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Maximum Temperature Limits for Chinook, Coho, and Chum Salmon, and Steelhead Trout in the Pacific Northwest

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Wild salmon stocks in the Pacific Northwest are imperiled by a variety of anthropogenic environmental modifications, not the least of which is increasing maximum water temperatures. While many reports have been written on physiological or population-level influences of temperature in terms of the decline of wild salmon, synthesis of these diverse sources is needed for evaluation of numeric temperature criteria and their potential in salmon recovery planning. Various sensitive life stages and biological processes are impacted differently for different salmon species. This article reviews the literature for chinook, coho, chum, and steelhead, which are currently listed in the Columbia River Basin under the Endangered Species Act. Spawning, incubation and early fry development, juvenile rearing and growth, smoltification, and migration are considered. Swimming speed, disease susceptibility, chemical considerations, and lethality are also reviewed. Regional population growth and climate change will exacerbate the difficulties of recovering Northwestern salmon beyond remnant runs. Ethical analysis of the assumptions underlying recovery policy decisions, proposals for regime-based water quality standards, and a systems level vulnerability analysis are components of the recovery planning discussions. Specific numeric maximum temperature criteria that can be integrated into a broader recovery planning process are described for sensitive life stages of three species of Pacific Northwest salmon and steelhead.

Keywords salmon, steelhead, temperature, habitat

Introduction

Adequate water quality is important to all salmonids at all life-history stages. The evolutionary histories of native salmonid fish in the Pacific Northwest and their historical distributions are strongly tied to temperature conditions in their habitats (Brannon et al., 2004). Because water temperature affects the health of individual fish, it also affects entire populations and species assemblages. Temperature may directly affect salmonids in obvious ways, or indirectly through interaction with other important variables (Dunham et al., 2001). For example, given sufficient magnitude and time, high temperatures can cause weight loss, disease, competitive displacement by species better adapted to the prevailing temperature, or death (Sullivan et al., 2000).

When fish are stressed by any one process, they are less able to deal with other stressors (Wedemayer et al., 1980; Wedemayer and McLeay, 1981). Salmonids already stressed by high water temperature are less able to deal with a second stressor (e.g., toxic pollutant, pathogen). For example, warmer temperatures often increase the infection rate or virulence of fish pathogens and lessen the ability of a fish to withstand disease (Fryer and Pilcher, 1974; Materna, 2001).

Human Influence on Thermal Regimes

In many streams that were once inhabited by large salmon runs, temperature regimes are now inhospitable. An important factor in the recovery of salmonid populations is the restoration of temperature regimes (Poole et al., 2001a, 2001b, 2004). Salmon recovery poses an enormous challenge due to competing societal priorities and regional population growth (Lackey, 2003; Lichatowich, 1999) and projections concerning climatic change that will alter the hydrology of the Pacific Northwest (Mote et al., 2003).

Human activities can affect thermal regimes by simplifying the physical structure of aquatic systems, thereby eliminating natural thermal buffers and insulators (Poole and Berman, 2001). Clearing and developing land, dredging or straightening streams, grazing, and other land-use activities influence temperature regimes by altering factors external to the stream, and the amount of water flowing in the stream (Poole et al., 2001a, 2001b). These activities often directly or indirectly simplify the structure of stream channels or riparian zones, as has occurred in the lower Willamette River, Oregon (Sedell and Froggatt, 1984). This type of channel simplification can potentially increase temporal variability and decrease fine-scale spatial variability in stream temperature, both of which may have negative consequences for salmonids (Poole et al., 2001b; Poole and Berman, 2001). Removing riparian vegetation in small streams, where shading is important, can increase daily variation in stream temperature (Beschta, 1997), and empirical manipulation of streams reveals complex relationships between maxima, minima, and mean temperatures and different temperature drivers (Johnson, 2004). For streams where groundwater buffers temperature, change in groundwater temperature or flow dynamics can alter the seasonal availability of cold water, increasing seasonal variation in water temperature (Poole and Berman, 2001). Altered flow regimes with concomitant effects including temperature changes and regional expressions of global climate change, have influenced chinook and steelhead migration over the last 50 years (Brannon et al., 2004).Water temperature is an indicator of habitat quality, acting as an integrator of what is happening in a watershed (Poole et al., 2001b).

Thermal refugia are important in maintaining salmonid populations because salmonids may be exposed to stressful or lethal temperatures for part of the day when daily variation in stream temperature is high. Small-scale thermal refugia provide important habitat for salmonids during periods of warmer water temperatures (Berman and Quinn, 1991; Ebersol, 2002; Gibson, 1966; Kaya et al., 1977; Torgerson et al., 1999) and changes in temperature extremes, or mean temperature, can result in loss of the refugia and therefore the salmonids. At peak summertime temperatures, only a patchwork of fish habitat in some streams may be cool enough (Cavallo, 1997; Kaya et al., 1977). Loss of riparian vegetation, the elimination of beaver populations, removal of large woody debris, channel simplification, reduced groundwater discharge due to changes in upland vegetation or urbanization, water withdrawals, and other human activities cause the loss of the fine-scale spatial distribution of appropriate thermal habitats upon which salmon rely (Poole et al., 2001b). This can cause fish to migrate greater distances to find appropriate habitats or not find them at all.

In the same way, seasonal variation in temperature can create thermal barriers to salmonid immigration and emigration. Human activities can increase the coarse scale temporal variation of streams, exposing salmonids to extremes beyond the normal range of variation and resulting in habitat fragmentation and elimination of large, well-connected tracts of high-quality thermal habitat. This habitat fragmentation has been shown to degrade both fish population structure and persistence (Dunham and Reiman, 1999; Poole and Berman, 2001; Poole et al., 2001b; Reiman and Dunham, 2000).

In a recent U.S. Environmental Protection Agency (EPA) document entitled EPA Region 10 Guidance for Pacific Northwest State and Tribal Water Quality Standards (EPA 910-B-03-002), (Environmental Protection Agency, 2003), the EPA recommended a multifaceted approach for state and tribal temperature standards to support native salmonids. This approach includes the adoption of: (1) new or revised numeric water quality temperature standards to protect salmonids at each life stage, and a set of "uses," including spawning, egg incubation, fry emergence, juvenile rearing, smoltification, and migration. It also recommended (2) criteria that focus on summer maximum temperature conditions related to human activities, which are the greatest water temperature concern in the Pacific Northwest (see also Lackey, 2003). These would include criteria to protect temperature-sensitive salmonid uses at times of the year in spring-early summer or late summer-fall where additional protection is required. Provisions were also made to (3) protect water temperatures that are currently colder than the numeric criteria, to protect the last strongholds of the Endangered Species Act (ESA)-listed salmonids. Finally, provisions were made to (4) protect salmonids from thermal plume impacts, to prevent instantaneous lethal temperatures, thermal shock, migration blockage, and other adverse impacts on sensitive life stages.

The EPA Guidance (EPA, 2003) provides for case-by-case EPA reviews of situations where the numeric criteria are unachievable or inappropriate, for example, in cases where a use-attainability analysis indicates that high natural background temperatures might prevent criteria from being achieved. The integrity of scientific analysis involved in such case-by-case EPA reviews will be critical in the conflicting societal milieu (Lackey, 2003) of the region. Recent events in development and implementation of scientifically based policy concerned with salmon recovery planning (Union of Concerned Scientists, 2004) compels a process ensuring undistorted scientific reviews by technically qualified scientists.

This article summarizes the large body of information about thermal effects on salmonids. It will be specific to life stages and species and use the information to evaluate and make recommendations pertaining to numeric water temperature criteria. Several groups have recently produced white papers on this topic: Pacific Northwest Salmon Habitat Indicator Work Group (PNSHIWG), the Sustainable Ecosystems Institute (SEI), the EPA Water Temperature Criteria Technical Workgroup, the Columbia River Inter-Tribal Fish Commission, and the Washington State Department of Ecology (WDOE).

The participating agencies in the PNSHIWG are the British Columbia Ministry of Environment, Lands, and Parks; the Alaska Department of Environmental Conservation; the Idaho Division of Environmental Quality; the Oregon Department of Environmental Quality; the WDOE; Environment Canada; and the U.S. EPA (Region 10). In 1997, directors of these agencies asked PNSHIWG to pilot development of regional indicators associated with risks to salmonid stocks. Indicators were required to: (1) have data available, (2) be integral to measuring the performance of salmon issues for PNSHIWG agencies, and (3) be able to be reported cost-effectively in a monitoring program.

Martin Environmental, Parametrix Inc., and Weyerhaeuser Company participated in the SEI review, which was funded by the Oregon Forest Industries Council, Washington Forest Protection Association, and Weyerhaeuser Company. The SEI developed a risk-based approach to analyze summer temperature effects on juvenile salmon species in their publication, *An Analysis of the Effects of Temperature on Salmonids of the Pacific Northwest with Implications for Selecting Temperature Criteria* (Sullivan et al., 2000). This report reviewed the aspects of temperature affecting the rearing of salmonid species in the freshwater environment and discussed lethal (acute) as well as sublethal (chronic) effects. The main focus of the report was on temperatures affecting growth and mortality (Sullivan et al., 2000).

The EPA established the Water Temperature Criteria Technical Workgroup to assist in developing temperature criteria guidance for EPA Region 10. The purpose of the EPA guidance is to help Pacific Northwest states and tribes adopt water temperature standards that (1) meet the biological requirements of native salmonid species (Pacific salmon, trout, and charr) for survival and recovery pursuant to the ESA; (2) provide for the protection and propagation of salmonids under the Clean Water Act (CWA); and (3) meet the salmonid restoration goals of federal trust responsibilities with treaty tribes. The technical work-group, a panel of experts on salmonid biology and stream temperature, represented the following agencies: EPA, U.S. Forest Service, WDOE, NOAA Fisheries, U.S. Fish and Wildlife Service, Columbia River Inter-Tribal Fisheries Commission, Idaho Department of Environmental Quality, Oregon Department of Environmental Quality, U.S. Geological Survey (USGS) Biological Resources Division, and USGS Water Resources Division. In 2001, the technical workgroup submitted a final summary report to the policy workgroup of the EPA Region 10 Water Temperature Guidance Project entitled *Technical Synthesis: Scientific Issues Relating to Temperature Criteria for Salmon, Trout, and Charr Native to the Pacific Northwest.* Five technical summaries on the major physical and biological considerations for developing water temperature standards were developed to provide a scientific foundation for the project:

1. thermal effects on salmonid physiology (McCullough et al., 2001),
2. thermal effects on salmonid behavior (Sauter et al., 2001),
3. interactions between multiple stressors—thermal and other—affecting salmonids (Materna, 2001),
4. thermal influences on salmonid distribution (Dunham et al., 2001), and
5. spatial and temporal variation in patterns of stream temperature (Poole et al., 2001a, 2001b).

McCullough (1999) prepared a summary report for EPA Region 10 in which he reported that significant impacts to survival due to temperature regime can occur in all life stages. Sublethal impacts to life processes, which include growth, survival, reproductive success, migration success, disease, feeding, territoriality, aggressiveness, swimming, and bioenergetics, can cumulatively diminish survival and population production.

The WDOE Water Quality Program released a draft discussion paper and literature summary addressing temperature criteria that included recommendations for chinook, coho, and chum salmon and steelhead at critical life stages (WDOE, 1999). The recommendations were based on a review of the literature and laboratory data adjusted for application to natural waters.

The following sections discuss the scientific findings on thermal effects and requirements of salmonids, in general and by individual species, drawing together materials from the primary literature and the documents listed above.

General Salmonid Data

Smoltification

High temperatures during the smolt phase can result in outright lethality, premature smolting, blockage of seaward migration, desmoltification, shifts in emigration timing resulting in decreased survival in the marine environment, and other stresses detrimental to fitness. Temperatures reported to impair smoltification are above a range from approximately 12° to 15°C or more (Adams et al., 1973; Hoar, 1988; Marine, 1997; Wedemeyer et al., 1980; Zaugg and McLain, 1976; Zaugg and Wagner, 1973). From a behavioral perspective, Sauter et al. (2001) suggested that water temperature affects duration of freshwater rearing and outmigration timing. Elevated water temperatures (from 12° to 17°C, depending on species, McCullough et al., 2001) inhibit the activity of gill ATPase, an enzyme that prepares juvenile salmonids for osmoregulation in seawater during emigration. Decreased gill ATPase activity is associated with loss of migratory behavior in anadromous juvenile salmonids. Spring water temperatures must not exceed 12°C for successful smoltification in steelhead (Adams et al., 1975; Hoar, 1988; Zaugg and Wagner, 1973). For spring chinook and coho this value is 15°C (Zaugg and McLain, 1976), and it may be higher for summer migrating fall chinook subyearlings (Zaugg and Wagner, 1973).

Adult Migration

Thermal blockages to adult salmon migration have also been identified. Migration blockages occur consistently in the temperature range of 19° to 23°C (McCullough et al., 2001). For chinook and sockeye salmon and steelhead in the Columbia River, 21.7° to 23.9°C has been cited as the temperature range blocking migration (Fish and Hanavan, 1948).

Spawning

Elevated temperatures can cause migration delays in salmonids that alter timing of key processes, such as spawning, or they can lead to stress, disease, bioenergetic depletion, or death. If salmonids are exposed to temperatures above approximately 13°C just before or during spawning, gametes held internally in adults can be severely affected, resulting in a loss of viability that manifests in reduced fertilization rate and embryo survival (Berman, 1990; Brett, 1952; Flett et al., 1996; Hokanson et al., 1977; Leitritz and Lewis, 1976). Egg mortality, alevin development, and egg maturation are negatively affected by exposure to temperatures above approximately 12° to 15°C (Beacham and Murray, 1985; Dong, 1981; Flett et al., 1996; Garling and Masterson, 1985; Heming, 1982; Murray and McPhail, 1988; Neitzel and Becker, 1985; Olson and Foster, 1955; Ringler and Hall, 1975; Tang et al., 1987). A spawning temperature range of 5.6° to 12.8°C (maximum) appears to be a reasonable recommendation for Pacific salmon, unless colder thermal regimes provided the evolutionary backdrop for the salmonid population in a specific tributary (Brannon et al., 2004; McCullough et al., 2001).

Lethality

Analysis of lethal temperature suggested that a threshold of 26°C for annual maximum temperature signals an imminent risk of direct mortality (Sullivan et al., 2000). A site-specific analysis of duration of exposure when annual maximum temperature is between 24°C and 26°C is also recommended to ensure that duration/magnitude thresholds are not exceeded. These annual maximum temperature values are intended to apply to all salmon and trout species in natural rivers and streams in the Pacific Northwest (Sullivan et al., 2000).

Distribution

After review of field studies for chinook salmon, steelhead, and rainbow trout, McCullough (1999) determined the distributional limit of these salmonids corresponds approximately to a mean daily water temperature of 20°C and a maximum daily water temperature of 22° to 24°C. Hokanson et al. (1977) showed that water temperatures greater that 23°C, even for short periods (hours), result in Pacific salmon and trout moving into cold-water refugia. Eaton et al. (1995) proposed a higher (95th percentile) weekly mean temperature tolerance for chinook (24°C) and coho (23.4°C) salmon, when the fish temperature database matching system (FTDMS) approach was used to evaluate various distribution records for 30 common North American fish species. However, when using the FTDMS approach, the existence of thermal refugia provides a potential source of error (Eaton et al., 1995), and leads to recommendations inconsistent with other studies. In general, juvenile salmonids appear to have temperature preferences in the range 11.7° to 14.7°C (Ferguson, 1958; Coutant, 1977; Jobling, 1981; McCullough, 1999).

In addition, higher water temperatures and longer exposure to warm water increase the feeding rate of predatory species consuming juvenile salmonids. Interspecific competition also appears to play a role in the distribution and thermal preferences of juvenile salmonids (Sauter et al., 2001).

Water Quality

Many chemical constituents are affected by temperature. Most notably, dissolved oxygen (DO) decreases with increasing temperature. When fish experience temperature stress, they may also experience some stress from low DO levels (Alabaster, 1988, 1989; Hallock et al., 1970). McCullough (1999) concluded that adult migration of chinook salmon can be impeded when temperature and DO requirements are not met. Although there is no single pattern that explains the effects of temperature on the toxicity of pollutants to aquatic organisms, some evidence shows that temperature may change the rate of toxic effects under chronic exposures (Mayer et al., 1994). Since rising temperatures increase metabolic processes, gill ventilation must also rise proportionately (Heath and Hughes, 1973). Black et al. (1991) showed that an increase in water flow over the gills, which may result from increased gill ventilation at increased temperature, resulted in rapid uptake of toxicants via the gills. Sublethal exposure to some toxicants may reduce the upper lethal temperatures of fish, constricting the thermal tolerance zone (Paladino et al., 1980). Fish weakened by other causes may be more sensitive to toxic chemicals (Jobling, 1994), although whether this is observed or not depends on the toxicant and the species involved (Cairns et al., 1978; Mayer et al., 1994; Sprague, 1985). Temperature has been found to significantly increase the toxicity of some organic chemicals such as terbufors, trichlorfon, and 2,4 dinitrophenol (Howe et al., 1994), as well as some metals such as mercury (MacLeod and Pessah, 1973; Materna, 2001). Susceptibility to sediment toxicity has been reported to increase with temperature (Servizi and Martens, 1991).

Disease

Elevated temperatures do not uniformly increase mortality from all salmonid diseases. “Cold water disease” caused by *Cytophaga psychronophila* (Snieszko, 1974), bacterial kidney disease (BKD) caused by *Renibacterium salmoninarum* or *Corynebacterium* (Sanders et al., 1978) and perhaps infections hematopoietic necrosis (Snieszko, 1974; but see Hetrick et al., 1979) have higher mortalities at temperatures well within an otherwise optimal range. Other fish diseases are exacerbated by higher water temperatures (Ordal and Pacha, 1963) and can infect salmon at many life stages. Many important salmonid diseases become virulent above approximately 15.6° to 16°C, which makes the impact to population production potentially more severe, because as temperatures rise toward the limits to salmonid growth, the mortality rate increases (Fish, 1948; Fryer and Pilcher, 1974; Fryer et al., 1976; Fujihara et al., 1971; Groberg et al., 1978; Holt et al., 1975; Ordal and Pacha, 1963; Wade, 1986). Diseases associated with warm water in the Pacific Northwest are well documented. They include the bacterial infections columnaris, caused by *Flexibacter columnaris*; the bacterial pathogens *Aeromonas salmonicida*, *A. punctata*, *A. hydrophila*; and the protozoan parasite *Ceratomyxa shasta*. Evidence from Idler and Clemens (1959), Williams et al. (1977), and Ordal and Pacha (1963) indicates that temperatures of 16.7° to 20°C or higher, lead to infection of adult salmon with columnaris, even with exposure to low-virulence strains, and infection can occur at even lower temperatures with high-virulence strains. Evidence from Colgrove and Wood (1966) indicates that temperatures between 13.9° and 15.6°C constitute a transitional temperature region below which recovery from columnaris after infection could occur, and above which infection and mortality increase. Laboratory and field studies by numerous investigators show that infection and morality by columnaris disease were negligible at temperatures $\leq$12.8°C, but temperatures $\geq$15°C produced significantly increased mortalities. Not only do juvenile survival rates decrease with increasing temperature, but Fryer and Pilcher (1974) also showed that time to death decreases with increasing temperature for juvenile chinook salmon, coho salmon, and steelhead (Materna, 2001).

Bacterial kidney disease is also a prevalent disease in which temperature has a complicated effect on mortality of infected salmonids. In an experiment involving infected sockeye, coho, and steelhead exposed from 4° to 20.5°C, the highest mortalities occurred at 12.2°C, with declining mortalities at higher or lower temperatures (Fryer and Sanders, 1981).

Groberg et al. (1978) studied the relationship of water temperature to infections of coho salmon, chinook salmon, and steelhead with *A. salmonicida* and *A. hydrophila*. Among the three salmonid species, at 3.9° and 6.7°C, mortality in fish infected with *A. salmonicida* varied from 2 to 26%; at 20.5°C, 93 to 100% died within 2 or 3 days; at 6.7°C or lower survival was 12 to 23 days. Results from experiments with *A. hydrophila* gave similar results. At 20.5°C, mortality ranged from 64 to 100%; at 9.4°C or below, no deaths occurred.

Ceratomyxa shasta infection is temperature-dependent in salmonids. Fryer and Pilcher (1974) reported extremely low mortality due to *C. shasta* in coho held at 9.4°C and below, ranging upwards to nearly complete mortality at 20.6°C and above. However, juveniles originating in waters where the disease is prevalent may be more resistant than juveniles from areas lacking the disease, and genetic dilution of resistance by hatchery hybrids has been documented (Bakke, 1997; Hemmingsen et al., 1986).

Chinook Salmon Data

Incubation and Early Fry Development

Olson and Foster (1955) reported fall chinook incubation at 10°–16.7°C. Heming (1982), Neitzel and Becker (1985), and Garling and Masterson (1985) reported incubation for fall Chinook at 10°–12°C. Constant temperatures above 12° reduced alevin survival substantially (Ringler and Hall, 1975). Bjornn and Reiser (1991) reported incubation from

5°–14.4°C. Constant temperatures above 9° to 10°C may reduce embryo and alevin survival, with reliable survival at lower percentages when temperatures increase to 11°–12°C (Baily and Evans, 1971; Burrows, 1963; Donaldson, 1955; Eddy, 1972; Heming et al., 1982; McCullough et al., 2001; Raleigh et al., 1986; Seymour, 1956). Incubation temperatures of 9.9°–16.7°C produced significant mortality, with complete mortality from 13.9–19.4°C (Hicks, 2000).

McCullough et al. (2001) recommended that temperatures be maintained below 12°C for incubation and fry development, and Hicks (2000) recommended an adjusted 7-day average of the daily maximum temperatures (7-DAM) of 11° to 12°C at the time of fertilization of chinook salmon eggs. Both McCullough et al. (2001) and Hicks (2000) indicated individual daily maximum temperature limits (1-DM) of 13.5° to 14.5°C are required to provide optimal protection for stages from fertilization through early fry development. For these and subsequent recommendations, Hicks utilized the multiple lines of evidence (MLE) approach, which selects the midpoint of individual lines of evidence (ILOE), unless concerns with any specific line of evidence would invalidate this technique (Hicks, 2000).

Juvenile Rearing and Growth

Optimal rearing temperatures at natural feeding regimes are in the range of 12.2° to14.8°C for chinook salmon (Hicks, 2000). Garling and Masterson (1985), Clarke and Shelbourn (1985), Brett et al. (1982), and Marine (1997) reported optimum growth temperatures, determined from feeding on full rations, that range from 14.8° to 20°C. Ration size in the laboratory and food supply in nature can have significant effects on optimal temperatures for rearing. Feeding rates below the satiation level, typical of field situations (Brett et al., 1982) were associated with reduced temperature optima for growth (Elliott, 1981). Brett et al. (1982) reported an optimal growth temperature of 19°C for chinook maintained in the laboratory at maximal daily ration. In the field, with a projected feeding level of 60% of maximal daily ration, Brett et al. (1982) projected an optimal growth temperature of 14.8°C. Heat shock proteins (hsp70) were induced after several hours exposure to 20°C for juvenile fall chinook from the Hanford Reach of the Columbia River (Mesa et al., 2002).

McCullough (1999) suggested using the growth optimum of 15.6°C for spring chinook salmon as the temperature standard, because temperatures lower than this cause no reduction in survival while temperatures higher than this begin to reduce growth and lead to increasing mortality rates. A synthesis of evidence from Bisson and Davis (1976), Garling and Masterson (1985), Brett et al. (1982), Marine and Cech (1998), Wilson et al. (1987), Reiser and Bjornn (1979), and Brett (1952), led McCullough et al. (2001) to recommend an optimum production temperature zone of 10.0° to 15.6°C. Adjusting laboratory temperatures to naturally fluctuating stream temperatures, Hicks (2000) recommended that a 7-DAM of 14.2° to 16.8°C during the peak of summer provides for optimal growth conditions for chinook salmon. The Independent Science Group (1996) concluded that juvenile chinook rearing is optimal between 12°–17°C with most optimal at 15°C.

Smoltification

The temperature threshold for impairment of smoltification was found to be 12°C by Zaugg (1981) in spring chinook yearlings. Marine (1997) found it to occur at 17°C or above in fall chinook subyearlings. Brett (1952) reported sublethal and lethal loading stress at 18°–21°C. Brannon et al. (2004) provide evolutionary arguments for chinook and steelhead that may account for the range of variability seen in the chinook smoltification literature.

Adult Migration

Immigrating spring chinook salmon in the Willamette River have experienced thermal blockages at 21° to 22°C (when dissolved oxygen was 3.5 mg/l) (Alabaster, 1988). A temperature of 21°C blocked migration of spring chinook salmon in Clearwater, Idaho, (Stabler, 1981), as well as summer chinook salmon (Stuehrenberg et al.,1978; Dauble and Mueller, 1993) of the Snake River. A temperature of 21.1°C blocked spring chinook in the Tucannon River (Bumgarner et al., 1997) and fall chinook in the Sacramento River were blocked at 19° to 21°C (oxygen ∼ 5 mg/l) (Hallock et al., 1970). Temperatures between 21.7° and 23.9°C blocked migration in the Columbia River (Fish and Hanavan, 1948). Bell (1986) and Spence et al. (1996) reported adult migration for summer chinook from 13.9°–20°C and adult migration for fall chinook from 10.6°–19.4°C. Adult migration for spring chinook from 3.3°–13.3°C has been reported (Bell, 1986; Bjornn and Reiser, 1991; Spence et al., 1996). Hicks (2000) recommended that daily maximum temperatures should not exceed 20° to 21°C in order to prevent migration blockage of adult chinook salmon.

Spawning

The following authors reported spawning temperature ranges in daily average temperatures (DAT) for chinook salmon. For spring chinook salmon, Olson and Foster (1955) reported 4.4° to 17.8°C. For fall/summer chinook, Raleigh et al. (1986) reported 5° to 13.4°C. The majority of the temperature observations reviewed in Hicks (2000) cited a maximum spawning temperature below 14.5°C for chinook salmon.

Lethality

For chinook salmon, the upper incipient lethal temperature (UILT) (the temperature at which 50% of the population is dead after indefinite exposure) has been recorded at 25.1°C (acclimation temperature 20° and 24°C) by Brett (1952), and 24.9°C (acclimation temperature 21.1°C) by Orsi (1971). Berman (1990) reported 17.5°C as the upper sublethal to lethal range for spring chinook. Brett et al. (1982) reported a lethal level of 25°C for an acclimation at 20°C. However, Snyder and Blahm (1971) reported that a 3-day test over which temperature changed from 10°C to 21.1° produced no mortality. Snyder and Blahm (1971) reported that 26.7°C produced mortality beginning at 100 sec and complete mortality at 4 min. Baker et al. (1995) studied smolt escapement in the lower Sacramento River and determined an upper lethal temperature of 23°C. Using live-box tests on juveniles, Burck (1993) found high mortalities with daily maximums in the range of 23.8°–25.5°C. Treatments ranging from 20.0°C to 22.7°C maxima yielded inconsistent results, perhaps due to differing daily minima (Burck, 1993).

Hicks (2000) recommended that to protect fish from acute lethality, daily maximum temperatures not exceed 22°C. In addition, he recommended that thermal plumes should not even briefly expose fish to water warmer than 30° to 32°C.

Behavior

For subyearling spring chinook salmon in the Dungeness River, Brett (1952) found the acute preference temperature to be 12° to 13°C at all acclimation temperatures and the mean final preference temperature was 11.7°C. Sauter (1996) found that spring chinook salmon smolts on unlimited ration have a final temperature preference (a preference expressed in a thermal gradient within 24 h, independent of acclimation temperature (Reynolds and Casterlin, 1979a, 1979b)).

Coho Salmon Data

Incubation and Early Fry Development

From data in Dong (1981), Tang et al. (1987), Murray and McPhail (1988), Velsen (1987), Davidson and Hutchinson (1938), and Sandercock (1991), it appears that egg survival for coho salmon is consistently best at constant temperatures of 2.5° to 6.5°C. Egg survival may still be acceptable for many stocks at temperatures of 1.3° to 10.9°C (Tang et al., 1987). Alevin and fry survival and health may be best at constant temperatures of 4° to 8°C, but survival may remain acceptable up to 10.9°C (Tang et al., 1987). A constant 12°C may form the upper threshold for optimal development of coho salmon eggs and alevin (McCullough et al., 2001; Hicks, 2000). Murray and McPhail (1988) reported increased mortality above 11°C, Brett (1952) and Reiser and Bjornn (1979) reported egg mortality at 14°C.

Flett et al. (1996) investigated the cause of low survival to hatch of embryos (42%) of coho salmon from the Fairview, PA stock in Lake Erie in 1988. They suggested the low survival was due to delayed oocyte maturation, ovulation, and vent maturation, caused by exposure to water above 20°C. Another stock (Simcoe) showed no such impairments during late ovarian maturation and migration at temperatures 2°–4°C lower (Flett et al., 1996).

Juvenile Rearing and Growth

Beschta et al. (1987) reported preferred rearing temperatures from 11.8°–14.6°C, Bell (1986) suggested 12°–14°C, Coutant (1977) suggested 11.4°C, Reiser and Bjornn (1979) and Brett (1952) suggested 11.8°–14.6°C. Beschta et al. (1987) reported upper lethal temperature at 25.8°C. Cessation of growth has been reported above 20.3°C (Reiser and Bjornn, 1979; Brett, 1952). Adjusting laboratory temperatures to naturally fluctuating stream environments resulted in a recommendation of a 7-DAM of 9° to 12°C to fully support the pre-emergent states of coho salmon (McCullough et al.,2001; Hicks, 2000). Everson (1973) found that, depending on food availability, growth optima occur at 15°C. Average or constant temperatures of 12° to 15°C probably best characterize optimal rearing conditions (Hicks, 2000).

Adjusting for a naturally fluctuating stream environment resulted in a recommendation of 14° to 17°C for the 7-DAM to fully protect juvenile coho salmon rearing (Hicks, 2000). Sullivan et al. (2000) developed and used a bioenergetics-based approach to evaluate salmon growth in relation to environmental temperature, and to suggest sublethal temperature thresholds for coho salmon. An upper threshold for the 7-DAM temperature of 16.5°C was proposed assuming a 10% reduction in growth represents an appropriate risk level (Sullivan et al., 2000). A corresponding temperature range of 12°–17°C was proposed (Sullivan et al., 2000).

Smoltification

Both Zaugg and McLain (1976) and Adams et al. (1975) reported the temperature threshold for impairment of smoltification of coho salmon to be 15°C. Brett et al. (1958) suggested limits of 12–15.5°C. Spence et al. (1996) reported smoltification from 2.5–13.3°C, and observed that most fish migrate before temperatures reach 11°–12°C.

Adult Migration

Brett (1952), Reiser and Bjornn (1979), and Beschta et al. (1987) suggested that adult migration occurs between 7.2°–15.6°C. Flett et al. (1996) reported that adults migrating through waters frequently warmer than 20°C had reduced quality and rapid deterioration of eggs.

Spawning

Spawning activity was proposed to occur over the widest temperature range by Bell (1973), with a range of 7.2° to 15.6°C. However, Bell (1991) reported a DAT of 10° to 12.8°C for spawning coho salmon. Reiser and Bjornn (1979) and Brett (1952) reported a spawning range of 4.4°–9.4°C. Hicks (2000) suggested a typical spawning range of 4.4°–13.3°C.

Lethality

For coho fry, Brett (1952) reported UILT at 25.0°C (acclimation temperatures of 20° and 23°C). Konecki et al. (1995) tested juvenile coho salmon fry critical thermal maximum (CTM, the temperature at which a fish loses equilibrium and dies, which depends on acclimation temperature). Mean CTMs from three populations captured in the field in Washington State were 28.2°, 29.1°, and 29.2°C, which exceed published data from some laboratory tests for juvenile coho (Beschta et al., 1987; DeHart, 1975; McGeer et al., 1991). The population from a relatively cool stream had a lower CTM (28.2°C) than two populations from warmer streams (29.1°C, 29.2°C). After 3 months in the laboratory under constant temperature regimes, the CTMs no longer differed. This indicated that the population-specific differences resulted from different acclimation regimes rather than from genetic adaptation. Constant exposure to temperatures of 22° to 23°C poses a risk of causing direct lethality to juvenile coho salmon (Hicks, 2000). Servizi and Martens (1991) reported that susceptibility to sediment toxicity was 33% higher when temperatures reached 18°C. Coutant (1970) reported a lethal limit of 21°–22°C for migrating adult fish collected from the Columbia River during the summer. Hicks (2000) concluded that the lethal limit was 22° to 23°C. Subtracting a 2°C safety factor resulted in a recommendation of 20° to 21°C to avoid direct lethality to coho salmon (Hicks, 2000).

Behavior

For subyearling coho salmon, Brett (1952) reported a range of 12° to 14°C for their temperature preference, which is affected by acclimation temperature. Konecki et al. (1995) reported 11.6°C (range 7° to 21°C) and 9.9°C (range 6° to 16°C) as temperature preferences for subyearling coho salmon in two different creeks; preferred temperatures were influenced by ration. Reutter and Herdendorf (1974) reported that adult coho have a final temperature preference of 16.7°C and Spigarelli (1975) reported that adults prefer a field temperature of 17.3°C. For fall chinook salmon, Sauter (1996) found parr to prefer a mean 16.7°C, while advanced smolts preferred 10.9°C.

Swimming Speed

Brett et al. (1958) investigated the effect of temperature on the cruising speed of young coho salmon. Cruising speeds of subyearling and yearling coho were determined for acclimation temperatures ranging from 1° to 24°C. Optimum cruising speed for juvenile coho occurred at 15°C.

Disease

Groberg et al. (1983) studied the effects of water temperature in the laboratory on experimental infection by the predominantly marine pathogen *Vibrio anguillarum* in juvenile coho salmon at seven water temperatures range from 3° to 21°C. More rapid death and higher mortality were observed at water temperatures above 12°C. Growth rates of *V. anguillarum* were directly related to temperature.

Chum Salmon Data

Incubation and Early Fry Development

Beacham and Murray (1985) reported 6–10°C as the range for maximum yolk-to-tissue conversion efficiency, and that at 12°C alevin mortality took place 1–3 days after hatching. Bjornn and Reiser (1991) reported incubation from 4.4°–13.3°C. Constant incubation temperatures from 4° to 12°C commonly produce excellent incubation results for chum salmon Beacham and Murray (1985) and Zinichev and Zotin (1987;) however, there may be less than optimal survival near the edges of this range. Both McCullough et al. (2001) and Hicks (2000) suggested that constant initial incubation temperatures of 8° to 10°C would be most consistently optimal for chum salmon. Responses to temperatures above 12°C depend upon the stock involved (Beacham and Murray, 1985, 1986; Zinichev and Zotin, 1987) and early stocks (e.g., Hood River Canal, WA) must be adapted to temperatures above 8° to 10°C. Hicks (2000) recommended that the 7-DAM should not exceed 10° to 12°C for fertilization through fry emergence. Many stocks have heavy losses above 12°C (Beacham and Murray, 1985, 1986).

Juvenile Rearing

Rearing temperatures are described as 11.2–14.6°C preferred and 13.5°C optimum by Beschta et al. (1987), with upper lethal at 25.8°C. Brett (1952) reported preferred temperatures of 12°–14°C. Bell (1986) reported rearing at 10–12.8°C.

Spawning

Chum salmon are most consistently observed to spawn within a range from 7°–12.8°C (Beacham and Murray, 1986; Bell, 1986; Hicks, 2000; Bjornn and Reiser, 1991).

Lethality

Brett (1952) reported the UILT for chum salmon fry at 23.7° and 23.8°C (acclimation temperature 20° and 23°C, respectively). Hicks (2000) stated that significant lethality to chum salmon can result from constant exposure to 22° to 23°C. Snyder and Blahm (1971) reported 50% mortality in less than 50 min. for fish transferred from 15.6°C to 26.7°C, 50% mortality in 60 sec. with a transfer from 15.6°C to 29.4°C, and 100% mortality in 15 sec. with a transfer from 15.6°C to 32.2°C. With a 2°C safety factor, Hicks (2000) recommended that daily maximum temperatures should not exceed 20° to 21°C to prevent direct lethality to chum salmon. In addition, fish should not be exposed even briefly to temperatures greater than 33° to 34°C (Hicks, 2000).

Behavior and Adult Migration

Brett (1952) reported that juvenile subyearling chum salmon have an acute (rapid) preference temperature of 12° to 14°C at all acclimation temperatures and final preference temperature (Reynolds and Casterlin, 1979a, 1979b) of 14.1°C. Groot and Margolis (1991) reported adult migrant chum have an acute preference temperature of 7° to 11°C.

Steelhead Data

Incubation and Early Fry Development

Bell (1986) indicated that 10°C is preferred steelhead egg hatching temperature, Rombough (1988) found elevated embryonic mortality at 15°C, Redding and Schreck (1979) reported smaller steelhead emerging at 16°C. Velsen (1987) found high incubation survival (>92%) from 4°–9°C and fair (>78%) from 3–15°C. Survival became very poor (7%) above 16°C (Velsen, 1987). Based on the literature and adjusting for a naturally fluctuating river environment, Hicks (2000) recommended 13.5° to 14.5°C for the single daily maximum temperature for the period from fertilization through hatching. Based upon data from Bell (1986), Rombough (1988), and Redding and Schreck (1979), McCullough et al. (2001) suggested an optimal constant incubation temperature occurs below 11°–12°C.

Juvenile Growth

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

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

Smoltification

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

Hicks (2000) projected constant temperature range data onto a fluctuating stream environment, and recommended a 7-DAM of 13.3° to 14.3°C would be protective for emigrating steelhead smolts. McCullough et al. (2001) noted that depending upon the run of steelhead investigated (Adams et al., 1973; Wedemeyer et al., 1980; Zaugg and Wagner, 1983), inhibition and even reversal of smoltification occurred between 11.3°C and 13.6°C.

Adult Migration

Stabler (1981) reported 21°C as the temperature blocking adult steelhead migration in the Snake River. Snyder and Blahm (1971) reported that temperatures of 23.9°C produced a migration barrier that remained until temperatures declined to 21.1°C. In a study of movement into and out of pools, Nielson et al. (1994) found that temperatures above 22°C generally elicited avoidance. Coutant (1970) reported an incipient lethal temperature at a constant 21–22°C for migrating steelhead adults. Fish and Hanavan (1948) reported that steelhead congregated in cool tributaries when the river's mainstream reached 21.7°–22.8°C.

Based on the consistency of several studies, Hicks (2000) recommended that temperatures remain lower than 21° to 22°C (1-DAM) to prevent thermal barriers to migrating steelhead, and that water in which steelhead migrate or hold not exceed a 7-DAM of 16° to 17°C. McCullough et al. (2001) noted that 21°C has been reported (Stabler, 1981) to block adult migration in the Snake River.

Lethality

Nielsen et al. (1994) reported upper lethal temperature at 24°C for juvenile steelhead. Redding and Schreck (1979) reported mortality within 20.5h for fish acclimated to 12°C rapidly (6.25 h) raised to 26.5°C. Coutant (1970) reported for steelhead taken during the peak adult migration in the Columbia River, the incipient lethal temperature was 21°–22°C. Hicks (2000) recommended that daily maximum temperatures remain below 19° to 20°C to prevent directly lethal conditions to steelhead.

Spawning

For steelhead spawning, Bell (1991) reported a daily average temperature range of 10° to 12.8°C.

Behavior

For subyearling and yearling steelhead in the South Umpqua River, the preferred temperatures were 15.0°C and 17.8°C, respectively (Roper and Scarnecchia, 1994). Nielsen et al. (1994) observed that 65% of the juvenile steelhead in Rancheria Creek, CA moved into thermal refugia—in the form of adjacent stratified pools—during periods of high ambient stream temperatures of 23° to 28°C. Just before moving into these pools, foraging behavior declined and agonistic activity increased. On the Middle Fork Eel River, CA summer-run steelhead adults were found in deep, thermally stratified pools throughout the summer, when midday ambient stream temperatures ranged from 26° to 29°C. These cold water pockets averaged 3.5°C cooler than the stream. Where stream temperatures reached upper incipient lethal levels, these thermally stratified pools provided refuge habitat for significant numbers of young-of-the year, yearling, and adult steelhead.

A Synthesis of Numeric Temperature Criteria

The EPA (2003) recommends that temperature-limit criteria be based upon upper optimal physiological temperature preferences known to support requisite biological processes of recognized salmonid life-history stages. Fish-habitat relationships indicate a critical need for criteria to help direct human activities so that habitat conditions are prevented from continuing to deteriorate in a region where climatic cycles can temporarily mask underlying processes (Anderson, 1998; Beschta et al., 1987; Brannon et al., 2004; Chao et al., 2000; Hicks, 2000; Independent Science Group, 1996; Lackey, 2003; McCullough, 1999; McCullough et al., 2001; Mote et al., 2003; PNSHIWG, 1998; Poole and Berman, 2001; Poole et al., 2001a; Sedell and Froggatt, 1984). Temperature-based criteria for the long-term recovery of threatened and endangered salmonids under the Endangered Species Act, written to be consistent with EPA upper optimal temperature values, require two basic parts:

1. A requirement that the 7-DAM (7-day average of the maximum daily temperature) maxima must not increase over the course of 20 years within the habitats of ESA-listed salmonids. This is consistent with EPAs call (2003) for protection of high quality habitat whose water is currently colder than numeric temperature criteria. The EPA (2003) believes that the thermally optimal waters that do exist will be crucial for the survival of ESA-listed salmonids, and that their additional warming would jeopardize the potential to control water temperatures in warmer habitats downstream. This requirement of thermal nondeterioration is a challenging target in the face of regional population growth (Lackey, 2003) and climate change projections (Mote et al., 2003). Twenty years is a sufficient duration to avoid confounding by temperature oscillations driven by the Pacific Decadal Oscillation (PDO) (Anderson, 1998, Chao et al., 2000), which has considerable effects on climate in the Pacific Northwest.
2. Upper optimal temperature criteria, above which recovery planning would have to propose ways to fix the thermal regime regardless of whether or not the direction of change is nondeteriorating (Table 1). Sufficient data exist to propose 7-DAM temperatures (EPA, 2003) and also weekly mean temperature criteria. The latter provide an additional layer of insurance against global and regional environmental challenges including altered flow regimes and water temperatures associated with human activities and projected regional population growth (Lackey, 2003; Mote et al., 2003).

Table 1
Upper optimal temperature criteria

Life stage	7-Day-average maximum daily temperatures	Weekly mean temperatures
Spawning and incubation	13°C (55°F)	10°C (50°F)
Juvenile rearing	16°C (61°F)	15°C (59°F)
Adult migration	18°C (64°F)	16°C (61°F)
Smoltification except steelhead	16°C (61°F)	15°C (59°F)
Steelhead smoltification at fourth-level HUC[a] watershed	14°C (57°F)	12°C (54°F)

[a] HUC = hydrologic unit code.

For all these criteria, the significant challenge of defining the spatio-temporal range over which they should be applied remains. Those spaces occupied by threatened and endangered salmonids need to be regulated at the times of year that sensitive life stages are present, and defining the bodies of water involved and the times to apply the standards requires additional consideration and research. The complex life histories of salmonids, the variety of habitats used by their different life stages, and the spatially and temporally dynamic nature of the habitats involved, make this an enormous scientific undertaking (Brannon et al., 2004; Hicks, 2000; McCullough, 1999; McCullough et al., 2001; Poole and Berman, 2001; Poole et al., 2001a). Salmonid populations have evolved to intimately fit into the intricate thermal regimes of the Northwest (Brannon et al., 2004) making an understanding of the species-habitat relationships crucial in the face of accelerating regional (Lackey, 2003) and global (Mote et al., 2003) environmental changes, as well as natural periodic sources of variability (Anderson, 1998; Chao et al., 2000). Laboratory studies cannot fully substitute for field data, because of difficulties in replicating acclimation conditions, food availability, social interactions including territoriality, diurnal physiochemical periodicity, and the complexities of microhabitats accessible to fish in nature (Poole et al., 2001). Historic thermal regimes are often poorly understood, making evolutionary interpretations required for salmonid recovery efforts (Brannon et al., 2004) an even greater, although no less important, challenge (Poole et al., 2001).

Using use-attainability analysis, as prescribed by the existing Clean Water Act, there is no obligation to attempt to achieve unattainable conditions (in this case to apply the temperature criteria). Use-attainability analysis can be brought into play in situations where numeric criteria cannot be achieved, and under limited circumstances (EPA, 2003) a state or tribe can adopt a different use for that water, and temperature criteria sufficient to protect that new use. The EPA (2003) indicated that the new use should be "the most protective salmonid use that is attainable," and that all uses attained since 1975 must be protected. A new use is considered "compromised" or "degraded," and may only be in effect for part of the year (e.g., summer) and "unqualified, healthy salmonid use may be attainable other times of year and therefore may be the appropriate use then" (EPA, 2003). Factors that might preclude attainment include dams and other hydrologic modifications that cannot be operated in compliance with numeric temperature standards, and pollution that would cause more environmental damage to remediate than to leave in its existing state (EPA, 2003). Appropriate applications of numeric criteria in conjunction with use-attainability analysis is discussed in EPA (2003) section VI.1.C, and thermal heterogeneity is discussed in Ebersol (2002). Evidence for nonattainability would include the anthropogenic factors involved (EPA, 2003) the density, size, and duration of thermal refugia (Ebersol, 2002), and data pertaining to the physiological consequence for the existing salmonid population. The relationships between individual species data and the numeric criteria in the preceding table are described briefly in the following paragraphs.

Spawning and Incubation

The 10°C weekly mean temperature and 13°C 7-DAM criteria are consistent with the upper temperature range for optimum survival of chinook salmon embryos and alevins and are within reported temperature ranges for successful spawning (Baily and Evans, 1971; Bjornn and Reiser, 1991; Burrows, 1963; Donaldson, 1955; Eddy, 1972; Garling and Masterson, 1985; Heming, 1982; Heming et al., 1982; Neitzel and Becker, 1985; Olson and Foster, 1955; Raleigh et al., 1986; Ringler and Hall, 1975; Seymour, 1956).

For coho salmon, the weekly mean temperature criterion of 10°C and 13°C 7-DAM criterion are beyond their optimal temperature but within the upper end of their acceptable incubation temperature range (Davidson and Hutchinson, 1938; Dong, 1981; Murray and McPhail, 1988; Tang et al., 1987; Velsen, 1987; Sandercock, 1991). These criterion are within the generally accepted range of coho spawning temperatures (Hicks, 2000; Bell, 1973; McCullough et al., 2001).

For chum salmon, the 10°C weekly mean temperature criterion is within their safe temperature range for spawning and incubation (Beacham and Murray, 1985, 1986; Bjornn and Reiser, 1991; Hicks, 2000; McCullough et al., 2001; Zinichev and Zotin, 1987).

Steelhead spawning occurs at temperatures within the range protected by the 10°C (weekly mean temperature criterion), as does their early fry development (Bell, 1986; McCullough et al., 2001; Redding and Schreck, 1979; Rombough, 1988; Velsen, 1987).

Juvenile Rearing

The 15°C weekly mean temperature criterion is within the acceptable range of rearing temperatures for chinook with a natural feeding regime (Brett et al., 1982; Clarke and Shelbourn, 1985; Garling and Masterson, 1985; Marine, 1997).

The 15°C weekly mean temperature criterion is beyond their preferred temperature and at the upper end of the temperature range providing acceptable rearing conditions for chum salmon (Brett, 1952; Beschta et al., 1987; Hicks, 2000).

The 15°C weekly mean temperature criterion is within the acceptable range for coho rearing (Bell, 1986; Beschta et al., 1987; Brett, 1952, Coutant, 1977; Hicks, 2000; Reiser and Bjornn, 1979).

Optimal growth temperatures for juvenile steelhead are in the vicinity of 13° to 15°C (Grabowski, 1973; Hicks, 2000), although in a laboratory setting slightly higher temperatures were associated with a food supply in excess of that characteristically available in nature (Cech and Myrick, 1999; Wurtsbaugh and Davis, 1977).

Smoltification

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

The weekly mean temperature criterion of 15°C may be more protective of fall chinook salmon (Marine, 1997) than spring chinook (Zaugg, 1981). Hicks (2000) found that temperatures above 13.8°C did impair smoltification in chinook. Brannon et al. (2004) ascribe variability in chinook populations to diversity in the evolutionary landscape of the Columbia River Basin.

For coho salmon, the 15°C weekly mean temperature criterion is at the threshold temperature that causes smoltification impairment (Adams, 1975; Brett et al., 1958; Zaugg and McLain, 1976).

Adult Migration

The proposed weekly mean temperature criterion of 16°C and 7-DAM of 18°C are within the acceptable migration range reported for chinook temperature maxima (Alabaster, 1988; Bjornn and Reiser, 1991; Bumgarner et al., 1997; Dauble and Mueller, 1993; Fish and Hanavan, 1948; Hallock et al., 1970; Spence et al., 1996; Stabler, 1981; Stuehrenberg et al., 1978) and seems protective for coho survival during adult migration as well (Brett, 1952; Beschta et al., 1987; Flett et al., 1996; Reiser and Bjornn, 1979). Adult migrant chum have a somewhat lower temperature preference of 7° to 11°C (Groot and Margolis, 1991) but this does not indicate the temperature at which blockage occurs. Adult steelhead migration is not blocked until 21°C (Coutant, 1970; Stabler, 1981; Snyder and Blahm, 1971). Steelhead have been reported to make use of deep stratified pools as thermal refugia when midday ambient stream levels ranged above 22°C (Nielsen et al., 1994), or to congregate in cool tributaries when the mainstem reached 21.7–22.8°C (Fish and Hanavan, 1948).

Framework for Temperature Criteria

Salmonid survival and recovery will require more than the attainment of numeric temperature goals. A rich data set (e.g., Brannon et al., 2004) shows that in terms of thermal tolerances, disease resistance and physiological adaptation in general, salmonid stocks native to specific bodies of water may be better adapted to local conditions than are members of stocks originating in substantially different spawning habitats. Definitive criteria for salmonid recovery should eventually define ways to incorporate spatio-temporal variability into them in a realistically complex fashion and have as their eventual goal a process that realigns the distribution of current environmental variables so that they overlay historic conditions rather than simply act as a floor or ceiling. Poole et al. (2004) proposed the development of regime-based water quality standards that would describe spatio-temporal distributions of desirable characteristics over entire cachments. This stream-dynamics based approach would require scientifically rigorous monitoring programs (Ralph and Poole, 2003) and build upon natural flow regimes (Lytle and Poff, 2004; Poff et al., 1997). The challenge of this task is exacerbated by the multiple salmonid life stages whose distributions over space and time will need identification and monitoring. Brannon et al. (2004) provide compelling arguments that temperature has been the dominant environmental influence responsible for the evolution of historical chinook and steelhead population structure in the Columbia River Basin: if dominant in their evolution, temperature will surely be a dominant factor in their survival or extirpation. Projections for regional climate changes suggest summer flows will be decreased and water temperatures increasing (Mote et al., 2003). The complexity of any solution to the problem of salmonid survival will need to balance all of these considerations while achieving temperature regimes suitable for the persistence of salmon.

The challenge of having anything beyond remnant runs of wild salmonids present at the turn of the next century is complex, societal, and involves a wide array of concerns beyond the narrow temperature considerations described here (Lackey, 2001, 2003; Poole et al., 2004). However, understanding and articulating such numeric temperature criteria are a necessary (if far from sufficient) component of salmon recovery planning. Ethical analyses of the assumptions underlying salmon recovery policy are called for (Butkus and Kolmes, 2003) and current policy trends that violate basic components of an environmental ethic are apparent. Basic assumptions upon which scientific modeling is based (e.g., the 5% acceptable risk of extinction for an evolutionarily significant unit over 100 years adopted by NOAA Fisheries, or proposals that would prioritize recovery efforts to specific streams while allowing thermal deterioration of others) (McElhaney et al., 2000; McElhaney et al., 2003) are in fact ethical decisions made prior to scientific analysis and often presented as though they were scientific themselves (Butkus and Kolmes, 2003). Realistic recovery planning needs to acknowledge and address difficult truths and distinguish science, ethics, and predictable future scenarios if we are to make progress (Lackey, 2001, 2003; Mote et al., 2003; Butkus and Kolmes, 2003). A system level approach to vulnerability analysis and careful design of long-term monitoring regimes are necessary in the analysis of coupled human-environment systems for sustainability planning (Larsen et al., 2004; Turner et al., 2003).

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