above the normal temperature" it is likely that he was conducting his investigation during the winter months. Nathenson et al. (2002) listed the water temperature at Big Springs as 11.6°C and in nearby Hidden Ranch Spring as 13.9°C. Our measurements of Clear Springs, located on the Shasta River above the confluence with Parks Creek, revealed a temperature of 13.6°C (Chesney et al. 2009). The temperature of Big Springs, as well as nearby springs listed in Table 1, is generally higher in the winter in comparison to most springs in the Shasta River basin and in the vicinity of Mount Shasta (Nathenson et al. 2002). Nathenson et al. (2002) introduced the term "slightly thermal springs" to define springs (i.e., Big Springs) that do not meet the criterion for thermal springs (10°C above air temperature), but that are warmer than non-thermal springs in the area.

The presence of these springs can have a moderating effect on main-stem Shasta River water temperatures. It is noteworthy that these springs produce water that is within the optimum temperature range for juvenile coho salmon. During winter, this water can regulate very cold winter water temperatures at the lower end (8°C-10°C) of the optimal range for rearing coho salmon. As main-stem Shasta River and Parks Creek temperatures increase during the summer, unimpaired flow of spring water can counter-balance the effects of higher water temperatures and decrease the magnitude of diel fluctuations over certain temporal and spatial scales.

The term “slightly thermal” should be understood correctly when discussing the temperature characteristics of these springs outside of a geothermal or geological context. It should not be inferred that these springs contribute to the warming of the Shasta River, especially during the summer. In light of available historical accounts, these springs, albeit slightly warmer than other cold springs within the region during the winter months, have been crucial in maintaining optimum water temperatures for salmonids during both summer and winter months.

The majority of the springs in the upper Shasta River springs complex have been impounded and are used for irrigation. With the exception of Big Springs itself, the water temperature benefits from the springs listed above are limited due to their small volume, and only occur periodically when irrigation is not taking place.

Under current management, Bridge Field, Black Meadow, Kettle and Clear springs are intermittently diverted during the irrigation season. Diversion of spring flows for flood irrigation impacts rearing habitat by reducing the quantity of cold water available to rearing fish. In addition, spring flow used for flood irrigation may return to the stream as tailwater. In 2008, 2009, and 2011 we documented rearing juvenile coho salmon displaced from summer rearing habitat below Kettle Springs (a tributary to Parks Creek), due to reduced flows, through dive surveys and the detection of PIT tagged individuals leaving the area. In summary, while we do find that there is a small remnant of cold water habitat remaining in the river that functions to support rearing, the downstream effects of this water, namely low temperatures and suitable flow, are quickly diminished due to a number of causes, including water diversions and concomitant tailwater returns.

Due to the present status of Shasta River coho salmon, the maximum extent of summer rearing habitat should be maintained through maximum spring flows. The spatial distribution of rearing habitats for juveniles in summer may provide a key to population productivity (McCullough 1991). Monitoring stations should be established in spring reaches to track water temperature conditions on a real-time basis. We propose that when temperatures at monitoring points reach 15.5°C, management practices contributing to warming of the water temperatures be determined and modified, if possible, to preclude the possibility of water temperatures reaching suboptimal or detrimental levels. This single value temperature threshold is a more conservative approach than the mean weekly maximum temperature (MWMT). High temperature events of even relatively short duration can initiate thermoregulatory behaviors leading to the displacement of fish from previously suitable areas. If action can be undertaken to reduce rising temperatures prior to reaching detrimental levels, there is a greater likelihood of minimizing risk and potentially reducing the duration and impacts of high temperature events.

In guidance provided to the Environmental Protection Agency, Sullivan et al. (2000) proposed water temperature standards with an upper threshold of 16.5°C for the MWMT. Above that threshold, coho salmon may be assumed to experience at least 10% and up to 20% growth loss. A 7-day MWMT exceeding 22.5°C could cause fish to experience greater than 20% growth loss. Sullivan et al. (2000) believed this 10% threshold to be an acceptable level of risk. Growth or lack of it, and direct temperature-induced mortality are relatively easy to quantify and incorporate into temperature models and criteria. However, several variables are not readily quantifiable, such as changes in competitive interactions or disease incidence, but these may begin to exert some pressure upon rearing salmonids as temperatures increase. From a management standpoint, growth loss of 10% may appear to be an acceptable risk, but this loss is likely accompanied by other significant, albeit unquantified, changes that may be operating increasingly to the detriment of juvenile salmonids. Running 7-day MWMT values are usually strongly correlated with instantaneous maximum temperatures, and high temperature occurrences are seldom short-lived, but these are commonly the beginning of events that have longer durations of temperatures outside the preferred range for juvenile salmonids. As mentioned above, a single value approach is a more sensitive threshold that could reduce, if not eliminate, risk of mortality due to a peak in temperatures that is averaged over 7 days.

Because of the precariously low numbers of coho salmon remaining in the Shasta River, it is inappropriate to use a risk management approach to achieving temperature compliance as described in Sullivan et al. (2000). Standards for coldwater biota should reflect biologically optimum conditions, not the upper limits of distribution, and also not incorporate some percentage reduction in productivity (McCullough 1999). Therefore, we propose that a single maximum summertime temperature should be used for the purpose of monitoring water temperatures in the Shasta River and its tributaries. One alternative would be to choose the temperature that defines the maximum of the suboptimal range. However, setting this temperature as a maximum instantaneous temperature standard would serve little purpose as a management tool. If all stream reaches were increased to this standard, coho salmon would be eliminated throughout the stream system. It makes far more sense to set the growth optimum as the standard (McCullough 1999). The use of a single value defining threshold trigger at 15.5°C would reduce the exposure of juvenile coho salmon to conditions known to affect survival. To maintain suitable habitat conditions for rearing coho salmon, we propose that this thermal threshold be set at temperature monitoring stations located throughout the upper Shasta River springs complex. Exceedance of the temperature threshold would be the trigger to initiate adaptive watershed management (McCullough 1999).

In light of historical accounts, the restoration potential in the Shasta River, especially within the areas immediately downstream of the spring complexes, is very high. Historically, the spring flow ensured that the river remained comparatively thermally homogenous and provided favorable water temperatures for salmonids throughout the summer. The restoration of riparian cover along certain reaches of the Shasta River would further help to restore optimum temperature conditions downstream of the cold water springs. The Shasta River system is unique among Klamath River tributaries in that flow and temperature were historically based on spring inflows. Extensive diversion of water for irrigation and livestock grazing have severely altered the natural flow characteristics and water quality parameters of the Shasta River such that the river currently is subjected to highly variable daily fluctuations in flow and water temperature. Although such conditions can and do occur naturally in many systems throughout the Pacific Northwest, this is not the case with the Shasta River, at least from a historical perspective. Temperature and flow heterogeneity in the Shasta River is mostly due to anthropogenic modifications, and is not indicative of the natural state of the system.

A recent change in ownership and management of the Big Springs Ranch (formerly the Louie Ranch) has resulted in improvements in riparian habitat and stream temperature

(Jeffres et al. 2009). This property encompasses 4.8 km of the upper Shasta River, as well as 3.5 km of the spring fed Big Springs Creek. By reducing tail water and excluding cattle from the steam, The Nature Conservancy has demonstrated that it is possible to operate an effective cattle operation and improve stream habitat conditions for salmonids. Successful recovery of coho salmon populations will require similar efforts to protect and restore the remaining spring habitat and maximize the extent of habitat where optimal temperatures exist in the upper Shasta River.

Climate change could make water temperature an even greater issue than it is currently for coho salmon in the Klamath basin. It has been suggested that interior basins like the Shasta River may be more resilient than other tributaries in the event of increases in temperature and changes in precipitation patterns (National Research Council 2004). The implication is that the spring flows of the Shasta River could have even more significance for coho salmon persistence at the population level in the Klamath Basin as climate change occurs.

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