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Issue Paper 5

Summary of Technical Literature Examining the Physiological Effects of Temperature on Salmonids

Prepared as Part of EPA Region 10 Temperature Water Quality Criteria Guidance Development Project

Dale McCullough, Columbia River Intertribal Fish Commission

Shelley Spalding, U.S. Fish and Wildlife Service

Debra Sturdevant, Oregon Department of Environmental Quality

Mark Hicks, Washington Department of Ecology

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Dale McCullough, Shelley Spalding, Debra Sturdevant, and Mark Hicks

Abstract

The chief objective of this paper is to provide a literature review of the role temperature exerts on the physiology of various salmonids. The fish are affected as species and within the stages of their life history. The thermal environment, perhaps more than any other aquatic habitat feature, influences the distribution, health and survival of our native salmonids. Temperature tolerances for salmonid species typically refer to effects of temperature on an individual. Because we are interested in sustainable populations of salmonids, this paper also reviews information on the optimal or preferred ranges of temperatures that will be needed to promote long-term survival, growth, and reproductive success.

Thermal stress occurs when a temperature or a change in temperature produces a significant change to biological functions leading to decreased likelihood of survival. Thermal stress can lead to lethal effects either immediately, in a period of days, or even weeks or months from the onset of the elevated temperature. Thermal stress can also result in "sublethal" or indirect effects resulting in death or reduced fitness that impairs processes such as growth, spawning, smoltification, or swimming speed. Metabolic processes are directly related to temperature, and the metabolic rate increases as a function of temperature. Fish are metabolically efficient and most likely to thrive within the preferred range of temperatures.

Different species of salmonids have evolved to utilize different thermal regimes, although there is much overlap in their utilization of these regimes. Anadromous salmonids and coastal cutthroat and rainbow trout tend to have similar temperature requirements; however, where multiple species and life stages are present, temperature criteria need to protect the most sensitive species and life history stage. For this guild, maximum growth and swimming speed occur at 55.4-68°F (13-20°C) under satiation feeding; reduced ATPase levels are experienced at temperatures as low as 51.8-55.4°F (11-13°C), potentially resulting in delayed or ineffective smoltification; adult migration may be blocked at 69.8-73.4°F (21-23°C); and temperatures of 42.8-50°F (6-10°C) or lower during incubation result in maximum survival and size at emergence. Bull trout have lower temperature requirements than other salmonids with optimal incubation occurring at 35.6-42.8°F (2-6°C), spawning being initiated as temperatures drop below 48.2°F (9°C), and the maximum growth rate at satiation feeding occurring at 60.8°F (16°C). For other salmonids such as redband trout, westslope cutthroat trout, and mountain whitefish, little information is available on the effects of temperature on their physiology.

Introduction

The distribution, health, and survival of our native fish species are inextricably linked to the thermal environment. Temperature, perhaps more than any other environmental parameter, greatly affects the status of fish and other aquatic life. With respect to thermal effects, lethal temperatures do occur in the field and can be locally problematic in defining usable and unusable habitat. Sublethal effects of temperature determine the overall well-being and patterns of abundance of our native fish populations. Temperature exerts its control through its effect on the physiology of the individual species and their life stages. In addition, individuals within a species population vary in their responses (e.g., lethal, growth) to temperature, generally according to a bell-shaped distribution. As species individually or relative to one another experience temperatures outside their physiological optimum range, the mix of species present in any given waterbody may drastically change. Aside from direct mortality caused by very high temperatures, temperature influences the abundance and well-being of organisms by controlling their metabolic processes. Every species, including disease organisms, has optimal metabolic ranges. Community composition is shaped by the level of numerous components of the habitat system, including temperature, food, water, light, substrate, and so on, each of which can provide optimal or suboptimal conditions. Temperature is one of the single most influential determinants of habitat quality and can also act synergistically with other habitat elements.

Temperature through its effect on physiology influences the ability of fish to grow, reproduce, compete for habitat, and escape predators. This issue paper examines the role of temperature in the physiology of the salmonids native to the Pacific Northwest, and the importance of lethal temperature effects compared with various types of sublethal effects in controlling the survival and health of native fishes.

For further information on the effects of temperature on salmonids, we suggest you refer to both the Behavior and Temperature Interaction issue papers in this series. This issue paper is drawn heavily from existing extensive reviews of thermal effect literature (Berman 1998, EPA and NMFS 1971, Hicks 1999, 2000, McCullough 1999, ODEQ 1994) and is intended to extract from this large body of literature the key documents illustrating various concepts and effects. For additional guidance to the literature on thermal effects, we recommend starting from these references.

The intention of this paper is to review physiological effects of temperature regimes for all salmonids. However, the authors acknowledge the scarcity of relevant bull trout information and have avoided including observations or case studies that are difficult to extrapolate, as is the case with much of the bull trout temperature literature. In cases where there is information available on a closely related charr species, that information may be included.

In the following questions and answers, we first summarize thermal requirements for salmonid incubation and early fry development, growth, smoltification, swimming speed, migration to spawning, and adult holding and spawning, and discuss lethal effects. Then we present detailed documentation and references.

SUMMARY OF THERMAL REQUIREMENTS

What are the thermal requirements for incubation and early fry development?

During incubation and early fry development, salmonid embryos and young fish have different habitat requirements from those of spawning adults, even though the adult-selected spawning site is the incubation environment for the progeny. During incubation, water temperature affects the rate of embryo and alevin development, the amount of dissolved oxygen in the water, and, to a significant extent, the survival of early fry (Bjornn and Reiser 1991). Within an acceptable range, the higher the temperature is the faster the rate of development will be and the shorter the incubation period and time to emergence (Beacham and Murray 1990).

The effects of water temperature in regulating developmental rates of incubating eggs are well documented (Hicks 2000, McCullough 1999). Temperatures from 39.2 to 53.6°F (4-12°C) tend to produce relatively high survival to hatching and emergence, with approximately 42.8-50°F (6-10°C) being optimum for most salmonid species. However, although salmonids should avoid temperatures that are too cold or too warm during initial stages of incubation, the entire thermal history (including accumulation of degree days) during incubation is of great importance to ensure proper emergence timing. That is, a thermal regime that cools rapidly from 53.6°F (12°C) and achieves low winter temperatures (according to natural cooling processes and rates) is essential for acquiring the necessary thermal units to ensure proper emergence timing and high egg survival. Unless water releases from dams alter winter thermal regimes in egg incubation habitat, it is assumed that controlling summer rearing temperatures (maximum and diel fluctuation) will also provide proper winter temperatures during incubation. Management "control" of summer temperatures means taking those actions that would restore the thermal regimes consistent with the system potential for the stream.

Char can be characterized as a stenothermal species because they require a narrow range of cold temperatures to rear and reproduce and may thrive in waters too cold for other salmonid species (Balon 1980). The literature suggests that the optimum water temperature range for bull trout and Dolly Varden incubation occurs just below the optimal range for the other salmonids native to the Pacific Northwest.

Native stocks of salmon, trout, and char are closely tied to their natal streams and have evolved with natural fluctuations in stream temperatures and other environmental variables. Some streams may have winter temperatures that are lower than the minimum recommended as optimal for most salmonid species other than char; however, eggs are usually able to develop normally because spawning and initial embryo development occur when temperatures are in the suitable range. The presence of groundwater inflows close to spawning areas also helps ameliorate seasonal temperature extremes that might be harmful to developing embryos.

What are the thermal requirements for growth?

Growth is one of the most sensitive indicators of overall fish health and is vulnerable to changes in basic environmental conditions such as temperature. Unless a fish can grow it cannot complete its life functions. For example, a fish must reach a sufficient size at hatching or

emergence to have a high likelihood of survival. Size attained at the time of hatching or emergence partially depends on egg size, which in turn is related to adult size and nutritional status at spawning. If growth rates are too low during the summer rearing period, body fat is not sufficient to sustain a fish during the winter rearing period (Hokanson 1977). If the size during overwintering is too small or the growth rate prior to emigration is too low, smolt size will be insufficient to ensure successful transition to the marine environment (Folmar et al. 1982). Growth rates during egg incubation are affected by temperature in the gravel. In streams with low winter temperatures (e.g., <42.8°F [6°C]), feeding and total fish activity tend to be very low, and consequently growth is minimal.

Growth rates of juvenile fish during summer are used as a convenient means of monitoring the thermal impacts of most freshwater environments. Riparian canopy removal or channel widening, which lead to increased maximum water temperatures during summer, are also associated with lower minimum winter temperatures as well as increased diel fluctuations in both seasons. Optimum growth temperatures for a variety of salmonids, many of which are native to the Pacific Northwest, are listed in Table 1. These optimum temperatures for feeding at full ration range from 53.6 to 68°F (12-20°C). Because food availability in the field typically provides less than satiation feeding, optimum growth temperatures in the field can be substantially reduced (Elliott 1981).

Table 1. Selected growth optima for salmonids determined from feeding on full rations

Species	Optimum growth temperature (°C)	Reference
Chinook (*Oncorhynchus tshawytscha*)	15	Banks et al. (1971) (as cited by Garling and Masterson 1985)
	17	Clarke and Shelbourn (1985)
	19	Brett et al. 1982
	20	Marine (1997)
Sockeye (*Oncorhynchus nerka*)	15	Brett et al. 1969
Coho (*Oncorhynchus kisutch*)	15	Everson (1973, as cited by Sullivan et al. 2000)
Rainbow trout (*Oncorhynchus mykiss*)	17.2-18.6	Hokanson et al. (1977)
	16.5	Wurtsbaugh and Davis (1977)
	15	Grabowski (1973)
	15	Railsback and Rose (1999)
(redband trout)	20	Sonski (1983b)
Brook trout (*Salvelinus fontinalis*)	12.4-15.4	McCormick et al. 1972
Lake trout (*Salvelinus namaycush*	12.5	Edsall and Cleland (2000)
Brown trout (*Salmo trutta*)	13.9	Elliott and Hurley (1999)
	13.1	Elliott et al. (1995)
Atlantic salmon (*Salmo salar*)	18	Siemien and Carline (1991)
Arctic char (*Salvelinus alpinus*)	14	Jobling (1983)
	15.1	Larsson and Berglund (1997)
European grayling (Thymallus thymallus)	17.3	Mallet et al. (1999)
Bull trout (*Salvelinus confluentus*)	12-16	McMahon et al. (1999)

Optimum growth temperature is that temperature which provides the most favorable conditions for growth. Other biological performances such as feeding rate and conversion efficiency may have other optimum temperatures. For example, feeding rate and conversion efficiency both are influenced by temperature, but each can have a slightly different optimum temperature. Because growth rate is more directly linked to energy assimilated (the result of the combination of feeding rate and conversion efficiency), it seems most appropriate to emphasize growth rate as a key biological performance indicator of the thermal environment quality rather than the other two performances.

Growth rate is a function of temperature but also of food availability (Elliott 1981, Elliott 1994). Food availability in the field is normally thought to be substantially less than that needed to provide satiation feeding. Consequently, if stream productivity restricts salmonid feeding to levels less than satiation, then lower temperatures are required to ensure optimum growth rates. Although laboratory-derived temperature growth optima are probably adequately defined for various feeding levels, an absolute growth rate in the laboratory may not be matched in the field given the differences in food quality. In hatchery culture situations, satiation feeding on hatchery diets can produce excessive accumulation of lipid (i.e., hatchery fish are often obese compared with wild fish). This is not to say that optimum growth temperatures are not a useful biological index to temperatures providing healthful conditions for salmonids residing in the center of their distribution in the field. Instead it indicates that artificially increasing temperature in the field above optimum produces a relative reduction in growth rate. Also, in order to provide the greatest population production capacity (contributing to biomass, abundance, and fecundity—all indicators of fitness and population long-term viability), it is important to provide the full range of natural potential temperature longitudinally. This means very cold headwaters, cold midreaches, and cold/cool lower reaches. This will produce, in general, lower than optimum growth in headwaters, optimum growth in midreaches, and lower than optimum growth downstream. Eliminating cold-water habitats upstream shrinks suitable habitat, converts more habitat to suboptimal growth zones, and reduces potential production.

Optimum temperature can have another connotation. When we consider the effects of temperature at any given life stage, multiple performances must often be achieved. For example, if the highest growth rate were produced only under temperatures so high that a large portion of the population would die from disease, the optimum temperature for satisfying overriding needs (e.g., sustainability) of the population might be closer to the optimum for protection against disease. If the disease resistance temperature optimum is so low that growth and reproduction are low, the optimum would have to lie in a more intermediate position. However, as previously described, most key biological performances are well correlated and have similar optima. Preferred temperatures, optimum growth temperatures, and high disease resistance from common warm-water diseases (e.g., furunculosis, columnaris) tend to be similar (Jobling 1981). Consequently, we are able to survey the literature about optimum growth temperatures, compare these temperatures with optima for other performances such as disease resistance or swimming ability, and find a temperature range that would satisfy growth objectives but also meet other key needs influencing survival.

The physiological optimum is the temperature under which a number of physiological functions, including growth, swimming, spawning, and heart performance, are optimized. Physiological optimum temperature can be estimated as the average of growth optimum and final

preferendum (Armour 1990, McCormick and Wegner 1981). Physiological optimum has been used as the basis for estimates of suitable temperatures for fish survival (NAS 1972). Because growth optima heavily influence the physiological optimum, optimum growth is intimately linked with temperatures producing high survival. Optimum growth during the warm, maximum growth season (generally summer) is then linked with high survival. Optimum growth depends on food availability. As food availability declines, the temperature producing optimum growth also is lowered. The growth optimum is also found near the temperature for maximum metabolic scope (Brett 1952). The greater the scope, the greater the ability of fish to divert energy to either somatic growth or gamete production. Obviously, maximizing growth is not desirable at all times. For example, rapid egg development throughout incubation would result in improper emergence timing, and rapid, early juvenile growth would result in early smolt emigration (Holtby et al. 1989). On the other hand, inadequate size attained by smolts leads to poor ocean survival (Metcalfe and Thorpe 1992). These contrasting demands imply that it is important to achieve high growth rates during the growth season and to minimize the loss of energy during the remainder of the year. At a stream system scale, this maximization of growth rates would occur only in the center of the geographic distribution of the species according to the natural potential of the system to produce the corresponding thermal regime. Exceeding the temperature producing optimum growth (e.g., in the center of distribution) results in diminished growth rate, increased disease incidence, and increased sublethal stress (see Elliott 1981).

Recommendation of temperatures for protection of fish species must emphasize high survival by life stage (e.g., egg, juvenile, smolt, adult). High ability to perform all key life functions (e.g., feeding, growth, swimming, migration, reproduction, mate selection) is also an important link to fitness and population viability.

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

What are the thermal requirements for smoltification?

Smoltification occurs in juvenile fish as they prepare to move from a freshwater habitat to a marine habitat. The parr to smolt transformation involves changes in activity, coloration, shape, and physiological tolerance to seawater. The ultimate biological goal of smoltification is to increase survival of smolts upon entering the marine environment.

Effects of temperature on the smolting process have been studied in terms of changes in growth, condition factor, body silvering, body moisture and lipid content, salinity tolerance, and gill Na-K-ATPase activities (Johnston and Saunders 1981). 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, or other stresses detrimental to fitness.

Salmon and steelhead during the smolt phase have various degrees of sensitivity to elevated water temperatures (e.g., Adams et al. 1973, Zaugg and McLain 1976, Hoar 1988). Temperatures that have been reported in the literature as impairing smoltification range from approximately 53.6-59°F (12-15°C) or more (Table 2). Steelhead appear to be most sensitive during this stage, as opposed to their greater resistance to high temperatures during other juvenile stages. Although some bull trout do enter the nearshore marine environment, little is known about their smoltification process and sensitivities. Smolt migration during periods of high water temperatures can cause inhibition or reversal of the smoltification process or a termination of migration (i.e., return to freshwater residency for an additional year). Qualitatively, this effect can be linked to changes in visual or physiological indicators, such as gill Na+-K+ ATPase activity. These qualitative indices, in turn, are linked to a lowered survival of smolts when subjected to seawater challenges. Lowered survival is associated with inability to osmoregulate due to altered physiological status. Because sensitivity of smolts to elevated mainstem temperatures varies by species and because species and stocks vary in migration timing, the significance of effects of mainstem temperatures on smoltification and survival require consideration of thermal regime during the migration period by species.

Table 2. Temperatures that have been linked to impairment of smoltification, ability of smolts to migrate, or survival during smolt migration

Species	Temperature (°C) threshold for impairment	Reference
Chinook	12	Wedemeyer et al. (1980)
	17-20	Marine (1997)
	12	Wedemeyer et al. (1980)
Coho	15	Zaugg and McLain (1976)
	12	Wedemeyer et al. (1980)
	15	Adams et al. (1975)
Steelhead	>13	Hoar (1988)
	>12.7	Adams et al. (1975)
(summer steelhead)	>13.6	Zaugg et al. (1972, as cited by Zaugg and Wagner 1973)
	12	Zaugg (1981)
Sockeye	12-14	Brett et al. (1958)

To provide a thermal regime protective of smoltification, temperature should follow a natural seasonal pattern (Wedemeyer et al. 1980). Varying temperatures are common in the natural environment, and fluctuating temperatures are more stimulating to steelhead smoltification than constant temperatures (Wagner 1974 as cited by Hoar 1988, Zaugg and Wagner 1973). An extreme example of the interference of elevated and constant temperatures on smoltification can be found in the mainstem Columbia River reservoirs, where environmental conditions are of considerable concern. The large thermal inertia due to the volume of stored water in the reservoirs alters the seasonal, as well as diel, thermal regimes (Bennett et al. 1997, Karr et al. 1992, 1998).

What are the thermal requirements for swimming speed?

Beamish (1978) classified swimming performance of fish into three categories: sustained, prolonged, and burst swimming. Sustained swimming performance is that swimming speed that can be maintained for long periods (>200 min) without fatigue. Prolonged swimming speed defines a performance of shorter duration (20 s to 200 min). Burst swimming speed is the speed a fish can swim for a few seconds. Swimming speed for fish of a certain species and size can have maximum swimming speeds defined by the number of body lengths traveled per second (Bjornn and Reiser 1991) or in absolute terms of distance/time.

According to Bell (1986), sustained speed is used for passage through difficult areas, prolonged or cruising speed during migration, and dart or burst speed for escape, feeding, and rapid movement through swift water. During adult migration, if water temperature is high or oxygen concentrations are low, swimming speed can be impaired and the fish may refuse to migrate, migrate back downstream, or seek shelter in tributaries or other available cold-water refuges (Fish 1948, Schreck et al. 1994). Under these conditions the migration may be delayed or restricted. Smolts, on the other hand, benefit from availability of rapid current flow because their downstream progress depends on water velocity rather than their swimming speed. However, swimming speeds of smolts must not be impaired because swimming is vital to maintaining position in the current to control rate of descent and avoid obstacles.

Small fish generally have lower swimming speeds (ft/s) than large fish at any given temperature. Large predators can easily overtake small fish, so that ability to avoid predators with burst swimming is essential. Burst swimming used during avoidance behavior requires recovery time, and excessive stress can lead to death. Burst swimming can be impaired under high temperature or low oxygen conditions. Predaceous species more adapted to warm water such as northern pikeminnow (native), walleye (exotic), and smallmouth bass (exotic), for example, find their optimum swimming speeds at temperatures greater than those of salmon and steelhead.

Water temperature and oxygen are significant controls on swimming speed. Swimming performance also depends on prior acclimation temperature in relation to exposure temperature. Disease has been shown to adversely affect the swimming performance of mature sockeye salmon caught in Port Alberni Inlet and transferred to Simon Fraser University for swimming tests at 66.2-69.8°F (19-21°C) (as cited in Macdonald et al. in press). Critical swimming performance was reduced to 65% of normal by diseases. Stress can also adversely affect

swimming performance. High plasma lactate levels are known to negatively affect swimming performance (Farrell et al. 1998 as cited in Macdonald et al. in press). Telemetry studies at Hell's Gate suggest that fish that failed to negotiate Hell's Gate exhibited one or more periods >10 min in which they swam at speeds greater than their estimated critical swimming speed. Stress is believed to induce such frantic behavior and cause the fish to be washed downstream.

Field studies with Fraser River sockeye (as cited in Macdonald et al. in press) reportedly support the work of Brett (1971, 1995) (optimum swimming performance at 59-64.4°F [15-18°C]) and found the temperature optimum to be 62.6°F (17°C) for swimming endurance, with almost a 20% reduction in swimming speed at 69.8°F (21°C).

In 1997, researchers reportedly found that because of high water velocity some sockeye salmon depleted their lipid stores more quickly than in previous years. Consequently, muscle protein and glycogen reserves were utilized earlier in the migration than was expected under normal conditions; many fish failed to reach the spawning grounds (Donaldson et al. 2000, Higgs et al. 2000; as cited in Macdonald et al. in press). Given that water temperature in 1998 exceeded the average by 3.6-7.2°F (2-4°C), the authors expected that metabolic stores would have been reduced at least 25% faster during river migration.

What are the thermal requirements for migration to spawning?

Salmonids often migrate great distances (intrabasin or upstream/downstream anadromous migrations) in river systems during the warm season. The success of these migrations can depend substantially on water temperatures. Most stocks of anadromous salmonids have evolved with the temperature regime of the streams they use for spawning and migration, and alteration of the normal temperature pattern can result in reduced fitness. Migration blockages occur consistently among species in the temperature range 66.2-73.4°F (19-23°C) (Table 3).

Elevated temperatures in mainstem rivers that provide migration corridors (especially those dominated by reservoirs) are harmful for survival and reproduction of bull trout, chinook, steelhead, and sockeye (especially, because of their adult migration timing). These effects occur via several mechanisms: (1) direct lethality to adults and smolts under high temperature conditions, (2) delay in migration and spawning, (3) depletion of energy stores through heightened respiration, (4) deformation of eggs and decreased viability of gametes, and (5) increased incidence of debilitating diseases. See the Behavior issue paper for a discussion of the effects of temperature on the migratory behavior of salmonids.

Macdonald et al. (in press) studied the high mortality rates in sockeye and chinook salmon that occurred in the Fraser River Watershed of British Columbia, Canada. They found temperature to be the likely cause of both en route and prespawning losses. On the basis of their review of the historical database, the authors suspected that losses in spawning runs occur when mean daily river temperatures exceed 62.6-64.4°F (17-18°C) for prolonged periods. Migration blockages, susceptibility to disease, impaired maturation process, increases to stress parameters, reduced efficiency of energy use, and reduced swimming performance were all cited as potentially serious hazards as daily mean temperatures exceed 62.6°F (17°C). In examining fertilization success, the authors found significant impairment (only 10% success) in stocks that

Table 3. Studies that identify thermal blockages to adult salmon migration

Species	River	Temperature cited as blocking migration	Reference
chinook, sockeye, steelhead	Columbia	71-75°F (21.7-23.9°C)	Fish and Hanavan (1948)
spring chinook	Clearwater, Idaho	69.8°F (21°C)	Stabler (1981)
spring chinook	Tucannon	69.9°F (21.1°C)	Bumgarner et al. (1997)
spring chinook	Willamette	69.8-71.6°F (21-22°C) (at oxygen >3.5 mg/L)	Alabaster (1988)
summer chinook	Snake	69.8°F (21°C)	Stuehrenberg et al. (1978) (as cited by Dauble and Mueller 1993).
fall chinook	Sacramento	66.2-69.8°F (19-21°C) (oxygen ~5 mg/L)	Hallock et al. (1970)
steelhead	Snake	69.8°F (21°C)	Strickland (1967, as cited by Stabler 1981)
sockeye	Okanogan	69.8°F (21°C)	Major and Mighell (1967)
sockeye	Snake	71.9°F (22.2°C)	Quinn et al. (1997)
sockeye	Okanogan	73°F (22.8°C)	Hatch et al. (1993)
sockeye	Fraser	64.4-71.6°F (18-22°C)	Macdonanld et al. in press

migrated through the Fraser during 1998 (a record warm year) compared with success during cooler years. Dr . Craig Clarke (as cited in Macdonald et al. in press) found that a 2-wk exposure to 66.2°F (19°C) compared with 59°F (15°C) in the laboratory was sufficient to significantly depress the hormones controlling sexual maturation in sockeye salmon. This was viewed as consistent with the finding of Manning and Kime (1985, as cited in Macdonald et al. in press) that steroid biosynthesis was suppressed in rainbow trout testes at 62.6°F (17°C).

Migration has been observed to occur under a wide range of conditions for each salmon species (see Bjornn and Reiser 1991). This reflects a combination of characteristics about the fish: the seasonality of their migration period, temperatures that were available to them during their normal migration period, shifts in migration timing that may have occurred over time (e.g., effects of deliberate attempts by hatchery managers to create a run that does not overlap with a wild run, the response by the stock itself to shifts in river temperature regimes during the incubation, smolt migration, and/or adult migration periods), and in some species that migrate during warm seasons their tolerance to elevated temperatures. Bioenergetic stresses (ability to maintain long-term energy reserves), instantaneous power demands (ability to exhibit burst swimming, jump falls, escape predators, recover from stress [exertion, disease]), and ability to resist disease may all be of concern in the higher temperature range for migration. Just as distribution of juveniles relates to temperature in a stream system (i.e., from optimum to suboptimum to the distributional limits), migration temperatures can be assumed to have an

optimum that is less than the migration limit and migration can be impaired as the limit is approached.

Fall and spring chinook are examples of different life history types of a single species having differing migration and spawning timings. Given the similarity in ultimate upper incipient lethal temperatures of these two races (NAS 1972) and the minor differences in ultimate upper incipient lethal temperature (UUILT) among stocks of numerous species, it is reasonable to assume that fall and spring chinook have similar UUILT values for juvenile and adult stages, respectively. Because adult spring chinook migrate earlier in the year than fall chinook they encounter cooler water temperatures in mainstem rivers. However, spring chinook also must hold in tributaries until the autumn spawning season, so avoidance of high holding temperatures is their thermal challenge. For fall chinook, the thermal challenge is avoidance of higher thermal stress both during adult migration and during a more brief holding period. Temperature ranges for spring, summer, and fall chinook migration have been summarized (see Bjornn and Reiser 1991), and show that spring chinook tend to migrate under a range of temperatures having a lower maximum. Given the similarity in lethal temperatures within this species, the temperatures linked to successful migration for fall chinook might also adequately represent the capability of spring chinook, which are not normally tested because temperatures do not tend to be as high during their migration period. However, threshold temperatures linked to a complete inability to migrate are very similar between spring and fall chinook, as well as among many anadromous species that have been examined.

What are the thermal requirements for adult holding and spawning?

Full protection of salmonids during reproduction involves managing instream temperature during several phases of the reproductive cycle (prespawning, spawning, and postspawning). Successful reproduction can involve success (survival of adults and their gametes) during migration, holding prior to spawning, mate selection, redd digging, egg deposition, and nest guarding. For fall-spawning fish (e.g., bull trout, chinook, coho, chum), temperatures typically reach their annual highs during migration and/or holding. Stocks that take advantage of the predictability of the most generally favorable seasons time their migration and spawning to complete life-cycle phases. Long-term alterations in temperature regimes can disrupt this timing. Disruptions in timing include a reduction in time available to complete a subsequent life-cycle process or a change in timing of this process.

Temperature can inhibit upstream migration of adult fish. This can result in seeking cold-water refuges such as deep pools in the mainstem, cold tributary mouths, or downstream mainstem areas. Inhibitory temperatures thus can cause migration delays that alter timing of key processes such as spawning or can lead to stress, disease, bioenergetic depletion, or death. If migration occurs at high temperatures just prior to spawning (such as in fall chinook or coho), gametes held internally in adults can be severely affected, resulting in a loss of viability that appears as poor fertilization or embryo survival. High temperatures during the holding or prespawning stages can also occur in many locations, even if adults have managed to escape high mainstem migration temperatures. Then, if water temperatures have not begun to decline below critical thresholds before spawning begins, fertilization and early incubation survival will be affected. Early incubation is very sensitive to elevated temperatures. In addition, salmonid

diseases can affect the egg stage as readily as other life stages.

The above section on migration detailed the inhibition of adult migration that occurs with elevated temperatures in migratory corridors. Spring chinook, summer chinook, and fall chinook all migrate during different seasons, but high water temperatures can be assumed to have similar effects on migration for all races. In addition, other species respond to the same thresholds. Furthermore, it is of great concern that UILT values for chinook and coho are approximately the same as the temperatures that inhibit migration. This implies that salmon will cease migrating at temperatures just below those required to kill a portion of the population.

What are lethal temperature effects?

National Academy of Sciences (NAS) (1972) recommendations for water temperature exposure for protection of aquatic life specify maximum acceptable temperatures for prolonged exposures (≥ 1 wk), winter maximum temperatures, short-term exposure to extreme temperature, and suitable reproduction and development temperatures. Lethal effects are thermal effects that cause direct mortality within an exposure period of less than 1 wk. Prolonged exposure temperatures and temperatures that interfere with normal reproduction and development can result in mortality or reduction in population fitness or production, but the effects may be delayed or indirect, or result from impairment of function or reduction in suitable habitat or food quantity and quality available.

Survival rates based on amount of time exposed and temperature of exposure are extremely well described in the scientific literature. These time-temperature relationships have been described using equations of the form log (time) = $a + b$ (temp.), where time is expressed in minutes, temperature is in degrees Celsius, and a and b are coefficients for intercept and slope of the regression, respectively, described for individual acclimation temperatures (NAS 1972). The regression describes the combinations of time and temperature that result in mortality (typically recorded as the point of estimated 50% mortality) at various acclimation temperatures. The upper incipient lethal temperature (UILT) is an exposure temperature, given a previous acclimation to a constant acclimation temperature, that 50% of the fish can tolerate for 7 d (Elliott 1981). Alternatively, UILT at a particular acclimation temperature has been determined as an exposure temperature producing 50% survival within 1,000 min (Brett 1952, Elliott 1981) or 24 h (Wedemeyer and McLeay 1981, Armour 1990). Within this variation in exposure times, we expect a slightly lower UILT at a 7-d than a 24-h exposure. The UILT becomes greater with increasing acclimation temperature until a point is reached at which further increase in acclimation temperature results in no increase in temperature tolerated with the same survival level. This is the ultimate upper incipient lethal temperature.

In addition to acclimating fish to a constant temperature prior to exposure to test temperatures, fish may be acclimated to a fluctuating temperature regime. It is possible to determine for a cyclic acclimation temperature a corresponding constant temperature, that is, an equivalent constant temperature. This is accomplished by experimentally determining the constant acclimation temperature within the range of the cyclic regime that produces the same response to an exposure temperature as the cyclic regime.

Because UILT varies with increasing acclimation temperature until the UUILT is reached, the UUILT is a good stable index for comparing thermal response among species. For salmonids, a survey of the literature indicates that acclimation temperatures above approximately 68°F (20°C) produce similar UILT values, although very small increases in UILT can occur at up to a 75.2°F (24°C) acclimation temperature. Consequently, it can be safely assumed that any UILT study in which acclimation temperature was ≥ 68°F (20°C) will produce a UILT nearly identical to the UUILT. UILT values compiled from the literature (taken from McCullough 1999) for various acclimation temperatures are presented in Table 4. Given the considerations above, these values can be interpreted as estimates of UUILT.

What conclusions can you draw for anadromous salmonids and coastal cutthroat and rainbow trout?

1. Five species of Pacific salmon—chum, *Oncorhynchus keta*; coho, *O. kisutch*; sockeye, *O. nerka*; chinook, *O. tshawytscha*; and pink, *O. gorbuscha*—and steelhead, *O. mykiss*, and coastal cutthroat trout, *O. clarki*, are stenothermic and have similar physiological requirements for cold water. Given their similarity in physiological requirements, a common temperature criterion could be established to protect these seven species as a single group. In those waterbodies where multiple species and life stages are present, temperature criteria would need to be oriented to the most sensitive species and life history stage.

2. Measures of maximum growth and swimming speed are useful in defining the optimal temperature range. However, these tests are typically conducted under controlled laboratory conditions and may not accurately reflect the influence of temperature under the more complex ecological context of natural stream systems. Laboratory results may need to be adjusted downward to account for the influences of reduced food availability, competition, predation, and other environmental variables. Also, laboratory results may not reveal sublethal effects associated with an increased risk of warm-water disease and physiological stresses of smoltification under elevated water temperatures.

    a. Maximum growth and swimming speed generally occur within the range of 55.4-68°F (13-20°C) for native salmon and trout under laboratory conditions in which fish are fed to satiation. Maximum swimming speeds appear to be at temperatures greater than those providing maximum growth rates. The ecological need for temperatures allowing maximum growth is greater than for maximum swimming speed. That is, of the two biological performances controlled by temperature, growth rates have a greater need to be optimized on a basinwide scale (see issue papers on Fish Distribution and Spatio-Temporal Effects as well as the final synthesis paper for a complete description of this concept). In addition, optimum growth temperatures provide nearly optimum swimming speeds.

    b. Streams with naturally low productivity or in which food availability is lower than under natural conditions (e.g., caused by stream channel sedimentation and high substrate embeddedness) can be expected to produce optimal growth at temperatures that are lower by at least 3.6-7.2°F (2-4°C) and, under certain conditions, as much as

Table 4. Upper incipient lethal temperature of various juvenile salmonids

Species	Common Name	Origin (river/lake)	Author(s)	Accl. Temp. (˚C)	UILT (°C)
Oncorhynchus tshawytscha	chinook salmon	Dungeness Hatchery, WA	Brett (1952)	20 24	25.1 25.1
		Sacramento River	Orsi (1971, as cited by CDWR 1988)	21.1	24.9
Oncorhynchus kisutch	coho salmon	Nile Cr. Hatchery, British Columbia	Brett (1952)	20 23	25.0 25.0
Oncorhynchus nerka	sockeye salmon	Issaquah Hatchery, WA	McConnell and Blahm (1970) (as cited by Coutant 1972) Brett (1952)	20 20 23	23.5 24.8 24.3
Oncorhynchus keta	chum salmon	Nile Cr. Hatchery, British Columbia	Brett (1952)	20 23	23.7 23.8
Oncorhynchus gorbuscha	pink	Dungeness Hatchery, WA	Brett (1952)	20 24	23.9 23.9
Oncorhynchus mykiss	rainbow trout	Lake Superior	Hokanson et al. (1977)	16	25.6
		France	Charlon et al. (1970)	24	26.4
		Lakes Erie, Ontario, Huron, Superior	Bidgood and Berst (1969)	15	25-26
			Cherry et al. (1977)	24	25
			Stauffer et al. (1984)	24?	26
		Ontario	Threader and Houston (1983)	20	25.9
			Alabaster (1964) (as cited by Threader and Houston 1983)	20	26.7
		Summerland Hatchery, British Columbia	Black (1953)	11	24
		Firehole River, MT Ennis Hatchery Winthrop Hatchery	Kaya (1978)	24.5 24.5 24.5	26.2 26.2 26.2

Table 4. Upper incipient lethal temperature of various juvenile salmonids (continued)

Species	Common Name	Origin (river/lake)	Author(s)	Accl. Temp. (°C)	UILT (°C)
	redband trout	Parsnip Reservoir, Oregon	Sonski (1983a)	20 23	27.4 26.8
		Parsnip Reservoir, Oregon	Sonski (1984)	20 23	26.2 26.2
		Firehole River, Wyoming		20 23	27.2 26.3
		Wytheville rainbow		20 23	26.8 27.0
Salmo salar	Atlantic salmon	England	Bishai (1960)	20	23.5
Salmo trutta	brown trout	England	Bishai (1960)	20	23.5
			Frost and Brown (1967)	23	25.3
			Cherry et al. (1977)	?	23
		England	Alabaster and Downing (1966) (as cited by Grande and Anderson 1991)	20	26.3
Salvelinus fontinalis	brook trout	Ontario	Fry, Hart, and Walker (1946)	20 24	25.3 25.5
			Cherry et al. (1977)	?	24
Salvelinus namaycush	lake trout	Ontario	Fry and Gibson (1953)	20	24.0-24.5
Thymallus arcticus	Arctic grayling	Montana	Lohr et al. (1996)	20	25
		Alaska	LaPerriere and Carlson (1973) (as cited by Lohr et al. 1996)	?	24.5

14.4°F (8°C) from temperatures producing optimal growth under satiation feeding. In the natural environment, food is often limited to less than satiation levels.

c.   Disease occurrence and severity are primarily determined by the specific strain of the pathogen, the temperature of the water, and the relative health of the exposed fish. The following general patterns can be identified from laboratory and field research: constant temperatures below 53.6-55.4°F (12-13°C) often reduce or eliminate both infection and mortality; temperatures above 59-60.8°F (15-16°C) are often associated

with high rates of infection and notable mortality; temperatures above 64.4-68°F (18-20°C) are often associated with serious rates of infection and catastrophic outbreaks of many fish diseases.

d. At the time of smoltification, anadromous salmonids experience reduced ATPase levels at constant or acclimation temperatures greater than 51.8-55.4°F (11-13°C). Reduced ATPase levels may result in delayed or ineffective transition to the marine environment and may result in smolts attempting to return to freshwaters to wait until the next spring. Temperatures above 64.4°F (18°C) may inhibit feeding in smolts, and temperatures of 57.2-59°F (14-15°C) may cause cessation of the seaward migration.

3. Stream temperatures vary through the spawning and egg incubation period, particularly for species that spawn in late summer and fall. There are several factors to consider in setting a criterion for these life history stages: temperatures that affect survival of gametes in adults prior to spawning, temperatures that affect the initiation of spawning behavior, temperatures that maximize the survival of eggs upon deposition in gravels and early embryo stages, and temperatures that allow for the correct timing and size of fry at hatch and emergence. In summary, it appears that a range of temperatures from 42 to 55°F (5.6-12.8°C) allows for successful spawning and incubation for different species of salmon.

a. For fall-spawning fish, spawning may be initiated in the field at temperatures of 57.2-60.8°F (14-16°C). Experiments done at constant incubation temperatures, however, show that survival of eggs under these conditions is low. Consequently, spawning temperatures >57.2°F (14°C) are considered to provide marginal to poor egg survival for these early-spawning fish.

b. For fall-spawning fish, spawning that is initiated as daily maximum temperatures fall below 53.6-57.2°F (12-14°C) results in greater incubation success, with 55°F (12.8°C) being adequate for most salmon species.

c. In laboratory studies, constant temperatures of 42.8-50°F (6-10°C) or lower during incubation consistently result in maximum survival and size at emergence for Pacific salmon, steelhead, and coastal cutthroat trout.

d. Constant incubation temperatures as low as 39.2°F (4°C) and as high as 53.6°F (12°C) can result in good to very good survival to hatching and emergence, with approximately 46.4°F (8°C) being optimal for most salmon species.

4. Laboratory and field studies show that when adult fish are exposed to constant or average temperatures above 55.4-60°F (13-15.6°C) during the final part of the upstream migration or during holding prior to spawning, there is a detrimental effect on the size, number, and/or fertility of eggs held in vivo.

5. Many studies have been done on the acute lethality of warm water temperatures on salmonids. Laboratory tests of acute lethality measure the temperature at which 50% of the

fish die after 1 to 7 d of exposure to a constant temperature (upper incipient lethal temperature, or UILT).

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

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

    c.   When fish are acclimated below 53.6°F (12°C), substantial lethality (LT50) can be expected to occur almost instantly (1-60 s) at temperatures above 86-93.2°F (30-34°C).

    d.   Migratory fish, particularly anadromous fish, may not be fully acclimated to warm mainstem temperatures.

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

6.   For all salmonids, figures can be compiled from the literature to depict temperature requirements by species and life stage. Such a diagram was developed by McCullough (1999) for spring chinook. The value of such diagrams is to highlight the ranges for normal function and high survival (e.g., egg incubation, adult migration), optimum growth ranges (e.g., juvenile stage), and thresholds for effects that become increasingly significant both above and below incipient lethal levels (e.g., disease, migration blockages, cold effects on egg incubation). For any life stage, there are multiple potential effects on survival, fitness, and growth. Recommendations for temperature criteria for a waterbody must account for the most sensitive species, most sensitive life stages of a species for any season, and the multiple effects on each life stage.

What conclusions can you draw for bull trout and Dolly Varden?

1.   Bull trout (*S. confluentus*) are not actually trout, but are char. Bull trout and Dolly Varden (*S. malma*) are the only native char found in Idaho, Washington, and Oregon. Members of the genus char live in the coldest, cleanest, and often most secluded waters.

2.   All char are fall spawners and cold water temperatures seem to be the proximate cue that initiates spawning behavior and defines distribution. Char are cold-water fish that are especially sensitive to thermal change and find optimal rearing conditions in a wide variety

of stream sizes that can provide the coldest water possible in the Pacific Northwest. Char are Holarctic in distribution and include the most northerly distribution of any fish found in freshwater. Char may be anadromous, resident, or freshwater migratory.

3. Little information is available for the physiological requirements of bull trout and Dolly Varden. Available research for bull trout includes information for incubation, fry and alevin growth and survival, growth rates for juvenile fish under variable feeding regimes, and juvenile lethality. This is substantially less than the broad range of metrics available for many other salmonids; however, it does include some important physiological characteristics for setting temperature criteria. Evidence from laboratory studies and distribution data indicates that bull trout have optimum temperature requirements substantially lower than the other salmonids examined in this paper, and that water temperatures protective of bull trout will require establishment of separate temperature criteria.

    a. Optimal incubation for bull trout eggs occurs at constant temperatures in the range of 35.6-42.8°F (2-6°C), with highest incubation success at 39.2°F (4°C). Temperatures in the range of 42.8-46.4°F (6-8°C) can produce variable but often substantially reduced egg survival and size at emergence.

    b. Under laboratory conditions, maximum growth temperature declines as ration declines. Growth rates in the studies conducted at satiation and 66% satiation were highest at constant temperatures of 60.8°F (16°C), although the growth rate was less in the lower (66%) ration test than at 100% satiation. At the 33% satiation ration the growth rate was maximized at 46.4-53.6°F (8-12°C). This conclusion is based on a single set of experiments on bull trout. Much more extensive studies of brown trout growth rates under a series of rations show similar declines in growth rate with decreased ration. From these studies we would expect growth optima to decline with each increment of decline in ration.

    c. The UILT for juvenile bull trout is 71.6-73.4°F (22-23°C) for a 7-d exposure.

What conclusions can you draw for other salmonids?

1. Interior native salmonid species found in Oregon, Washington, and Idaho include Westslope (*O. clarki lewisi*), Yellowstone (*O. clarki bouvieri*), Bonneville (*O. clarki utah*), and Lahontan cutthroat trout (*O. clarki henshawi*); redband trout (*O. mykiss gairdneri*); and mountain whitefish (*Propsipium williamsoni*).

2. Little information is available on the effects of temperature on the physiology of these salmonids. Although a few laboratory study results are available, we have referenced field distribution data.

3. Mountain whitefish were not reviewed because of limited information. It is assumed that temperature criteria established to protect other salmonid species protect whitefish where they occur.

SUPPORTING DISCUSSION AND LITERATURE

What are the advantages and disadvantages of laboratory and field data?

Our understanding of thermal effects on salmonids is based on a combination of laboratory and field evidence. In the adult life stage, much of the information available comes from field studies; on the other hand, for the juvenile life stages, most information on thermal effects comes from laboratory studies.

Some argue that laboratory studies have limited use in setting standards because of unrealistic conditions. In truth, each type of study is capable of providing useful information. In determining the usefulness and applicability of laboratory study results, it is important to assess the possible confounding variables such as whether wild fish or hatchery progeny were used, feeding rations, competition, or other ecological issues that may or may not be described in the methods for the laboratory study.

Reisenbichler and Rubin (1999) provide strong evidence that salmonids' fitness for natural spawning and rearing can be rapidly and substantially reduced through artificial propagation. Genetic differences in behavior and physiology can occur in the offspring of hatchery fish. Hatchery fish are often raised in waters with constant temperature and in warmer water more conducive to rapid growth at satiation feeding.

Laboratory studies of thermal effects on salmonids are most often conducted under constant temperature conditions, although what is considered constant can fluctuate as much as 1.8°F (1°C). It is obvious that in natural stream systems, temperatures fluctuate hourly. This pattern can be represented as a sine wave, with a maximum temperature in midafternoon and a minimum temperature in early morning. This cycle is summarized statistically according to its minimum, mean, or maximum temperature. However, from day to day these values can change, resulting in continually changing conditions in the stream. If temperature cycles were identical (i.e., their pattern and minimum and maximum remained steady) for several consecutive days, it would be easier to biologically describe acclimation conditions. Under such a repetitive cycle, a scientific challenge would be to identify the "effective acclimation temperature," that is, the temperature in a fluctuating thermal environment that produces acclimation equivalent to a constant-temperature acclimation.

Fluctuating temperature conditions lead to major issues that make it difficult to predict thermal effects. From laboratory tests using constant temperatures it is known that survival is a function of exposure temperature and exposure time, but the magnitude of the effect also depends on prior acclimation temperature. If water temperatures are variable during both the acclimation and the exposure phases of a test, it becomes difficult to make an accurate prediction of effects based on constant-temperature laboratory studies. Likewise, in the absence of any laboratory studies, it would be difficult to create a predictive model of survival under a thermal regime in which acclimation and exposure history are both varying.

Laboratory tests of survival under thermal stress have several distinct advantages. Laboratory studies allow both acclimation and exposure temperature to be precisely controlled.

Acclimation and exposure temperatures can be made either constant or fluctuating, and if fluctuating, they can conform to precise, repeatable cyclic patterns. Under laboratory conditions, we know precisely what temperatures fish are actually experiencing. That is, fish are not able to seek thermal refuges during survival tests as they could in the field. In the laboratory the condition (diseases, prior feeding history, gut contents prior to testing) of the test organisms can be controlled.

Laboratory results can sometimes be an artifact of laboratory methods, conditions, or apparatus. For example, "tank effects" can result from behavioral interactions between test organisms. If crowding is an issue, fish can be stressed from agonistic behavior. If current speeds are not similar to those the fish would experience in a field setting, many unexpected effects could occur. For example, various performances of a population can change with current speed—behavior, energy expenditure during swimming, oxygen uptake rate in the gills, or recovery from stress (Milligan et al. 2000). Attention must be given to photoperiod for certain performances to be meaningfully represented (Clarke et al. 1992). Disturbance to test organisms during testing must be controlled (e.g., minimizing startling the fish during observation). For some kinds of tests, such as temperature preference, equipment can affect results. For example, it can make a difference whether fish are allowed to seek their temperature preference within a vertical versus a horizontal thermal gradient.

Field testing of fish survival under high temperatures is not usually done. One possible field method is to catch fish from a stream after having monitored the ambient temperature conditions for several days. This acclimation history would then be used as a basis for interpreting exposure results. Fish could be tested in an experimental apparatus at streamside. This method would rely on artificial equipment (tanks) to test their response, but would involve uncertainty in effective acclimation temperature. An alternative method could be to monitor fish densities weekly and water temperatures hourly in a stream reach netted off to prevent emigration or immigration. This would be a "realistic" field test, but would involve uncertainty in effective acclimation temperature and difficulty in integrating exposure temperatures. Also, reduction in fish density would be attributable to natural mortality factors (developmental causes, disease, predation) that would need to be controlled, as well as temperature effects.

If such methods were feasible, the improved realism would be helpful. For example, it would be useful to know the influence of food availability as mediated by thermal regime and other environmental conditions (light, nutrients, organic inputs, competition for food and space), as well as associated natural disease occurrence, in regulating mortality under thermal stress from acclimation phase to exposure phase in the field. These combined effects during acclimation would likely result in greater mortality under field conditions than in laboratory settings, in which multiple stresses are limited. Although these multiple effects constitute the realism that ecologists are interested in, the best chance of adequately understanding these effects is to study them in controlled laboratory tests and then compare predictions from laboratory experience with field data.

If our most precise understanding of thermal effects is from laboratory tests, what methods can be used?

Tests of survival under thermal stress have conventionally been done using either the ILT (incipient lethal temperature) or the CTM (critical thermal maximum) methods. It has generally been accepted that the ILT methodology presents the best means of assessing acute effects because it does not allow for the variable levels of partial acclimation that occur in CTM tests having varying rates of heating. In the ILT method the test endpoint is death; in the CTM test, the endpoint is either loss of equilibrium or death.

Conventional use of the ILT method is to acclimate test organisms at a constant temperature and then immediately transfer them to a constant test temperature. This and other methods are possible as shown in the table below:

No.	Acclimation	Exposure	Methodology
1	constant	constant	Conventional ILT (e.g., Fry 1947, Brett 1952)
2	constant	cyclic	Hokanson et al. (1997), Golden (1976)
3	cyclic	constant	Threader and Houston (1983)
4	cyclic	cyclic	Golden (1976)
5	constant	constant, with multiple exposures	
6	constant	stepped increase	CTM variant
7	constant	continuous increase	conventional CTM (e.g., Becker and Genoway 1979, Elliott and Elliott 1955)

Test condition 1 is the conventional ILT methodology and allows the most accurate knowledge of effective temperatures. Given data from these tests, it is possible to determine the percentage mortality of a salmonid test population at temperatures such as 77, 78.8, 80.6, 82.4, and 84.2°F (25, 26, 27, 28, and 29°C), for example, as well as time to death. With a mathematical expression of these results, it is feasible to estimate percentages of a lethal dose that could be acquired during exposure to a cyclic temperature regime.

Test condition 2 allows accurate knowledge of acclimation history. Subsequent exposure to a cyclic regime could produce mortality in a test population that could be attributed to a mean temperature, maximum temperature, or some intermediate temperature. Mortality under a cycle could also be predicted from knowledge of exposure times at each thermal increment under a cyclic regime and application of mortality rate coefficients for each temperature increment (e.g., Coutant 1972) developed in constant-temperature experiments. A lethal dose may be estimated by this summation technique for a single cycle (McCullough 1999, cumulative mortification, see Fry et al. 1946 as cited by Kilgour and McCauley 1986). Alternatively, mortality from a

constant-temperature exposure can be contrasted with that from a cycle having the same mean temperature. Results of this comparison vary with the magnitude of the cycle and whether the mean temperature is less than or greater than the optimal temperature (Hokanson et al. 1977).

Condition 3 presents the best opportunity to estimate an equivalent acclimation temperature for a cyclic temperature regime in the acclimation phase. Percentage survival is determined in a constant temperature exposure environment, given acclimation to a cyclic regime. This is then related to that constant acclimation temperature that would have provided the same survival (or growth or swimming speed, depending on experiment) as observed in a cyclic temperature exposure. Experiments such as this demonstrate that equivalent acclimation temperatures in a cyclic thermal regime are equal to acclimation to temperatures ranging from the mean to the maximum of the cycle (Heath 1963, Golden 1975, Clarke 1978, Jensen 1990), with much evidence indicating that a temperature intermediate between the mean and the maximum is a good representation of equivalent acclimation temperature.

Condition 4 provides a temperature environment during acclimation and exposure phases that can mimic reasonably occurring field situations. This provides the most "natural" laboratory conditions, but imposes the need to compare results with combinations of constant acclimation and/or exposure temperatures. Mortality data obtained for cyclic temperature exposures from this method are best interpreted against data for constant temperature exposure. Otherwise, cumulative percentage of a lethal dose could be established as in condition 2 exposure based on constant temperature laboratory data and the derived survival coefficient for each test temperature.

Condition 5 provides a constant acclimation and a constant exposure temperature. This framework would be effective in testing cumulative mortality from multiple exposures. Cumulative exposures were tested by DeHart (1975), Golden (1975, 1976), and Golden and Schreck (1978) using cyclic temperatures. They found that mortality could be produced if 100% of a lethal dose were accumulated in periods of approximately 2 d. A more effective test of cumulative mortality could be gained by multiple exposures to constant temperatures. It would be helpful to know whether lethal doses can be accumulated over 3, 4, 5, or more consecutive days.

Constant temperature acclimation followed by stepped or continuous increases in temperature provides survival results similar to those of CTM tests. Depending on the rate of increase, a certain degree of partial acclimation can occur, leading to a test endpoint. If the heating rate approximates that found in field conditions under a thermal cycle involving high maximum temperatures, the CTM experiment based on thermal regime number 7 (or its cousin, number 6) can be helpful in inferring harmful temperature fluctuations. There are some difficulties in making effective use of CTM data. As in all laboratory or field experiments, properly inferring effective acclimation temperature is an issue. In the CTM test, the heating rate determines the degree of partial acclimation that is feasible. Variability in response of individuals needs to be considered in using CTM data because mortality occurs at temperatures below the median level. Also, CTM data are based on uniform heating rates. In the field, if high temperatures are sustained for variable time periods, exposure time and subsequent mortality to the most lethal conditions can vary substantially.

Is there enough significant genetic variation among stocks or among species to warrant geographically specific water temperature standards?

At the time of the 1994 Oregon Triennial Water Quality Review, which involved water temperature criteria, Oregon's water temperature standards applied a standard of 68°F (20°C) to salmon-bearing streams of northeastern Oregon and 57.9°F (14.4°C) to Oregon Coast Range streams. The technical committee concluded that there was no evidence for significant genetic variation in sensitivity to high water temperatures such that different standards (especially ones differing by 10.1°F [5.6°C]) could be justified for different regions of the State.

Climatic conditions vary substantially among regions of the State and the entire Pacific Northwest. Maximum and minimum annual air temperatures, rainfall and streamflow patterns and magnitudes, cloud cover, humidity, and other climatic features all influence downstream water temperatures and trends. Climate also indirectly influences density and type of riparian vegetation that itself has a role in controlling water temperature. Regional environmental variations can establish a template to which a species might make evolutionary adaptations. For example, a species found in a region with streams having a range of maximum summer water temperatures from 46.4 to 78.8°F (8-26°C) (headwaters to mouth) might become adapted over time to warmer water temperatures than the same species located in a region having temperatures ranging only from 46.4 to 68°F (8-20°C). These hypothetical examples may represent historical extreme conditions in large stream systems in coastal versus eastern Oregon streams. Such conditions could potentially have led to evolutionary adaptations, resulting in development of subspecies differences in thermal tolerance.

Acclimation is different from adaptation. Adaptation is the evolutionary process leading to genetic changes that produce modifications in morphology, physiology, and so on. Acclimation is a short-term change in physiological readiness to confront daily shifts in environmental conditions. The extent of the ability to tolerate environmental conditions (e.g., water temperature extremes) is limited by evolutionary adaptations, and within these constraints is further modified by acclimation.

The literature on genetic variation in thermal effects indicates occasionally significant but very small differences among stocks and increasing differences among subspecies, species, and families of fishes. Many differences that had been attributed in the literature to stock differences are now considered to be statistical problems in analysis, fish behavioral responses under test conditions, or allowing insufficient time for fish to shift from field conditions to test conditions (Mathur and Silver 1980, Konecki et al. 1993). It is also possible that tests intended to differentiate stock performance (e.g., survival, growth) could inadvertently use test individuals emphasizing one or a small number of family groups. For example, when tested at suboptimal temperatures, family groups of rainbow trout showed much greater variation in growth rates than at optimal temperatures (Wangila and Dick 1979).

Are there evolutionary differences among salmonid species in the Pacific Northwest?

Within the species *O. tshawytscha* (chinook salmon) there is great variation in run timing, life histories, and habitat selection. This species has stream-type and ocean-type forms, featuring

significant differences in length of freshwater residency. Even so, no subspecies have been designated for chinook or any other salmon species. Genetic variation does exist, however, within the chinook and other salmonids in the Pacific Northwest, as shown in classification tree diagrams drawn by agencies such as the National Marine Fisheries Service (NMFS). These genetic relationships are based on enzyme frequencies. An accumulation of genetic differences between populations can eventually become great enough that subspecies are recognized. However, this has apparently not happened within the salmon, despite the fact that species such as chinook range from Alaska to mid-California and from temperate coastal mountain streams to continental interior streams.

There are many possible explanations why salmon have not made a significant adaptation to high temperatures in streams of the Pacific Northwest. Temperature tolerance is probably controlled by multiple genes, and consequently would be a core characteristic of the species not easily modified through evolutionary change without a radical shift in associated physiological systems. Also, the majority of the life cycle of salmon and steelhead is spent in the ocean rearing phase, where the smolt, subadults, and adults seek waters with temperatures less than 59°F (15°C) (Welch et al. 1995). It would be unlikely for optimal growth conditions and associated physiological processes to be radically different in freshwater systems than in ocean environments, especially when food abundance in freshwater is so much more limited.

What are the major differences in thermal tolerance among and within important families?

One way to look at evolutionary differences among salmonids is to compare the Salmonidae with other fish families. Given the data compilation for Salmonidae in this report (Table 4) and the compilation by Coutant (1972) (see McCullough 1999, Tables 13 and 14), one can infer a range of UUILT for the families Salmonidae, Cyprinidae, and Centrarchidae to be 73-78°F (23-25.6°C), 84-91°F (29-33°C) (Table 13), and 91-98.6°F (33-37°C) (Table 14), respectively. The range for Salmonidae accounts for the response of chinook, coho, sockeye, chum, and pink salmon; steelhead; Atlantic salmon; and brown, brook, and lake trout. There appears to be very little variation in UUILT among species in family groups, except for a higher lethal limit for redband trout and a lower one for bull trout. These two species appear to broaden the UUILT range to 71.6-80.6°F (22-27°C) for the Salmonidae. The Cyprinidae and Centrarchidae are significantly more tolerant of warm water. However, they are effective competitors to the cold-water species that are the primary native species in the Pacific Northwest, because they are very active feeders at temperatures >68°F (20°C). This capability allows Cyprinidae and Centrarchidae to increasingly exclude cold-water species at temperatures in this range. This is a partial explanation for the disappearance of salmonids from streams when maximum temperatures are in the range of 71.6-75.2°F (22-24°C) (see McCullough 1999).

The small range in UUILT among all the salmonids surveyed and the lack of overlap with the ranges expressed by the cyprinids and centrarchids indicates fundamental differences among major families of fish and a narrow window within which potential adaptations would likely be expressed. If the differences among species within a family are so minimal, it is unlikely that significant differences would emerge within a species (i.e., at a stock level).

The UUILT values listed above for salmonids represent essentially the juvenile life stages. Studies have been cited here showing that UUILT values for adult salmon tend to be 3.6-5.4°F (2-3°C) lower than those for juveniles of the species. This response of adults in freshwater may be linked to the preferred temperatures in ocean environments that the fish inhabited for several years prior to their entry into rivers.

Differences in response in thermal tests can usually be attributed in part to test conditions. Numerous factors can be listed as reasons for differences in responses among studies for a given species. Different test results appear to be more common in tests of temperature preference than in UILT tests. Test apparatus has a role in determining results as well as season, sex, size, and so on. Because preference involves behavioral traits and appears to be less precise an index to estimate, UILT values are emphasized in this discussion.

Studies of UILT on salmonids, cyprinids, and centrarchids conducted by Cherry et al. (1977) can be assumed to eliminate potential methodological variations. These researchers found that the UUILTs for these fish families were 73.4-77, 78.8-96.8, and 95-96.8°F (23-25, 26-36, and 35-36°C), respectively. The salmonids tested in this study included rainbow trout, brown trout, and brook trout. Brett (1952) measured UUILT on several salmon species (*O. tshawytscha*, *O. kisutch*, *O. gorbuscha*, *O. keta*, and *O. nerka*). Brett's work is the most complete analysis of thermal effects on fish physiology available in the literature. It provides a useful comparison of these five species and can also be said to eliminate variation attributed to methodology. He found that among species of Pacific salmon the UUILT values varied only from 74.8 to 77.2°F (23.8-25.1°C). Similarly, when CTM method was used to test thermal tolerance of five species of trout (rainbow, brown, brook, Gila, and Arizona trout), CTM values of 84.9, 85.8, 85.6, 85.3, and 84.9°F (29.4, 29.9, 29.8, 29.6, and 29.4°C,) respectively, were determined (Lee and Rinne 1980). All species were collected in the southwestern United States. The rainbow, brown, and brook trout were introduced and the Gila and Arizona trout were native to this climatic region. Despite these differences in geographic origin, species, and cultural history (hatchery/wild), CTM values differed by a maximum of 0.9°F (0.5°C) among species. (Note that CTM and UILT test methodologies are fundamentally different and yield different kinds of information on thermal tolerance.)

A recent study (Myrick and Cech 2000) of thermal physiology in two rainbow trout strains (Eagle Lake and Mt. Shasta) from California lakes revealed no strain-related differences in thermal tolerance, and moreover found that CTM values for these rainbow trout strains were very similar to values found for many other salmonids, including brook trout, brown trout, Atlantic salmon, Gila trout, another rainbow trout stock, and Little Kern River golden trout.

What is the variation in thermal response within a species?

One of the most extensive and earliest evaluations of geographic variation in UILT available is by Hart (1952). Comparisons were made of stocks from 10 species ranging in distribution from Ontario to Tennessee to Florida. Stock differences in UILT were found in only three of these species, but in these cases the stocks were taxonomically distinct subspecies that also were differentiated morphologically. In two species, each having recognized subspecies, there were no differences in UILT or lower incipient lethal temperature (LILT) values. Another

two species having subspecies were not different in UILT but might have differed in LILT. In two species having no recognized subspecies, the stocks sampled over this large geographic range had no geographic differences in UILT. Hart concluded that the southern stocks of a species had no greater resistance to high temperature than the northern stocks, the exception being if they were taxonomically and morphologically distinct. Even then there were not always differences. Among the species studied, each tended to occupy similar thermal regimes across the extent of its range.

Similar results were found by McCauley (1958) in thermal tolerance tests of *Salvelinus spp*. McCauley found that two stocks of *Salvelinus fontinalis* failed to reveal any difference in response. However, McCauley reported a difference in response between two subspecies of *S. alpinus*, (*S. a. willughbii* and *S. a. alpinus*). However, the geometric mean resistance at 1,000 min exposure occurred at approximately 76.5°F (24.7°C) with *S. a. willughbii* and at 75.9°F (24.4°C) with *S. a. alpinus*. Even though McCauley reported a highly significant difference between the subspecies, the actual difference in thermal tolerance was negligible in a management context.

In CTM tests of two stocks of Lahontan cutthroat trout, Vigg and Koch (1980) found that variation owing to strain differences was approximately 0.18-0.9°F (0.1-0.5°C), but that differences owing to water source (i.e., alkalinity) were 36.8-7.2°F (2.7-2.9°C). Konecki et al. (1993) found that when acclimatization effects were eliminated for Washington coho stocks collected from streams with greatly different thermal environments, there was no significant difference in CTM values. Sonski's (1984) test of three stocks of rainbow trout, including redband trout, revealed no more than 1.4°F (0.8°C) difference in UILT values. In thermal testing of two subspecies of largemouth bass (Florida and northern) acclimated to 89.6°F (32°C), CTM values were 41.8°C ± 0.4 SD and 40.9°C ± 0.4 SD, respectively (Fields et al. 1987). But the authors questioned whether these differences were biologically meaningful; they considered the chronic thermal maximum to be more meaningful. These values were 39.2°C ± 0.64 and 37.3°C ± 0.60, respectively. These differences were expressed only at the highest (i.e., 89.6°F [32°C]) acclimation temperature and may indicate a selective advantage of the Florida subspecies over the northern under conditions of high thermal stress. Again, these differences are only expressed at a subspecies level and are not great in magnitude.

Beacham and Withler (1991) studied the survival of ocean-type and stream-type juvenile chinook in high water temperatures. Twenty separate full-sib families of the ocean-type (hatchery) and 32 full-sib families of the stream-type chinook (wild) were produced from gamete collections and matings of 1 male with each of 2 females. The stream-type population, rearing at 70.7°F (21.5°C), had a total mortality of 79% after 16 d. The ocean-type population, rearing at 71.6°F (22°C), had a total mortality of 74% after 18 d. These populations responded very similarly to high temperature (approximately 71.6°F [22°C]) in about 18 d of exposure, but the cumulative mortality curves were very different. The stream-type population had approximately 70% mortality after 8 d, whereas the ocean-type population suffered only 3% mortality in the same time period. These different patterns of mortality are likely a result of adaptive differences in the populations (Beacham and Withler 1991). The authors speculated that ocean-type chinook are better adapted to warmer water conditions because they spend a greater portion of their life cycle in coastal waters.

A study of thermal influences on physiology of two rainbow trout strains (Eagle Lake and Mt. Shasta) revealed no differences in thermal tolerance as measured by the CTM method (Myrick and Cech 2000). The Eagle Lake rainbow trout (*O. m. aquiliarum*), originally native to Pine Creek, California, has been artificially propagated since 1956 because of concerns for habitat degradation. The Mt. Shasta strain is an inbred hatchery strain derived from a southeast Idaho trout farm and Hot Creek strain rainbow. In addition, the authors found no differences in conversion efficiency, oxygen consumption rates, or swimming performance.

Is there significant genetic flexibility within a stock that would allow for adaptation to thermal regimes?

Beacham and Withler (1991) hypothesized that the ocean-type population, having a shorter period of freshwater residence than the stream-type population, is better adapted to warmer waters as found in the ocean and also in its freshwater habitats. Consequently, the ocean-type population is better adapted to short-term exposure to high water temperature than is the stream-type population. It is interesting that despite the differences in response to temperature within the first few days, the two British Columbia populations had similar cumulative mortalities over a 16- to 18-d period.

These authors speculated that the UILT for salmonids may vary by population, depending on their history of adaptation to temperature regimes. Differences in thermal tolerance were noted in time to death. At 70.7°F (21.5°C) the entire stream-type test population (i.e., all families of the stream-type population) had a mean time to death of 3.4 (0.10) d. At 71.6°F (22°C) the ocean-type population had a mean time to death of 13.3 (0.11) d. The standard error for the stream-type population in time to death was approximately 3%; that among the ocean-type population was approximately 0.8%. The ocean-type population had a greater short-term tolerance of warm water temperatures than the stream-type population, but had a reduced additive genetic variation in mean time to death. The estimated heritability of mortality rate and time to death for the ocean-type chinook population was zero. These results indicate that the ocean-type population had very little capacity for increased adaptation to warmer water temperatures because it was fully adapted to the warmer summer conditions found in its coastal stream. However, the stream-type population had additive genetic variation for survival at high temperatures and time to death that could allow it to further adapt to high water temperatures.

Besides survival, what other key biotic responses influenced by temperature vary among stocks?

Growth. Growth is a good indicator of performance of a species at various temperatures. When fed to satiation, chinook achieved maximum growth rates at 66°F (19°C) (Brett et al. 1982). However, at this temperature, under satiation feeding, Big Qualicum chinook juveniles (approximately 3 g) grew at a rate of 3.5%/d, whereas the Nechako stock had a significantly lower growth rate of only 2.9%/d. Brett et al. (1982) considered this difference to be a genetically controlled means for one stock to achieve greater growth, especially in the optimum temperature range. In addition, examination of growth rates on Sacramento River chinook revealed that at 68-69.8°F (20-21°C), sublethal growth stress becomes significant for fish fed to

satiation (Marine 1997). These data indicate consistency in temperature thresholds, whereas actual growth rates differ somewhat among stocks.

Wangila and Dick (1988) studied the growth response of two strains of rainbow trout (*O. mykiss*) and their hybrid at 45 and 59°F (7 and 15°C). The two strains, Mt. Lassen and Tagwerker, were symbolized as LAS and TAG. There were four families of LAS, three of TAG, and four crosses of LAS x TAG. Each family was produced by matings of a single pair of parents. Progeny of each family were divided into four groups of 75 individuals each, two of which were tested at 45°F (7°C) and the other two at 59°F (15°C). Trout were fed three times per day to satiation, so growth rates should be considered maximum at each temperature. Wangila and Dick found significant differences among strains and hybrid in specific growth rates as a function of body weight during growth between July 8 (mean starting weight 3.3-4.5 g) and October 15 (ending weights 10.5-13.9g). Growth was modeled with the equation $\log_e G = a + b \log_e W$.

Slopes for the regression of specific growth rate on mean weight were significantly different among the two strains and hybrid at 45°F (7°C), but not at 59°F (15°C). The high degree of heterogeneity of slopes at 45°F (7°C) suggests that genetic differences were significant among stocks when growth took place at temperatures far below the growth optimum. However, at temperatures near the growth optimum, heterogeneity in slopes for this regression was very low. This study leaves unanswered how the stocks would respond under a temperature above the growth optimum. It could be that under stress, one stock would be able to convert more of its food intake to growth, or its ability to feed at high temperatures might be greater than for the competing stock.

Sadler et al. (1986) tested differences in specific growth rate (a measure that assumes exponential growth) for two rainbow trout strains at constant temperatures of 50°F (10°C) and 61°F (16°C). Significant differences in strain N and S occurred at 10°C (1.80 ± 0.04 vs. 2.03 ± 0.02) (±SE) and at 16°C (2.29 ± 0.11 vs. 3.00 ± 0.09), respectively. Both stocks achieved higher growth rates at the higher temperatures, which would be nearer the preferred temperature of rainbow. The authors attributed the greater growth rate of the S stock (Soap Lake, US, domesticated stock) to its hatchery selection for high growth rate compared with the N strain derived from wild stock from a river in Ontario.

A study of two strains of rainbow trout from California lakes (Eagle Lake subspecies and Mt. Shasta strain) revealed no differences in food consumption, gross conversion efficiency, resting routine oxygen consumption rate, upper CTM, or critical swimming velocity. However, over a temperature range including 50, 57.2, 66.2, 71.6, and 77°F (10, 14, 19, 22, and 25°C) constant temperature growth experiments, the Mt. Shasta strain had a significantly greater growth rate than the Eagle Lake strain only at 71.6 and 77°F (22 and 25°C). At 71.6 and 77°F (22 and 25°C), growth rates for these two strains were 2.97% vs. 3.51% body weight/d and -0.35% and 0.05% body weight/d, respectively. When compared with other rainbow stocks from widely separated geographic locales at 71.6°F (22°C), the growth rates were similar to those from Rainbow Springs Hatchery, Ontario, reported by Alsop and Wood (1997), lower than those for Lake Superior rainbow trout (3.94% body weight/d) (Hokanson et al. 1997), and greater than reported for Oregon juvenile steelhead (1.7% body weight/d, at 72.5°F [22.5°C]) (Wurtsbaugh and Davis 1977b, as reported by Myrick and Cech 2000). However, Myrick and Cech (2000)

attributed much of the difference among stocks to differences in juvenile weight. Weight of test specimens in the studies above by Myrick and Cech (2000), Hokanson et al. (1997), Wurtsbaugh and Davis (1997b), and Alsop and Wood (1997) were 2.3-4.2 g, 0.2-0.3 g, 1-1.2 g, and 6-7 g, respectively. On the basis of studies of growth at constant temperatures within the overall range 50-77°F (10-25°C), Myrick and Cech (2000) inferred an optimal growth rate between 57.2 and 66.2°F (14 and 19°C), bracketing the optima found by both Hokanson et al. (1977) and Briggs and Post (1997, cited by Myrick and Cech 2000).

Swimming speed. Myrick and Cech (2000) measured the critical swimming velocities of two rainbow trout strains assumed to be genetically different (juvenile Eagle Lake and Mt. Shasta trout from California lakes) over a temperature range from 50 to 66.2°F (10-19°C). They reported that length-specific critical swimming velocities were not statistically different. By plotting critical swimming speeds (Figure 1) from the literature summarized by Myrick and Cech (2000), it appears that the various trout stocks (rainbow/steelhead and golden trout) had swimming optima of 57.2-59°F (14-15°C). Only the Little Kern River golden trout exhibited a sharp decline in critical velocity at temperatures above 57.2°F (14°C). No studies were conducted at temperatures greater than 68°F (20°C), but one would assume that at some temperature between 68 and 77°F (20 and 25°C) a more dramatic decline in swimming speed would take place. The literature summarized in Figure 1 indicates that critical swimming velocity (BL/s or body length per second) generally declines with total body length in juveniles over the range 85-287 mm, although this conclusion is formed by lumping all trout stocks. Body length then appears to be more significant as a source of variation in critical swimming speed than is genetic differences. However, at 50°F (10°C), Myrick and Cech (2000) noted a significantly greater critical swimming velocity in strains of coastal cutthroat trout (Aberdeen strain) and steelhead (Aberdeen strain) than for Eagle Lake rainbow, Mt. Shasta rainbow, Little Kern River golden trout, and coastal cutthroat trout (Shelton strain), which were more similar. Stocks tested at 50°F (10°C) varied in length from 89 to 120 mm. Differences in swimming speed were not obviously related to body length.

Which temperatures provide optimum conditions for incubation and early fry development in the following species?

Chinook salmon. Once spawning has taken place, the eggs of chinook salmon hatch in about 2 months and the young remain in the gravel for 2-3 wk before emerging. Many researchers have tested incubation survival at constant exposure to various test temperatures. Complete mortality (100%) has been noted at incubation temperatures from 57 to 66.9°F (13.9-19.4°C) (Donaldson 1955, Garling and Masterson 1985, Seymour 1956, Eddy 1972, as cited in Raleigh et al. 1986). Significant mortality (over 50%) has been noted at constant incubation temperatures from 49.8 to 62°F (9.9-16.7°C) (Donaldson 1955, Seymour 1956, Burrows 1963, Bailey and Evans 1971, as cited in Alderdice and Velsen 1978; Hinze 1959, as cited in Healy 1979). A constant incubation temperature of 46.4°F (8°C) produced more robust alevin and fry survival than constant exposure to either 39.2 or 53.6°F (4 or 12°C) in a study by Murray and Beacham (1986), and Velsen (1987) compiled data showing that the best survival (>92.9%) occurred between 44.9 and 49.2°F (7.2 and 9.6°C). Heming (1982), however, found good survival at both 50 and 53.6°F (10 and 12°C). Heming tested survival in both incubation trays
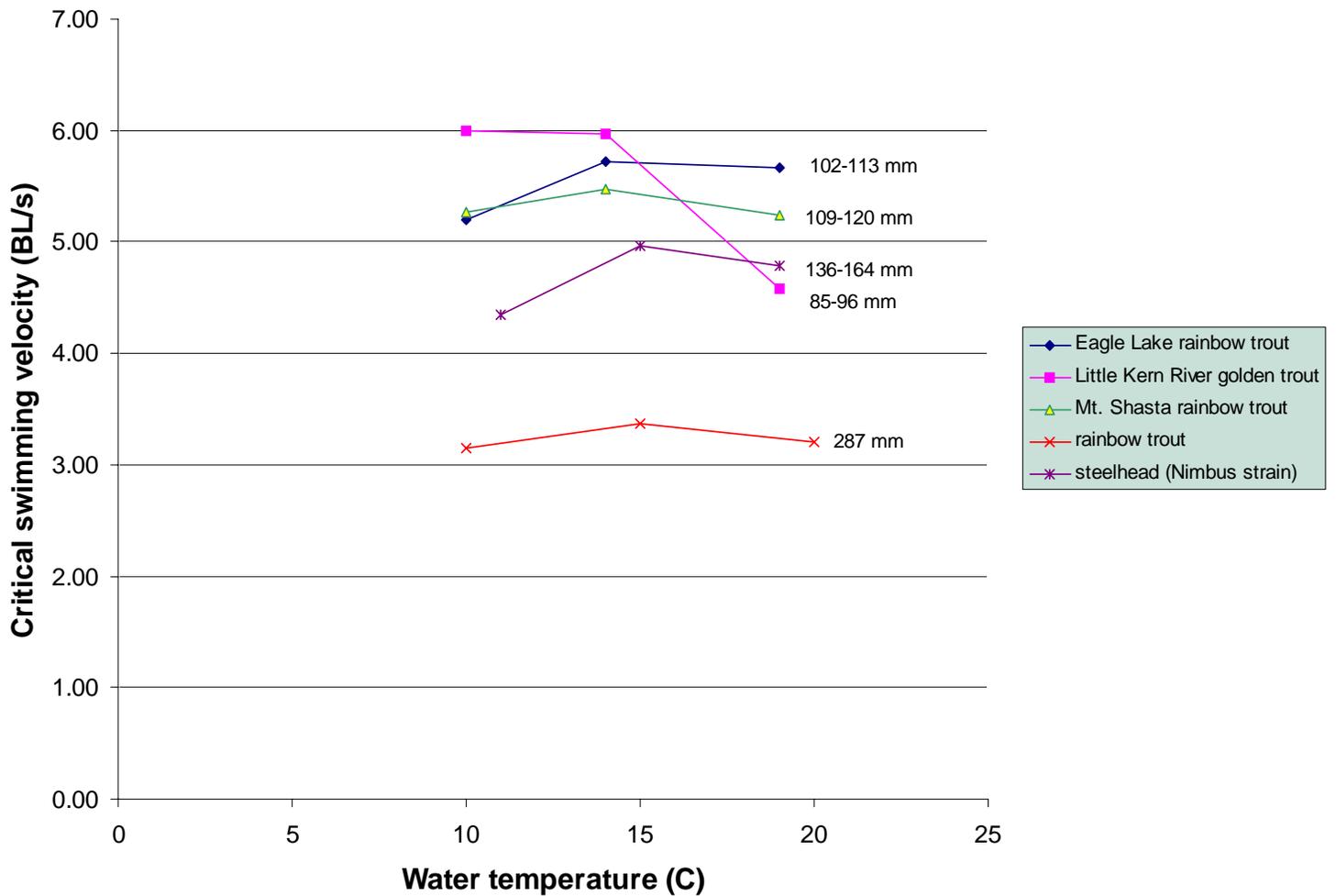
Figure 1. Critical swimming velocity as a function of water temperature. Data source was tabulated in Myrick and Cech (2000).

and artificial redds. Survival rates declined as the temperatures increased from 42.8 to 46.4, 50, and 53.6°F (6-8, 10, and 12°C). The greatest survival (91.7%-98%) occurred at 42.8 and 46.4°F (6 and 8°C), but it was still very good (90.2%-95.9%) at 50°F (10°C). Incubation at 53.6°F (12°C) consistently had the lowest survival (84.6%-89.3%). Heming also tested survival rates from incubation to hatching against survival rates from hatching through complete yolk absorption. His work suggests higher incubation temperatures may create a metabolic energy deficit for pre-emergent salmon that increases mortality. Once alevin have hatched and absorbed their yolk sacs they will need to make a transition to active feeding. Heming and McInery (1982) found that temperatures of 42.8, 46.4, and 50°F (6, 8, and 10°C) resulted in an average survival of 98.4% during this transitional period, while 53.6°F (12°C) was associated with a decrease in survival to 89.2%. The maximum conversion of yolk to tissue weight was reported by Heming (1982) (as cited by Beacham and Murray 1986) to occur at 42.8°F (6°C) or below. Seymour (1956) noted a ninefold increase in abnormalities in fry incubated at 60°F (15.6°C) and

higher when compared with those incubated between 39.9 and 55°F (4.4-12.8°C). Seymour also noted that fry incubated at 39.9°F (4.4°C) emerged at a larger size than those reared at higher temperatures; however, subsequent fry growth was maximized at 55°F (12.8°C).

Considered together, the work of the authors cited above most strongly suggests that constant temperatures above 48.2-50°F (9-10°C) and below 41°F (5°C) may reduce the survival of chinook salmon embryos and alevins. Although constant temperatures of 51.8-53.6°F (11-12°C) can still result in good success, the results are consistently less than what is produced at lower temperatures. As discussed previously in this paper, constant laboratory test temperatures of 48.2-50°F (9-10°C) should be considered roughly equivalent to naturally fluctuating stream temperatures with daily maximums of 51.8-53.6°F (11-12°C).

Some researchers have tried to mimic the naturally fluctuating and falling temperatures actually experienced by incubating eggs, or have stepwise reduced the incubation temperatures as incubation progressed. Initial incubation temperatures from 60 to 62°F (15.6-16.7°C) have been associated with significant to total losses of young fish through the incubation to early fry development phase (Healy 1979, Johnson and Brice 1953, California Department of Water Resources [CDWR] 1988, and Jewett 1970 as cited in CDWR 1988). Rice (1960) found that source waters declining from 60 to 46.9°F (15.6-8.3°C) resulted in satisfactory egg development, although he did not provide survival rates or clearly consider survival through to the fry stage. Johnson and Brice (1953) found survival often exceeded 90% where initial water temperatures (as a daily mean) were below 53.9°F (12.2°C). Healy (1979) found that highest survival (97%) occurred in creek water where the daily maximum reached 55°F (12.8°C) only a few times during the first 2 wk of development, but also noted that survival was still very good (90%-94%) where the initial temperatures were between 55 and 57.5°F (12.8 and 14.2°C). Olson and Nakatani (1969) found 53.7%-88% survival in egg lots started at 54.5°F (12.5°C), experiencing a brief increase to 58.4°F (14.7°C) in the first wk, and then quickly dropping back to 53.6-54.5°F (12-12.5°C) and assuming a seasonal downward trend in temperature (test water paralleled both diel and seasonal fluctuations). Olson and Foster (1955) found the greatest survival at an initial test temperature of 52.8°F (11.6°C) (92.2%), but reported no appreciable differences in survival rates at initial test temperatures of 56.8, 59, and 60.8°F (13.8, 15, and 16°C) (89.9%-83.9%) (test water paralleled seasonal daily average temperatures). Seymour (1956) tested four geographically distinct stocks of chinook. Taking into consideration both mortality and growth rate, the optimum temperature was estimated as 52°F (11.1°C) for eggs and fry. The mortality rate was considered low at all stages of development for lots reared between 39.9 and 55°F (4.4-12.8°C). Lots with initial temperatures of 64.9°F (18.3°C) had the highest mortality (11%, 24%, 40%, and 100%). In the cyclic and fluctuating temperature tests reviewed here, temperatures at the beginning of incubation that are below 51.8-55°F (11-12.8°C) are typically associated with optimal survival rates. This compares well with the adjusted optimal range of 52.7-54.5°F (11.5-12.5°C) suggested above based on examining the constant temperature exposure studies. This range also compares well with the optimal temperature range of 46.4-53.6°F (8-12°C) recommended by the Independent Scientific Group (1996) study.

Donaldson (1955) transferred eggs to more optimal 50-55°F (10-12.8°C) incubation temperatures after various periods of exposure to higher temperatures. He found that tolerance to temperature exposure varies with the stage of development. He also found 20% mortality could be induced by exposing eggs to 66.9°F (19.4°C) for 1 d, 64.9°F (18.3°C) for 3 d, and

62.9°F (17.2°C) for less than 10 d. Donaldson's work lends further support to the observations made by other authors such as Jewett (1970, as cited in CDWR 1988) that the latent effects of holding eggs at higher than optimal temperatures continues through the period of absorption of the yolk sac; thus, using mortality estimates at the time of hatching underestimates the total temperature-induced mortality. Donaldson found the developmental stages associated with the greatest percentages of temperature induced mortality were: (1) the time up until the closure of the blastopore (200 T.U.); (2) the period just previous to and during hatching; and (3) when fry are adapting themselves to feeding. He also found that when eggs were exposed to test temperatures 62.9, 64.9, and 66.9°F (17.2, 18.3, and 19.4°C) past the eye pigmentation stage (350 T.U.), the time necessary for complete hatching doubled, and the frequency of common abnormalities increased with both the higher temperatures and longer exposures. Murray and Beacham (1986) found that initial incubation at 39.2°F (4°C) reduced survival even with later transfer (at completion of epiboly) to warmer waters 46.4 and 53.6°F (8 and 12°C). Transfers after epiboly or completion of eye pigmentation from 39.2 to 53.6°F (4-12°C) and from 53.6 to 39.2°F (12-4°C) also caused an increase in alevin mortality. The authors also found that decreasing temperature produced longer and heavier alevins and fry. Combs (1965) found that eggs developed to the 128-cell stage at 42.4°F (5.8°C) could then tolerate 35°F (1.7°C) for the remainder of the incubation period with only moderate losses. Mortality of 14.5% was observed with a transfer time of 72 h, whereas only 3.3% mortality occurred with a transfer at 144 h. These three works together suggest that the effects of suboptimal initial incubation temperatures may not be nullified by later changes in the temperature regime to more optimal levels; that sudden changes in temperature at either early or later stages of development, regardless of the direction of that change, can be harmful to pre-emergent life stages; and that initial incubation at optimal temperatures may condition eggs and embryos such that they can withstand very low winter temperature regimes.

In addition to Donaldson (1955), Neitzel and Becker (1985) conducted work on the effects of short-term increases in temperature that can be used to support daily maximum temperature criteria. Neitzel and Becker used chinook salmon to determine the effects of short-term dewatering of redds by hydropower facilities. Neitzel and Becker found that sudden increases in temperatures from 50°F to above 71.6°F (10-22°C) for 1-8 h significantly reduced survival of cleavage eggs in chinook salmon. Controls held at 50°F (10°C) had very low mortalities (less than 2%). Mortality in treatment groups was 8%-10% at 71.6°F (22°C) after 2-h exposure, and was 22% after a 1-h exposure at 74.3°F (23.5°C). They further found that decreasing the temperature from 50°F (10°C) to near freezing 32°F (0°C) for up to 24-h did not increase mortality in eggs, embryos, or alevin. Considering the work of Neitzel and Becker, it would appear that chinook salmon eggs and embryos are relatively tolerant of short-term increases in temperature up to 71.6°F (22°C). However, because Donaldson (1955) found that 66.9°F (19.4°C) produced 20% mortality in 1 d and 64.9°F (18.3°C) produced 20% in 3 d, setting a more restrictive single daily maximum temperature limit is certainly warranted. Furthermore, as described above, incubation conditions where daily maximum temperatures were in the range of 57.9-60.8°F (14.4-15.6°C) produced reduced survival rates, so further caution may be warranted in allowing daily maximum temperatures to exceed 56.3-58.1°F (13.5-14.5°C) during incubation.

Although there is some disagreement, the literature is consistent overall regarding optimal incubation requirements for chinook salmon. Providing for optimal protection from fertilization

through initial fry development requires that constant or acclimation temperatures be maintained below 48.2-50°F (9-10°C) and that individual daily maximum temperatures generally not exceed 56.3-58.1°F (13.5-14.5°C).

Coho salmon. Embryo survival is consistently maximized in tests at constant temperature exposures between 36.5 and 43.7°F (2.5-6.5°C) and is only slightly less successful between 34.4 and 51.6°F (1.3-10.9°C) (Dong 1981, Tang et al. 1987, Murray et al. 1988, Velsen 1987). Davidson and Hutchinson (1938, as cited in Sandercock 1991) suggested that optimum temperature for egg incubation is 39.2-51.8°F (4-11°C). Mortalities tend to become moderate (74%-79%) at 51.8-54.5°F (11-12.5°C), and at 54.5-56.3°F (12.5-13.5°C), mortalities of 50% can be expected. Above 57.2-57.9°F (14-14.4°C), tests commonly report 100% mortality or close to it. Alevin survival may be excellent (97%) at 34.3-51.6°F (1.3-10.9°C) (Dong 1981, Tang et al. 1987), and the most robust fry are at incubation temperatures of 39.2-46.4°F (4-8°C) (Dong 1981, Murray et al. 1988). Alevin mortalities of 51%-59% occur at 54.5°F (12.5°C) (Dong 1981), and 100% mortality occurs at 57.2-57.9°F (14-14.4°C) (Dong 1981, Murray et al. 1988).

From the studies discussed above, we are relatively confident that egg survival is consistently best at exposure to constant temperatures of 36.5-43.7°F (2.5-6.5°C), but may still be excellent for many stocks at temperatures of 34.4-51.5°F (1.3-10.9°C). Alevin and fry survival and health may be best at exposure to constant temperatures of 39.2-46.4°F (4-8°C), but survival may remain excellent up to 51.6°F (10.9°C). This review of the available literature suggests that a constant 44.6-50°F (7-10°C) may form the upper threshold for optimal development of coho salmon eggs and alevin. Adjusting this laboratory-based naturally fluctuating stream environment (as discussed previously) results in the recommendation that to fully support the pre-emergent stages of coho development, the 7-d average of daily maximum temperatures should not exceed 48.2-53.6°F (9-12°C).

No information is available that suggests coho salmon embryos and alevins are more sensitive to short-term (daily peak) increases in temperature than any other Pacific salmon. The one study reviewed that looks at short-term temperature changes for coho was by Tang et al. (1987). In that study, incubation temperatures were increased from 50.3 to 62.6°F (10.2-17°C) and lowered from 50.3 to 39.2°F (10.2-4°C) for 8 h. In neither test did these modest changes result in any statistically significant increase in mortality. Additionally, one field study reported coho alevins capable of at least partial survival (substantial change in later numbers of juveniles) when daily peak temperatures rose from 14 to 20°C during the month of May while some were still in the gravels. The control stream had no change in later abundance of juveniles and had temperatures of 51.8-54.5°F (11-12.5°C) (visually interpolated from graph) during May. In the impacted stream, summer maximum temperatures in two successive years were 75.2 and 86°F (24 and 30°C), and in the unimpacted stream, summer temperatures remained below 59°F (15°C) (Hall and Lantz 1969). In the review of the literature, no clear basis was found for setting a daily peak temperature specific to coho incubation.

Chum salmon. Incubation survival from fertilization to emergence is variable, but can be excellent anywhere from 39.2 to 53.5°F (4-12°C) (Murray and Beacham 1986, Beacham and Murray 1985). In the initial period of embryo development, temperatures of 46.4-53.6°F (8-12°C) produce the highest survival. However, in later stages of incubation, temperatures of 41-46.4°F (5-8°C) produce the best survival as well as the largest and heaviest alevin and fry (Beacham and Murray 1986). Temperatures of 53.6°F (12°C) in the later developmental stages can result in heavy losses in some stocks (Beacham and Murray 1985, Beacham and Murray 1986). The optimal temperature range for conversion of yolk to tissue weight was estimated to be 42.8-50°F (6-10°C) (Beacham and Murray 1986), and optimal respiration efficiency has been estimated to range from 51.8 to 54.5°F (11-12.5°C) for prolarvae and larvae (Zinichev and Zotin 1988). Constant incubation at temperatures of 57.7 and 60.8°F (14 and 16°C) as well as at 36.5°F (2.5°C) have been associated with embryonic mortalities of 50% (Beacham and Murray 1990). The alevin stages of development (late), however, were shown to have very high survival rates when exposed to temperatures as low as 35.6°F (2°C).

Based on the literature reviewed, constant incubation temperatures from 39.2 to 53.6°F (4-12°C) commonly produce excellent incubation results; however, some researchers have noted less than optimal survival occurring at the edges of this range. It appears that constant initial incubation temperatures of 46.4-50°F (8-10°C) would be most consistently optimal for chum salmon. In reviewing the literature, no specific basis was found for setting a daily peak temperature for incubating chum.

Pink salmon. The range for successful incubation has been suggested to be from 39.9 to 55.9°F (4.4 to 13.3°C) (Beschta et al. 1987, Bonar et al. 1989). Murray and Beacham (1986) reported excellent survival (91%-97%) with initial fertilization occurring at 57.2°F (14°C) and a 0.9°F (0.5°C) drop in temperature every 3 d down to 41°F (5°C). When they allowed temperatures to drop further to 39.2 and 35.6°F (4 and 2°C), survival was reduced. Murray and McPhail found survival of 94% from fertilization to emergence at 41°F (5°C), and Beacham and Murray (1986) found the greatest survival for 5 stocks and 21 families of pink salmon tested at 46.4°F (8°C). Velsen (1987) compiled data showing that the best, although highly variable, survival (generally >89.5%) occurred between 46.4 and 55.4°F (8 and 13°C). Survival decreased at an incubation temperature of 51.8°F (11°C) in a test by Murray and McPhail (1988), and was 50% at 59-60°F (15-15.5°C) (Beacham and Murray 1990). Temperatures of 41-46.4°F (5-8°C) produced the largest alevins in a study by Murray and McPhail (1988), and 46.4°F (8°C) produced the longest (Beacham and Murray 1986) and heaviest (Murray and McPhail 1988) fry.

Survival of the alevin life stage was found to be generally excellent (>97%) for 21 families of pink salmon tested at temperatures ranging from 39.2 to 35.6°F (4-2°C) (Beacham and Murray 1986). Survival to emergence was reportedly low, at 57.2°F (14°C) (Murray and McPhail 1988).

Examining low incubation temperatures, Beacham and Murray (1986) found that temperatures of 39.2°F (4°C) consistently resulted in the lowest survival for 5 stocks and 21 families of pink salmon, and in a 1990 study found 50% mortality at 41°F (5°C). Murray and McPhail (1988), Beacham and Murray (1990), and Bailey and Evans (1971) found 100% mortality at incubation temperatures of 35.6°F (2°C). Murray and Beacham (1986) transferred

embryos in a late stage of development from 46.4°F to 33.8°F (1-8°C) and found that while northern stocks had 100% survival, southern stocks had mortalities ranging from 38% to 60%.

Based on the research cited above, constant temperatures of 40.1-53.6°F (4.5-12°C) and a constantly declining temperature regime beginning at 57.2°F (14°C) can produce excellent and perhaps optimal survival rates of incubating pink salmon. However, a constant temperature of 46.4°F (8°C) appears to produce the most consistently optimal results; and although tests up to 53.6-55.9°F (12-13.3°C) were found to produce optimal results, several tests found temperatures of 51.8-53.6°F (11-12°C) (as well as ones conducted at 40.1-41°F [4.5-5°C]) to produce less survival and smaller fry. Furthermore, in natural streams the temperatures do not decline at a steady rate, and temperatures of 59-60.8°F (15-16°C) have resulted in high mortality. In consideration of all of these issues, we should assume that constant or acclimation temperatures in the range of 46.4-50°F (8-10°C) represent optimal conditions for embryonic development. No specific information was reviewed that examined the effect of short-term and infrequent peaks of temperature on developing pink salmon.

Sockeye salmon. Murray and McPhail (1988) and Combs (1965) reported that sockeye salmon are more tolerant of low incubation temperatures and less tolerant of high incubation temperatures than the other Pacific salmon. At constant exposure, Combs (1965) reported that temperatures of 39.9-54.8°F (4.4-12.7°C) produced similarly high survival rates (85.8%-90.9%), with the highest occurring at 42.4°F (5.8°C). Combs found that incremental increases in mortality of 53%-67% occurred when the temperature was lowered from 42.4 to 39.9°F (5.8 to 4.4°C) or raised from 54.8 to 57.5°F (12.7-14.2°C). Velsen (1987) found that while survival rates were highly inconsistent between 34 and 59°F (1.1-15°C), the best survival generally occurred between 35.8 and 42.4°F (3.1 and 5.8) (generally >90%), with fair survival (>70%) occurring in the range 35.8-54.9°F (2.1-12.7°C), and survival rates consistently poor (17%-76%) above 57.2°F (14°C). Murray and McPhail (1988) found that survival was highest at 46.4°F (8°C) (79%) but only 40% at both 51.8 and 41°F (11 and 5°C). Andrew and Geen (1960) reported that in the first 2 years of a 4-year field study, the Salmon Commission found that eggs initially incubated at temperatures of 45°F (7.2°C) had lower survival than those initially incubated at 50, 55, and 60°F (10, 12.8, and 15.6°C). In a followup experiment the following 2 years, they found that eggs exposed to temperatures of 60-62°F (15.6-16.7°C) for short periods suffered severe losses during the exposure, and that temperatures of 62-64.9°F (16.7-18.3°C) caused extensive losses both during and following exposure. In a study by Craig et al. (1996), the temperature range of 46.4-50°F (8-10°C) resulted in the optimum 1:1 male-to-female sex ratio in offspring, although the study design really only allows the conclusion that temperature in the early stage of development affects sex determination.

The data on sockeye incubation survival are highly variable. Overall, however, it can be said that constant or acclimation temperatures in the range of 39.2-54.5°F (4-12.5°C) produce variable but often excellent survival rates in sockeye salmon, but that the range 46.4-50°F (8-10°C) appears most consistently optimum. No specific studies were found to suggest a basis for a single daily maximum temperature limit during the incubation period for sockeye salmon.

Steelhead. In establishing a State standard to protect spawning, we should consider temperature recommendations established to protect embryo development. Fuss (1998) considered the range 42-52°F (5.6-11.1°C) to be optimal for steelhead egg survival in the

Washington State hatchery program, and Bell (1986) suggested that 50°F (10°C) is the preferred hatching temperature for steelhead eggs. Rombough (1988) found less than 4% embryonic mortality at 42.8, 48.2, and 53.6°F (6, 9, and 12°C), but noted an increase to 15% mortality at 59°F (15°C). Alevin mortality was less than 5% at all temperatures tested, but alevins hatching at 59°F (15°C) were considerably smaller and appeared less well developed than those incubated at the lower test temperatures. Redding and Schreck (1979) similarly found that emergent fry were larger at 53.6°F (12°C) than at 60.8°F (16°C). Based on the works reviewed above, it appears that an optimal constant incubation temperature occurs below 51.8-53.6°F (11-12°C). No specific research results were found that could be used to suggest a single daily maximum temperature limit for waters containing incubating steelhead.

Nonanadromous rainbow trout. Kamler and Kato (1983) tested incubation survival at 48.2, 50, 53.6, 57.2, and 60.8°F (9, 10, 12, 14, and 16°C). They found the highest survival of eggs at 50 and 53.6°F (10 and 12°C), slightly lower survival at 57.2F (14°C), and abrupt drops in survival at both 48.2°F (9°C) and 60.8°F (16°C). Velsen (1987) compiled data on the incubation survival of both rainbow trout and steelhead trout that showed survival was consistently high (>92%) between 39.2 and 48.2°F (4 and 9°C), and fair (>78%) between 37.4 and 59°F (3 and 15°C), but very poor (7%) above 60.8°F (16°C). Survival to the swim-up stage in two strains of rainbow trout had 94%-98% survival at 44.6°F (7°C), 72%-95% at 39.2°F (4°C), and <12%-41% survival at 35.6°F (2°C) (Stonecypher and Hubert 1994). Kwain (1975) found that the lowest mortalities occurred at 44.6 and 50°F (7 and 10°C), Billard and Breton (1977) found a drop in fertility at temperatures higher than 50°F (10°C), and Kashiwagi et al. (1987, as cited in Taylor and Barton 1992) found optimal hatching occurred at 50°F (10°C). Humpesh (1985) found that optimal hatching (>90%) occurred between 44.6 and 51.8°F (7 and 11°C), and Alekseeva (1987, as cited in Taylor and Barton 1992) suggested that optimal incubation occurs with temperatures rising from 41.5°F to 50.9°F (5.3-10.5°C). Rombough (1988, as cited in Taylor and Barton 1992) found that at temperatures less than 53.6°F (12°C) there was less than 4% mortality. Constant temperatures above 53.6°F (12°C) have produced variable, but generally lower survival during incubation temperatures, with often severe losses occurring at temperatures of 59-60.8°F (15-16°C) (Velsen 1987, Billard and Breton 1977, Kwain 1975, Kamler and Kato 1983, and Rombough 1988, as cited in Taylor and Barton).

On the basis of the literature cited above, we can generally conclude that constant or acclimation temperatures in the range of 44.6-50°F (7-10°C) are optimal for incubation and embryonic development of rainbow trout. No specific studies were found that test the ability of *O. mykiss* eggs or alevin to survive high single daily maximum temperatures.

Cutthroat trout. Eggs of sea-run cutthroat incubate 6-7 wk before they hatch, and the alevin remain in the gravel for about another 2 wk before they emerge (Trotter 1989, Pauley et al. 1989). Fry may emerge from March through June, depending on the location and time of spawning, but peak emergence occurs in mid-April (Trotter 1989, Wydoski and Whitney 1979). Pauley et al. (1989) cite studies demonstrating that the optimum temperature for incubation is 50-60.8°F (10-11°C). Bell (1986) has suggested that the range for hatching of cutthroat trout eggs is from 39.9 to 55°F (4.4-2.8°C). Smith et al. (1983) found that west-slope cutthroat trout eggs

held in creek water with a fluctuating temperature of 35.6-50°F (2-10°C) had significantly better survival than eggs held at a constant 50°F (10°C).

Hubert and Gern (1995) found 68.6% survival in a control population held at 44.6°F (7°C) when testing the effects of lowering incubation temperatures in the early stage of development. Mortality rates were no different from controls when temperatures were lowered to 37.4°F (3°C) at least 13-15 d after fertilization but were higher if the cooling took place sooner. Stonecypher and Hubert (1994) found that survival to swim-up stage in Snake River cutthroat trout was 95% at 44.6°F (7°C), approximately 87% at 39.2°F (4°C), and less than 16% at 35.6°F (2°C).

It is somewhat problematic to set standards to protect the incubation of cutthroat trout that can be reasonably applied statewide. Cutthroat are a spring spawning species that often spawns high in the watershed and has a very broad period of spawning when examined statewide. Stocks that exist in lower or warmer watersheds spawn as early as February when temperatures rise above 42.8°F (6°C), whereas stocks that exist in high-elevation snow-melt streams may need to wait until late June or July for waters to be sufficiently warm (42.8-51.8°F [6-11°C]) for successful spawning. If there were no risk of egg loss from sudden late winter and spring freshets, we could suggest that the spring spawning strategy is relatively unencumbered by changes in the temperature regime. Although earlier spawning exposes cutthroat eggs to higher risks of physical damage, the earlier hatch also places surviving resident fry in a good position to maximize summer growth and thus increase their survival opportunities over the following winter. It may well be that the superior growth of anadromous salmonids in the ocean phase makes increases in weight gain from earlier emergence of less value, but this relationship remains to be tested. In general, specific stocks will have adapted their spawning and emergence periods to optimize both incubation survival and early fry growth. Significant changes in the temperature regime, such as earlier spring warming, will bring unknown risks to individual populations. Therefore, although an optimal temperature regime is recommended in this paper for cutthroat trout, it would be best to tailor it to the historic spawning patterns found in specific stocks. To initiate spawning in most stocks, the water temperatures must at least warm up to daily maximums of 42.8-44.6°F (6-7°C), although some stocks may not begin spawning until temperatures reach 51.8°F (11°C). Specific studies on incubation survival suggest that incubation may be optimized with constant or acclimation temperatures in the range of 44.6-50°F (7-10°C). No specific basis was found in the literature for setting single daily maximum criteria for the incubation of cutthroat trout.

What are the conclusions for incubation requirements?

Spawning signals the beginning of the life-cycle stage (egg deposition and initial egg incubation) that is most sensitive to warm waters. Critical spawning temperatures for a variety of salmonids are summarized in Table 5. Because the spawning period, egg fertilization, and initial incubation are sensitive life stages dependent on thermal regimes, special consideration must be given to ensure that criteria to protect incubation are applied at the proper time of year.

Table 5. Upper optimal temperature regimes based on constant or acclimation temperatures necessary to achieve full spawning protection of the nine key cold-water fish species indigenous to the Pacific Northwest

Fish species	Critical spawn temperatures	
	Upper optimal temperature range °F (°C)	Single daily maximum temperature °F (°C)
Chinook	48.2-50 (9-10)	56.3-58.1 (13.5-14.5)
Pink	50-53.6 (10-12)	
Chum	46.4-50 (8-10)	
Char	35.6-42.8 (2-6)	42.8 (6)
Sockeye	46.4-50 (8-10)	
Coho	44.6-50 (7-10)	
Cutthroat	44.6-50 (7-10)	
Rainbow	44.6-50 (7-10)	
Steelhead	51.8-53.6 (11-12)	

For growth, what are the demands for energy and how is the balance determined by temperature?

In terms of energy budgets, fish production energy (P) equals the sum of growth (G), reproduction (Rp), shed scales (Ex), and secretions (S), as shown in the following equation:

$$P = G + Rp + Ex + S.$$

Energy assimilated from food equals the difference between energy ingested and defecated, or $A = I - F$.

Energy assimilated is distributed into production (P), respiration (R), and excretion (U), as follows:

$$A = P + R + U.$$

The symbols used above follow terminology of Ricker (1968) and Odum (1968).

Energy is needed to maintain the basic metabolic rate and is fundamental to sustain life. In addition, some energy must be diverted to activity (swimming) to perform the functions of food capture, escape from predators, migration, and so on. If the active metabolism is not sufficiently high, energy is not available for feeding activity and, subsequently, growth and reproduction. When water temperatures rise toward lethal conditions, resting metabolism rate increases

dramatically and feeding rate declines to zero. When water temperatures are high, most of the fish's assimilated energy may be required simply to keep up with basic metabolic demand. When active metabolism (energy expenditure for swimming) declines so the fish can divert available energy to basic metabolic demands, feeding declines. And, even when food is available, feeding no longer occurs if the temperature is above the feeding temperature limit. This may have an adaptive benefit, because digesting food under high temperature conditions incurs a metabolic demand (specific dynamic action). The more overall energy the fish expends in basic metabolism and food digestion, given a declining food intake, the lower will be the assimilated energy that the fish can utilize for growth, reproduction, or resistance to environmental extremes. This latter use of energy is needed for resistance to disease and recuperation from cumulative stresses of predator avoidance, migration, high temperature stress, and so on (Kelsch 1996).

Why is it important to be concerned with growth rate, production, and fish density?

Production is the elaboration of tissue by a population over a specified period of time, regardless of the fate of the tissue (Warren 1971). Production energy is stored as body tissue growth, gametes, or released as secretions (e.g., mucus). Production (e.g., growth) for any time period in which growth rate is relatively constant can be calculated as the product of the growth rate (e.g., mg/g/d) and mean biomass (e.g., g/m^2). Production for longer time periods is calculated as the summation of production for the short time intervals in which growth rate is relatively constant. Production can also be computed graphically as the area under the curve where number of individuals in the population at an instant in time is plotted against the mean weight of those individuals (Warren 1971). Regardless what method is used to calculate production, production is clearly a function of population size, survival, and growth rate, which in turn may be influenced by water temperature, other water quality factors, food availability, level of predation, and so on.

Temperature regime is an important influence on fish density. Control on density can occur through a combination of survival effects, behavioral avoidance, and interspecific competition. Li et al. (1993) reported a decline in steelhead biomass from 18 g/m^2 at a maximum summer water temperature of 60.8°F (16°C) in tributaries of the John Day River to 0 g/m^2 at a maximum temperature of 82.4°F (28°C). The sharp reduction in biomass with increasing temperature is an indication of either progressive mortality or emigration from zones exceeding temperature preferenda. Likewise, Ebersole et al. (in press) reported for tributaries of the Grande Ronde River, Oregon, that rainbow trout density declined steadily between a mean daily maximum temperature of 53.6°F (12°C) to zero at approximately 75.2°F (24°C). The literature on the effect of water temperature in controlling fish density is extensive (McCullough 1999).

Because fish are mobile and migration to avoid high water temperatures is sometimes an option, it is not easy to extrapolate temperature-fish density effects to a whole watershed to estimate total population size or population production. Nonetheless, the numerous studies showing a decline in fish density with increasing water temperature probably indicate lethal and sublethal effects and preference for habitats in which growth is optimum as much as they indicate simple avoidance behavior. Production is calculated as the product of growth rate and mean biomass (see above). Energy stored as production is distributed primarily in somatic

growth and reproduction. The ability to divert energy to reproduction is feasible when there is sufficient scope for activity and this depends on ambient temperatures and food availability. In addition, population viability is related to population abundance.

What is the optimum range or optimum temperature for growth of various salmonids?

Chinook. Chinook production in an experimentally modeled stream at 53.6°F (12°C) was 65% higher than at 60.8°F (16°C) (Bisson and Davis 1976, as cited by CDWR 1988, p. 31). An optimum growth temperature of 59°F (15°C) was recommended by Banks et al. (1971 as cited by Garling and Masterson 1985). Brett et al. (1982) recommended 58.6°F (14.8°C) as the growth optimum for juvenile chinook feeding on a food ration of 60% of the maximum (assumed to be a typical level in nature). Marine and Cech (1998) determined that growth rates of fall chinook under sublethal rearing temperatures (69.8-75.2°F [21-24°C]) were substantially less than growth rates at 55.4-60.8°F (13-16°C). Wilson et al. (1987) recommended 50.9°F (10.5°C) as the midpoint of the growth optimum for Alaskan chinook, based on studies in southeastern and southcentral Alaska. Preferred rearing temperatures for chinook were reported as high as 58.3°F (14.6°C) (Reiser and Bjornn 1979). The preferred temperature range for fingerlings was 53.6-55.4°F (12-13°C) (based on determination of mean of the distribution) when the fish were acclimated to temperatures ranging from 50 to 75.2°F (10-24°C) (Brett 1952). If growth temperatures are maintained between 50 and 60°F (10-15.6°C), growth rate would be >80% of the maximum level observed in feeding at 60% satiation (a level considered by Brett et al. [1982] to correspond to naturally occurring food availability levels). Growth rate under 60% satiation feeding at 58.6°F (14.8°C) is expected to be approximately 1.8%/d (Brett et al. 1982). Lower levels of food availability would reduce the optimum growth temperature. Temperatures above 60°F (15.6°C) significantly increase the risk of mortality from warm-water diseases. A synthesis of this evidence leads to a recommended optimum production temperature zone of 50-60°F (10.0-15.6°C).

The optimal growth zone of 50-60°F (10-15.6°C) falls within the range for positive growth at 40.1°F (4.5°C) (lower limit) and 66.4°F (19.1°C) (upper limit) (see Armour 1990). The 39.4 and 66.4°F (4.1 and 19.1°C) limits tabulated in Armour (1990) are zero net growth limits for a chinook population. Brett et al. (1982) reported a zero individual growth rate under 60% satiation feeding at 70.5°F (21.4°C) (see Figure 2). If chinook were to have unlimited rations, the optimum growth temperature would be approximately 66.2°F (19°C) (Brett et al. 1982).

Sockeye. Good growth of sockeye, with low mortality, occurred at 53-62°F (11.7-16.7°C) (Donaldson and Foster 1941). The upper limit to growth was similar to that observed by Brett et al. (1982) for chinook feeding at 60% of satiation. Sockeye (7-12 months old) feeding at satiation had a growth rate optimum at approximately 59°F (15°C). Growth rates declined at both higher and lower temperatures. Growth rates reached zero at approximately 75.2°F (24°C) under satiation feeding. When feeding rate was lowered to 1.5%/d, the optimum growth temperature declined drastically to 41°F (5°C). At this feeding rate, growth rate (%/d) was zero at approximately 59°F (15°C) (Brett et al. 1969). Feeding rates of Skaha Lake sockeye at 62°F (16.7°C) were 2.3%-3.2%/d (fresh weight; based on a sample of the 2-wk periods having mean temperatures of 62°F [16.7°C]). Feeding rates were approximately 2.2%/d at 50°F (10°C), but the optimum growth occurred at this low temperature (Donaldson and Foster 1941). Optimum
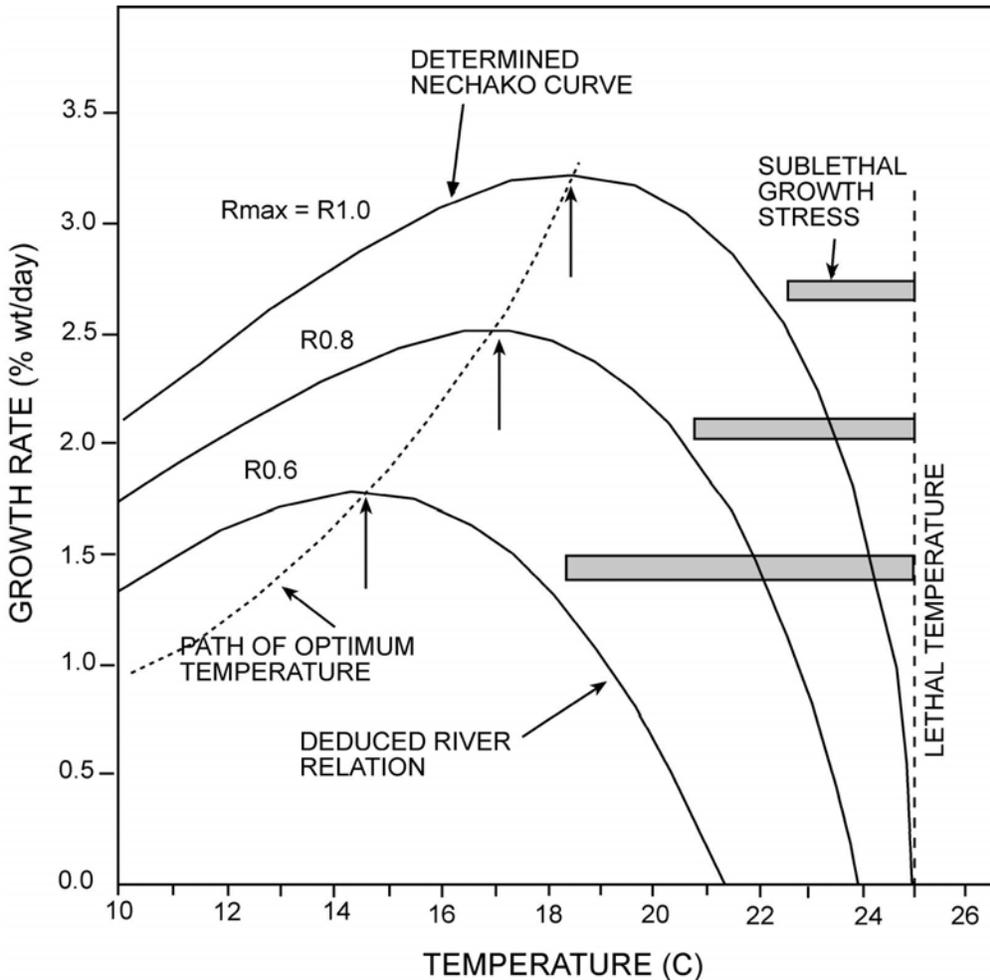
Figure 2. Optimum growth rates of spring chinook under various feeding regimes and constant temperatures.

growth temperature was 59°F (15°C) at a ration of 6%/d, but this declined to an optimum growth temperature of 41°F (5°C) at a ration of 1.5%/d (Brett et al. 1969).

   Steelhead. Wurtsbaugh and Davis (1977) studied growth of steelhead trout in laboratory streams under three fluctuating temperature regimes (natural cycle, natural +5.4°F [3°C], and natural +10.8°F [6°C]) in all four seasons and found that trout growth could be enhanced by temperature increases up to 61.7°F (16.5°C). During the summer season the control temperature (natural cycle) was 61.2°F (16.2°C) (mean) and the elevated temperatures averaged 67.1°F (19.5°C) and 72.5°F (22.5°C). The average diel temperature range for the summer growth period was about 38.1°F (3.4°C) under the three treatments. Growth rates under food consumption rates of 5%-15% dry body wt/d were higher under the control temperature regime

than at the elevated fluctuating regimes. Under the high temperature regime (mean of 72.5°F [22.5°C]) growth rate was zero at a food consumption rate of 7%/d. Gross food conversion efficiency decreased as temperatures increased from 61.2 to 72.5°F (16.2-22.5°C). Maintenance rations increased by a factor of three over the temperature range 44.4-72.5°F (6.9-22.5°C).

What more is specifically known about growth rearing requirements of rainbow trout?

Final preferred and optimal temperatures for rainbow trout have been reported at 53.6-66.2°F (12-19°C) (Bell 1986, Taylor and Barton 1992), and scope of activity and growth for juvenile fish are commonly reported to be optimal between 59 and 69.8°F (15-21°C) on a satiation diet (Moyle 1976, McCauley and Pond 1971, Dickson and Kramer 1971, Kwain and McCauley 1978, and Huggins 1978 as cited in Kwain and McCauley 1978). However, some authors have suggested lower optimal temperature ranges. Piper et al. (1982) set the optimal at 50-62.1°F (10-16.7°C), although Sadler et al. (1986) found that growth and food conversion efficiency were greater at 60.8°F (16°C) compared with 50°F (10°C). McCauley and Huggins (1975) found that large (150-250 g) rainbow trout had a preferred mean temperature of 62.1°F (16.7°C), and that the fish actively traveled at temperatures between 56.8 and 64.4°F (13.8-18°C) in a thermal gradient. Behnke (1992) suggested that the optimum temperature for growth and food assimilation in salmonids occurs between 55.2 and 60.8°F (13-16°C). Ferguson (1958) cites 56.5°F (13.6°C) as the final preferred temperature for rainbow trout, and Mckee and Wolf (1963, cited in Wedemeyer et al., no date) found 55.4°F (13°C) to be optimum. Kwain and McCauley (1978) suggest that fish over 1 year old may have a final preferred temperature of 55.4°F (13°C) (citing the works of Garside and Tait 1958, Christie as reported in Fry 1971, and McCauley et al. 1977, as cited in Kwain and McCauley 1978) although as noted above, the work of McCauley and Huggins (1975) suggests that older fish sometimes demonstrate more intermediate temperature preferences.

Dockray et al. (1996) found that in a fluctuating temperature environment, temperature increases benefited growth up to daily maximum temperatures of 64.4°F (18°C), above which long-term growth was inhibited. De Leeuw (1982) found that stream temperature increases that raised the summertime maximum temperature from 53.6 to 61.7°F (12-16.5°C) were associated with an increase in growth rates in three streams in British Columbia, Canada. Hokanson et al. (1977) found that a constant exposure to 63°F (17.2°C) produced the greatest growth rates in trout fed to satiation over a 40-d test period. Increased mortality was observed in temperatures above this growth optimum. They also noted that in fluctuating temperature experiments, growth was accelerated when the mean temperature was below the constant temperature optimum (63°F [17.2°C]), and growth was retarded by mean fluctuating temperatures above this optimum. The highest growth rate in the fluctuating temperature environment occurred at a mean of 59.9°F (15.5°C) (range of 53-66.7°F [11.7-19.3°C]). A statistically nonsignificant decrease occurred at a mean of 63.1°F (17.3°C) (range of 56.3-70°F [13.5-21.1°C]). The authors also concluded that rainbow trout acclimate to some temperature between the mean and the maximum daily temperatures. Sometimes, warmer waters may provide secondary benefits to rainbow trout. Cunjak and Green (1986) found that rainbow trout were able to compete better with brook trout at 66.2°F (19°C) than at either 46.4 or 55.4°F (8 or 13°C).

Bisson and Davis (1976, as cited in Li et al. 1994) found that streams with daily maximum

temperatures of 60.8-73.4°F (16-23°C) had greater standing crops of trout than did streams with warmer maximum temperatures (78.8-87.8°F [26-31°C]). Frissell et al. (1992) studied the distribution of rainbow trout and found that although they could be found in water temperatures over 73.4°F (23°C), there was a general threshold response for age 1+ fish above 71.6°F (22°C) and for age 2+ fish above 69.8°F (21°C). Consistent with these results, Li et al. (1993, 1994, and 1991 as cited in Spence et al. 1996) noted that even though rainbow trout might not show avoidance reactions when stream temperatures were below 68°F (20°C), they actively avoided waters warmer than 73.4-77°F (23-25°C). Linton et al. (1997) noted that rainbow trout fed to satiation continued to feed and grow at a mean temperature of 68.9°F (20.5°C), a 30% reduction in food intake occurred at 71.6°F (22°C), and juvenile fish continued to feed near their thermal maximum. Linton et al. (1997) found that increasing the temperature regime by 3.6°F (2°C) over the natural (base) level for Lake Ontario trout resulted in increased spring and early summer growth, which was lost later in the summer due to suppression of appetite and growth. Mortality rates increased from 6% to 13.1% in the warmer test water during the late summer in the first summer of testing when the mean monthly base temperature in August was 73.4°F (23°C). Mortality was almost nonexistent through the following summer, which had a mean August base temperature of 64.4°F (18°C) (the test waters should have had a mean of 68°F [20°C]). The threshold temperature for cessation of feeding, and subsequently growth, differed from >68°F (20°C) to <68°F (20°C) over the two summers, and thus also fish size and age. Behnke (1992) cited work showing that trout reduce and finally cease feeding as temperatures rise to between 71.6 and 77°F (22-25°C), often well below the lethal temperature.

Although the works of Li et al. (1991, 1993, 1994) cited above were conducted on interior forms of rainbow trout, Behnke (1992) reported finding redband trout in the desert basins of southern Oregon and northern Nevada where temperatures regularly kill other trout. Trout in these intermittent desert streams were found actively feeding in water of 82.9°F (28.3°C). Behnke suggested that redband trout from an Oregon desert basin have an optimum feeding temperature at some untested temperature higher than 66.2°F (19°C). These desert redband might have a functional feeding temperature that is higher than that of rainbow trout, which have evolved in less harsh environments of temperature and water flow. A test was evaluated that compared an introduced population of rainbow trout in the Firehole River in Montana with two hatchery stocks. Temperatures in the Firehole River in summer at times reached as high as 85.1°F (29.5°C) due to thermal springs. The introduced population had been living in the river for approximately 20 generations, yet it was found that neither the functional feeding temperature nor the upper incipient lethal temperature had increased compared with the hatchery stocks. The author concluded that thousands of years of adaptation to a dry environment have enabled Oregon desert redband trout to feed at high temperatures, but 60-70 years seem too few to have allowed the introduced rainbow trout to raise their functional feeding temperature in the Firehole River. Kaya et al. (1977) found that daily maximum temperatures exceeding 77°F (25°C) caused rainbow trout to move out of the mainstem of the Firehole River in Montana. These fish would move into tributary streams that averaged 10.8-18°F (6-10°C) lower in temperature.

The above research shows a wide range in the estimates of optimal temperature for rearing rainbow trout. This wide range may reflect the fact that the individual subspecies and specific stocks have evolved differently to fit the characteristics of their home streams. Also, different ages and sizes of fish were used in the research. Equally plausible is that some of the

temperatures for redband trout that were higher than noted for rainbow trout or other salmonids might have been based on an improper assumption that temperatures measured in the vicinity of the fish were actually those that the fish inhabited—that is, fish might actually inhabit microhabitat or habitat-scale refugia to maintain their populations in otherwise hostile conditions (see Ebersole et al. in press). Because criteria must protect both adult and juvenile forms of rainbow trout, an optimal temperature regime seems to most consistently occur in the range of 55.4-60.8°F (13-16°C).

What is the relationship between growth temperatures and other physiological responses?

When fish demonstrate temperature preference in a thermal gradient, this is an adaptive mechanism that allows them to be positioned in an environment where they can achieve optimum physiological performance (Coutant 1987, Hutchison and Maness 1979). Hutchison and Maness (1979) cited numerous physiological processes that achieve optimum performance near the thermal preferendum: growth rate, appetite, food conversion efficiency, digestion, egestion, metabolic scope, oxygen debt load, maximum sustained speed, maximum volitional speed, resting and active blood pressure, active cardiac work, cardiac scope, learning and memory, immune response, renal function, hormone secretion, reproductive function, elimination of anaerobically produced lactate, and enzyme activity.

Temperatures preferred or avoided are highly correlated with key physiological indices (Stauffer 1980). Final temperature preference is correlated with optimal growth temperature (Jobling 1981, Kellogg and Gift 1983, Christie and Regier 1988). Kellogg and Gift (1983) found for four fish species that nearly all preferred temperatures measured were in a range that provided 75% of maximum growth rate. The physiological optimum is derived by averaging the growth optimum and preferred temperature (Brett 1971). Preferred temperature also is correlated with the temperature providing the maximum metabolic scope. This, in turn, is related to the temperature providing the maximum critical swimming speed (Kelsch and Neill 1990). Also, fish tend to be more immunologically resistant to pathogens at their preferred temperatures (Sniezko 1974, Cuchens and Clem 1977, Avtalion et al. 1980, O'Neil 1980, Rijkers et al. 1980, Avtalion 1981, Wishkovsky and Avtalion 1982, all cited in ODEQ 1995).

The preferred temperature range for chinook fingerlings was 53.6-55.4°F (12-13°C) (based on determination of mean of the distribution) when acclimated to temperatures ranging from 50 to 75.2°F (10-24°C) (Brett 1952). If growth temperatures are maintained between 50 and 60°F (10-15.6°C), growth rate would be >80% of the maximum level observed in feeding at 60% satiation (a level considered by Brett et al. [1982] to correspond to naturally occurring food availability levels).

For sockeye, Brett (1971) found that swimming capacity, metabolic scope, growth on excess rations, and ingestion were maximized at 59°F (15°C). The temperature producing the growth optimum (59°F [15°C]) also was the final thermal preferendum determined by acute tests (Brett 1952, 1971). A correlation between final preferred temperature and optimum growth has been found in numerous other fish species (Christie and Regier 1988). In coho, it was found that swimming speed was maximum at 68°F (20°C), but growth reached a maximum on excess food

rations at 62.6-68°F (17-20°C) (Griffiths and Alderdice 1972).

What are temperature feeding limits for salmonids?

Temperature feeding limits are the upper and lower temperatures that result in inhibition of feeding. The ability to consume food does not guarantee that growth occurs. Food intake rate and conversion efficiency (assimilation rate) at any temperature dictate the amount of energy assimilated. However, if metabolism rate exceeds energy assimilation rate, no energy is available for growth. In fact, the fish would lose weight because energy stored in tissue is used for metabolism.

Brett et al. (1982) observed feeding behavior of juvenile chinook from the Nechako River, in British Columbia, and the Big Qualicum River, on Vancouver Island. They reported good feeding response to unlimited food supply at 71.6°F (22°C), but feeding became more sporadic between 73.4 and 77°F (23-25°C), at which point it ceased.

Fingerling sockeye began losing appetite at 73.9°F (23.3°C) and stopped feeding at 75.2°F (24°C). Maximum feeding rate was measured as 8% dry body wt/d at 68°F (20°C). Redband trout can be expected to set the upper limit for feeding response for all salmonids of the Pacific Northwest. No feeding was observed by Sonski (1982 as cited by Sonski 1984) for juvenile redband at 77.9-80.6°F (25.5-27°C). Comparing thermal tolerance by three rainbow trout species, Sonski (1984) found that no redband trout or Wytheville rainbow would feed at temperatures >78.8°F (26°C). The Firehole River stock would not feed beyond 80°F (26.7°C).

In CTM (critical thermal maximum) experiments in which the heating rate was 3.6°F (2°C)/d, five species of juvenile salmonids were observed feeding up to temperatures that were 1.8-3.6°F (1-2°C) less than the LT50 (Grande and Anderson 1991). Lake trout, brook trout, brown trout, rainbow trout, and Atlantic salmon were observed feeding at temperatures of 74.8, 78.2, 79.1, 79.9, and 82.6°F (23.8, 25.7, 26.2, 26.6, and 28.1°C), respectively, reached during CTM experiments. A similar CTM experiment with *Salmo apache* in which temperature was increased 1.8-2.7°F (1-1.5°C)/d showed that fish began refusing food at 68°F (20°C) and totally stopped feeding at 70.1°F (21.2°C) (Alcorn 1976). In northern California streams, juvenile steelhead were seen actively feeding in water temperatures as high as 75.2°F (24°C) (Nielsen et al. 1994). However, once temperatures reached 71.6°F (22°C), rate of foraging began to decline.

How is feeding rate affected by acclimation temperature?

The highest temperature for normal feeding in brown trout varies with acclimation temperature, as is probable for all fish species. Elliott (1981) determined that the highest temperature for normal feeding in brown trout that were acclimated to 59°F (15°C) was 19.1°C ± 0.27 (SE). Similarly, Frost and Brown (1967) determined that feeding rate declined sharply above 66.2°F (19°C) in brown trout. When fish were acclimated to 68°F (20°C), no feeding took place. Under cold temperature regimes, when brown trout were acclimated to water at 50°F (10°C), normal feeding occurred when fish were subjected to 2.9°C ± 0.27. When acclimated to even lower temperature 41°F (5°C), normal feeding occurred at 0.4°C ± 0.21.

What are temperature growth limits for salmonids?

Temperature growth limits for salmonids are those lower and upper temperatures that result in zero growth on an individual basis or zero net growth of the population. The zero net growth temperature is the temperature at which net elaboration of tissue of the population is zero or the temperature at which fish mortality balances the gain in growth.

With chinook, the bounds for positive growth occur at 40.1°F (4.5°C) (lower limit) and 66.4°F (19.1°C) (upper limit) (see Armour 1990). The 39.4°F (4.1°C) and 66.4°F (19.1°C) limits tabulated in Armour (1990) are zero net growth limits for a chinook population. Brett et al. (1982) reported a zero individual growth rate under 60% satiation feeding at 70.5°F (21.4°C).

Juvenile sockeye had a positive growth response between 39.2 and 69.8°F (4-21°C) in laboratory experiments with feeding to satiation once per day (Donaldson and Foster 1941). Growth rate was negative at 73°F (22.8°C), and at this temperature mortality was significant. Good growth with low mortality occurred at 53-62°F (11.7-16.7°C) (Donaldson and Foster 1941). The upper limit to growth was similar to that observed by Brett et al. (1982) for chinook feeding at 60% of satiation rations.

Brown trout growth can be high in the temperature range 44.6-66.2°F (7-19°C), but growth is poor above 68°F (20°C) (Frost and Brown 1967).

Wurtsbaugh and Davis (1977) studied growth of steelhead trout in laboratory streams under three fluctuating temperature regimes (natural cycle, natural +5.4°F [3°C], and natural +10.8°F [6°C]) in all four seasons and found that trout growth could be enhanced by temperature increases up to 61.7°F (16.5°C). During the summer season the control temperature (natural cycle) was 61.1°F (16.2°C) (mean) and the elevated temperatures averaged 67.1 and 72.5°F (19.5 and 22.5°C). The average diel temperature range for the summer growth period was about 6.1°F (3.4°C) under the three treatments. Growth rates under food consumption of 5%-15% dry body wt/d were higher under the control temperature regime than at the elevated fluctuating regimes. Under the high temperature regime (mean of 72.5°F [22.5°C]), growth rate was zero at a food consumption rate of 7%/d.

How does food availability affect growth of salmonids at different temperature exposures?

In a laboratory setting, feeding rations can be controlled by the researchers. Feeding to satiation at a frequency of three to five times a day is not uncommon in growth experiments and is considered to provide growth rates comparable to those under continuous feeding with excess food. In other studies, varying feeding regimes may be used to determine the temperature effects on growth at different levels of food availability.

In the field, stream productivity and nutrient availability to salmonids depend on many factors including light; nutrients including inputs of litter, decomposing salmon carcasses, and coarse woody debris; sediment loading; temperature; and streamflow (Murphy 1998, Bilby et al.

1996). Other factors that may limit fish feeding in the wild include suitable instream cover and species- or density-dependent competition and predation (Richardson 1993).

Food limitations in trout streams commonly cause reductions in summer growth (Cada et al. 1987, Enseign and Strange 1990). If there is food limitation in the field, growth rates will be less than maximum for salmon and bull trout at temperatures that produce maximum growth under satiation feeding. Growth rates have been observed in the field that are less than those predicted in the laboratory under excess feeding and suggest that food limitation could be the cause (Preall and Ringler 1989, Cada et al. 1987). With food limitation, the upper temperature that produces zero growth would decline to a lower temperature. Under conditions where fish have reduced feeding rates due to food limitation, conversion efficiency can increase somewhat to compensate for the limitation in total energy intake. However, if the food limitation is significant, the energy demands of standard metabolism may be difficult to satisfy (Cada et al. 1987). This may limit the scope of activity required to acquire food. Behavioral inhibition in swimming at higher temperatures and lack of competitive ability in foraging compared with fish tolerant of warm water can place salmonids at a disadvantage in deriving maintenance energy requirements.

Gut fullness may be an indicator of food availability. Gut fullness was monitored on several fish species on various dates from late July to mid-October in several tributaries of the upper Yakima River as an index of food availability (James et al. 1998). During this sampling period, temperatures were >57.2°F (14°C). Species monitored included mountain whitefish, spring chinook, redside shiner, and rainbow trout. A high degree of diet overlap was found among the four fish species studied, indicating that competition for food is possible. Gut fullness and diet overlap together were assumed to indicate degree of competition. Summertime gut fullness for spring chinook averaged 14%, while mountain whitefish, rainbow trout, and redside shiner averaged 32%, 10%, and 10%, respectively. Low stomach fullness may indicate a low availability of food due to production of food and intense competition. It is not clear from this research, however, what gut fullness level would be expected under satiation feeding. Growth rates are the bottom line. Comparison of growth rates at various feeding levels in the laboratory with rates in the field under comparable temperatures appears to be the most direct means to infer food supply.

If food becomes limited, the positive growth zone can shrink dramatically (i.e., the maximum temperature at which growth is positive declines) and the optimum growth zone shifts to lower temperatures to compensate for elevated respiration/growth ratios (Elliott 1981, p. 231). McMahon et al. (1999) found that growth curves for bull trout clearly depict a shift to maximum growth at lower temperatures (46 and 53°F [8 and 12°C]) when energy availability is low. Elliott found that for brown trout the temperature at which growth is zero drops from 66.2 to 46.4°F (19-8°C) when food rations are reduced from maximum to 12.5% of maximum. Because the growth optimum falls within 50-60°F (10-15.6°C) for chinook and because diseases become a significant mortality risk beyond this level, water temperatures in major salmon-rearing reaches must be managed on a stream network level from headwaters to mainstem so that temperatures can be maintained below 60°F (15.6°C) within the historic salmon rearing area and below 53.6°F (12°C) in bull trout historic rearing areas. Given that food rations under field conditions are typically less than satiation levels, a reduced growth zone expands the upper temperature zone

and causes loading stresses. This argues for keeping temperatures no higher than the optimum growth range.

Is there evidence for food limitation in natural streams?

A stream's capacity to produce food greatly affects both abundance and growth of fish. Some of the highest freshwater production value have been reported for trout in New Zealand; production values reported for the Pacific Northwest are considerably lower, by at least an order of magnitude (Bisson and Bilby 1998).

Factors influencing stream productivity include nutrient availability, input of organic matter from external sources, the channel's capacity to store and process organic matter, and light (Cederholm et al. 2000). The river continuum concept describes the predictable differences in stream productivity with changes in stream size (Vannote et al. 1980). Headwater streams in the Pacific Northwest are characterized by low levels of primary and secondary productivity (Gregory et al. 1987). In a large watershed, first- to third-order streams may produce only 10%-20% of the annual gross primary production, despite having more than 80% of total stream length (Murphy 1998). Coho, steelhead, cutthroat, bull trout, and spring chinook are among the salmonids that utilize these small headwater streams for spawning and rearing.

Productivity of Northwest streams has been further diminished by the recent decline of Pacific salmon. The role salmon populations play in maintaining ecosystem function by recycling energy and nutrients from the North Pacific Ocean to the inland Northwest has been acknowledged in numerous studies (see Cederhom et al. 2000). The carcasses of spawned-out salmon greatly influence the productivity of the otherwise generally oligotrophic ecosystems of the Pacific Northwest (Cederholm et al. 2000). With declines of Pacific salmon, it is estimated that only 3% of the marine-derived biomass once delivered by anadromous salmon to the rivers of Puget Sound, the Washington coast, the Columbia River, and the Oregon coast is currently reaching those streams (Gresh et al. 2000 in Cederholm et al. 2000).

Growth rates of wild rainbow trout in the field have generally been reported as <1%/d (see review by Wurtsbaugh and Davis 1977) but were higher in the laboratory in every season under the natural temperature regime (mean seasonal temperatures in the laboratory of 50, 44.4, 48.9 and 61.1°F [10, 6.9, 9.4, and 16.2°C] in autumn, winter, spring, and summer, respectively) when fish were fed to satiation. This study revealed that trout growth was improved by increasing temperatures up to a maximum of 61.7°F (16.5°C), but that this threshold applies to the field only under satiation feeding. Because the researchers measured field growth rates in an Oregon coastal stream that indicated food limitation, they concluded that temperatures less than 61.7°F (16.5°C) would be optimal.

In the field an increase in water temperature, when produced by canopy removal, can lead to increased primary production. Greater primary and secondary production can increase food availability to fish (Murphy and Hall 1981, Hawkins et al. 1983) provided that substrate sedimentation does not increase with canopy removal. However, as temperatures continue to increase, primary production can be in the form of algae not readily consumed or digested by benthic macroinvertebrates (e.g., blue-green algae rather than diatoms) (McCullough 1975,

McCullough et al. 1979), and macroinvertebrate production can be dominated by species not readily available to salmonids in the drift (Li et al. 1994). Even if food quality remains high with increasing temperature, feeding rate and growth decline beyond the optimum temperature. Additionally, over the long run, increases in primary production in early seral stage may eventually be outweighed by longer-lasting reductions as a result of increased shade in later seral stages (Murphy and Hall 1981). Second-growth hardwoods and young conifers produce a denser canopy and lack the gaps commonly found in old-growth forests (Murphy 1998).

Can growth rates be predicted under field conditions using thermal history identified under laboratory conditions?

Growth rates under controlled field conditions can be related to growth rates obtained under laboratory conditions if feeding rates and temperatures are known; however, many subtle variables in the field (recruitment to or movement out of the study area, varied caloric content of forage, inter- and intraspecies interactions) can complicate these comparisons. Differences between laboratory and field growth rates can be attributable to a great number of factors.

Typically, temperatures in laboratory experiments are kept constant (i.e., fluctuating less than ± 1.8°F [1°C] around the mean). First, to compare laboratory and field growth rate we must know the field water temperature regime. Growth rates should be measured over days to weeks to improve the ability to detect a change. The temperature regime must be described by an index (e.g., daily mean, daily maximum) in order to relate it to laboratory growth rates. For example, if growth rate under a constant laboratory temperature of 50°F (10°C) is 2%/d and under field conditions a 2%/d growth rate is experienced by fish under a 50°F (10°C) ± 3.6°F (2°C) diel temperature regime, then we might conclude that the mean diel temperature in the field adequately represents the growth conditions. However, food is generally limiting in the field. If this is the case and if the mean field temperature adequately represents the growth response, we would expect field growth rate to be lower than laboratory rates at the same constant mean temperature. The situation can be more complicated, however, because growth rate is related to acclimation temperature. In a fluctuating temperature regime, fish can acclimate to a temperature between the mean and maximum of the cycle. If this is so, the feeding rate in the field (and consequently growth rate) might be higher than under a constant diel temperature equal to the mean of the cycle, despite the lower food availability. That is, there may be some compensation for lower food availability due to fluctuating temperature conditions. In summary, field growth depends on the food availability and quality, the effective acclimation temperature, and the exposure temperature.

The ability to model brown trout growth in the laboratory and field under fluctuating temperatures arose from Elliott's (1975a,b) studies of brown trout growth under constant temperatures. This model has often been found capable of predicting growth under both constant and fluctuating temperatures (Elliott 1994). Elliott (1975a) found that growth rates in the laboratory over 42-d periods in which temperature fluctuated as much as ±4.1°F (2.3°C) around the mean for the entire period closely matched those predicted by entering the mean temperature into the growth model. Growth experiments in the field (a small stream near Windermere, England) were also conducted. In one experiment, temperature increased from 44.2°F (6.8°C) in March to 53.8°F (12.1°C) in June; in another, temperature decreased from 55.2°F (12.9°C) in

August to 45°F (7.2°C) in November. Estimates of growth in the field made by entering the mean weekly temperatures (calculated as the mean of seven daily mean temperatures) into the growth model revealed good agreement between predicted and actual final weights in a 4-wk growth period. Edwards et al. (1979) modeled brown trout growth on 10 British streams and were able to show that predicted growth was 60%-90% of potential growth, assuming feeding on maximum rations. Predicted monthly growth based on mean monthly temperatures was 2% different from computations based on temperatures taken every 4 h. Likewise, Preall and Ringler (1989) developed a computer model of brown trout growth based on Elliott's work and predicted potential growth for populations in three central New York streams based on initial weight, condition factor, and weekly mean temperature. These authors measured actual growth under fluctuating temperatures in the field that were 60%-90% of potential, as determined from their model. Jensen (1990) measured growth on 12 populations in Norwegian rivers and determined that mean growth rates of anadromous brown trout parr were 76%-136% of the maximum inferred from the temperature regime.

Jensen (1990) concluded from his field work that growth rates exceeding laboratory-derived maxima under constant temperatures and satiation feeding could be explained by interpopulation genetic differences or the ability of fish in the field to feed at greater rates under fluctuating temperatures than under constant temperatures. It is also possible that the ability to assess temperatures actually experienced in the field is poor and not well represented by mean reach temperature. Jensen (1990) noted that in two streams growth was best predicted by using the 75% temperature (the median between the mean and maximum), whereas for another stream growth was best predicted using mean temperature. Assuming that Jensen could measure the actual diel cycle experienced by brown trout in these streams, the similar ability of the 75% temperature in predicting growth and in estimating equivalent acclimation temperatures in UILT tests is interesting. It appears that physiological conditioning of fish in fluctuating temperatures adjusts their growth and thermal tolerance toward levels that would be predicted under constant temperatures located between the mean and the maximum.

Another possible explanation not given by Jensen (1990) for greater growth rates in the field is that food quality in the field is better than that provided in laboratory experiments. Also, fat content of macroinvertebrates in the drift could be higher than the average of prey available in the benthos and provide a high-calorie diet. Food quantity, however, is often considered limiting to fish growth in the field (Brett et al. 1982). Growth rates of wild rainbow trout in the field have generally been reported as <1%/d (see review by Wurtsbaugh and Davis 1977), but were higher than this in the laboratory in every season under the natural temperature regime (mean seasonal temperatures in the laboratory of 50, 44.4, 48.9, 48.9 and 61.1°F [10, 6.9, 9.4, and 16.2°C] in autumn, winter, spring, and summer, respectively) when fish were fed to satiation.

Other studies have noted that mean temperatures are useful in predicting growth rates. Growth rates of sockeye fry (Babine Lake, BC, stock) were measured at satiation feeding (3 times/d) from March to mid-May under three temperature regimes: constant 50°F (10°C), declining 23.4 to 12.6°F (13 to 7°C), and increasing 12.6-23.4°F (7 to 13°C). Mean temperature was 50°F (10°C) in each treatment. Rate of temperature change in the declining or increasing treatments was 1.8°F (1°C)/wk over a 56-d period. Although mean temperature can be a suitable

index to growth rate under a fluctuating temperature regime, the studies above did not subject fish to either extreme temperature maxima or extreme diel fluctuations.

Has acclimation to a temperature higher than the mean of a diel cycle been demonstrated?

In addition to the research discussed above, Clarke (1978) measured growth rates of juvenile sockeye in the laboratory at constant and fluctuating temperatures. At constant temperatures ranging from 45.5 to 63.5°F (7.5-17.5°C), growth rates increased linearly. This response was defined by the equation $y = 0.0660x - 0.311$, where x is mean temperature and y is growth rate (%wt/d). At 45.5°F (7.5°C), growth rate was approximately 0.2%/d and at 63.5°F (17.5°C) it was approximately 0.8%/d. At a constant 50°F (10°C) regime, growth rate was 0.35%/d (estimated by regression for all constant temperature growth experiments), but under fluctuating regimes of 44.6-55.4°F (7-13°C) and 41-59°F (5-15°C) (mean daily temperatures of 50°F [10°C]), growth rates were about 0.47%/d and 0.63%/d, respectively. This study indicated that specific growth rate (as %wt/d) at 44.6-55.4°F (7-13°C) was equivalent to that observed at a constant temperature of 52.5°F (11.4°C). Under the diel regime with great amplitude (41-59°F [5-15°C]), growth was equivalent to that observed at a constant temperature of 57°F (13.9°C). This indicates that under diel fluctuating regimes, there was an acclimation to an equivalent temperature between the mean and the maximum temperature. In terms of growth rates, this acclimation effect was similar to that observed in survival under thermal stress with prior acclimation in cyclic diel temperature regimes.

Are there seasonal differences in growth rates not related to temperature?

Jensen (1990) noted that a decreasing autumn temperature trend caused growth to be less at a given temperature than at the same temperature under a generally increasing temperature trend in spring. Such a seasonal effect has been observed in brown trout and Atlantic salmon by some authors, but others have not detected any seasonal difference at comparable temperatures (Jensen 1990). A study by Mortensen (1985 as cited by Jensen 1990) indicated that 0+ and 1+ brown trout growth rate in the field during spring was accurately predicted using Elliott's model, but growth rate was only 60%-90% of predicted rates in summer and 0%-30% in winter. Jensen attributed the realized growth rate to seasonal limitation in food availability.

What research seems to best describe the influence of fluctuating temperature on growth?

Probably the best study of the effect of fluctuating temperature on salmonids is that of Hokanson et al. (1977). It is especially useful as a central point for evaluating other studies because of the range of temperatures evaluated, the fact that both growth and survival were evaluated, and its consistency with the vast literature on thermal effects.

Hokanson and colleagues studied growth and survival of rainbow trout (*O. mykiss*) juveniles reared on maximum rations under fluctuating temperatures (T°F ± 6.8°F [3.8°C]) versus constant temperatures. The physiological optimum (PO) temperature of rainbow trout is 60.8-64.4°F (16-18°C). These authors noted that specific growth rate at mean temperatures less

than PO was lower for a given mean temperature under a constant (T°F) versus a fluctuating (T°F ± 6.8°F [3.8°C]) temperature regime. This indicates a benefit of a fluctuating regime when the mean temperature is less than PO. In this temperature zone, a constant temperature of T+2.2°F (1.5°C) provided comparable specific growth rate to juveniles reared at T°F ± 6.8°F (3.8°C). In other words, we would have to increase an initial constant temperature by 2.7°F (1.5°C) to provide growth rates equivalent to those exhibited under a fluctuating regime having a mean equal to the initial constant temperature. However, specific growth rates at mean temperatures greater than PO were higher at constant than fluctuating temperatures having the same mean temperature. This indicates that when water temperature under field conditions is greater than PO, it is not safe to assume that a fluctuating regime is protective on the basis of its mean, even if the mean itself is not injurious under constant temperature experiments. The negative influence of the diel cycle appears to come from exposure to temperatures higher than the mean when the mean is greater than PO.

This pattern led Hokanson and colleagues to suggest that the growth of rainbow trout appears to be accelerated under fluctuating temperatures when the mean temperature is below the constant temperature optimum for growth and retarded by fluctuating temperatures when the mean is higher. Hokanson et al. suggested that water quality standards (based on weekly mean values) should be set such that the average weekly temperature is below the constant test temperature producing maximum growth. They determined that rainbow trout growth rates under fluctuating regimes do not correspond to those in a constant temperature regime having a mean equal to that for the cycle. Rather, they acclimate to some value between the mean and maximum daily temperatures and consequently their growth rates reflect this "effective" temperature. Looked at another way, the optimal fluctuating regime had a mean of 59.9°F (15.5°C) with a range of 53-66.7°F (11.7-19.3°C), and the optimal constant test temperature of 63°F (17.2°C) fell approximately midway between the daily mean and the daily maximum of the optimal fluctuating test.

Most of the research on optimal growth temperatures is conducted at a constant temperature. Water quality standards, however, must apply to naturally fluctuating thermal environments. Because temperature directly affects the metabolism of fish, a fish kept continuously in warm water will experience more metabolic enhancement than one that experiences the same temperature for only 1 or 2 hours per day. Thus, constant test results cannot be reasonably applied directly to the daily maximum temperature in a fluctuating stream environment. Although the constant temperature test results could be used to represent daily mean temperatures, it is believed that the daily maximum temperature is more influential to the biology and should be the focus of any standards developed.

Clarke (1978) studied individual specific growth rates of underyearling sockeye salmon after 42 d at five constant temperatures ranging from 45.5 to 63.5°F (7.5-7.5°C) and two diel cycles of 44.6-55.4°F (7-13°C) and 41-59°F (5-15°C). At constant temperature, there was a linear increase in growth rate over the range 45.5-63.5°F (7.5-17.5°C). Both thermocycles had a mean of 50°F (10°C), but growth was greater on the 41-59°F (5-15°C) cycle. The author notes that the equivalent constant temperature for specific growth rate in length on the 44.6-55.4°F (7-13°C) cycle was increased significantly from 50°F (10°C) in one replicate (54.1°F [12.3°C]) but not in the other (51.4°F [10.8°C]). Specific growth rate in length on the 41-59°F (5-15°C) cycle was equivalent to that on a constant temperature of 59.5°F (15.3°C). Specific growth rate

in weight on the 44.6-55.4°F (7-13°C) cycle was equivalent to that on a constant 52.5°F (11.4°C); on the 41-59°F (5-15°C) cycle it was the equivalent of a constant 57°F (13.9°C). This study concludes that underyearling sockeye salmon exposed to diel thermocycles are able to acclimate their growth rates to a temperature above the mean of the cycle.

Dickerson et al. (1999 and unpublished data, as cited in Dunham 1999) conducted experiments with hatchery-reared Pyramid Lake strain Lahontan cutthroat trout. Fish were exposed to 1 wk fluctuating temperatures (68-78.8°F [20-26°C]; mean = 73.4°F [23°C]) and to constant temperatures of 55.4, 68, and 73.4°F (13, 20, and 23°C). Growth rates in the fluctuating temperature tests were lower than for fish exposed to constant temperatures of 55.4 and 68°F (13 and 20°C), but were similar to groups of fish held at a constant 73.4°F (23°C).

Hahn (1977) investigated the effects of fluctuating (46.4-66.2°F [8-19°C]) and constant (47.3, 56.3, 65.3°F [8.5, 13.5, 18.5°C]) temperatures on steelhead trout fry and yearlings. He found that as many fish remained in the fluctuating regime as in the constant 56.3°F (13.5°C) temperature water; twice as many remained in the fluctuating temperature regime as remained in the constant 65.3°F (18.5°C) temperatures; and twice as many fish remained in constant 47.3°F (8.5°C) water as in the fluctuating temperature regime. By inference, Hahn found the relationship among the three constant temperatures was the same as the relationship of each to the fluctuating temperature: twice as many fish in 56.3°F (13.5°C) as in 65.3°F (18.5°C), twice as many fish in 47.3°F (8.5°C) as in 56.3°F (13.5°C), and four times as many fish in 47.3°F (8.5°C) as in 65.3°F (18.5°C). We can conclude from Hahn's work that juveniles had equal preference for constant (56.3°F [13.5°C]) water and fluctuating (46.4-66.2°F [8-19°C]) water with a mean of 56.3°F (13.5°C). Although not a growth test, the Hahn study supports the general premise that daily mean temperatures are reasonable approximations of constant exposure test temperatures.

Grabowski (1973) conducted growth experiments with steelhead trout. Fish were fed a percentage of body weight according to feeding charts twice per day based on temperature and changes in body weight. To evaluate growth, fish were subjected to four test temperatures for 8 wk. These four regimes were a fluctuating test from 46.4 to 64.4°F (8-18°C) (mean 55.4°F [13°C]) and constant tests held at 46.4, 59, and 64.4°F (8, 15, and 18°C). Steelhead grew better at 59°F (15°C) than at other temperatures. Fish in the fluctuating test had the second highest growth rate and actual weight gain. Growth rate in the fluctuating test was only 13% less than that at the constant test of 59°F (15°C), while growth rates at 46.4 and 64.4°F (8 and 18°C) were 47% and 21% less, respectively. Plotting the data using the midpoint in the fluctuating test as a surrogate for a constant test condition creates near linear growth from 46.4 to 59°F (8-15°C), with a steep drop as temperature progresses to 64.4°F (18°C). Thus the mean of the fluctuating treatment appears generally comparable to a constant test temperature of the same value.

Thomas et al. (1986) investigated the effects of diel temperature cycles on coho salmon. Temperature cycles (50-55.4, 48.2-59, 46.4-62.6, and 43.7-68°F [10-13, 9-15, 8-17, and 6.5-20°C]) were used to simulate observed temperatures in clearcuts of southeastern Alaska. Different levels of feeding, including starvation, were used in each of the tests. Cyclic temperatures for 40 d, averaging 51.8°F (11°C) daily, did not influence growth of age-0 fish on any ration in comparison to the controls (kept at a constant 51.8°F [11°C]). Plasma cortisol and glucose concentrations were significantly greater in fish maintained for 20 d in the 43.7-68°F

(6.5-20°C) cycle, which may be an indicator of long-term stress. Thus, in the work by Thomas et al. (1986) the daily mean of the fluctuating test and the constant test exposures produced essentially equivalent results, but stress conditions were noted to occur in cycles with daily peak temperatures of 68°F (20°C).

Everson (1973) used the data of Averett (1969) to show that growth rates and gross efficiencies of food conversion of fish kept at moderate constant temperatures (59.9°F [15.5°C]) were somewhat greater than those of fish exposed to temperatures that fluctuated about a similar mean value (60°F [15.6°C]), whereas at higher average temperatures the fluctuation of temperature markedly benefited the growth and food conversion efficiency of the fish. Thus Everson showed support for the assumption that fluctuating temperatures can produce greater benefits to growth than can higher constant temperatures.

What is the range of laboratory growth rates under fluctuating temperature vs. constant temperature?

There appears to be considerable controversy regarding the effect of fluctuating temperatures vs. constant temperatures on juvenile growth rate. Peterson and Martin-Robichaud (1989) studied growth of Atlantic salmon under daily temperature cycles of 53.6-68°F (12-20°C) and 60.8-68°F (16-20°C) relative to constant temperatures of 60.8 and 68°F (16 and 20°C) and could find no differences.

Thomas et al. (1986) measured growth of juvenile coho for 40-d periods under constant 51.8°F (11°C) temperature vs. diel temperature cycles of 50, 55.4, 48.2, 59, 46.4, 62.6, and 43.7-68°F (10-13, 9-15, 8-17, and 6.5-20°C), all of which averaged 51.8°F (11°C). They found that the growth rates of 0+ age fish at any of the food rations were not significantly different among temperature regimes, although the growth at 4% and 8% ration (i.e., 8% of body weight/day) was better than at 1%.

Konstantinov et al. (1989) reported that under fluctuating thermal regimes coho salmon have a decreased respiration rate and increased growth rate relative to that at constant temperatures. This coupling of respiration and growth causes greater efficiency in use of assimilated energy in growth. Konstantinov and Zdanovich (1986 as cited by Behnke 1992) measured greater growth rates in several fish species under fluctuating vs. constant temperature regimes. Konstantinov et al. (1989), summarizing several of their studies on effect of fluctuating thermal regimes on fish, stated that growth rate under a fluctuating regime tends to be 10%-40% greater than at constant temperatures equal to the mean of the cycle.

Biette and Geen (1980) reported variable response of 0+ age sockeye to cyclic temperature regimes relative to constant temperatures depending on food ration. Under zooplankton rations equal to 4.0%-6.9% dry body weight/d and a fluctuating temperature similar to that experienced in the field in diel migrations, sockeye grew as well or more rapidly than under constant temperatures of 60.6, 59.5, 52.3, or 43.1°F (15.9, 15.3, 11.3, or 6.2°C). This ration was estimated to be comparable to that consumed under field conditions in Babine Lake. Rearing sockeye underwent diel vertical migrations between the hypolimnion, having temperatures of 41-48.2°F (5-9°C), and the epilimnion, with 53.6-64.4°F (12-18°C) water. During periods of

maximum lake temperature, sockeye inhabited the epilimnion for 2 h in early afternoon and 2 h in early evening. At higher food rations, growth at constant high or intermediate temperatures exceeded that under cyclic temperatures. At both high and low rations, food conversion efficiency and growth were greater in a constant temperature regime than under fluctuating conditions during daily vertical migrations in the field.

Wurtsbaugh and Davis (1977) studied growth of steelhead trout in laboratory streams under three fluctuating temperature regimes (natural cycle, natural +5.4°F [3°C], and natural +10.8°F [6°C]) in all four seasons and found that trout growth could be enhanced by temperature increases up to 29.7°F (16.5°C). During the summer season the control temperature (natural cycle) was 61.1°F (16.2°C) (mean) and the elevated temperatures averaged 67.1 and 72.5°F (19.5 and 22.5°C). The average diel temperature range for the summer growth period was about 6.1°F (3.4°C) under the three treatments. Growth rates under food consumption rates of 5%-15% dry body wt/d were higher under the control temperature regime than at the elevated fluctuating regimes. Under the high temperature regime (mean of 72.5°F [22.5°C]) growth rate was zero at a food consumption rate of 7%/d. Gross food conversion efficiency decreased as temperatures increased from 61.1 to 72.5°F (16.2-22.5°C). Maintenance rations increased by a factor of three over the temperature range 44.4-72.5°F (6.9-22.5°C). This study revealed that trout growth was improved by increasing temperatures up to a maximum of 61.7°F (16.5°C), but that this threshold applies to the field only under satiation feeding. Because researchers measured field growth rates in an Oregon coastal stream indicating food limitation, they concluded that temperatures less than 61.7°F (16.5°C) would be optimal for the trout. Food limitations in trout streams not uncommonly cause great reductions in summer growth (Cada et al. 1987).

Laboratory growth experiments were run on juvenile rainbow trout reared in Lake Ontario water (Dockray et al. 1996). Growth was measured for juveniles over a 90-d period in which "control" temperatures followed the ambient lake diel fluctuations and also varied in daily mean temperature from 55.4 to 75.2°F (13-24°C) over this summer period. A water treatment facility resulted in increasing control temperatures by 3.6°F (2°C) over background for each day of the growth study. Growth rate over this period was significantly less for the warmer regime, having mean daily temperatures of 59-78.8°F (15-26°C). A comparison of the day 0-30 initial growth period with the day 60-90 growth period is revealing. The initial period had daily control temperatures varying from 55.4 to 64.4°F (13-18°C); the final period had temperature variation from 66.2 to 75.2°F (19-24°C). The treatment temperature regime was equal to the daily control temperatures +3.6°F (2°C). In the first 30-d period, food conversion efficiencies were 42.4% and 45.6%, respectively, for the control and treatment fish. For the final 30-d period, conversion efficiencies were 27.3% and 6.2%, respectively. The warmer temperature regimes in the final 30-d period substantially reduced conversion efficiency from the initial period. This effect was very pronounced in the 69.8-78.8°F (21-26°C) regime for treatment fish in the final 30-d growth period. In addition, growth was just barely positive for the last 30-d growth period for fish in the 69.8-78.8°F (21-26°C) regime.

Troughs stocked at high density with rainbow trout were supplied with Columbia River water in tests of growth rate and disease susceptibility (Fujihara et al. 1971). Water in troughs was maintained at ambient conditions for July (63.8-71°F, mean 67.4°F [17.7-21.7°C, mean 19.7°C]), ambient–4°F (2.2°C), and ambient+4°F (2.2°C). Growth rate under the reduced

temperature was 44% greater than under the ambient condition, even though mortality rates associated with columnaris disease were comparable.

In another study on *O. mykiss* (steelhead parr from Dworshak National Fish Hatchery, Idaho), growth rate under a fluctuating temperature with feeding 2 times/d to satiation was contrasted with growth at constant temperatures of 46.4, 59, and 64.4°F (8, 15, and 18°C) for 2- and 8-wk periods. Best steelhead growth occurred at 59°F (15°C). By contrast, instantaneous growth rate under the fluctuating temperature was 11% less (Grabowski 1973). The thermocycle was sinusoidal, so a mean temperature of 55.4°F (13°C) can be inferred. Growth at constant temperatures of 46.4 and 64.4°F (8 and 18°C) was 36% and 29% less than at 59°F (15°C) (Grabowski 1973). These data allow one to hypothesize that the effective growth temperature for the 46.4-64.4°F (8-18°C) cycle was close to 59°F (15°C), but it is not possible to determine whether it was slightly above or below 59°F (15°C).

In summary, laboratory studies indicate that increasing food rations between 1% and 8% body weight/d results in an increased growth rate (Thomas et al. 1986, Elliott 1994). Growth rates have been found to be no different under fluctuating than under constant temperature equal to the mean of the cycle (Peterson and Martin-Robichaud 1989, Thomas et al. 1986). In contrast, growth rates under fluctuating regimes have been reported as greater than at constant temperatures equal to the mean of the cycle (Konstantinov et al. 1989, Konstantinov and Zdanovich 1986, Clarke 1978, Biette and Geen 1980). The study by Biette and Geen (1980) indicates that a fluctuating temperature regime might confer a growth advantage on juvenile sockeye under low, rather than high, food availability as typically found in lake environments. Enhanced growth under a fluctuating temperature regime might reflect an acclimation to a temperature higher than the mean of the cycle, similar to responses exhibited in tests of lethal temperatures in survival studies.

Other studies have reported that fluctuating temperature regimes are not all equal. For example, under three fluctuating regimes in which diel temperature varied approximately 6.1°F (3.4°C) in each, steelhead growth rate was greatest in the fluctuating regime with the lowest mean (61.7°F [16.5°C]) as opposed to those with means of 67.1 and 72.5°F (19.5 and 22.5°C) (Wurtsbaugh and Davis 1977). A very similar result was obtained with rainbow trout (Fujihara et al. 1971), in which the highest growth rate occurred at the lowest mean temperature (63.5°F [17.5°C]) in a fluctuating regime. In another study with steelhead, highest growth rate occurred at 59°F (15°C) under constant temperatures (Grabowski 1973). In this study a fluctuating regime (46.4-64.4°F [8-18°C]) with a mean of 55.4°F (13°C) had a growth rate less than that at 59°F (15°C). Studies that indicate a reduction of growth rate under fluctuating temperatures occurs when fluctuations extend above the zone of best constant temperature growth (approx. 55.4-60.8°F [13-16°C]) for salmonids under satiation feeding. Fluctuating temperatures appear to provide a growth benefit to salmonids when the mean of the cycle is lower than the constant temperature growth optimum. In this manner all the studies cited above are consistent with findings of Hokanson et al. (1977).

How is smoltification measured?

The rate of silvering during smoltification is related to temperature, presmolt size, migration timing, and photoperiod (McMahon and Hartman 1988). Silvering generally increases with increased temperatures (Hoar 1988). During the smolt transformation, body lipids decrease in quality and quantity and the smolt assumes a lower condition factor (weight per unit length) (Hoar 1988). Survival of smolts in the marine environment depends heavily on the degree of smoltification, which can be measured in terms of ability to regulate plasma sodium concentrations and grow in seawater (Mahnken and Waknitz 1979, Clarke and Shelbourn 1985).

What is physiological stress and at what temperatures does it occur in salmonids?

Many stressors can induce physiological stress in salmonids. These include temperature (high, low, or thermal shock), hyperosmotic stress (when juveniles enter the saline waters of the estuary or ocean), migration (physical exertion), crowding, and other factors. Stress can be detected via changes in the endocrine system. A promising indicator of smoltification is the sharp increase in thyroxine (T4) in blood plasma (Wedemeyer et al. 1980). Numerous other physiological tests are available to index the degree of stress on fish health (Wedemeyer 1980, Iwama et al. 1998, Beckman et al. 2000). Among these are measures of plasma glucose and cortisol as indices of acute or chronic stress (Wedemeyer 1980), changes in gill ATPase activity (Zaugg 1981), and heat shock protein production (Iwama et al. 1998).

Not all stress or associated endocrine changes are bad. Migration upstream in adults and downstream in juveniles or the smoltification process are stressful but essential aspects of salmon life history. These processes involve instantaneous to seasonal shifts in endocrine balance that reflect physiological processes over time. During smoltification there is a predictable pattern of gill ATPase activity throughout the downstream migration (Beckman et al. 2000). However, any physiological process can be disrupted. In terms of thermal influence, this can alter developmental rates (shift the timing of life history events), or impair or inhibit functions. Impairment caused by thermal stress can be increased when it is combined with other stressors (e.g., low dissolved oxygen). Habitat destruction and water pollution can act together, leading to a cumulative stress. The magnitude of the stress can be detected using endocrine (ATPase, cortisol), biochemical (e.g., lipid), morphological (e.g., body shape, condition factor, degree of silvering), or developmental (stage of egg development) indicators to detect deviation from normal range or rate of change.

Thermal stress is any temperature change that significantly alters biological functions of an organism and lowers probability of survival (Elliott 1981). Stress was categorized by Fry (1947 as cited by Elliott 1981) and Brett (1958) as *lethal* (leading to death within the resistance time), *limiting* (restricting essential metabolites or interfering with energy metabolism or respiration), *inhibiting* (interfering with normal functions such as reproduction, endocrine and ionic balance, and feeding functions), and *loading* (increased burden on metabolism that controls growth and activity). The latter three stresses can be lethal when continued over a long period (Elliott 1981).

Loading stress increases with temperature above the positive growth zone, but it also increases with reduction in food availability because this shrinks the growth zone. Thermal

stress can have a cumulative effect between the feeding limit (temperature at which feeding ceases, slightly beyond the chinook growth limit of 66.4°F [19.1°C]) and the UILT (Elliott 1981). Within this zone the combined effects of food limitation, low oxygen concentration, high turbidity, competition for space, and temperature can result in death (Elliott 1981, Wedemeyer and McLeay 1981). This is the so-called tolerance zone, identified by Elliott as the exposure/acclimation temperature bounded by the UILT for 7-d exposure. Reduced oxygen concentration and other factors can accentuate thermal stress (Wedemeyer and McLeay 1981) even within the growth zone and can lower the optimum growth temperature.

What are the seasons for passage of smolts of common anadromous species and how would this information be used?

The timing of smolt passage relative to the water temperature regime of migration habitat is vital to surviving the passage, feeding, avoiding predators, avoiding disease, and improving the level of smoltification during emigration. Some general dates of smolt passage past selected dams on the Columbia and Snake Rivers are given in Table 6 as a representation of the issues that need to be considered. For example, passage of any species or life history type can occupy an extensive time period. To allow full protection of the run, the total duration of the run must be known. However, there is considerable year-to-year variation in timing. In addition, the downstream passage of smolts and adults of the same stock may be different. That is, protection of a stock involves providing suitable water temperatures for all life stages.

What are heat shock proteins and what do they indicate?

Heat shock proteins (HSPs) are expressed in response to biotic and abiotic stressors (e.g., heat or cold shock, anoxia, diseases, chemical contaminants including heavy metals). These unique proteins are produced in cells and tissues of many organisms, including fish (Dietz 1994, Iwama et al. 1998) under environmental stress. They have many biochemical roles, including proper folding of cellular proteins and restoring thermally denatured proteins to their native state. Temperatures at which HSPs are induced can be mediated by acclimation temperature (Dietz 1994). Although HSPs can be related to thermal tolerance, their presence also indicates environmental stress. Although they help repair cellular protein damage caused by stressors such as high temperature, they are a useful indicator of thermal stress that requires tissue repair (Currie and Tufts 1997) and leads to irreparable cell damage.

What temperature range is recommended for reducing physiological stress?

The *optimum* temperature range provides for feeding activity, normal physiological response, and normal behavior (i.e., without thermal stress symptoms) and is slightly wider than the growth range. Deviation from this range implies greater stress, leading to greater impairment in physiological functions and greater mortality. Stresses of migration and acclimation to saltwater activate many low-grade infections by freshwater disease organisms (Wedemeyer et al. 1980) and the mortalities produced by these diseases go largely unnoticed. Optimum temperatures likewise minimize physiological stress. Growth temperatures that are optimum or lower tend to be minimally subject to warm-water diseases.

Table 6. Historical dates of smolt migration past selected dams on the Columbia and Snake Rivers. Data from Fish Passage Center (1993)

Monitoring Sites (dams)	Species	Historical Passage Dates[1]		
		10%	50%	90%
Lower Granite	Chinook 1's	4/17	4/27	5/24
	Chinook 0's	na	na	na
	Steelhead	4/28	5/12	6/01
	Sockeye	na	na	na
Rock Island	Chinook 1's	4/22	5/07	5/22
	Chinook 0's	6/06	7/04	8/02
	Steelhead	5/06	5/15	5/31
	Coho	5/13	5/21	5/29
	Sockeye	4/19	5/02	5/26
McNary	Chinook 1's	4/23	5/10	5/23
	Chinook 0's	6/15	7/03	7/20
	Steelhead	4/29	5/18	6/02
	Coho	5/16	5/21	5/31
	Sockeye	5/01	5/16	6/03
John Day	Chinook 1's	4/28	5/15	5/30
	Chinook 0's	6/08	7/21	9/01
	Steelhead	4/26	5/15	5/31
	Coho	5/06	5/13	5/31
	Sockeye	5/10	5/22	6/04
Bonneville	Chinook 1's	4/19	5/02	5/21
	Chinook 0's	na	na	na
	Brights[2]	6/07	6/27	7/29
	Steelhead	4/26	5/14	5/31
	Coho	4/27	5/10	6/01
	Sockeye	5/11	5/23	6/04

[1] Historical percentiles are based on passage data for 7 years (1984-90) at Lower Granite and McNary dams; 6 years (1985-90) at Rock Island Dam; 4 years (1986-89) at John Day Dam; and 4 years (1987-90) at Bonneville Dam for spring migrants and 3 years (1988-90) for summer migrants.

[2] "Brights" at Bonneville Dam refers to subyearling chinook arriving after June 1; this excludes most "tule" fall chinook originating from Spring Creek hatchery.

Why might it be advisable to use naturally reared vs. hatchery-reared salmonids to measure physiological status?

Significant differences between conditions in the field and in the hatchery can lead to different physiological responses in these environments. For example, these environments may have different seasonal temperature profiles, photoperiod, nutrition, and social interactions, which could produce variations in developmental timing, growth rate, size at age, and body composition (Beckman et al. 2000). Consequently, the physiological status of hatchery-reared fish may not relect that of naturally reared fish.

Differences in physiological indicators between hatchery and wild salmonids were reported for Columbia River chinook (Congleton et al. 2000). Cortisol concentrations were higher in wild than hatchery chinook in early, mid-, and late season. In this study, cortisol was used as an indicator of stress in barge transportation. However, for both wild and hatchery fish, cortisol declined during the barging in early and late season, but not mid-season. This effect was produced by social interaction with the high densities of steelhead that were loaded on barges in mid-season, causing stress in chinook. In addition, ATPase activity was significantly lower in migrating hatchery steelhead and chinook in the Columbia River than in the wild fish of these species. These differences were greatest in late April to early May. Hatchery rearing can result in suppression of gill ATPase activity for at least 7 wk after release (Congleton et al. 2000).

How does physiological status of smolting salmon change seasonally?

Few studies on smolting salmonids monitor a broad range of physiological indicators, much less study salmon in the wild throughout the year. Beckman et al. (2000) reported endocrine and physiological status of naturally reared spring chinook juveniles in the Yakima River, Washington. Status was measured in terms of condition factor, weight, stomach fullness, body appearance, liver glycogen, body lipid, gill Na+-K+ ATPase, plasma thyroxine (T4), and plasma insulin-like growth factor-I (IGF-I). The smolting period (April-May) was characterized by an increase in ATPase activity, plasma T4, and IGF-I. At the same time there was a decrease in condition factor, body lipid, and liver glycogen. Body lipid reached a high in late summer (5%-8%) and a low during winter of 2%-3.5%, and then increased to 4% by March. Body lipid again declined during April-May, when smolting occurred. Condition followed the same pattern as whole-body lipid content. Body weight of juveniles increased dramatically from February to May. A similar decline in body lipid content was reported for chinook and steelhead from the American River, California (Castleberry et al. 1991). High lipid content in juveniles is associated with high adult return rates. For example, fall chinook smolts with 7.9% whole body lipid had an adult return rate nearly 1.9 times greater than those having only 4.1% (Burrows 1969 as cited by Castleberry et al. 1991).

In springtime, plasma T4, IGF-I, and gill ATPase increased as fish migrated downstream in the Yakima River (Beckman et al. 2000). These indicators of smoltification have been reported in other studies. Other reported changes include increased growth rate, increases in plasma growth hormone (GH), and metabolic rates (Hoar 1988, as reported by Beckman et al. 2000). During smoltification there are two distinct phases—first anabolic, then catabolic. The anabolic phase in Yakima River spring chinook occurs from January through March and is characterized by an increase in condition factor, IGF-I, weight, and lipid. The catabolic phase which follows from April through May is characterized by an increase in condition factor and IGF-I, but a decline in weight and lipid content. A high plasma GH causes depletion of glycogen and lipid.

How does photoperiod influence growth rate and subsequent saltwater readiness of smolts?

Juveniles migrating downstream from freshwater to saltwater exhibit saltwater readiness in their ability to regulate plasma sodium concentrations. If high water temperatures impair smoltification processes, including the ability to regulate plasma sodium, survival in saltwater

would be reduced. The ability of a juvenile to regulate plasma sodium depends on its growth rate and consequent size. Growth rate is a function of temperature and food availability. A study of spring chinook growth rate under satiation feeding found that photoperiod experience at first feeding (i.e., after emergence) helps to set the potential growth rate. Juveniles exposed to a short-day photoperiod from February to mid-April followed by a long-day photoperiod had a significantly greater growth rate and final body weight by midsummer than juveniles that experienced only a long-day photoperiod (Clarke et al. 1992). A long-day photoperiod after emergence is apparently a developmental cue that produces a slower growth rate than in fish exposed to a short- then long-day photoperiod at the same temperature. This cue causes juveniles to overwinter at least 1 year before emigration. In saltwater challenge tests, the ability of juveniles to regulate plasma sodium by midsummer depended on their experiencing the natural sequence of photoperiods. It is questionable whether juveniles that experienced a long-day photoperiod at emergence would actually attempt to emigrate in the first summer. Growth rate and body size are vital in determining tendency to emigrate and subsequent survival (Bilton et al. 1982). The study by Clarke et al. (1992) does highlight the need to consider photoperiod history from emergence through rearing as well as food availability and temperature in comparisons of growth rates between stocks.

Salmon parr feed throughout the summer in streams, gaining weight, length, and lipid content (see Beckman et al. 2000). As autumn approaches, Atlantic salmon parr may become segregated into two size groups, indicating their ability to smolt the following spring (upper modal group) or the need to spend another year growing in freshwater (lower modal group) (Metcalfe and Thorpe 1992). Overwintering salmon undergo a period of anorexia (loss of body fat) coinciding with a loss of appetite and cessation of growth, even when food is present. The onset of anorexia is controlled by photoperiod (Thorpe 1986, as cited by Metcalfe and Thorpe 1992). However, the loss in body fat is controlled by variable "defended" energy levels. That is, fish that will smolt in the spring maintain a higher appetite and feeding rate. This balances energy costs of maintaining a feeding station and capturing food against the gain in growth rate and ability to smolt early, thereby avoiding mortality in a second overwintering period.

Are smolts affected by high temperatures during migration?

Migration during the smolt phase can be lethal. For example, in the lower Sacramento River, a 50% mortality was estimated over a 48-km migration distance, based on smolt releases during the May-June period, 1983-1990. These mortalities were associated with temperatures of 73.4 ± 1.9°F (23 ± 1.1°C) (Baker et al. 1995).

In addition to thermally induced mortality during migration, smolting juveniles can be indirectly affected by high temperatures. For example, subyearling chinook rearing in nearshore areas of the Columbia River can be forced into the main current to avoid increasing temperatures along river margins. This becomes significant above 62.6°F (17°C) (Connor et al. 1999). Reduced food in marginal areas of the river coupled with high water temperatures reduces the capability of the river to rear fish to proper smolt condition (Coutant 1999).

Gill ATPase is a useful indicator of smoltification. In the Columbia River, high levels of gill ATPase activity are frequently associated with longest travel time downstream through the

dams. However, subyearling fall chinook have occasionally exhibited slowest travel times with highest ATPase levels (Tiffan et al. 2000). Rapid juvenile growth in premigrants typically accompanies increasing ATPase levels, leading to increased ability to osmoregulate in seawater. Migration in an impounded river may alter the relationship between ATPase and time of ocean entry. Tiffan et al. (2000) determined that ATPase activity increased for Hanford Reach fall chinook from Hanford Reach to McNary Dam and decreased afterward. Even though saltwater mortality declined over this migration path, the decline in ATPase activity in 1994 appeared to be greater than in 1995. The greater 1994 loss may account for that year's higher mortality rate in saltwater challenges. Chinook smolts often migrate during reduced streamflows and elevated water temperatures. Mainstem dams cause significant delays in migration rates, and smolts in reservoir forebays undergo prolonged exposure to surface temperatures as high as 77°F (25°C) or more (Venditti et al. 2000). Such high temperatures limit fall chinook production by impairing the ability of juveniles to grow, smolt, and maintain appropriate migration timing. Late emigration results in the lowest survival rates (Connor et al. 1999).

Are smolts subject to cumulative stresses from thermal exposure?

Temperatures of 64.9-70°F (18.3-21.1°C) place smolts under either lethal or loading stresses that can impair metabolic activity (Brett 1958). For example, in subyearling fall chinook in the Columbia River, temperatures of 64.4-68°F (18-20°C) inhibit feeding. Heat shock proteins are produced after exposure to 68°F (20°C) for several hours (Sauter and Maule 1997).

What temperatures are required to inhibit smoltification in steelhead and salmon?

Smolt transformation in steelhead rearing in water >52.3°F (11.3°C) was inhibited (Adams et al. 1973); rearing temperatures >55.4°F (13°C) prevent increases in ATPase activity (Hoar 1988). This effect is stronger in steelhead than in coho, chinook, or Atlantic salmon (Adams et al. 1973, Adams et al. 1975 as cited by Johnston and Saunders 1981). Temperatures >56.5°F (13.6°C) do not permit smoltification in summer steelhead (Zaugg et al. 1972, as cited by Zaugg and Wagner 1973). In winter steelhead, a temperature of 54.1°F (12.3°C) is nearly the upper limit for smolting (Zaugg and Wagner 1973). Zaugg (1981) found that a temperature of 53.6°F (12°C) could inhibit successful migration to the ocean in winter steelhead. Because ocean entry in the Columbia River normally occurs in mid and late May and river temperatures typically reach 53.6°F (12°C) by mid-May, failure of steelhead smolts to enter the ocean may be attributed to low water flow and associated high water temperatures (Zaugg 1981). Dawley et al. (1979 as cited by Zaugg 1981) observed that peak steelhead migration to the ocean, as determined by capture at Jones Beach, coincided with river temperatures above 53.6°F (12°C).

In the American River, California juvenile steelhead (young-of-the-year) were captured during their downstream migration for measurement of Na+ -K+ ATPase (Castleberry et al. 1991). The authors reported that ATPase activity increased from capture temperatures of 60.8°F (16°C) to 68°F (20°C), and that increased river temperatures did not suppress smoltification, but may have enhanced it. However, they also noted that ATPase activity was uniform for fish of standard lengths from 60 to 100 mm. The authors interpreted this evidence to mean that steelhead did not develop into smolts at sizes below 100 mm SL. Furthermore, they did not sample steelhead longer than 100 mm but indicated they were not common. In the American

River, steelhead emerged from early April through early May and were abundant in the middle-lower river site from early May to early June. At this period, temperatures cycled daily from 61.7 to 66.2°F (16.5-19°C). In addition, capture temperatures up to mid-May were often as much as 3.6°F (2°C) greater than the average temperature for the 2-wk period prior to capture, meaning that the correlation of ATPase with temperature may not be as meaningful as believed. This study did not deal with yearling steelhead and did not describe successful smolt migration. Steelhead usually do not migrate to sea until reaching age 1 to 3 years (Moyle 1976, as cited by Castleberry et al. 1991), so it is not clear what relevance ATPase activity in age-0 juveniles has to smolt saltwater readiness, but it does indicate temperature ranges that juveniles experience in their pre-smolt migrations. These data do not appear to challenge the large body of literature detailing the sensitivity of steelhead smolts to migration temperatures >53.6-55.4°F (12-13°C).

Some smoltification processes are greatly retarded by water temperatures >55.4°F (13°C), and in some Pacific salmonids smolt stage cannot be attained at 60.8°F (16°C) (see references cited by Johnston and Saunders 1981). An apparent exception is that temperatures as high as 59°F (15°C) have been used to increase growth rate and onset of smolting in coho. However, desmoltification is also high at this temperature. Laboratory tests clearly showed that a high constant temperature regime of 68°F (20°C) during coho emigration caused a very restricted peak in gill ATPase activity compared with a normal 50°F (10°C) temperature regime. Under the elevated temperature regime, ATPase activity plummeted prior to ocean entry (Zaugg and McLain 1976). Fall chinook undergo an even greater desmoltification rate at temperatures of 59°F (15°C) (Wedemeyer et al. 1980). In work on Central Valley chinook stocks from California, Marine (1997) found that normal smolt development patterns can be altered or inhibited with prolonged rearing in a temperature range of 62.6-75.2°F (17-24°C) compared with rearing in a range of 55.4-60.8°F (13-16°C). Evidence for the effects of temperatures exceeding 62.6°F (17°C) came from changes in gill ATPase activity, reduced survival in acute seawater exposure, and a reduced hypo-osmoregulatory capability. In addition, juvenile chinook exposed for 2.5 months to 62.6-75.2°F (17-24°C) incurred increased loss to predation compared with juveniles exposed in the range 55.4-60.8°F (13-16°C), although the causal mechanism was not identified. Sockeye terminate their downstream migration if water temperature exceeds 53.6-57.2°F (12-14°C) (Brett et al. 1958), although coho can withstand some further increases. The influence on the smoltification process, though, may be common to both species.

What temperatures are required to reverse smoltification in steelhead?

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

Can incubation temperature affect smolt emigration timing?

Temperature regime can influence time of smolt emigration. Research on Carnation Creek, British Columbia, revealed that most variation in chum and coho emigration dates was attributed to mean stream temperatures between peak spawning and emergence (Holtby et al. 1989). Shifts in this portion of the annual temperature regime were linked to land-use practices (Hartman et al. 1984). Alteration in the emigration date in turn can affect survival in the marine environment (Thedinga and Koski 1984, Holtby et al. 1989). From laboratory studies, it would appear that an accelerated temperature regime during springtime would result in either earlier emigration (caused by more rapid development to the smolt stage) or less success in smoltification (caused by high temperature desmoltification or inhibitory effects) (see Zaugg and Wagner 1973).

What river temperatures are associated with peaks in migration?

Most steelhead emigration occurs before river temperatures rise above 53.6°F (12°C). Emigration can extend into temperatures as high as 61.7°F (16.5°C). The 53.6°F (12°C) limiting temperature normally does not occur until mid-May, but in low-flow years can occur in late April; this shift in thermal regime may cause a reduction in steelhead survival (Zaugg 1981). The South Umpqua River, a southern Oregon coastal river subject to thermal extremes, has a wild spring chinook run. This stock begins emigration when stream temperatures exceed 50°F (10°C). Approximately 50% of the emigration takes place at 54.5-59°F (12.5-15°C) and the upper tail of the run is generally complete before 68°F (20°C) is exceeded. Large fish that are presumably most ready to enter the ocean delay entry until temperatures warm beyond 50°F (10°C) (Roper and Scarnecchia 1999). In spring chinook from the American River, California, juvenile levels of gill Na+-K+ ATPase increased with increasing standard length between 30 and 80 mm and capture temperature from 53.6 to 64.4°F (12-18°C) (Castleberry et al. 1991). However, juveniles were no longer found in the lower river in early May. Maximum daily temperatures ranged from 64.4 to 69.8°F (18-21°C) and minimum daily temperatures were as low as 59°F (15°C). Juveniles were found in the middle upper site in late June when diel temperatures fluctuated regularly between approximately 59 and 64.4°F (15 and 18°C). These chinook typically enter the ocean 2-4 months after emergence at a size of 40-80 mm (sizes of juveniles captured at monitoring sites). These data indicate that temperatures as high as 64.4°F (18°C) do not prevent ATPase levels from increasing, but temperatures beyond this appear to eliminate juveniles from affected river reaches.

How do freshwater and ocean temperatures affect time of ocean entry?

The relation of the temperature of the lower reach of a river entering the ocean and the temperature of the ocean itself is important in determining growth rates in the early ocean phase and survival. Two of the most important factors regulating seawater adaptability, such as ability to regulate plasma sodium, are freshwater rearing temperature and time of transfer to seawater. The relative growth rate of fall chinook in seawater was greatest after rearing in freshwater in temperatures of 46.4-57.2°F (8-14°C), followed by transfer to 55.4-58.1°F (13-14.5°C) in early May to early June. Freshwater rearing at 60.8°F (16°C) resulted in growth rates that were 70% of those at 50°F (10°C) (i.e., a temperature within the preferred range).

Smolts must be able to regulate plasma sodium, maintain their silver color (indicative of their degree of smoltification), and maintain a high growth rate. The temperatures present in the freshwater environment and ocean during the smolt's emigration and ocean entry, as well as its timing of ocean entry, are critical in determining initial growth rates. Freshwater temperatures must be low enough during emigration so that complete smoltification can take place prior to ocean entry. If all these conditions are met (and also the size of migrants leaving the natal tributaries is optimum), a smolt will likely be able to maintain critical size before ocean entry. Otherwise, desmoltification can take place, smolts fail to maintain a critical size, and they become parr-revertants (Mahnken and Waknitz 1979, Folmar et al. 1982). By losing their smolt status, juveniles fail to enter the ocean, die, or attempt to rear in the lower river to await smoltification in a subsequent year, which is unlikely.

Hatchery releases should be timed to avoid extreme temperatures during smoltification to ensure maximum passage survival. Releases should coincide with historic migration times, however (Wedemeyer et al. 1980). If historic migration timing now coincides with adverse temperatures, naturally produced salmon and steelhead are likely to be affected. Altered (e.g., earlier) times of release of hatchery fish to avoid human-caused thermal stress may result in inappropriate ocean entry timing and lower overall survival.

What is the role of temperature in migratory response and seawater adaptation?

A maximum temperature of approximately 53.6°F (12°C) is recommended for chinook and coho to maintain migratory response and seawater adaptation in juveniles (Wedemeyer et al. 1980, CDWR 1988, p. 4).

Wedemeyer et al. (1980) recommended that winter and spring hatchery water temperatures below 53.6°F (12°C) would protect the smoltification process for chinook, coho, and steelhead. Their recommendations apply to proper physiological development during the smoltification process, timing of saltwater entry, and high marine survival.

How can multiple stresses during the smolting phase be reduced?

Infection of fish with freshwater diseases should be minimized because the stresses of migration and acclimation to saltwater can increase mortality from disease (Wedemeyer et al. 1980). Warm-water diseases can be transmitted through hatchery practices, by contagion in migration through dam passageways, and in barging.

Human-caused increases in estuary temperature must be restricted. In addition, numerous chemical contaminants, such as herbicides, that can become concentrated in the estuary have been shown to inhibit smolt function and migratory behavior (Wedemeyer et al. 1980). The smoltification process is physiologically stressful to fish. Additional stresses associated with elevated temperature or other pollutants should be avoided. (See Multiple Effects issue paper for a detailed discussion of these effects.)

How is swimming speed measured?

Sustained swimming performance is a swimming speed that can be maintained for long periods (>200 min) without fatigue. This activity is totally aerobic, so no oxygen debt builds up. Sustained swimming during migration tends to occur at 15%-20% of maximum swimming speed (Bell 1991). Some tests have documented swimming for periods of 2 wk without fatigue for a variety of species. Prolonged swimming speeds define a performance of shorter duration (20 s-200 min) that involves both aerobic and anaerobic metabolism. Exhaustion of glycogen stores can result in fatigue. Within the range of speeds that define prolonged swimming at a particular temperature, the faster the speed, the more anaerobic metabolism is responsible. Critical swimming speed is a special case of prolonged swimming. It may be measured in fish swimming at a particular temperature (either a temperature to which they are fully acclimated or as an acute performance at a test temperature) or by increasing swimming velocity in increments (such as 10 cm/s) to determine the maximum speed at which swimming can be maintained for a fixed period (e.g., 60 min). If a fish can swim 60 min continuously at 50 cm/s but only a fraction of that time at 60 cm/s, the critical speed is interpolated. A median performance for a test group of fish is taken as the critical swimming speed. Comparisons among sizes within a species can be made in terms of body length/s rather than cm/s. Burst swimming is the maximum swimming rate that can be achieved for periods up to 20 s and is largely independent of temperature. This is essential for prey capture, predator avoidance, and rapid migration through swift water. During burst swimming, fish consume some oxygen but are powered mostly by anaerobic metabolism. Burst swimming can reach approximately 22 ft/s in chinook, coho, and sockeye and up to 27 ft/s in steelhead (Bell 1991).

It is interesting to compare swim speeds determined from laboratory studies with those from field studies. Hinch and Rand (1998) used electromyogram radiotelemetry on Fraser River sockeye to measure tail beat frequency (TBF). TBF was then converted to swim speeds using laboratory regressions of TBF against swim speed. Swim speeds varied by reach within study sections in accordance with constrictions, channel form, and probably associated flow patterns. In a 7.6-km study section in the lower Fraser River, including the Fraser River canyon, average swim speeds varied from approximately 75 to 125 cm/s in the 10 consecutive study reaches. In this river section, water temperatures ranged from 60.8 to 66.2°F (16-19°C) during tracking. Speeds varied by river reach depending on constrictions and channel bank form. Male sockeye swam at mean speeds of 118 cm/s and females at 90 cm/s. In another study year, male average swim speed was only about half as fast (i.e., 62 cm/s). Near the spawning grounds approximately 900 km further upstream, water temperatures ranged from 68 to 71.6°F (20-22°C) and average swim speeds declined to 50-60 cm/s (Hinch and Rand 1998). This decline in swim speed may be associated with the warm river temperatures. Other explanations might be that those individuals that migrate at very high swim speeds when encountering complex flow patterns (see Hinch and Bratty 2000) were already eliminated from the population by exhaustion, or the population in general might have suffered energy depletion that impaired swimming capacity.

Combinations of swimming speeds and time periods exceeding critical time limits may build up lactic acid in tissues and require resting periods of up to 3 hours before further swimming can occur (Paulik et al. 1957). Rate of recovery from anaerobic metabolism is a

function of water temperature and oxygen concentration.

At what swimming speeds do metabolic transitions occur?

Data from Bainbridge (1960, 1962) for rainbow trout and Brett (1964) for sockeye, as summarized in a single figure by Beamish (1978), illustrate the sharp differentiation among sustained, prolonged, and burst swimming performances at a fixed temperature. As swimming speed is reduced in the prolonged swimming zone (i.e., performance time of 20 s-200 min), swimming can eventually be performed without fatigue; this point denotes the transition to sustained swimming (i.e., the temperature-swimming time period combination that allows continuous swimming for long periods). At higher swimming speeds in the prolonged swimming zone, a transition occurs in the plot of log (time to fatigue) versus velocity that denotes a transition from prolonged to burst swimming (Beamish 1978). This transition (i.e., of the critical swimming speed) occurs at approximately 3 and 5 body lengths/s in rainbow and sockeye, respectively. At these velocities, fatigue occurs in approximately 20 s. Burst swimming speed increases only as time to fatigue decreases. Because of evidence such as this for many fish species, 20 s is generally taken as the period producing this metabolic transition.

Critical swimming speed is a physiological performance measure that can indicate the ability of a fish to function in a natural flowing-water environment. It indicates ability to capture prey and avoid predators (Castleberry et al. 1991). Sharp reductions in critical swimming speed at high temperatures indicate environmental risk for a given life stage and fish size (see Griffiths and Alderdice 1972, Brett and Glass 1973).

Why is swimming speed vital to adults during migration?

During adult migration, swimming speed is important in maintaining progress toward holding or spawning areas upstream. At falls, rapids, or fish ladders, adult migratory fish must often be able to swim in the sustained speed range, and for challenges at significant falls or under high water velocities, instantaneous burst swimming must be available. The swimming velocity needed to leap a falls depends on the height of the falls; the higher the falls, the greater the speed that must be attained when thrusting through the water surface.

Water temperature and oxygen concentrations are significant controls on swimming speed. However, progress upstream also depends on other factors, such as water velocities along the migratory path and barriers to migration (e.g., falls, debris jams, or dams). In moderate water velocities, as found in reservoirs, migration rates of chinook can match or exceed those in free-flowing reaches (Bjornn 1998c, as cited by NMFS 1999). Very high flows can impede migration. Under normal river flow rates the tradeoffs between difficult passage at dams and easier swimming in reservoirs make it difficult to estimate the net effect (NPPC 1999). It is possible that to the degree that adults would be stressed by repeated dam passage enroute to spawning grounds. Maintenance of migratory ability remains dependent on proper flow direction and olfactory cues and cool temperatures (NPPC 1999). If water temperature is high and/or oxygen concentrations are low, swimming speed and migration rates can be impaired; fish may refuse to migrate, migrate back downstream, or seek shelter in tributaries or other cold-water refuges if such are available (NMFS 1999, draft white paper). Under these conditions, net upstream movement may be reduced or extremely delayed. Holding in warmed pools can result in spread of warm-water diseases.

Swimming speeds can be substantially impaired at temperatures above the swimming optimum. Fraser River sockeye have an optimum temperature of 62.6°F (17°C) for swimming endurance, but this is reduced 20% at 69.8°F (21°C) (Macdonald et al. in press). This takes on ecological significance given the varying temperatures in the river. At Hell's Gate on the Fraser River, temperatures were >64.4°F (18°C) for a 60-d period during summer; upstream temperatures reached a maximum of >71.6°F (22°C). Zones of elevated temperature create stressful conditions that impair swimming capability in demanding passage conditions (Macdonald et al. in press). The tendency for some sockeye migrants at Hell's Gate to become hyperactive and exhibit a "burst-then-sustained speed" pattern under high flows at passage constrictions would make them even more susceptible to combined effects of high temperature and hypoxia if these conditions coincided with high flows (Hinch and Bratty 2000).

Why is swimming speed vital to smolts during migration?

Smolts migrating downstream have different problems with current velocities than do adults. For adults, high current velocity can impede upstream migration, but with moderate temperatures and oxygen concentrations, their upstream movement tends to be easier because they can seek conditions in which sustained or prolonged swimming speed exceeds current velocity, thus allowing net upstream travel. Smolts, on the other hand, benefit from rapid current flow because their downstream progress depends on water velocity rather than swimming speed. Downstream migrants, such as subyearling fall chinook, are capable of controlling their downstream rate of travel by swimming toward shore, where they feed in shallows. If marginal areas are too warm and if the warm water, fine sediment substrate conditions, and slow water do not produce abundant macroinvertebrates that can serve as prey (see Coutant 1999), growth rates and survival may be low.

With downstream smolt migration, swimming speeds must not be impaired because swimming is vital to controlling rate of descent and avoiding obstacles. Temperature must not be so high that swimming is inhibited. In addition, for juveniles (including smolts), nonimpairment of swimming capability is important because of the increased vulnerability to predation that accompanies the effect of high water temperature on swimming performance (Bams 1967, Schreck 1990, Kruzynski and Birtwell 1994, all as cited by Marine 1997). However, some reduction in swimming capacity is expected during smoltification (Smith 1982, as cited by Castleberry et al. 1991), resulting in reduced ability to maintain position in current and the tendency to be swept downstream more rapidly.

How does temperature affect juvenile swimming speed?

Brett (1958) provided a useful graph of the relationship between cruising speed (ft/s) and acclimation temperature for underyearling sockeye and coho. Sockeye acclimated to 59°F (15°C) achieved their maximum cruising speed (approx. 1.12 ft/s). Coho acclimated to 68°F (20°C) attained their maximum cruising speed (approx. 1.02 ft/s). Sockeye swimming speed was reduced to approximately 58% of maximum as water temperature was increased to upper incipient lethal levels. Coho swimming speeds were reduced to approximately 91% of maximum at these temperatures. This information reveals a decline in performance when acclimation temperature increases above optimal levels. The percentage decline in swimming performance

appeared to be greater in sockeye than in coho. However, upper incipient lethal levels would not permit indefinite swimming because lethal effects would emerge. In addition, sublethal effects such as energy depletion and exhaustion would likely occur. Although swimming performances of adults would be expected to follow a similar pattern (i.e., optimum at an intermediate temperature with decline at higher and lower temperatures), adults are much more sensitive to thermal stress than are juveniles (Becker 1973).

How do temperature and oxygen jointly affect juvenile swimming speed?

Davis et al. (1963) found that as oxygen concentrations declined below 9.0 mg/L, maximum swimming speed of coho was reduced. Swimming performance increased from 59°F to 68°F (10-20°C), as noted in the previously cited studies by Brett (1958). Dahlberg et al. (1968) studied coho final swimming speed at 68°F (20°C) under various oxygen concentrations and found a dramatic reduction in swimming speed below a dissolved concentration of 7-8 mg/L. With a DO of 5 mg/L (53% saturation) swimming speed was reduced 10% below maximum. Further reductions in DO caused a precipitous reduction in final speed (See Temperature Interactions issue paper for additional detail on effects.)

How are physiological optimum, growth optimum, preferred temperature, swimming maximum, and metabolic scope derived?

The physiological optimum is derived by averaging the growth optimum and preferred temperature (Brett 1971). Preferred temperature also is correlated with the temperature providing the maximum metabolic scope. This, in turn, is related to the temperature providing the maximum critical swimming speed (Kelsch and Neill 1990). Swimming speed is highest at the preferred temperature (Kelsh 1996).

How can allocation of energy to metabolism and swimming be used to interpret fitness and resistance to disease?

The standard metabolic rate (SMR) is calculated in terms of oxygen consumption extrapolated to zero activity and indicates the resting metabolic rate of unfed fish (Priede 1985). The scope for activity defines the performance capacity of the organism. The rate of oxygen consumption at the maximum aerobic swimming rate defines the active metabolic rate (Priede 1985, Evans 1990), which is that found for a fasted fish swimming at critical speed (Beamish 1978, Kelsh and Neill 1990). The specific dynamic action (SDA) is the metabolic rate attributable to digestion of a meal. In fish, feeding and peak digestion tend to be cyclic and are correlated with water temperature and photoperiod. In addition, power (i.e., the short-term allocation of metabolic resources, see Priede 1985) devoted to SDA is related to the size and quality (e.g., protein content) of the meal consumed. Therefore, the power demand for SDA varies and consumes variable portions of the available energy defined by the scope for activity. In ecological terms, the greater the available power at any given temperature in excess of the basic demands of SMR and SDA, the greater the fitness (Evans 1990). Fish operating under a temperature that allows only a small power output in excess of SMR and SDA needs have little ability to deal with additional power demands caused by disease, the need to apply burst swimming to escape predators or swim against currents, and so on. The seriousness of this

situation is reflected in the danger of feeding cultured fish at high temperatures, despite the fact that more energy is required. With the heightened power demand for SDA at high temperatures, any unnecessary stress can lead to metabolic power overload and mortality (Priede 1985).

In addition to the correlation between the maximum scope for activity and preferred temperatures, median survival has other ecological importance. Survival of an individual fish is probably maximized by temperatures in the mid-range of its scope for activity. The temperature range that maximizes scope for activity tends to be correlated with the center of distribution of the species and maximum production. The ability of the organism to adapt to its thermal environment is related to its ability to maximize available power (Evans 1990).

How do temperature, light intensity, and photoperiod influence swimming speed?

A plot of prolonged swimming performances for a variety of species relative to temperature, as summarized by Beamish (1978), indicates that sockeye attain maximum speed at 59°F (15°C), whereas coho and lake trout reach maximum prolonged swimming speeds at approximately 62.6-64.4°F (17-18°C).

Diel changes in swimming speed by factors of approximately 2-3 have been observed in sockeye in coastal waters (Madison et al. 1972) and chinook in the Columbia River (Johnson 1960); speeds were lower at night than during the day. Quinn (1988 as cited by Quinn et al. 1997) also reported that sockeye swimming speeds were lower in coastal waters at night. Light intensity or photoperiod apparently provides a behavioral regulation of swimming speed. However, Hatch et al. (1993), using video time-lapse recording, detected significant adult sockeye movement past Zosel Dam on the Okanogan River between 2000 and 0600 h. In fact, most passage occurred during nighttime. Such was not the case at Tumwater Dam on the Wenatchee River, where daytime passage was predominant. Sockeye on the Okanogan can apparently take advantage of nighttime passage. Provided that nighttime water temperature is lower than daytime temperature, sockeye might escape significant thermal stress. High net migration rates (up to 3.4 km/h) were observed in these sockeye populations (Quinn et al. 1997), which could either decrease exposure time to thermal stress or produce dangerous levels of fatigue under warm river conditions.

How do fish size and acclimation temperature affect swimming?

Small-size sockeye held a swimming advantage relative to larger size sockeye over the length range 8-60 cm (Brett and Glass 1973). That is, critical swimming speed (60-min sustained speed) was 6.7 body lengths/s at the smallest size and decreased to 2.1 body lengths/s at the maximum size when measured at 68°F (20°C).

Swimming performance also depends on prior acclimation temperature in relation to exposure temperature. This effect can be measured in acute temperature exposure tests. Griffiths and Alderdice (1972) found that for juvenile coho over a temperature range of approximately 35.6-77°F (2-25°C), a low acclimation temperature of 35.6°F (2°C) produced maximum critical speed (5 lengths/s) at a test temperature of 57.2°F (14°C). As acclimation temperature was increased, so did the test temperature producing the maximum critical speed.

At an acclimation temperature of 68°F (20°C), a test temperature of 68°F (20°C) produced a critical speed of 6.0 lengths/s. Critical swimming speed declined dramatically as test temperature was increased above 68°F (20°C). An acclimation and test temperature of 68°F (20°C) provided the highest critical swimming performance (Griffiths and Alderdice 1972). For juvenile coho salmon a temperature of 68°F (20°C) appeared to provide maximum metabolic scope and swimming speed, given unlimited food.

Can disease affect swimming speed?

Tests of critical swimming performance on Fraser River adult sockeye at 66.2-69.8°F (19-21°C) indicated that diseases, including fungal infections, reduced swimming speed 35% from control conditions (Jain et al. 1998, as cited by Macdonald et al. in press).

What is known about swimming speed for three species of char?

Beamish (1980) measured critical swimming speed for three species of char: arctic char, *Salvelinus alpinus*; brook trout, *S. fontinalis*; and lake char, *S. namaycush*, at 41, 50, and 59°F (5, 10, and 15°C). Median critical swimming speed for each species increased with temperature over the range of 41 to 59°F (5-15°C). Swimming performance and oxygen uptake decreased as temperatures exceeded 59°F (15°C).

Can swimming act as an indicator of sublethal stress?

Swimming performances have been suggested for assessing sublethal effects of water quality (temperature and other combined pollutants) on fish (Brett 1967, as cited by Beamish 1978). Upstream migration requires a combination of all three modes of swimming (sustained, prolonged, and burst). Swimming to exhaustion in coho requires up to 18-24 h for complete recovery (Paulik et al. 1957). After 3 h of rest, recovery is only 67% complete. Exhaustion may be produced by repeated attempts to negotiate falls or fish ladders, escape predators, or struggle against the line of a sport angler. But lower energy reserves, decreased scope for activity, or unacceptable delays in reaching holding or spawning areas because of need for metabolic recovery mean that the cumulative effect of swimming stress may result in prespawning mortality or reduced reproductive success.

How are adult swimming speeds and migration rate related?

Brett (1965 as cited by Brett 1983) plotted the swimming efficiency of 2.3-kg sockeye as the energy cost (kcal/kg/km) vs. swimming speed (km/h). Low speeds (<1 km/h) required too much energy expenditure because of the large metabolism requirement in a prolonged migration period. Intermediate speeds (1.0-2.6 km/h) had the least energy expenditure. Optimum efficiency was achieved at 1.8 km/h. Interestingly, the mean current velocity of the Columbia River is 7 km/h, whereas maximum sustainable swimming speed is 5 km/h. The energy expenditure observed in sockeye was equated to a swimming speed of 4.3 km/h by Brett (1965 as cited by Brett 1983). This implies that sockeye must be able to travel largely in low-velocity currents to conserve energy. Fastest migration speeds, determined by radio tracking in mid-run spring chinnok in the Willamette River (late May-early June) were 1.8 km/h, although most of

the migration occurred at speeds of 1.3-1.7 km/h at 55.4-66.2°F (13-19°C) (Schreck et al. 1994). Further investigation of energy and swimming speeds is needed because the total distances traveled are uncertain. Adult salmonid migration can involve considerable downstream and upstream exploration for a given net distance traveled upstream (Schreck et al. 1994). If frequent fall-back through dams occurs, total travel distances and energy expenditure could become great, placing the individuals in considerable bioenergetic stress.

Recent studies using EMG radiotelemetry on volitionally swimming adult sockeye in the Fraser and Nechako Rivers in British Columbia revealed the average swim and migration speeds in different river reaches that presented various migration challenges attributable to channel constriction. Average swim speeds in these reaches varied from 1.8 to 4.5 km/h. Migration speeds in these same reaches ranged from 0.2 to 2.2 km/h (Hinch and Rand 1998). Swim speeds were much more constant than migration speeds, indicating that sockeye have a preferred or optimum swim speed (Hinch and Rand 1998). However, application of EMG telemetry at Hell's Gate, a major constriction in the Fraser River, showed that adult sockeye that were unsuccessful at passing this impediment swam for prolonged periods at speeds exceeding critical velocity, depleted energy reserves, and required prolonged recovery periods (Hinch and Bratty 2000). Although complex flow conditions associated with channel constrictions and fish ladders can lead to fatigue in unsuccessful upstream migrants, low oxygen concentration and high temperature can reduce the success rate even further (Hinch and Bratty 2000). By modeling bioenergetics of sockeye swimming up the Fraser River and accounting for the temperature variations as experienced over a 44-year period in which maximum temperatures of 69.8°F (21°C) occurred periodically, it was determined that 8% of the sockeye run over this time period was subject to energy depletion and prespawning mortality (Rand and Hinch 1998). Because as much as 20% of initial energy must be conserved to complete spawning, factors that contribute to energy depletion (high temperature, high velocity flows, passage barriers and constrictions, confusing flow patterns) need to be reduced.

What temperatures are associated with migration?

Migration is generally considered to occur or be feasible to some extent for summer and fall chinook at 57-68°F (13.9-20.0°C) and 51-66.9°F (10.6-19.4°C), respectively (Bell 1991). However, a migration threshold at a temperature of 69.8-71.6°F (21-22°C) is documented by numerous studies across major migratory salmonid species in the Columbia River (Table 3).

Summer water temperatures in many streams of the Pacific Northwest can be high enough to cause migration difficulties. The Snake River provides an example. In each of the Snake River reservoirs there is an approximately 2-month period during which water temperatures exceed 69.8°F (21°C) (Dauble and Mueller 1993, p. 39). At Lower Granite reservoir this period extends from mid-July to mid-September. This period in which water temperature exceeds adult migration thresholds overlaps the adult migration periods of summer chinook, fall chinook, sockeye, and summer steelhead (Dauble and Mueller 1993, Fish Passage Center data sheet) (also see Table 7) and the smolt outmigration of fall chinook and sockeye at Lower Granite Dam (Fish Passage Center 1998). Even spring chinook migration to spawning grounds can be inhibited for continuous periods of more than 2 months by temperatures in major tributaries of the Snake (i.e., Tucannon River) (Bumgarner et al. 1997). Chinook, sockeye, and steelhead of the Snake River

Table 7. Adult migration period for chinook and steelhead

Reservoir	Spring chinook	Summer chinook	Fall chinook	Steelhead
Ice Harbor	4/1-6/8	6/12-8/11	8/12-10/31	4/1-10/31
Lower Monumental	4/1-6/13	6/14-8/13	8/14-10/31	4/1-10/31
Little Goose	4/14-6/15	6/16-8/15	8/16-11/15	4/1-10/31
Lower Granite	3/1-6/17	6/18-8/17	8/18-12/15	4/1-10/31

Note: Adult sockeye passage at Lower Granite Dam extends from June 15 to August 20 (Dauble and Mueller 1993). Steelhead migration includes the group A run from April 1 to August 25 and the B run from August 26 to October 31.

are all listed under the ESA as either threatened or endangered, migrate during periods affected by warm water, and require consideration for their migration success and survival.

Fall chinook historically entered the Snake River from late August through November with a peak in September (Snake River Subbasin Plan 1990). At Ice Harbor Reservoir during 1990, water temperatures were 73.4°F (23°C) on August 15 (i.e., the initiation of the migration period) but declined to only 71.6°F (22°C) by September 16 (Karr et al. 1992). As an example of the problem posed for fall chinook migration, 1990 water temperatures in Lower Granite Reservoir peaked on approximately August 13 at 77°F (25°C) and gradually declined to about 69.8°F (21°C) by September 16 (Karr et al. 1992). Temperature histories for Snake reservoirs such as these indicate that migration blockages of 4 wk can occur. Since September 1990, attempts have been made to reduce Snake River reservoir temperatures by releasing water from Dworshak Dam. Releases of cold water of up to 14 kcfs have been made to improve fish migration and survival.

Periodic inability to migrate because of high water temperatures was almost certainly one of a number of environmental challenges presented to salmon under historic conditions. However, unimpounded rivers have thermal regimes that are different from those of impounded rivers. Even if a free-flowing river experienced a maximum daily temperature that impeded upstream migration, it would not have continuous temperatures beyond the migration threshold, nor would they be present for many consecutive days. A healthy stream system would provide abundant cold-water refuges along the entire migration route. Large reservoirs on mainstem rivers, channel alterations (loss of pools via removal of large woody debris or sedimentation, channelization), and altered cold-water input sources (e.g., wetland loss, interception of shallow groundwater flow by the road system) lengthen exposure to temperatures that could block migration, shift maximum temperatures to later in the year, eliminate cold-water refuges, result in more constant daily temperatures, and heat river margin habitats (Coutant 1999). These habitats would be best for juvenile rearing (especially fall chinook migrating slowly to the ocean), if not for the high temperatures present during summer and early autumn months.

If adults or smolts were able to seek colder water at depth, they could avoid the migration

barriers. However, there is very little temperature stratification in the reservoirs (Bennett et al. 1997, Karr et al. 1998). Adult salmon in the vicinity of the Snake River mouth are known to hold in the much cooler Columbia River to avoid adverse temperatures. However, they have a limited opportunity to then migrate through the Snake River, find a mate, and spawn. This window is predetermined by their stored body energy, their maturation during holding, and their need to deposit eggs in sufficient time for development and emergence. Although salmon have some inherent flexibility in their life cycle, this can easily be overwhelmed by stresses imposed in river management. In addition, salmon's range of tolerance to high temperatures in their environment can easily be exceeded, lowering their survival.

The year 1998 set record high temperatures throughout the Fraser River Watershed in British Columbia, Canada. It also set records for high losses to the river's sockeye salmon run. Macdonald et al. (in press) evaluated the effects of temperature, flows, disease, and other stressors to determine the likely cause of the estimated in-river loss of 3,394,000 adult fish and increased prespawning mortality in some early-run stocks. Temperature was the main cause of both en route and prespawning losses to the 1998 Fraser River sockeye runs. Mean daily water temperatures at Hell's Gate (a lower mainstem site) were the highest recorded for most days during the summer of 1998, frequently exceeding 68°F (20°C) in late July and early August (warmest mean summer temperatures in the 51 years of record). From their review of the historical database, the authors suspected that losses in spawning runs occur when mean river temperatures exceed 62.6-64.4°F (17-18°C) for prolonged periods. They noted that chinook salmon also appear susceptible to high temperatures in the Fraser River system. In 1998 unusually large losses (25% of population) occurred in the South Thompson River, where summer mean temperatures were frequently above 68°F (20°C) and reached a high of approximately 73.4°F (23°C). The only other year with reports of large chinook losses was 1994, also an unusually warm year.

Migration stress and reproductive impairment in salmon populations may result from the cumulative effects of exposure to less than optimum environmental conditions. Macdonald et al. (in press) suggested that migration blockages, susceptibility to disease, impaired maturation, increases to stress parameters, reduced efficiency of energy use, and reduced swimming performance are all more common as daily mean temperatures exceed 62.6°F (17°C). The authors found that measuring physiological indicators of stress and reproductive condition is useful in evaluating the effects of temperature on migratory sockeye salmon.

How can stress during migration affect later reproductive success in salmonids?

Macdonald et al. (in press) monitored stress and reproductive state in both prespawning and postspawning sockeye from the Horsefly River stock (midsummer run). The Horsefly River stock entered the Fraser River during the warmest period of the year. During migration to the spawning grounds, temperatures were well over 68°F (20°C). Four stress parameters and three reproductive parameters were examined. In addition, some of the fish collected were artificially spawned and their eggs placed in capsules in the gravel of their natal stream and examined to determine both fertilization and hatching success.

In 1998, Horsefly sockeye (midrun stock) females had plasma cortisol levels (a primary

indicator of stress) that reflected exposure to acute stress and that were generally higher than those in other migrating Fraser River sockeye stocks in previous years. The levels of lactate (a secondary indicator of stress) in Horsefly salmon at all reproductive stages examined showed that these fish had engaged in stressful exercise even though the flow rates in 1998 were substantially lower than in 1997, when water flows created very challenging migration conditions. There were several indications that the early portion of the 1998 Horsefly run was suffering from impaired maturation. Many of the females, particularly those in poor condition, had low estradiol and progesterone levels, possibly from high-temperature stress that caused suppression of estrogen synthesis and an inability to switch to the synthesis of 17,20P (an indicator of final maturation in males and females). These processes are known to be linked. Testosterone (an indicator of maturation in males and females) also was depressed in females in poor condition, further evidence that these fish would probably not reach maturity or spawn viable eggs. Elevated but sublethal temperatures are known to negatively affect secretion of the hormones controlling sexual maturation in sockeye salmon in the Fraser River. The likely physiological consequences of these reduced hormone levels are poor spawning success, poor egg quality and viability, and senescent death prior to spawning. All three of these reproductive impairment problems were evident in 1998 in each of the stock groups.

What temperatures are recommended for holding?

Hatchery managers have long known that highest survival of chinook adults occurs when water temperatures do not exceed 57.2°F (14°C) (Leitritz and Lewis 1976, Piper et al. 1982). Fish (1944) reported very high holding survival of sockeye when temperatures were <60°F (15.6°C), but survival was only 51% under a fluctuating regime of 48.9-73.9°F (9.4-23.3°C).

Can temperature affect viability of gametes developing in adults?

Temperature can influence the reproductive success of fish well before spawning. Prespawning effects can be separated into at least two time periods: before ovulation and after ovulation. Before ovulation, reproductive success can be hampered by mortality to the adult spawner (Andrew and Geen 1960, Bouck et al. 1975, Schreck et al. 1994, Cooper and Henry 1962, as cited in Gilhousen 1980) and interference with ovulation and spermatogenesis. After ovulation, reproductive success can be harmed through decreased egg and sperm fitness and reduced embryonic survival rates. Here we discuss only the impact of temperature on ovulation and subsequent egg survival.

Hatchery managers have long known that highest survival of chinook adults occurs at water temperatures less than 57.2°F (14°C) (Leitritz and Lewis 1976, Piper et al. 1982). When adults hold in higher water temperatures, egg survival increasingly declines (Hinze 1959, Hinze et al. 1956, as cited by Marine 1992).

After ovulation in females and sperm maturation in males, the effect of elevated water temperature on rainbow trout egg and sperm viability becomes important (Billard 1985). Holding females at 68°F (20°C) for 70 h reduced viability of eggs held in the body cavity, compared with holding females at 50°F (10°C) (Billard and Breton 1977, as cited by Billard 1985). To promote female maturation and egg development, holding at temperatures from 42 to

55.9°F (5.6-13.3°C) is essential (Leitritz and Lewis 1976).

Smith et al. (1983) and Piper et al. (1982) cited work demonstrating that rainbow trout adult broodfish should be held at temperatures below 53.9-55.9°F (12.2-13.3°C) before spawning to produce good-quality eggs, whereas holding temperatures above 55.4°F (13°C) have been found to reduce in vivo postovulatory egg survival (Flett et al. 1996, Billard and Gillet 1981, as cited in Billard 1985). Temperatures of 64.4°F (18°C) or higher were found to reduce the volume of male sperm, and a temperature of 68°F (20°C) was found to cause a drop in egg fertility in vivo to 5% after 4.5 d (Billard and Breton 1977). At 50°F (10°C), fertility of the eggs held in the hen trout remained high. Saki et al. (1975, as cited in de Gaudemar and Beal 1998) found that embryonic and posthatching survival in *O. mykiss* decreased significantly if eggs remained ripe in the body cavity for more than 5-7 d after ovulation, and fertility could approach zero after 2 wk (Stein and Hochs 1979, as cited in de Gaudemar and Beal 1998).

When ripe adult chinook females were exposed to temperatures beyond the range 55.9-60°F (13.3-15.6°C), prespawning adult mortality became pronounced and survival of eggs to the eyed stage decreased. Prespawning adults exposed to prolonged temperatures of 60-62°F (15.6-16.7°C) had survival of eggs to the eyed stage of 70% when incubated at 54.8-55.9°F (12.7-13.3°C) and survival of 50% when incubated at 60-62°F (15.6-16.7°C). Adults exposed to 55-59°F (2.8-15°C) water temperature had egg survival of 80% to the eyed stage when then incubated at the same temperatures (Hinze 1959, as cited by CDWR 1988). The highest survival of eggs (95%) to the eyed stage was in those taken from adults held at 53-53.9°F (11.7-12.2°C) (Hinze et al. 1956 as cited by CDWR 1988). Eggs taken from chinook held at constant temperatures >55.4-59°F (13-15°C) have poor viability (Hinze et al. 1956, as cited by Marine 1992, Rice 1960, Leitritz and Lewis 1976).

Berman (1990) held adults at 63.5-66.2°F (17.5-19°C) for a 2-wk period before spawning. Control fish were held at 57.2-59.9°F (14-15.5°C). Progeny of the elevated treatment group had higher prehatch mortality and a much greater rate of developmental abnormalities than the control group. In addition, alevin weight and length were less in the elevated group. The smaller alevin size could be attributable to the smaller size of eggs in the elevated group. It is interesting that even though no differences were observed in fertilization rates of eggs between the elevated and control groups, numerous delayed effects occurred.

Two coho stocks migrating to spawning grounds in eastern Lake Erie had very different survival of embryos to hatch, attributable to the water temperatures on the migration route. The stock that migrated in waters >59°F (20°C) in mid-August to early September had deformed eggs with mean survival rates to hatching of low to 0%, depending on the year. The neighboring stock had very little warm shoal water to traverse during migration, were exposed to temperatures 3.6-7.2°F (2-4°C) lower, and had normal eggs with high viability (84% embryo survival) (Flett et al. 1996).

Hokanson et al. (1973) measured a significant effect of prespawning temperature exposure on brook trout broodstock. When brook trout were spawned at 50.7°F (10.4°C) or at 55.7°F (13.2°C) and subsequently reared at 50°F (10°C), percentage of normal hatching was 65% and 38%, respectively. When brook trout were spawned at 50.7°F (10.4°C) or 55.7°F (13.2°C) and subsequently reared at 60.8°F (16°C), percentage of normal hatching was 0% in each case.

Percentage of normal hatching was >90% at constant incubation temperatures of 40.8-46.4°F (6-8°C) and declined steadily to 0% at 60.8°F (16°C). The highest percentage of viable eggs per female was found at 46.4°F (8°C). An increase in spawning temperature from 50 to 60.8°F (10-16°C) resulted in a steady decline to near zero in spawnings per female, viable eggs per female, and total eggs per female. The temperature range 42.8-60.8°F (6-16°C) may represent the right portion of a bell-shaped survival curve. This study provides important evidence that adult holding water temperatures and temperature at fertilization are as important as incubation temperature in determining egg viability. In female brook trout the maximum temperature for maturation and ovulation is 60.8-66.2°F (16-19°C). Males can achieve functional maturity at temperatures as high as 62.2°F (19°C). However, at 66.2°F (19°C) development of ova becomes inhibited and ova can be resorbed. Hokanson et al. recommended that for brook trout in the month prior to spawning, maximum water temperature should be <66.2°F (19°C) and mean temperature should be <60.8°F (16°C). During the breeding season maximum water temperature should be <53.6°F (12°C). Optimal spawning activity, gamete viability, and embryo survival would take place at mean spawning temperatures <48.2°F (9°C).

Egg survival during egg development has also been studied in rainbow trout. Postovulation survival of eggs in the body cavity of rainbow trout females held at >55.4°F (13°C) was much lower than at lower holding temperatures (Billard and Gillet 1981, as cited by Billard 1985).

Forced delays in spawning, such as are frequently caused by difficulties in passing dams, can cause decreases in reproductive success. In Atlantic salmon a delay in spawning from any source causes overripening in females. Prolonged holding of eggs after ovulation reduces egg viability and increases retention and malformation. As little as a 1-wk delay in spawning after full maturation causes a marked reduction in egg quality (de Gaudemar and Beall 1998).

In addition to the effects on egg viability caused by holding adult female salmon at elevated water temperature (>59-60.8°F [15-16°C]), warm water can also lower viability of eggs of nonanadromous salmonid adults by influencing their nutrition during their feeding period (see Hokanson 1977). A lowered food intake leading up to egg deposition, when growth is normally rapid, may accompany elevated water temperature. Poor growing conditions for salmonids that achieve maturity in freshwater can result in poor reproductive success (Coutant 1977). A rapid decline in quality of rainbow trout eggs within the body cavity after ovulation has been reported at holding temperatures of 55.4-59°F (13-15°C) by numerous authors (see citations in Flett et al. 1996, Billard 1985, Smith et al. 1983). Cutthroat females held at temperatures fluctuating from 35.6 to 50°F (2-10°C) produced eggs of significantly higher quality than females held at 50°F (10°C) (Smith et al. 1983).

Bouck et al. (1975) studied survival of sockeye acclimated to 55.4°F (13°C) and adjusted to test temperatures at a rate of 3.6°F (2°C)/d. Adults holding at a test temperature of 71.6°F (22°C) died after 3.2 d from thermal effects. Holding for 11.7 d at 68°F (20°C) resulted in 100% mortality from indirect thermal effects (infection by columnaris). Fish held at 61.7°F (16.5°C) had lower health and reproductive indices than fish held at 50°F (10°C). Among these indices were the absence of fat reserves at 61.7°F (16.5°C) vs. abundant reserves at 50°F (10°C), the doubling of weight loss, enlarged liver, and reduced egg size at the higher temperature. The noninfectious pathology at 61.7°F (16.5°C) occurs precisely during the major period of reproductive development in the Columbia River. For these reasons, Bouck et al. concluded that

50°F (10°C) was more favorable for maturing sockeye than 61.7°F (16.5°C), and in addition, did not subject these fish to the greater risk of thermal death and disease associated with 60.8 and 68°F (16 and 20°C) holding.

Water temperatures can speed up, slow down, or stop entirely the ripening of gonads and ovulation in fish (Flett et al. 1996, Gilhousen 1990, Gillet 1991 as cited in Baroudy and Elliott 1994, and Reingold 1968 as cited in Bailey and Evans 1971). Billard and Breton (1977) found that temperatures as high as 64.4°F (18°C) had no adverse effect on male rainbow trout spermatogenesis, but sperm volume and gonadotrope secretion were both higher at 50°F (10°C) than at 64.4°F (18°C). At temperatures above 55.4°F (13°C), ovulation may still occur in rainbow trout, but postovulatory egg survival in the body cavity is much shorter. Taranger and Hansen (1993) used Atlantic salmon (*Salmo salar*) to test the timing of ovulation under different temperature regimes. Water temperature was either increased from 50°F (10°C) to 55.4-57.2°F (13-14°C) (warm water), decreased abruptly from 50°F (10°C) to 41-44°F (5-7°C) (cold water) or gradually decreased from 50 to 46.4°F (10-8°C) (ambient control) from November 1 onward. Median ovulation time was delayed by 5 wk in the warm-water group compared with ambient controls, with 43% of the females remaining nonovulated at the end of the study. Only minor effects were observed on timing of ovulation in the cold-water group compared with the ambient controls. Survival of eggs to the eyed stage was significantly higher in the cold-water group (92.1%) than in both the ambient control group (84.5%) and the warm-water group (76.6%). The results indicate that high water temperature during the spawning season may inhibit ovulation and have a detrimental effect on gamete quality. Morrison and Smith (1986, as cited in Taranger and Hansen 1993) found that low water temperature delayed ovulation in winter spawning rainbow trout and that an increase in water temperature could accelerate ovulation.

Although eggs in the body cavity of the female are less sensitive than they are outside the female (roughly several weeks compared with a few days) (Billard and Gillet 1981, Billard and Breton 1977), once ovulation has occurred the quality of the eggs will begin to decline as they overripen (Gillet 1991 as cited in Baroudy and Elliott 1994, Bouck and Chapman 1975, Flett et al. 1996, Sakai et al. 1987 as cited in Flett et al. 1996, de Gaudemar and Beal 1998). Bry (1981), as cited in Flett et al. (1996), found that eggs retained in the body cavity after ovulation show a high, significant decline in quality by 9-12 d after ovulation at 54°F (13°C). Escaffre et al. (1977), as cited in Flett et al. (1996), reported a rapid decline in egg quality when water temperature exceeded 57.2-59°F (14-15°C). De Gaudemar and Beal (1998) found that 8 d after ovulation in Atlantic salmon, egg survival already seemed affected. In rainbow trout, Sakai et al. (1975), as cited in de Gaudemar and Beal (1998), showed a decrease in embryonic and posthatching survival if ova were kept more than 5-7 d in the abdominal cavity after ovulation. They also found that after 15 d ova underwent a decrease in fertility, which could even be close to zero after 2 wk according to Stein and Hochs (1979), as cited in de Gaudemar and Beal (1998).

Bouck and Chapman (1975) found that 50°F (10°C) would be more favorable for sexually maturing adult sockeye salmon than 61.7°F (16.5°C). Body weight losses for females averaged 8.5% at 50°F (10°C) and 13.2% at 61.7°F (16.5°C). Although fat reserves were abundant in the 50°F (10°C) group, they were absent at 61.7°F (16.5°C). Higher temperatures, 61.7°F versus 50°F (16.5 vs. 10°C), were associated with advanced development of secondary sexual characteristics (snout and dark skin) and diminished development of gonads. Females bore

similar numbers of eggs at 50 and 61.7°F (10 and 16.5°C), but eggs were 11% less in weight in the 61.7°F (16.5°C) group, which was correlated with percentage body weight loss. Bouck (1977) found results very similar to those reported in Bouck and Chapman (1975).

Exposure of ripe adults and eggs to water temperatures above 55.9°F (13.3°C) is commonly assumed to result in greater than normal losses and abnormalities of young fish (Morat and Richardson 1983, Weidlein 1971, Dunham 1968, as cited in CDWR 1988). Rice (1960) tested hatchery holding facilities to determine the best conditions for holding, spawning, and incubating chinook salmon stocks from the American River in California. He determined that a facility with temperatures below 44.96°F (7.2°C) was too cold for successful incubation, but one with temperatures ranging between 46.94 and 60°F (8.3 and 15.6°C) was satisfactory for egg development.

Billard and Breton (1977) found that temperatures above 55.4°F (13°C) allowed ovulation to occur in rainbow trout, but postovulatory egg survival time in the body cavity was much shorter than at lower temperatures. The authors noted that in vivo survival of ovulated eggs (4 d) in rainbow trout was high (approximately 95%) for 70 h at 68°F (20°C), but beyond this point survival dropped rapidly and dramatically (to approximately 5% at 110 h). This demonstrated that rainbow trout broodfish must be held at water temperatures not exceeding 55.9°F (13.3°C) (preferably not above 53.9°F [12.2°C]) for a period of 2-6 months before spawning to produce eggs of good quality (Smith et al. 1983 as cited by Bruin and Waldsdorf 1975, Leitritz and Lewis 1976).

Temperatures shown to affect salmonid egg quality vary. Flett et al. (1996) suspected that the low survival to hatching observed in adult coho salmon migrants was caused by traveling through waters warmer than 68°F (20°C). Temperatures greater than 60°F (15.6ºC) were noted to decrease egg survival and contribute to coagulated yolk in sac-fry (Hinze et al. 1956 as cited by CDWR 1988, Olson and Foster 1957). Greatest survival occurred in eggs taken from fish when water temperature was in the 53.1-54°F (11.7-12.2ºC) range. Furthermore, it was noted that early embryonic damage may be manifested during the latter part of the fry stage and just after feeding has begun in the fingerling stage, so rates of survival to hatching may underestimate the detrimental effect of prespawning temperatures. Rice (1960) found that holding broodstock in hatchery waters that were consistently above 60°F (15.6°C) reduced survival of eggs to the eyed stage by 12.7% compared with holding the broodstock between 46.9 and 60°F (8.3-15.6°C). Bouck et al. (1970, as cited in EPA and NMFS 1971), however, found no apparent adverse effects on coho salmon eggs in utero after prolonged exposure of adult fish to 62°F (16.7°C). When females hold in warm water, eggs tend to be smaller with less stored energy, which means less energy for alevin development and the necessity for earlier feeding to sustain life. Berman and Quinn (1989) cited a personal communication with B. Ready, the manager of the Kalama State Fish Hatchery, showing egg mortalities of 50% or more from adults held in river waters fluctuating from 57.9 to 66.9°F (14.4-19.4°C). The current supervisor of the Kalama Falls Hatchery, Ron Castaneda, acknowledges that they incur some increased losses at holding temperatures around 60-64°F (15.6-17.8°C), but they have not had mortality as high as 50%. It is perhaps useful to note that this hatchery incubates in the natural river water as well.

In an unpublished 1995 study, Dr. Craig Clarke (cited in Macdonald et al. in press) exposed early Stuart sockeye salmon captured at Hell's Gate to two temperature treatments (59 and

66.2°F [15 and 19°C]) for 2 wk. Two weeks of exposure to 66.2°F (19°C) in the laboratory reduced plasma testosterone levels significantly in both sexes compared with 59°F (15°C) exposure. Levels of 11-ketotestosterone and estradiol were low and below the detection limit in many fish at 66.2°F (19°C). Furthermore, circulating levels of the major hormones controlling sexual maturation were also depressed at 62.2°F (19°C). Similarly, Manning and Kime (1985 as cited in Macdonald et al. in press) found that steroid biosynthesis was suppressed in rainbow trout testes at 62.6°F (17°C). Clearly, the potential for suppression of sexual development and intergenerational impairment existed in 1998 when migration temperatures exceeded 62.2°F (19°C) at many locations and times. This possibility was supported further by an experimental assessment of the spawning success of the early Stuart and Horsefly stocks. Macdonald et al. (in press) monitored stress and reproductive state in both prespawning and postspawning sockeye from the Horsefly River Stock (midsummer run). The Horsefly River stock entered the Fraser River of British Columbia during the warmest period of the year. During migration to the spawning grounds, temperatures were well in excess of 68°F (20°C). Four stress parameters and three reproductive parameters were examined. In addition, a portion of the fish collected were artificially spawned and their eggs placed in capsules in the gravel of their natal stream and examined to determine both fertilization and hatching success. Fertilization success was found to be lower in 1998 than in 1997. Horsefly fish that arrived on the spawning grounds in early 1998 suffered even lower fertilization success rates than the Stuart fish, and only 10% of their eggs hatched. Egg hatching success (but not fertilization success) was influenced by the condition of the spawning female as estimated by stress and reproductive parameters. Females that arrived late tended to have lower levels of testosterone and spawned eggs that hatched more successfully. These late arrivals likely experienced less severe water temperatures during their entire migration than did early fish. The likely difference at Hell's Gate was that mean daily temperatures were 64.4-66.2°F (18-19°C) versus 69.8-71.6°F (21-22°C). These observations suggested that the upper threshold temperature for successful migration lies between 64.4 and 71.6°F (18 and 22°C).

Based on the information reviewed above, it can be concluded that holding migratory fish at constant temperatures above 55.4-60.1°F (13-15.6°C) may impede spawning success. Maximum constant temperatures of 50-54.5°F (10-12.5°C) may provide better reproductive conditions in most salmon and trout.

How is survival of prespawning adults affected by water temperature?

Leitritz and Lewis (1976) and Piper et al. (1982) recommended chinook broodstock holding temperatures of 42.8-57.2°F (6-14°C). Conventional hatchery practice is to consider chinook broodstock thermally stressed at temperatures >59°F (15°C); survival declines dramatically when temperatures exceed 62.6°F (17°C) (Marine 1992). Raleigh et al. (1986) described adult chinook prespawning temperatures as maximal in the range 46.4-54.5°F (8-12.5°C) but declining to zero at 75.2°F (24°C). A study by Fish (1944) revealed that adult chinook survival under fluctuating temperature regimes of 48.9-73.9°F (9.4-23.3°C) (mean = 10.8°F [16°C]) was only 36%, but at 52-60°F (11.1-15.6°C) (mean = 53°F [11.9°C]) survival was 75% after holding in ponds for approximately 2 months. This study highlights the benefit of holding adults under cold water temperatures to promote survival. However, in this Grand Coulee Fish Salvage Program, disease outbreaks (especially columnaris) in the holding pond environments made

cold-water holding particularly necessary to inhibit pathogens.

Prespawning mortality of wild spring chinook in the Warm Springs River varied from 34% to 75% during the period 1977-1986. In 1980 and 1981 prespawning mortality averaged 74%. BKD was implicated in this high mortality because it was responsible for mortality in the hatchery. Even though all adults released to the Warm Springs River above the hatchery were inoculated for BKD in 1982-1986, mortality was still high (24%-59%). In the Rogue River, Oregon, furunculosis and columnaris were the primary cause of mortality of wild and hatchery adults from 1977 to 1981. Prespawning mortality in wild and hatchery fish was 12% and 36%, respectively, during this period (Cramer et al. 1985 as cited by Lindsay et al. 1989). Wild spring chinook in the lower Rogue River exhibited high prespawning mortality in May-July 1992 as water temperature ranged from 64.4 to 69.8°F (18-21°C) (M. Everson, ODFW, pers. comm., as cited by Marine 1992). The foregoing studies point out the variability of prespawning salmonid mortality in the wild and the magnitude of disease effects observed under thermal stress.

What temperature ranges are associated with the adult spawning period?

There is conflict between the fish's inherent temperature preferences and its need to spawn within a limited time frame. That is, given a prolonged high-temperature period during adult holding, adults may be forced to spawn during adverse conditions, leading to poor egg and sperm, embryo, alevin, or fry survival. For this reason, fish habitat managers must use discretion in selecting suitable spawning temperatures. Even though fish may have been observed spawning under warm temperatures, as during the initial days of the spawning period, there is no guarantee that embryo survival is high for the early-spawning fish. There is some plasticity in timing of life stage events relative to annual climatic patterns (i.e., if sufficient energy remains in the adult body in the prespawning stage, some delay in spawning is feasible), and adjustments can be made throughout the life cycle, but inability to compensate fully tends to be expressed as population mortality, poor growth, reduced fecundity, and reduced fitness.

Spawning of chinook in a wide variety of locations has been reported for a composite temperature range of 35.9-66°F (2.2-18.9°C) (Mattson 1948, Burner 1951, both as cited by Raleigh et al. 1986, Crawford et al. 1976 as cited by Vigg and Watkins 1991, Olson and Foster 1955, Chambers 1956 as cited by Andrew and Geen 1960, Snyder et al. 1966 as cited by Parker and Krenkel 1969, Wilson et al. 1987). Recommended spawning temperatures for spring, summer, and fall chinook given by Reiser and Bjornn (1979) and Bjornn and Reiser (1991) in their literature review were 42-57°F (5.6-13.9°C). These limits were extracted from Bell (1986). EPA and NMFS (1971) recommended a maximum temperature of 55°F (12.8°C). Bell (1991) gave a range of 42-57.5°F (5.6-14.2°C) as the preferred spawning zone, with 51.8°F (11°C) as a preferred temperature based on an extensive summary of literature.

What temperatures or thermal regimes are required to initiate spawning?

In autumn-spawning species such as the Pacific salmon, it can be assumed that the highest temperatures associated with the spawning period are temperatures that allow spawning to be initiated. For chinook, the extreme high temperature at spawning was 66°F (18.9°C). However, egg survival at these temperatures cannot be assumed. In general, 60.4°F (16°C) is the maximum associated with initiation of fall chinook spawning (Groves and Chandler 1999).

It has been reported that spawning is initiated when temperatures decline. Chambers (1956 as cited by Raleigh et al. 1986) found that spring chinook normally spawn as water temperature declines from 55 to 40.1°F (12.8-4.5°C) and fall chinook spawn under a 56.1-41°F (13.4-5°C) decline. The critical temperature threshold of approximately 55°F (12.8°C) and declining temperature are apparently associated with ability to complete the spawning act, maximum long-term viability of eggs and alevins, and better resistance to death by disease in adults and eggs. Although prespawning mortality attributed to bioenergetic stress may be a significant factor in overall adult mortality up to spawning time, it is uncertain how to separate disease and bioenergetic stress effects.

Spawning can be initiated only under a limited temperature range. In the Hanford Reach of the Columbia River, the median date for peak spawning was November 11, based on surveys from 1948 to 1992. On this date the mean weekly temperature was 54.5°F (12.5°C) and the maximum weekly temperature was 57.2°F (14°C) (Dauble and Watson 1997). However, in both the Hanford Reach and Snake River spawning zones, spawning activity begins as weekly mean water temperatures decline below 60.8°F (16°C) and continues up to 41°F (5°C) (Groves and Chandler 1999). Because studies of egg survival and development after fertilization for chinook and other salmon species indicate reduced survival under temperatures of 53.6-60.8°F (12-16°C), preferred spawning temperatures of 55°F (12.8°C) (maximum) have typically been recommended (see EPA and NMFS 1971, review of McCullough 1999). These data indicate that it is essential for mainstem temperatures to decline rapidly below 60.8°F (16°C) so that spawning activities can commence and also so that egg survival continues to improve during the spawning period.

Fall chinook, sockeye, and coho were all reported to spawn on falling temperatures starting at peaks of 51-55°F (10.6-12.8°C) (Chambers 1956 as cited by Andrew and Geen 1960). Sockeye spawning success was only 45% when mean daily temperatures during spawning were 57.9-61°F (14.4-16.1°C). On the Fraser River, spawning temperatures >55°F (12.8°C) were associated with an increasing number of females that died without spawning (Andrew and Geen 1960). Temperatures >53.6°F (12°C) can inhibit or delay spawning by Atlantic salmon (Beall and Marty 1983, as cited by de Gaudemar and Beall 1998). In the laboratory, brook trout spawning was typically initiated at 50°F (10°C) but occurred under temperatures as high as 60.8°F (16°C) (Hokanson et al. 1973). Spawning of brook trout begins to occur after the weekly mean temperature falls below 55.4°F (13°C) (approximately early October). During the spawning period, water temperatures steadily decline from approximately 55 to 44.8°F (12.8-7.1°C) (Hokanson et al. 1973). Based on a survey of temperature effects on all aspects of spawning in fall-spawning salmonids, it appears that spawning temperatures in the spring and fall chinook spawning habitats having a 55°F (12.8°C) peak and that a declining trend would

satisfy biological requirements. Keying the spawning period to rapidly falling temperatures is common among fall-spawning salmonids and has been documented for chinook of the Pacific Northwest (Groves and Chandler 1999, Lindsay et al. 1986).

Although spawning for bull trout may begin as early as mid-August, spawning activity is reported to be initiated when water temperatures begin to fall to 48.2°F (9°C) or lower (McPhail and Murray 1979, Shepard et al. 1982, Kraemer 1994, Brenkemen 1998). Both the coastal rainbow and the redband trout spawn in the spring, stimulated by rising water temperatures. Behnke (1992) suggested that along the Pacific coast a water temperature of about 37.4-42.8°F (3-6°C) may initiate some spawning activity, but spawning does not usually occur until temperatures reach 42.8-48.2°F (6-9°C). Although this spawning activity would typically occur from late December through April, in some very cold headwater streams local temperatures may delay spawning until July or August for some stocks. Beschta et al. (1987) suggested that rainbow trout spawn between 35.9 and 68°F (2.2 and 20°C), Bell (1986) set the range at 35.9-66°F (2.2-18.9°C), and Piper et al. (1982) concluded the range was 50-55°F (10-12.8°C).

Conclusions for spawning. Egg mortality, alevin development linked to thermal exposure of eggs in ripe females or newly deposited in gravel, and egg maturation are negatively affected by exposure to temperatures above approximately 54.5-57.2°F (12.5-14°C). Therefore, a spawning temperature range of 42-55°F (5.6-12.8°C) (maximum) appears to be a reasonable recommendation for Pacific salmon, unless colder thermal regimes are natural in any tributary.

What is the utility of UILT data and how has it been applied?

Upper incipient lethal temperature data were tabulated in NAS (1972) for juveniles and adults of many fish species. UILT values for many salmonid species have since been added to the literature; a cross-section is summarized in Table 4, extracted from McCullough (1999). The UILT values correspond to the highest acclimation temperatures, and consequently, are very similar to UUILT values. Given prior acclimation to temperatures lower than listed in the table, however, the UILT values would likely be lower. This means that in the field, mortality can be induced at temperatures significantly lower than UUILT levels.

Studies of the effect of elevated water temperature on survival of a wide variety of salmonids using transfer to high constant temperature (UILT experiments) show much consistency among species. In those tests in which acclimation temperature was 68°F (20°C) and the UILT was approximately equal to the UUILT, UILT values found ranged from 73.4 to 80.6°F (23-27°C). Redband trout tend to be the most heat resistant of the salmonids; UILT values for all other species ranged from 73.4 to 78.8°F (23-26°C).

NAS (1972) recommended that for any acclimation temperature, short-term exposure be limited to UILT (factor of safety, 3.6°F [2°C]). This assumes that at the UILT temperature, 50% of the population would die within the test period (at least 1,000 min), but if the temperature is reduced by 3.6°F (2°C), no mortalities would occur in this time period. Although this assumption may generally be valid, it also relies on no incidence of disease or other sublethal effects. When this method was proposed, cumulative effects of repeat exposure to high temperatures were not well known (see DeHart 1975, Golden 1975, Golden 1976, Golden and

Schreck 1978).

Although temperatures of 73.4-78.8°F (23-26°C) are generally considered the UUILT for most salmonids, UILT values are typically 1.8-3.6°F (1-2°C) less than UUILT. The UILT values are incipient lethal temperatures that correspond to acclimation temperatures lower than the UUILT. Because we can never assume that fish in the field will be acclimated to the highest acclimation temperature, the more appropriate lethal temperature in the field may be up to 3.6°F (2°C) less than UUILT. The factor of safety would then have to be applied to this value, and even then the additional sublethal or cumulative lethal concerns remain.

The 73.4-78.8°F (23-26°C) UUILT range for salmonids applies to the juvenile life stage. Although information on salmon adults is much more limited, it indicates that adults are far more sensitive than juveniles to high temperatures. Becker (1973) identified the thermal tolerance of chinook jacks to be 69.8-71.6°F (21°-22°C) on the basis of a 168 h TLM test. Coutant (1970) identified the incipient lethal temperature for chinook jacks as 71.6°F (22°C) with prior acclimation to 66.2°F (19°C) (estimated from ambient river temperatures). Columbia River steelhead, acclimated to a river temperature of 66.2°F (19°C) had a lethal threshold of 69.8°F (21°C) (Coutant 1970). These lethal limits are 9.9°F (5.5°C) lower than for juvenile rainbow acclimated to 64.4°F (18°C) (Alabaster and Welcomme 1962, as cited by Coutant 1972).

Servizi and Jensen (1977) found that the geometric mean survival times (GMST) for adult sockeye were less than for juveniles. They also reported that the median survival times (MST) for adult coho found by Coutant (1969) were similar to those of sockeye over the exposure range 80.6-86°F (27-30°C). The GMST for adult sockeye was 1,000 min at 75.2°F (24°C) with acclimation at 60.4-64.9°F (15.8-18.3°C). Survival time at 78.8°F (26°C) was only 100 min. Time to loss of equilibrium and survival time of adults were plotted vs. exposure temperature on the same graph. The curve for loss of equilibrium was considerably lower than the time-to-death curve. For this reason, Servizi and Jensen (1977) considered the loss of equilibrium temperature more ecologically significant. Furthermore, because sockeye exposed to temperatures of approximately 64.4-69.8°F (18-21°C) become highly susceptible to *Flexibacter columnaris*, researchers took this temperature range as a greater thermal threat to continued stock survival.

Although UUILT or UILT temperatures are well known and consistent for the various salmonids, they are probably not useful in setting temperature standards. Certainly they represent the upper limits to tolerance, but salmonids in a stream system tend to be restricted to maximum temperatures that are 3.6-7.2°F (2-4°C) lower than UILT values. In general, a maximum temperature of 71.6-75.2°F (22-24°C) represents the normal upper temperature limit in the field (see McCullough 1999). As this limit is approached, juvenile density declines to zero. Using the presence/absence threshold as a temperature standard for salmon habitat can only be done when density is at or near zero.

Although the UILT has limited value in establishing the temperature standard itself, the *a* and *b* coefficients for a given acclimation temperature are useful in estimating exposure times that will result in 50% mortality. In addition, NAS (1972) recommended (MWAT) as an index to tolerable prolonged exposures. This index was estimated as either:

[(opt. temp. + zng temp.)/2],

where the zng or zero net growth temperature is that temperature which results in zero net growth of a population (i.e., subtracting tissue lost as population mortality from that added in growth)

or

opt. temp. + (UILT – opt. temp)/3.

Each formula is based on the assumption that adequate growth rates can be maintained if the weekly average maximum temperature falls between the optimum and the UILT or the zero net growth temperature. However, the decline in growth rate can be very steep if temperature is above the optimum. Consequently, limiting reductions in growth rates to, for example, 80% of maximum levels can lead to much greater reductions in growth, given errors estimating the relationship or managing temperature in a watershed.

Are there potential weaknesses in reliance on MWAT?

Hokanson et al. (1977) advised caution in using short-term exposure experiments to calculate long-term exposures, such as with MWAT. They reported for *O. mykiss* that, given a physiological optimum of 60.8-64.4°F (16-18°C) and a UILT of 78°F (25.6°C) (at 60.8°F [16°C] acclimation), one would calculate an MWAT of 66.2°F (19°C) and a maximum temperature (applying the 2°C safety factor of Coutant 1972) of 75.2°F (24°C) for short-term exposure. Measurement of rainbow trout growth showed that at a fluctuating temperature of 71.6 ± 6.8°F (22 ± 3.8°C) specific growth rate was zero. Under this temperature regime mortality rate was 42.8%/d during the first 7 d. For experiments within the optimum range (59.9-63.1°F [15.5°C-17.3°C] for a fluctuating regime), average specific mortality was 0.36%/d. Combining data on specific growth and mortality rates, the authors were able to predict yield for a hypothetical population under the temperature regimes. A rainbow trout population would exhibit zero increase over a 40-d period (maintenance) at a constant temperature of 73.4°F (23°C) and a fluctuating temperature with a mean of 69.8 ± 6.8°F (21 ± 3.8°C) because growth balances mortality. Several sources report temperatures of 69.8-73.4° (21-23°C) as the upper limit of rainbow trout distribution in the field (Hokanson et al. 1977). Numerous authors have reported upper limits to salmonid distribution as approximately 71.6-75.2°F (22-24°C).

With this laboratory information and corroborating field information, Hokanson et al. (1977) recommended a mean weekly temperature of 62.6 ± 3.6°F (17 ± 2°C) for rainbow trout so that maximum yield is not reduced more than 27% under normal fluctuating temperature regimes. Production has been shown to be substantially reduced even just above the physiological optimum. This paper has great significance. It was published 5 years after the National Academy of Sciences recommended the use of MWAT to establish prolonged exposure temperatures. The NAS acknowledged that growth rate should be expressed as net biomass gain or net growth. Yield is that portion of the population available to humans; the remainder is lost as mortality, which can be substantial if temperatures are high. Also, if temperatures are high, much of the energy assimilated from food is lost as excessive metabolism. If the MWAT is 66.2°F (19°C), and yield is reduced 27% from maximum, even at a mean weekly temperature of 62.6 ± 3.6°F (17 ± 2°C) it is obvious that MWAT is not protective.

In addition to concern for the inadequacy of the MWAT, this criterion also covered reproduction and development needs of salmonids. A quote from NAS (1972) is useful:

> Uniform elevations of temperature by a few degrees during the spawning period, while maintaining short-term temperature cycles and seasonal thermal patterns, appear to have little overall effect on the reproductive cycle of resident aquatic species, other than to advance the timing for spring spawners or delay it for fall spawners. Such shifts are often seen in nature, although no quantitative measurements of reproductive success have been made in this connection.

However, significant recent research has shown that calculated MWAT temperatures (e.g., 66.2°F (19°C) for rainbow trout) result in damage to gametes during reproductive stages. On the basis of these technical findings, any temperature criterion that can result in a 27% reduction in biomass and affect gamete viability must be questioned.

How can UILT data be evaluated against UUILT data?

Temperatures as low as 73.4°F (23°C) have been found to produce 50% mortality (LT50) over the course of a week in rainbow trout acclimated to very cold (39.2°F [4°C]) waters (Sonski 1982, Threader and Houston 1983 as cited in Taylor and Barton 1992), with the lethal temperature rising to 75.2°F (24°C) in moderately cold-water-acclimated 42.8-51.8°F (6-11°C) fish (Black 1953, Stauffer et al. 1984, Bidgood 1980 as cited in Taylor and Barton 1992). However, at most acclimation temperatures likely to be encountered during the spring through fall seasons (53.6-68°F [12-20°C]), lethal levels are consistently in the range of 77-78.8°F (25-26°C) (Bidgood and Berst 1969, Hokanson et al. 1977). With cautious acclimation to temperatures in the range of 73.4-75.2°F (23-24°C), rainbow trout may not experience LT50 effects until a week at 78.8°F (26°C) (Charlon et al. 1970 as cited in Grande and Anderson 1991). Even with careful acclimation, 77°F (27°C) results in high or complete mortality in less than 24 hours (Charlon et al. 1970), and temperatures of 84.2-86°F (29-30°C) result in 50% mortality in 1-2 hours (Kaya 1978, Craigie 1963, Alabaster and Welcomme 1962 as cited in Taylor and Barton 1992).

How can prolonged exposure to cyclic temperatures be evaluated?

Under fluctuating temperature test conditions, rainbow trout have experienced 50% mortality in a week of daily cycles from 69.8 to 77°F (21-27°C) (Lee 1980). Sonski (1983), however, was able to culture rainbow trout in ponds that reached 84°F (28.9°C), and Chandrasekaran and Subb Rao (1979) reported that rainbow trout were largely able to survive in rearing ponds with months of daily maximum temperatures of 78.8-84.2°F (26-29°C).

It seems important, given the low lethal levels reported in the literature, to evaluate whether individual research results would unduly influence the temperature recommendations. In Figures 3 and 4, lethality data for salmon and char species (extracted from the summary by Hicks 2000) are combined and examined in two different ways to develop a stronger basis for regional daily maximum criteria.

In Figure 3, all of the available 7-d LT50 data (50% of test organisms die over a 7-d constant exposure test) for char and salmonids are presented by acclimation temperature. This distribution is then used to make criteria recommendations for acclimation temperatures. At low acclimation temperatures, constant exposure to just above 72.5°F (22.5°C) would be expected to result in 50% mortality over a week. Reducing this value to a level where no lethality would be expected to any adults or juveniles would result in a daily maximum not to exceed 68.9°F (20.5°C).

Figure 4 considers resistance against short exposures to high temperatures, as might occur in a natural fluctuating stream environment. Resistance time is very important to estimating potential lethality; it is the time spent above a lethal threshold that determines whether short-term lethal effects will occur. Different peak temperatures (e.g., 71.6, 75.2, 80.6, and 86°F [22, 24, 27, and 30°C]), may be lethal to an organism, but the organism can likely withstand these temperatures for variable lengths of time. A population of fish may be able to withstand 69.8°F (21°C) for 7 d of constant exposure without any mortality, but have 50% of the population die after 2 d at 75.2°F (24°C). At 80.6°F (27°C), 50% mortality may occur after less than 2 h of exposure, and at 86°F (30°C) complete mortality may occur in just a few minutes.

In considering the effect of repeated hot days, it is important to incorporate cumulative effects. DeHart (1975) found that lethal effects depend on the area of the temperature time curve that is above a fish's UILT. Thermal effects accumulate over several days when the daily temperature cycle fluctuates above the UILT, and the time above the UILT influences the thermal resistance time regardless of any lower test temperatures. In other words, the ability of a fish to resist a single day's exposure to a lethal temperature may not be sufficient, and 15 minutes spent at 7.2°F (4°C) over the UILT is of more consequence than the same time spent at 3.6°F (2°C) over the UILT.

In Figure 3, LT50 results are plotted for durations of 1 hour or less. At acclimation levels less than 53.6°F (12°C), 50% mortality can be expected at 77°F (25°C) with a 1-h exposure, or at 75.5°F (24.2°C) with a 2-h exposure. Reducing these values to levels where no lethality would be expected would result in temperatures not exceeding 73.4 or 71.6°F (23 or 22°C), respectively. Because adults are considered more sensitive than juveniles (all of the 1-h or less data were for juvenile fish), and the effects of lethal exposures are cumulative, we can assume that death may occur with repeated exposure to daily maximum temperatures greater than 69.8-71.6°F (21-22°C). This estimate is very similar to the results (68.9-70°F [20.5-21.1°C]) at low acclimation temperatures in the approach shown in Figure 2.

Acclimation Temperature °F (°C)	Combined LT50 for all Salmonids	Estimated LT1 with NAS Adjustment
41 (5)	72.46 (22.48)	68.9 (20.5)
50 (10)	73.56 (23.09)	70 (21.1)
39 (15)	74.66 (23.7)	71.06 (21.7)
68 (20)	75.75 (24.31)	72.14 (22.3)
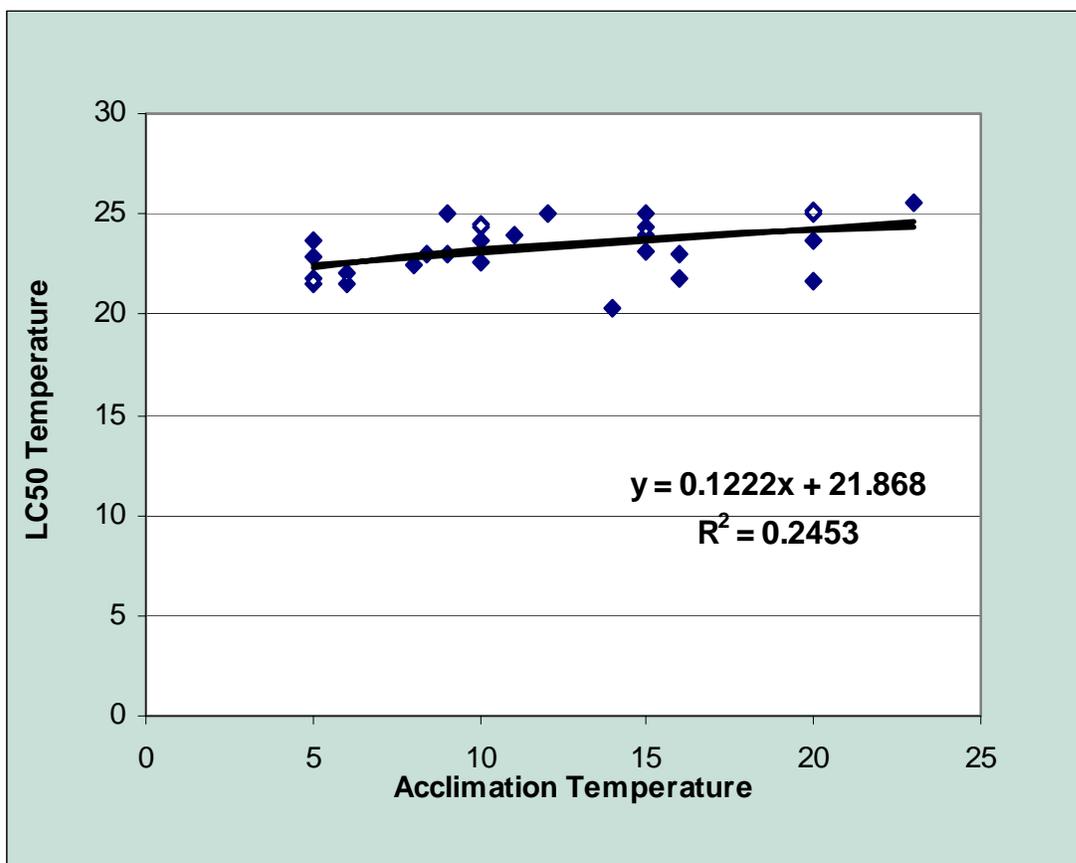
Figure 3. Combined lethality data for all salmonid species (based on 7-d LT50 constant temperature exposure test results).

What are the thermal requirements of bull trout and Dolly Varden?

Incubation. For bull trout, McPhail and Murray (1979) compared egg survival and water temperature and reported the highest egg survival to hatching (80-95%) in water temperatures of 35.6-39.2°F (2-4°C). Shortest hatch, largest alevins, and largest *hatching* fry were also associated with these low temperatures 35.6-39.2°F (2-4°C).

Research suggesting that spawning does not peak until temperatures fall to below 44.6°F (7°C) is consistent with the results of studies determining temperatures necessary for the successful incubation of char eggs. These studies show that char require temperatures below 42.8°F (6°C) to achieve optimal egg survival (Buchanan and Gregory 1997). It is generally agreed that poor survival occurs at temperatures above 44.6-46.4°F (7-8°C). Under test conditions where temperatures were held constant, 46.4-50°F (8-10°C) resulted in very poor survival of eggs (0%-20%) in tests by McPhail and Murray (1979), and test temperatures in the range of 44.6-51.8°F (7-11°C) were reported
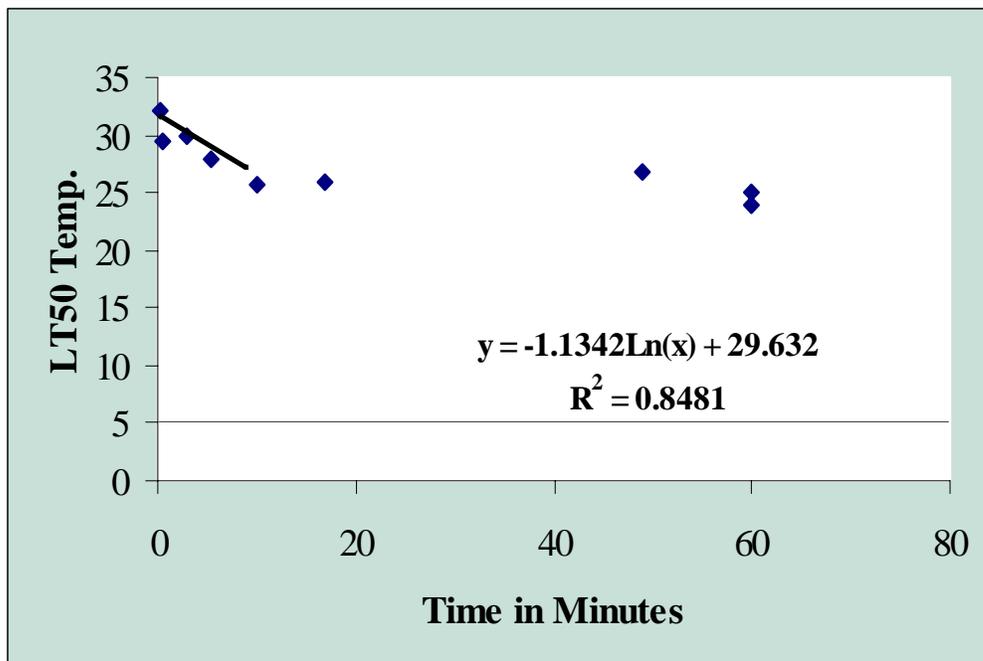
Time to LT50	Temperature (C)
1 sec	34.32
30 sec	30.42
1 min	29.62
60 min	24.99
120 min	24.2

Figure 4. Instantaneous mortality for char and salmon combined (based on LT50 data for exposures of less than 1 hour and acclimation to <12C).

to result in poor survival in hatchery culture by Brown (1985). McPhail and Murray (1979) found a temperature of 42.8°F (6°C) to produce variable survival rates (60%-90%), and the range of 35.6-39.2°F (2-4°C) produced the best survival (80%-95%). In studies on the related species of Arctic char, Humpesch (1985) reported optimal incubation to occur at 41°F (5°C).

In conclusion, for bull trout, temperatures falling to 48.2°F (9°C) and below may initiate spawning, but colder temperatures during incubation and yolk absorption produce the largest size and greatest number of fry (McPhail and Murray 1979). Although spawning tends to peak at 44.6°F (7°C), water temperatures continue to decline as the spawning season progresses and drop toward the optimum incubation temperatures of 35.6-42.8°F (2-6°C). Bull trout tend to select redds directly adjacent to or below areas of groundwater upwelling, resulting in relatively

constant cold water temperatures for egg incubation with little diel fluctuation (Baxter and Hauer 2000).

Growth. In a laboratory study by McMahon et al. (1999), limited rations lowered the optimal temperature for growth. For satiation-fed and 66% of satiation-fed juvenile bull trout, optimum growth occurred at a temperature range of 53.6-60.8°F (12-16°C). When energy availability was low (one-third satiation-fed fish), maximum growth occurred at lower temperatures (46.4-53.6°F [8-12°C]). In a related species, Arctic char, the upper thermal limits to both feeding and growth were 70.7-71.2°F (21.5-21.8°C) (Thyrel et al. 1999).

In a study analyzing the temperature effects on bull trout distribution in 581 sites, Rieman and Chandler (1999) found that juvenile/small bull trout appeared most likely to occur at summer-mean temperatures of 42.8-48.2°F (6-9°C) or single maximums of 51.8-57.2°F (11-14°C). When given a choice of temperatures from 46.4 to 59°F (8-15°C) in a large plunge pool, juvenile bull trout showed a clear preference for the coldest water available (6.4-48.2°F [8-9°C]) (Bonneau and Scarnecchia 1996).

Migration. Upstream spring migration of adult bull trout may be related to water temperatures and flows. In Rapid River, Idaho, a review of trap counts and temperature for 1985 through 1992 reported a general trend of increasing upstream bull trout counts as water temperatures reached 50°F (10°C) (Elle et al. 1994). McPhail and Murray (1979) found peak upstream movement coincided with water temperatures of 50-53.6°F (10-12°C).

Spawning. Bull trout spawning areas are often associated with cold-water springs, groundwater infiltration, and the coldest streams in a given watershed (Pratt 1992, Rieman and McIntyre 1993, Rieman et al. 1997). Bull trout spawning is initiated as temperatures drop to 48.2°F (9°C) or lower, and egg mortality is lowest and alevin development is strongest at colder temperatures (McPhail and Murray 1979). In Indian Creek, tributary to the Yakima River, bull trout spawning activity peaked when stream temperatures were 42.8-46.4°F (6-8°C) (James and Sexauer 1994). In the North Fork Skokomish River, bull trout spawned in October after water temperatures dropped below 43.7°F (6.5°C) (Brenkman 1998). Mean daily river temperatures ranged from 38.3 to 45.5°F (3.5-7.5°C) during the remainder of the spawning period. This does not differ significantly from descriptions of temperatures initiating bull trout spawning in Montana (Shepard et al. 1982), Oregon (Ratliffe 1992), or Washington (Kraemer 1994).

Although spawning for bull trout may begin as early as mid-August, spawning activity is reported to be initiated when water temperatures begin to decrease and fall to 48.2°F (9°C) or lower and does not peak until temperatures fall below 44.6°F (7°C) (McPhail and Murray 1979, Shepard et al. 1982, Kraemer 1994, Brenkemen 1998). Kraemer (1994) noted that when stream temperatures rise to above 46.4°F (8°C) once spawning has been initiated, spawning usually stops or slows.

Bull trout require a narrow range of cold temperatures to rear and reproduce and may thrive in waters too cold for other salmonid species (Balon 1980). McPhail and Murray (1979) reported that 0%-20%, 60%-90%, and 80%-95% of bull trout eggs from a British Columbia river survived to hatching at water temperatures of 46.4-50, 42.8, and 35.6-39.2°F (8-10, 6, and

2-4°C), respectively. In Montana, Weaver and White (1985) found that 39.2-42.8°F (4-6°C) was needed
for bull trout egg development. Buchanan and Gregory (1997) defined a range of 33.8-42.8°F (1-6°C) that would meet bull trout egg incubation requirements in Oregon.

Although data are not shown directly for char species, other salmonids are known to undergo some conditioning in the early stage of incubation that allows excellent survival at very low temperatures. Where conditioning does not occur, and the eggs are incubated at an early stage at very low temperatures, significant reductions in survival have been noted (Murray and Beacham 1986, Seymour 1956). Thus even if 35.6°F (2°C) is suboptimal at a constant incubation temperature, natural seasonal declines in temperature to 35.6°F (2°C) in the incubation period may not decrease survival. This assumption is supported by work showing that newly hatched Arctic char (*Salvelinus alpinus*) alevins are tolerant of temperatures near 32°F (0°C) (Baroudy and Elliott 1994) and that the lower limit for hatching in Arctic char is less than 33.8°F (1°C).

On the basis of the information examined, the initiation of spawning behavior and in vivo egg development will be fully supported by keeping maximum temperatures in the spawning areas below 44.6-46.4°F (7-8°C) during the spawning season. Given that excellent survival has been noted in tests at 42.8 and 43.7°F (6 and 6.5°C), that some increased problems with disease may be initiated at the higher end of this range, and that a variety of impacts to spawning have been noted above 44.6°F (7°C), it appears that constant or acclimation temperatures in the range of 37.4-42.8°F (3-6°C) are optimal for the incubation of char. Because char are highly resistant to low temperatures and low temperatures discourage disease organisms, water temperatures that swiftly decline to 35.6-39.2°F (2-4°C) as the incubation season progresses appear highly favorable.

What are the thermal requirements for Lahontan cutthroat trout?

Growth. Laboratory studies of growth conducted at constant temperatures showed that growth remained the same at temperatures of 55.4, 68, and 71.6°F (13, 20, and 22°C) (Dickerson et al. 1999, as cited in Dunham 1999). Growth was significantly reduced at 75.2°F (24°C). Tests done under a fluctuating temperature regime of 68-78.8°F (20-26°C) with a daily mean of 73.4°F (23°C) for 1 wk showed growth rates were lower under this temperature regime than for fish exposed to constant temperatures of 55 and 68°F (13 and 20°C). The growth rates under the fluctuating regime were similar to growth rates of fish held at a constant 73.4°F (23°C).

Thermal stress—heat shock proteins. Lahontan cutthroat trout begin to produce heat shock proteins immediately when exposed to 78.8°F (26°C) water temperature. Fish exposed to 75.2°F (24°C) water temperature began to produce heat shock proteins within 24 h. Fish exposed to 71.6°F (22°C) water temperature did not produce heat shock proteins, even after 5 d of exposure.

Occurrence. Dunham (1999) found that the distribution limit of most Lahontan populations corresponded closely to a maximum summer water temperature of 78.8°F (26°C).

The Willow Creek population in Oregon occurred in water with daily maximum temperatures up to 83°F (28.4°C).

Lethal effects. It has often been assumed that Lahontan cutthroat trout have a greater tolerance for warm water than other salmonids because of their geographic distribution in warm climates. Although there are not abundant studies of Lahontan cutthroat thermal requirements, good evidence indicates that this species is comparable to other salmon and trout in its response to warm water.

Critical thermal maximum (CTM) tests of thermal resistance were conducted on two strains of Lahontan cutthroat trout by Vigg and Koch (1980). The two strains tested were Marble Bluff and the Summit Lake strain found in Pyramid Lake. The test was designed to determine the effect of alkalinity on CTM values. In both strains it was found that as alkalinity increased from 69 to 1,487 mg/L, the CTM decreased. Average CTM values determined for the death (D) temperature endpoint were approximately 72.3-67.2°F (22.4-19.6°C) over this alkalinity range (average values for the two strains). This CTM study employed a stepped temperature increase equal to 1.8°F (1°C)/d up to an exposure temperature of 68°F (20°C), starting from an acclimation temperature of 60.8°F (16°C). After 68°F (20°C) was reached, the increments were 1.8°F (1°C)/4d. Because of the stepped increases and the two different rates of heating, the study methodology is not completely analogous to conventional CTM technique. The initial period of increase to 68°F (20°C), however, could be considered to provide nearly full acclimation (given a 4-d acclimation at each step) before the subsequent heating schedule. The temperature increase rates for the two exposure periods averaged approximately 0.04°C/h and 0.01°C/h, respectively (averaging the thermal increase over the step time interval). CTM tests provide results that have a different meaning from UILT test results. Comparison of CTM values for other salmonids that have corresponding UILT values is useful to understand the relative thermal tolerance of Lahontan cutthroat. For example, appropriate comparisons of CTM values among species can be made by contrasting the Lahontan results with CTM values for salmonids whose temperature increase rates are 0.018-0.14°F (0.01-0.08°C)/h and starting from acclimation temperatures of 60.8-68°F (16-20°C) (McCullough 1999). Grande and Anderson (1991) measured a CTM of 79.3°F (26.3°C) for 2- to 3-month-old rainbow trout, 81°F (27.2°C) for 3- to 4-month-old brook trout, and 78.6°F (25.9°C) for 2- to 4-month-old lake trout. Elliott and Elliott (1995) reported CTM of 81.9°F (27.74°C) for Atlantic salmon and 76.6°F (24.8°C) for brown trout. The Lahontan cutthroat studies reported CTM for a death endpoint; the Grande and Anderson studies also used a death endpoint. If a loss of equilibrium (LE) endpoint is used to record CTM, the critical temperature is generally slightly lower than if a death endpoint is used. For example, at a heating rate of 1.8°F (1°C)/h, Becker and Genoway (1979) measured a CTM for coho salmon as 81.8 and 81.7°F (27.7 and 27.6°C) for the LE- and death-temperature endpoints, respectively. However, at a 64.4°F (18°C)/h heating rate, these values were 83.6 and 85.4°F (28.7 and 29.7°C), respectively. In conclusion, the CTM values for Lahontan cutthroat trout, compared with other salmonids tested in a similar manner (i.e., rainbow trout, brook trout, lake trout, Atlantic salmon, brown trout), are much lower. UILT values determined in other studies (see Table 4) for all the species that were contrasted above with Lahontan ranged from 73.4 to 79.5°F (23-26.4°C). Using CTM data as a guide, these results appear to indicate that Lahontan cutthroat would likely have lower UILT values than these other salmonids.

Dickerson and coworkers (1999, and unpublished data, in Dunham 1999) found in laboratory tests at constant temperatures that survival was 100% at 75.2°F (24°C) but dropped to 35% at 78.8°F (26°C). Tests done under a fluctuating temperature regime of 68-78.8°F (20-26°C) with a daily mean of 73.4°F (23°C) for 1 wk showed no mortality even though this regime provided 1-h/d exposure to 78.8°F (26°C) for 7 consecutive days, a temperature that produced mortality during longer exposures (Dickerson and Vinyard 1999). These data indicate that the UILT is probably between 77 and 78.8°F (25 and 26°C). However, temperature adjustment rates, starting from an initial temperature of 55.4°F (13°C), were 7.2°F/d (4°C/d) up to the test temperature. That is, a conventional time period for acclimation was not allowed prior to the final exposure temperature. This could result in a slight underprediction of UUILT.

What are the thermal requirements for westslope cutthroat trout?

Incubation and egg survival. In a study by Shepard et al. (1982), westslope cutthroat trout in the Flathead River basin, Montana, emerged in July and August following incubation temperatures ranging from 35.6 to 50°F (2-10°C). Fry were approximately 20 mm long at emergence. Adult westslope cutthroat trout held in cool 35.6-39.2°F (2-4°C) water temperatures produced more viable eggs than those held in constant water temperatures of 50°F (10°C) (Smith et al. 1983, in Shepard et al. 1982).

Growth. Westslope cutthroat streams are typically cold, nutrient-poor waters in which conditions for growth tend to be less than optimal (Liknes and Graham 1988).

Spawning. Initiation and timing of spawning activity is related to water temperatures. Adults move into tributaries during high streamflows and spawn in the spring when water temperatures are near 50°F (10°C) (Scott and Crossman 1973).

Occurrence. Westslope cutthroat trout and bull trout have similar life history patterns, often occupy the same headwater streams, and restrict themselves to the coldest sections of streams (Jakober et al. 1998, Behnke 1992). Westslope trout prefer cooler water temperatures than do both brook trout and Yellowstone cutthroat trout (B. Shepard, personal communication).

Westslope cutthroat trout and redband trout may occur in the same system. They can be allopatric or sympatric, but the redband generally inhabit lower reaches and cutthroat trout (often with bull trout) dominate the upper, higher gradient sections where annual temperature units are considerably less (Mullan et al. 1992).

What are the thermal requirements for redband trout?

Growth and feeding. Dwyer et al. (1986) conducted temperature experiments at 39.2, 44.6, 50, 60.8, and 66.2°F (4, 7, 10, 13, 16, and 19°C) on rainbow trout and redband trout collected from Threemile Creek, Catlow Basin. Redband trout from Threemile Creek showed the best growth at 66.2° (19°C) (no higher temperatures were tested), whereas rainbow trout exhibited the best growth at 59-60.8°F (15-16°C).

In a study by Sonski (1982, as cited by Sonski 1983b), redband trout reached their maximum growth rate at 68°F (20°C). Growth rates were less at both 59°F (15°C) and 73°F (22.8°C).

Redband trout are thought to exhibit the upper limit for feeding response for all salmonids of the Pacific Northwest. No feeding was observed by Sonski (1982 as cited by Sonski 1984) for juvenile redband at temperatures above 77.9-80.6°F (25.5-27°C). In a comparison of thermal tolerance by three rainbow trout species, Sonski (1984) found that no redband trout or Wytheville rainbow fed at temperatures higher than 78.8°F (26°C), and the Firehole River rainbow would not feed beyond 80°F (26.7°C).

Metabolic activity and swimming speed. Gamperl (in litt.) conducted temperature studies in Bridge Creek ("warm" stream) and Little Blitzen River ("cold" stream) in the Harney basin. Gamperl's studies found that despite the two streams' different thermal histories, redband trout from each stream exhibited a similar preferred temperature of 55°F (12.8°C). Bridge Creek trout had greater metabolic power and improved swimming efficiency at 75.2°F (24°C) than at 53.6-57.2°F (12-14°C) compared with the Little Blitzen River redband, which had similar values for metabolic power and swimming performance at 53.6-57.2°F (12-14°C) and 75.2°F (24°C). Gamperl concluded that some populations of redband trout can tolerate, and may have adapted to, warm environmental temperatures. However, these studies should be taken as preliminary because they were not replicated.

Occurrence. There are observations of redband trout feeding and surviving at relatively high temperatures for a salmonid (82.4°F [28°C], Behnke 1992; 81.3°F [27.4°C] Sonski 1986; 80.6°F [27°C] Bowers et al. 1979), although it is unclear whether temperatures were measured in the vicinity of the stream that the fish actually inhabited. These trout may rely on microhabitats or thermal refuges to maintain populations in desert environments (see Ebersole et al. in press).

Lethal effects. In a comparison of thermal resistance among redband trout, Firehole River rainbow, and Wytheville rainbow, Sonski (1984) found very little difference. He measured UILT values for subyearling trout acclimated at 73.4°F (23°C) of 79.1, 79.3, and 80.6°F (26.2, 26.3, and 27.0°C), respectively. These values are probably equivalent to UUILT values because it appears that resistance was not improved by acclimation beyond 59°F (15°C). It is interesting that redband trout were not significantly different in their thermal tolerance from other rainbow stocks, despite their reputation as being tolerant of higher water temperatures.

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