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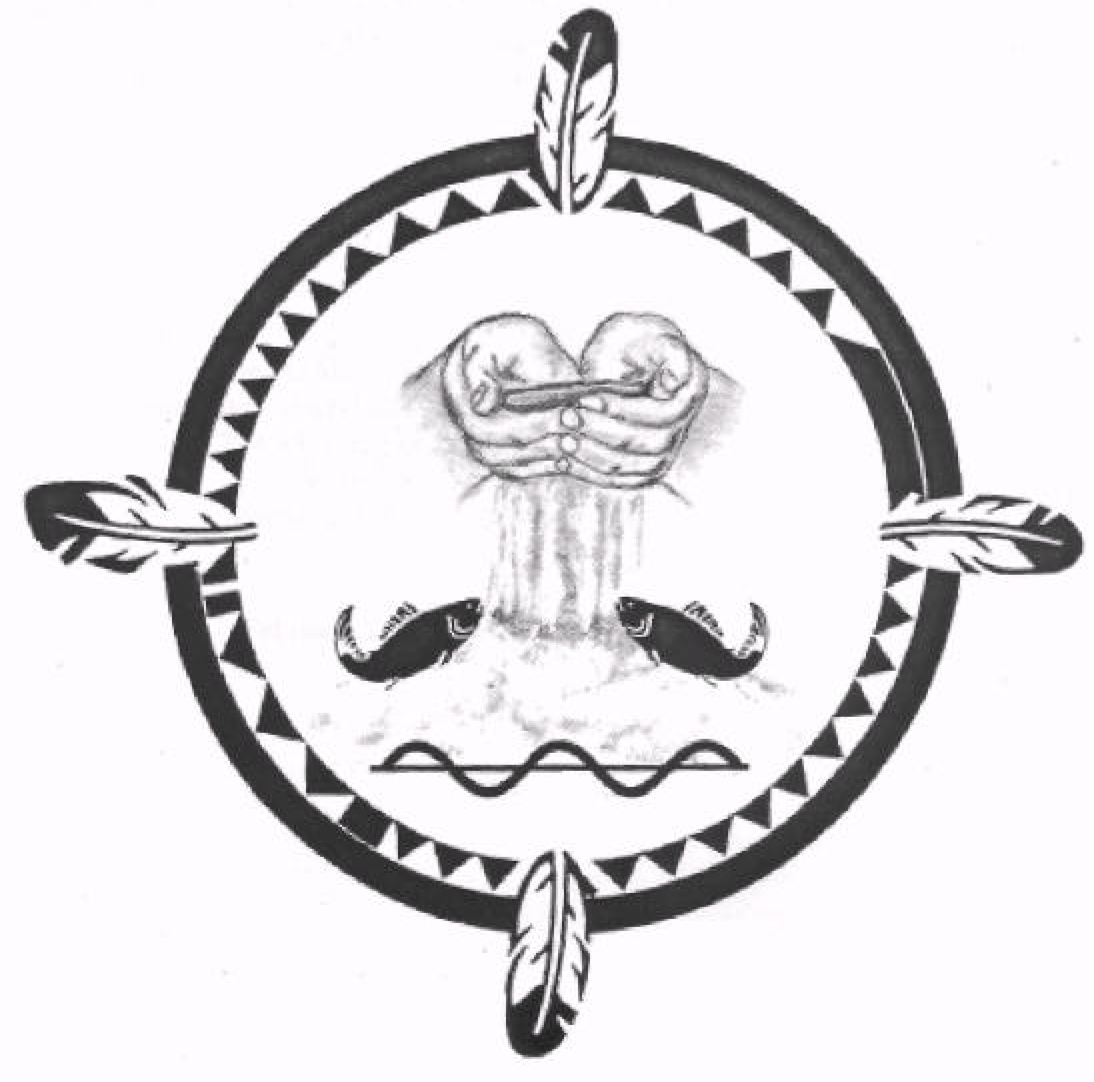
# A Review and Synthesis of Effects of Alterations to the Water Temperature Regime on Freshwater Life Stages of Salmonids, with Special Reference to Chinook Salmon



# A REVIEW AND SYNTHESIS OF EFFECTS OF ALTERATIONS TO THE WATER TEMPERATURE REGIME ON FRESHWATER LIFE STAGES OF SALMONIDS, WITH SPECIAL REFERENCE TO CHINOOK SALMON

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I would like to express appreciation to the Environmental Protection Agency —Region 10 for their funding of this project and their great patience in awaiting its completion. Donald Martin, as project manager for EPA, was very helpful with the entire project, and was especially encouraging throughout the project and a definite pleasure to work with. Much thanks also go to the Columbia River Inter-Tribal Fish Commission, Portland, Oregon for substantial financial support to complete this work. Fisheries Science Department manager Phil Roger was always supportive of the need for a report such as this. Colleagues at CRITFC (Roy Beaty, Jon Rhodes, and Matthew Schwartzberg) were greatly encouraging in sustaining the effort to complete the writing. Other CRITFC staff provided many kinds of assistance that also facilitated the work. In particular, I appreciate the efforts of the StreamNet Library staff (see www.streamnet.org) in securing numerous references for review.

The cover art was provided by Roberta Stone and Jeremy Crow, both of the CRITFC. We are especially grateful for their creative contribution to this document. The cover design reflects the circle of life, encompassing all of creation. The feathers symbolize the four treaty tribes of the Columbia River, the Yakama Indian Nation, the Confederated Tribes of the Umatilla Indian Reservation, the Confederated Tribes of the Warm Springs Reservation of Oregon, and the Nez Perce Tribe. They also symbolize the four directions. The hands indicate that humans are caretakers of life's resources. The tribes of the Columbia River have held for centuries, as a major part of their culture, that care for water and salmon and other wildlife was their responsibility. Water and fish are the givers of life to the tribes. The border design to the circle is common to beadwork of these tribes. The sine wave on the water represents the interaction of technology with culture. It is the influence of temperature cycles on water quality and salmon.

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# INTRODUCTION

## SALMON STATUS

Average annual adult salmon runs were estimated to be 10-16 million fish historically. Of this number there were 7.4-12.5 million salmon destined for above Bonneville Dam. Currently, this number has dwindled to 600,000, of which approximately 58% are produced by hatcheries (ODFW and WDFW 1995, as cited by CRITFC 1995). Passage mortalities through the system of dams average 15-30% per dam for juvenile emigration and 5-10% per dam for adult immigration. Cumulative dam mortality through 9 dams is 77-96% for juveniles and 37-51% for adults (NPPC 1986). Sources of mortality are numerous and include environmental effects of timber harvest, agriculture, livestock grazing, mining, urbanization, overfishing, and direct habitat destruction (e.g., estuary diking or filling), in addition to dam-related mortalities. These mortality sources taken cumulatively threaten the inherent capability of salmon populations to replace themselves.

Currently, the National Marine Fisheries Service has listed numerous stocks of salmon in the Columbia River basin under the Endangered Species Act. These include stocks listed as endangered (Snake River sockeye, upper Columbia River steelhead), and threatened (Snake River fall chinook, Snake River spring/summer chinook, Snake River steelhead, lower Columbia River steelhead). Other stocks recently have been proposed for listing as endangered (upper Columbia River spring chinook) and threatened (lower Columbia River chinook, upper Willamette River chinook, upper Columbia River spring chinook, Columbia River chum, upper Willamette River steelhead, and middle Columbia River steelhead) (NMFS 1998a). Numerous other species and stocks have been candidates for listing, such as coho, bull trout, cutthroat trout. Adverse stream temperatures caused by cumulative anthropogenic activities in the mainstem and tributaries of the Columbia River contribute significantly to making recovery of these stocks uncertain. Similarities in response to temperature perturbation make all these species and stocks vulnerable.

Among these listed stocks some population trends indicate the perilous biological status. For example, Snake River fall chinook were listed as threatened in 1992. This population numbered approximately 72,000 natural spawners in 1940 but in recent years (1992-1996) this declined to 500. Snake River spring summer chinook, which were also listed in 1992 have been estimated to have had 1.5 million adults in 1800, a number that has been reduced to 2500 natural spawners recently. The stream area utilized by such low population numbers of these stocks is very large. With a small overall population size distributed over a massive habitat area, population density for any individual stream can be so low as to make success in spawning marginal. In addition to these demographic effects, poor habitat quality impairs prospects for recovery. Among the most significant water quality parameters, elevated water temperature does not tend to be a problem confined to limited portions of these large spawning and rearing habitats.  Rather, the problem is extremely widespread throughout the range of these stocks.  Once water temperatures become warm along the course of any river they remain warm, except for stream reaches gaining significant groundwater inflow. Presence of dense riparian canopy can delay downstream warming trends, but when a stream is opened up and warmed, it does not cool appreciably in downstream shaded zones, but again has a delayed rate of warming.

## SALMON HABITAT STATUS

Since 1850 there has been a substantial loss in habitat **quantity** for the Columbia River basin's stocks of spring, summer, and fall chinook, chum, sockeye, coho, and steelhead.  The Columbia River before 1850 supported 12,935 miles of anadromous fish bearing stream and currently affords access to 8,916 miles, representing a loss of 31% in available stream length owing to water development (NPPC 1986, p.4).  Loss of anadromous fish habitat in the Columbia basin above Bonneville Dam over this same time period has been 38% (10,525 miles, reduced to 6537 miles).  What remains has been substantially altered in **quality**, leading to further reductions in potential anadromous fish production.  Historically, the majority of the high quality habitat of spring, summer, and fall chinook was on privately owned lands where degradation has been most severe.  Loss of habitat quantity and quality in the tributaries is responsible for a decline in the carrying capacity of tributary spawning and rearing areas (McCullough 1996) but carrying capacity for the salmon production system as a whole brings into question the quantity and quality of essential habitats throughout the entire migration pathway.

Loss of habitat quantity has resulted from land management actions such as building of mainstem hydroelectric dams, tributary irrigation dams, and installation of hundreds of culverts on road crossings over small tributaries, all of which can create passage impediments. In addition, summertime diversion of water from stream channels causes a partial or total loss of usable habitat area.  Loss of habitat quality in the Columbia River subbasins has arisen from land management actions that have increased stream water temperatures, increased sediment delivery and deposition of fine sediment in spawning and rearing substrate, increased stream channel width, reduced average depth, reduced pool volume and frequency, and reduced large woody debris volume and distribution in the channel.  Loss of quality has also been produced by cumulative impacts across the entire stream system that have resulted in habitat fragmentation and disproportionate loss of certain critical habitats for key life stages.  Evaluation of this site-specific loss of habitat quality can be made by accounting for spatial considerations, such as whether migration corridors are maintained or whether migration distances among components of habitat (e.g., spawning, summer rearing, overwintering areas) are acceptable.

Among these impacts to habitat condition, it is probable that the combination of increased water temperature and increased streambed sedimentation by fine sediments is a sensitive indicator to the biological effects of the majority of land management actions.  For example, land management activities in the riparian zone and on forest, range, and agricultural lands of the watershed tend to increase sediment delivery over natural background levels and result in loss of pool volume and frequency, degradation of spawning and rearing substrate, and increased width-to-depth ratio (W/D). Riparian timber harvest or vegetation removal (grazing, clearing, thinning) results in increased water temperature, reduction in recruitable woody debris, and frequently in reduced bank stability that leads to increased W/D, sediment delivery from bank erosion, and loss of primary pools and bank overhanging cover. Streambank impacts magnify the severity of water temperature elevation by increasing channel width and thereby the water surface area subject to direct solar radiation or heat exchange with the air. Water temperature and sediment effects are, themselves, among the most significant factors directly affecting salmonid habitat quality and production in the Columbia River and its tributaries (Rhodes et al. 1994).

A recent report by the USEPA, Region 10 (1992) prepared for the Northwest Power Planning Council tabulated the collective professional judgement of the Water Quality Committee of the Columbia River Water Management Group (represented by USGS, USFS, USFWS, SCS, EPA, COE, USBR, and BPA) and information submitted to EPA under Sections 305(b) and 319 of the Clean Water Act. Although this report did not identify the spatial extent or magnitude of temperature problems within a subbasin, it does reveal the pervasiveness of threats to salmon habitat. Temperature problems were noted for the Columbia River estuary, Mainstem Columbia from mouth to Chief Joseph Dam, Willamette, Coast Fork of the Willamette, Lewis, Cowlitz, Deschutes, John Day, Umatilla, Walla Walla, Yakima, entire mainstem Snake River, Clearwater, Tucannon, Palouse, Grande Ronde, Salmon, Imnaha, Burnt, Payette, Owyhee, Boise, Wenatchee, Entiat, Methow, Okanogan, Flathead, and Spokane rivers. Because of the extent of ecosystem alterations produced by years of logging, road building, grazing, and mining throughout the John Day River subbasin, the habitat usable by spawning chinook is currently limited to less than one third of probable historic habitat (Wissmar et al. 1994). This has restricted current distribution to headwaters of the mainstem, the Middle Fork, and the North Fork tributaries of the John Day.

Attempts have been made to quantitatively estimate the magnitude of thermal alterations made to tributaries and the mainstem of the Columbia River. Assessments by federal scientists indicate that in 85% of managed (i.e., those lands not designated as wilderness or roadless) watersheds maximum water temperatures have increased by ≥2°C over historical values (National Academy of Sciences 1996). In Oregon, Washington, and Idaho nearly 2500 waters have been assigned to State 303(d) lists. Of these waters, 1100 were listed for their temperature problems (Cleland 1997). "On federal lands in Oregon, 55 percent (20,400 miles) of the streams are moderately or severely impaired (Fig. V-7). On Bureau of Land Management lands, 7,300 miles of streams, and 4,900 miles of streams on Forest Service lands have water temperature problems. An additional, 8,000-11,000 miles have problems with turbidity, erosion, and bank instability" (FEMAT 1993). In the mainstem Columbia River there has been a trend during the last 50 years of increasing summer water temperatures and progressively earlier peak temperatures (Quinn and Adams 1996). This trend may be influenced to some extent by long-term climatic trends, but the current reservoir system has produced other related thermal changes. The large storage volumes, by virtue of thermal inertia, cause a several-week prolongation of temperatures exceeding critically high levels and a reduction in diel variation (Karr et al. 1992, Karr et al. 1998).

These assessments are useful attempts to map out the water quality status of streams throughout the region but unfortunately, the true extent to which temperature pollution undermines salmon production is vastly underreported. This situation is a product of lack of monitoring data (see McCullough and Espinosa 1996), lack of analysis and/or reporting of available data, lack of widespread recognition of the temperature requirements of salmon, political unwillingness to make the obvious linkages between land management causes and effects and to implement controls. Science, as practiced in the Columbia Basin, is also frequently at fault, for allowing spurious technical arguments to deflect attention from these known cause-effect relationships. For example, technical uncertainty over the degree of spatial/temporal variability in water temperature, the proportional role of natural events vs. management as causative agents, allowing the full range of natural variation in "unmanaged" watersheds to act as a reference condition for managed watersheds, or the use of unrealistically stringent statistical detection limits to demonstrate management effects (see Rhodes et al. 1994) are all frequently obstacles to applying the best of our understanding about managing watersheds.

Approximately 50% of the remaining anadromous fish habitat area in the Columbia River basin is federally owned and this portion constitutes the majority of the best remaining habitat for many species. Wilderness and roadless areas on these lands have taken on increasing importance as refuges where much of a subbasin's salmon production is concentrated, owing to the cold water and generally high habitat quality. The remaining relatively cooler streams providing habitat for chinook, steelhead, bull trout, and cutthroat trout or contributing cool water to downstream anadromous fish zones tend to be found on U.S. Forest Service land. The following tributaries and wilderness or roadless areas of these subbasins are key production areas: North Fork John Day River, North Fork John Day Wilderness in the John Day River subbasin; Wenaha-Tucannon Wilderness, Tucannon River and Wenaha River in the Tucannon and Grande Ronde River subbasins; North Fork Umatilla River and North Fork Umatilla River Wilderness in the Umatilla River subbasin; Minam River, Imnaha River, and Eagle Cap Wilderness in the Grande Ronde and Imnaha subbasins; Frank Church Wilderness and Middle Fork Salmon River in the Salmon River subbasin; White Sand Creek in the upper Clearwater River subbasin. Many of the roadless areas have been the focus of recent attempts to apply "new forestry" concepts in an attempt to restore "ecosystem integrity." Rationales for incursions into roadless areas have been reliant on salvage logging or thinning for reduction of disease or fire threat. Protection of the cold water resource vital to salmon production in these and other salmon strongholds has too frequently been compromised via an economic process of optimizing the rewards to the salvage operation and trading off habitat quality with the promise of recovery sometime in the future. Also, despite the good intentions of ecosystem management in forestry today, the physical linkages among water routing and sustained summer flows, basin-wide sediment delivery and channel morphology, natural or altered stream width and old growth tree height, stream width or pool volume and stream heating, air or soil temperature and groundwater temperature, loss of shade on intermittent streams and water temperature elevation, and cumulative effects of canopy reduction on a basin-wide scale and increase in the longitudinal temperature profile tend to be rapidly obscured when it comes to planning future management actions in watersheds that are already damaged. These "oversights" in management tend to aggravate water temperature and streambed sediment conditions in the short as well as the long term (see Espinosa et al. 1997).

## POTENTIAL FOR RECOVERY

The potential for recovery depends upon the severity of alterations to the physical state of the watershed and stream, the significance of relatively permanent engineered features (e.g., dams, roads), or biological events (e.g., extirpation, introduction of exotic fish species or disease vectors), the potential of the biogeoclimatic system (sensu Warren 1979, McCullough 1987, 1990), recovery actions applied, and the protection measures directed to the watershed and stream system in forest practices. Even if one were to assume that water quality was satisfactory for salmonid production in stream reaches whose watersheds are already developed, the prognosis for basin-wide water temperature control is not sanguine. Forest Practices rules in the Northwest states on private lands allow for harvest of riparian timber in perennial and intermittent fish-bearing and non-fish bearing streams tributary to salmonid production zones. Considering forestry rules on private and state lands in Oregon, Washington, and Idaho, the designated widths of riparian management areas vary considerably among states for various stream classes on the westside and eastside of the Cascades.

Protection afforded to the large, permanent, fish-bearing stream reaches is typically far less than what is needed to maintain optimum ecological function (shading, LWD delivery, sediment control) and the protection given to intermittent and non-fish bearing streams, which can comprise a large percentage of a watershed's stream miles, is reduced to negligible levels (Spence et al. 1996). Protection of riparian management areas required in federal land management strategies outlined in FEMAT and PACFISH for westside and eastside forests, respectively, is greater than for non-federal lands, but timber harvest or reduction in riparian buffer width is still allowed provided that it can be justified with a watershed analysis or to meet a riparian management objective. There are numerous approaches used to justify logging in riparian areas that frequently result in aggravating thermal regimes in either salmon-bearing streams or streams that are tributary to them, such as salvage, conifer disease reduction, thinning for growth release effects on remaining trees, stand conversion from alder to conifer, wildlife enhancement, etc. Some of these effects can be short-term (a few years) but if basin wide stream temperatures are already critically high, even a few years of increased temperature regimes could create a major biological impact.

The Forest Practice Act adopted by each state is considered by them to be a BMP that will result in meeting water quality standards, despite the fact that each state has different BMPs. Unfortunately, when BMPs are used, there is an assumption by managers that water quality will be maintained despite the amount of riparian area subject to harvest in any particular year. That is, the distribution in time of impacts from application of BMPs is not regulated, except if an integrated management plan (coordinated among landowners and regulated in time) is in effect. The same problem exists for federal lands. Even federal land managers seldom consider the cumulative effects of their actions in conjunction with those of non-federal land managers, partly because of an assumption that BMPs will not result in water quality degradation. The inadvisability of relying on BMPs is apparent when one realizes that even federal land managers frequently propose further impacts to riparian buffers before a stream has recovered to the point that it meets habitat standards (Espinosa et al. 1997).

The potential for recovery in water temperature regime in stream reaches and longitudinally in a stream system is well illustrated on the Tucannon River subbasin, Washington, by Theurer et al. (1985). They used the stream segment temperature model SSTEMP developed by the Soil Conservation Service and the US Fish and Wildlife Service to predict stream temperature profiles along the Tucannon's entire mainstem length under historic climax vegetation and channel morphology condition. This modeling exercise required extensive data on current and historic riparian cover and channel widths. It was estimated that by restoring riparian cover and channel morphology to predevelopment conditions, the mean daily water temperature for July observed at the mouth (22.4°C) could be reduced to 19.1°C. Current mean maximum water temperature for July measured at the mouth of the Tucannon River was 26°C (Theurer et al. 1985), but would be reduced to 22°C if all riparian and channel morphology restoration is done. This amount of temperature recovery does not account for limitations that may still be caused by loss of pool volume due to in-channel sedimentation, restoration of wetlands, reduction of road density, or riparian restoration on tributaries (see Rhodes et al. 1994).

Theurer et al. (1985) estimated the effect of improving the riparian cover and channel morphology for the Tucannon River mainstem. This restoration would result in an increase in adult returns from 884 currently to 2236 **(Fig. 1)**. Chinook rearing capacity would increase by a factor of 2.5 (i.e., from 170,000 to 430,000). Using this same framework, one could estimate by extrapolation on an areal basis that adult returns and juvenile rearing capacity would decrease to 704 adults and 135,000 juveniles if there is an additional 1.1°C temperature increase (J. Rhodes, Columbia River Inter-Tribal Fish Commission, Portland, OR, pers. comm.).

Similar results were achieved by EPA (Chen and Chen 1993, Norton 1996) in reconstructing the historic temperature regime for the upper Grande Ronde River, Oregon. These authors used aerial photography to evaluate current riparian condition. They used the HPSF model to estimate the degree of improvement achievable by restoring the entire riparian system to predevelopment riparian canopy conditions. Significant improvement was indicated for all stream reaches and a large increase in travel distance downstream of cold water from headwater tributaries was produced by the increased canopy cover. This resulted in an increase in total area available that meets minimum biological needs. This modeling did not account for improvements in usable area that could occur from restoration of channel morphology, wetland restoration, reduction of sediment impacts, or increase in pool volume and frequency.

Given the magnitude of the alterations to thermal regimes of streams of the Columbia River basin, the continued worsening of these conditions under existing forest practices and other land management practices, and the tendency to extend inappropriate management regimes to remaining high quality habitats having cold water temperatures, there is greater need than ever to understand the temperature requirements of coldwater species and the numerous mechanisms for detrimental biological impact at various salmonid life stages, how to evaluate the thermal environment, and how to improve and restore suitable conditions throughout the historic range of the species. This approach is based upon "full protection of beneficial uses" (refer to Clean Water Act) in its truest sense and the physical conditions that permit this. This approach is antithetical to current practices of setting temperature standards and then allowing new dispersed and ongoing thermal impacts to cumulatively limit or reduce suitable habitat, shrinking it headward to low order tributaries. Likewise, this approach points out the need to undertake restoration in a comprehensive watershed program rather than as site-specific, after-the-fact mitigation for continued dispersed degradation in other stream reaches. Impacts to the stream system (especially water temperature and substrate fine sediment) from land management actions and recommended protection and restoration were reviewed in Rhodes et al. (1994). This current report explores the varied biological effects of water temperature or temperature regimes on all life stages of salmonids. Today's multifaceted, comprehensive attack on the integrity of the ecosystem requires an equally comprehensive understanding of the biological impacts.

## OBJECTIVES AND APPROACH TO BE TAKEN IN LITERATURE REVIEW AND SYNTHESIS

Few stream habitat management issues are so controversial as control of land management impacts that increase water temperature, nor so prone to muddled understanding of biologic response. This is remarkable because the literature on effects of water temperature and temperature change on species and communities is so voluminous. Such effects have been described on survival, growth, metabolism, production, reproduction, behavior, competition, predation, swimming, etc. It may be largely the magnitude of information available on so many species and their life stages that makes full comprehension of the influence of temperature during a species' life cycle so difficult. And with so many kinds of effects and linkages between them, one has to evaluate the relative importance of these impacts and determine what kinds of temperature monitoring indices would be of use in scientific investigation and in management.

Numerous compilations have been made of thermal requirements of various fish species over the last 40 years (Parker and Krenkel 1969, EPA and NMFS 1971, Coutant 1972, 1977, Brungs and Jones 1977, Alabaster and Lloyd 1982, CDWR 1988). Despite the extent of the literature relevant to effects of temperature on fish, there is still great debate on how and whether all this information applies to conditions found in natural streams. The objectives of this review of the literature are to: (1) interpret and synthesize the literature on temperature effects to salmonids and other coldwater species and their life stages, (2) consider not simply effects during a single short-term exposure to a sustained high temperature but effects of altered temperature regimes under short-term and long-term exposure to constant or fluctuating temperatures, (3) compare and contrast response to temperature of several coldwater fish species, stocks, or family groups, (4) recommend standards that are biologically defensible, (5) review and recommend methods for evaluating water temperature regime to determine whether it meets biological requirements.

To meet these objectives this review will focus on the life stages of spring chinook (Oncorhynchus tshawytscha) as a template. Upon this foundation the results and conclusions from related studies on other coldwater fish species will be evaluated. This approach to review of salmonid response is reasonable because of the high degree of similarity exhibited among these species. Frequently, it will be found that when information on certain effects of temperature are lacking in chinook technical literature, information will be available for other salmonids. Taking the salmonid literature as a whole and by comparing and contrasting, the understanding of response to thermal experience by salmon and trout can become very robust. Selected coldwater non-salmonid literature will be considered to indicate those temperature conditions that both salmonids and other coldwater species would find suitable. Temperature requirements for common warmwater exotic species will also be noted to indicate the ecological problems faced by salmonids in competitive and predator-prey interactions and to provide a relative index by which to judge salmonid requirements (e.g., contrasting optimum conditions for coldwater and warmwater fishes). Significant differences among salmonids occur frequently via separate life histories. For example, spring chinook, which immigrate in the spring and spawn in 3rd to 5th order streams, face different migration and adult holding temperature regimes because of life history variation, fish size, and habitat selection than do summer or fall chinook, which spawn in streams of 5th order or greater as a rule. However, for similar life stages experiencing the same thermal regime (e.g, if spring and summer chinook juveniles have overlapping habitats), biological responses do not vary so much that different temperature standards are warranted, with a few exceptions.

It is important to gain a comprehensive understanding of responses to temperature regimes in order to adequately evaluate their suitability with respect to a given life stage or the entire life cycle. This kind of understanding can only be gained by synthesizing both field and laboratory observations. This review is an attempt to synthesize experience on salmonids during their life stages and their associated responses (avoidance, preference, growth, survival, reproductive success, migration (upstream, downstream, intrabasin) success, disease, feeding, territoriality, aggressiveness). All of these aspects of fish ecology are useful in identifying temperature requirements and the potential consequences of temperature modification. Cursory evaluations of the literature can be prone to overlooking synergistic effects, cumulative effects during the life cycle, and can mistake tolerable for optimal in the short term and long term.

Examples of the complexities in evaluating biological significance of temperature regimes are numerous. For example, temperatures under which migration occurs in streams are potentially misleading because of the difference between preferred (or optimal) conditions and those experienced by fish given few alternatives. Also, migration temperatures identified as optimal may not be suitable when fish are confronted with combinations of other stressors (e.g., low dissolved oxygen, chemical pollutants). Egg incubation might be able to occur with high percentage survival at 10°C, but a specific number of degree days may also be essential to ensure proper hatching and emergence timing. Because establishing habitat standards on the basis of existing conditions can lead to progressive erosion of quality, it is important to distinguish between optimum and marginal conditions. Observations of juvenile salmonids in warm stream margins may be misleading because age 0+ fish can have higher preferred temperatures than older age classes. Even the age 0+ fish might not have the relatively high temperatures as optimal growth temperatures because their occurrence in stream margins might be merely a means of escaping predation in deeper water. Observations of adults in warm water in riffles can be misleading because they might be spending the majority of their day in cold thermal refuges and never let their internal body temperatures become warmed. Field growth rates depend largely on temperature, but proper measurement of temperature regime can be controversial. In addition, growth rate and optimum temperature are also functions of food availability, alkalinity of the water, degree of competition, etc. Results of laboratory experiments, likewise, need interpretation and analysis because of many of the same reasons as just expressed about field work. Also, laboratory methodology can influence biotic response.

Although field observations are often considered more meaningful because they are not an artifact of experimental equipment (e.g., horizontal or vertical temperature gradient apparati, swimming tunnels, laboratory streams), much of the most reliable information on temperature requirements comes from laboratory studies because experimental conditions permit strict use of controls. Experimental work has been indispensable in determining fish survival and preference under constant or fluctuating temperatures. Laboratory studies on egg development rate and survival and juvenile survival and growth rate under constant temperatures are most commonly relied upon to establish water temperature standards in tributaries. These biological responses can be very precisely described mathematically (responses are highly repeatable) but the responses in the field can vary slightly from those predicted from constant temperature experiments depending on field temperature regime (i.e., diel fluctuating temperatures, temperature trends throughout the incubation period). A portion of the observed variability can be attributed to the difficulty of knowing the thermal exposure of a monitored population in the field or its previous exposure history, the complexity of the thermal pattern in the field compared with temperatures used in establishing laboratory-based relationships, or the possibility that field responses are significantly influenced by one or more other factors.

There are many notable field and laboratory studies illustrating the effects of temperature on chinook salmon in streams of the Northwest. Where necessary this database was supplemented with experience from populations spanning the range from the Sacramento River to Alaska. A significant portion of the body of literature on temperature criteria for chinook is summarized in **Figure 2**. Further review on temperature effects on salmonids was made by reviewing literature on species from California to Alaska, the entire Pacific Northwest, the Rocky Mountains, the Great Lakes, east coast of the United States, Greenland, Iceland, Europe, Russia, and New Zealand.

# TERMINOLOGY

## THERMAL STRESS

Thermal stress is any temperature change producing a significant alteration to biological functions of an organism and which lower 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** (restriction of essential metabolites or interference in energy metabolism or respiration), **inhibiting** (interference in normal functions such as reproduction, endocrine and ionic balance, and feeding functions caused by low or high temperatures), and **loading** (increased burden on metabolism that controls growth and activity). The latter three stresses can also be lethal when continued over a long period (Elliott 1981). Brett (1958) plotted the loading level for sockeye, for example, which represents the upper temperature boundary permitting growth, given combinations of acclimation and exposure temperatures. The temperature polygon defined within acclimation and temperature exposure axes and between the upper loading and the lower inhibiting levels defines a zone where growth can occur. Given acclimation temperatures ranging from 4 to 20°C, a loading line can be plotted for juvenile sockeye between 17 and 20°C exposure temperatures (Brett 1958). This line represents an upper limit to growth and activity. Upper lethal limits are just beyond the loading line. When food or oxygen are restricted (i.e., are limiting stresses), the loading stresses occur at lower temperatures and the growth zone is reduced in size.

## TEMPERATURE RANGES

The **optimum** temperature range provides for feeding activity, normal physiological response, and normal behavior (i.e., without thermal stress symptoms). The optimum range is slightly wider than the growth range. **Preferred** temperature range is that which the fish most frequently inhabits when allowed to freely select temperatures in a thermal gradient. The **acute temperature preference** is that temperature preferred when a fish acclimated to a certain temperature is rapidly presented a temperature gradient in which it selects a temperature (Elliott 1981). Up to 2 h are allowed in a thermal gradient to identify acute preference (Reynolds and Casterlin 1979a). The **final temperature preference** (or final preferendum) is a preference made within 24 h in a thermal gradient and is independent of acclimation temperature (Reynolds and Casterlin 1979a, 1979b). Fry (1947) (as cited by Jobling 1981) defined this term in two ways: (1) that temperature that individuals will ultimately select regardless of thermal experience, and (2) that temperature at which preferred temperature equals acclimation temperature. These two definitions stimulated two separate methods of determination. The "gravitation" method requires determination of a final preference (or range of preference) in a thermal gradient after a sufficiently long time for variation of the selected temperature to be maximally reduced. The second definition requires that acute preference is determined across a wide range of acclimation temperatures. Preferred temperature is then plotted against acclimation temperature. The point at which this line crosses the line of equality defines the final preference. The acute preference generally exceeds the acclimation temperature for acclimation temperatures below the crossover point and are less than acclimation temperatures above the crossover point (Reynolds and Casterlin 1979b).

The **tolerance** temperature range is a set of temperatures relative to corresponding constant acclimation temperatures that define an upper and lower tolerance limit. The **tolerance zone** exists between the incipient lethal level and the feeding limit (Elliott 1981). 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 days (Elliott 1981). Fish may also be acclimated to a fluctuating temperature regime which may be related to 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 cycle. 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 (UUILT)**. Generally, UILT at a particular acclimation temperature is determined as an exposure temperature producing 50% survival within 1000 min (Brett 1952, Elliott 1981) or 24 h (Wedemeyer and McLeay 1981, Armour 1990). Brett (1952) indicated that exposure duration might need to be as much as 7 d for some species, because as long as mortality continues to occur on exposure to high temperature the organisms are in the resistance zone. Exposure times reaching 7 d have been studied in relation to shorter exposure times (Hart 1947, Coutant 1970, Elliott 1981). The UILT (i.e., the temperature required to produce 50% survival), given any acclimation temperature, increases as the exposure time permitted is reduced.

The **upper lethal temperature (ULT)** is the temperature at which survival of a test group is 50% in a 10-min exposure, given a prior acclimation to temperatures within the tolerance zone (Elliott 1981, Elliott and Elliott 1995). Resistance temperatures are those temperatures within the boundaries defined by the UILT and the ULT. If fish are held within the resistance zone after acclimation to temperatures within their tolerance range, they will succumb within a period of 10 min to 7 days. The **ultimate upper lethal temperature (UULT)** is the maximum ULT achievable and is reached by increasing acclimation temperature to a point beyond which no further increase in ULT is produced.

**Acclimation** temperature is a temperature within the tolerance zone under which an experimental fish is held prior to being subjected to an exposure temperature. An acclimation temperature is generally a constant temperature but can also be a dielly fluctuating temperature regime (Fry 1971) Fish collected in the field or obtained from a hatchery are conditioned gradually to the acclimation temperature using daily increments of 1-2°C to adjust initial temperatures to the desired acclimation level. Once a desired acclimation temperature is reached, test organisms are generally held at that temperature for about 3-4 d (Bidgood and

Berst 1969, Hartwell and Hoss 1979) to about 2 wk (Dwyer and Kramer 1975, Lee and Rinne 1980, Elliott and Elliott 1995) prior to exposure to a test temperature. Bennett et al. (1998) showed that the acclimation times required for channel catfish, determined as rate of change in thermal tolerance with acclimation time, depended upon the direction in change in acclimation temperatures, magnitude of the change, and final acclimation temperature reached. Rate of acclimation to a reduced temperature was far slower than rate of acclimation to a higher temperature. Fish are often not fed for approximately 1 d before testing (Bidgood and Berst 1969). Physiological acclimation of an organism is a reversible process given enough time; that is, the organism can be acclimated to another constant or cyclic temperature regime (Fry 1971). However, the response to an exposure temperature after acclimation to a given constant temperature in one season may be different from that in another season. This is partly explained by the organism becoming acclimatized to a total environmental complex prior to a test acclimation and exposure temperature (Fry 1971). **Acclimatization** involves exposure of an organism to ambient temperatures available in the field during its development prior to a test (Hart 1952). In tests of differences in response to temperature among fish stocks of a given species, it is important to attempt to eliminate the influences of acclimatization by careful acclimation (Fry 1971). A fish removed from the field has an acclimatization state that is a product of its exposure to varying field temperatures and also numerous non-thermal factors, such as photoperiod, season, age, chemicals, biotic interactions, and nutritional state (Reynolds and Casterlin 1979a). **Adaptation** is an evolutionary process that involves selection of individuals with traits that lead to survival under certain environmental conditions or that improve fitness (i.e., increase fecundity and thereby result in greater frequency of alleles for the adaptive traits in the next generation). Because salmonids live in so many different environments (marine, estuarine, freshwater) that each have seasonally and annually varying environmental conditions, the adaptations that are successful vary from generation to generation. Early emergence and emigration from freshwater may have selective advantages in the freshwater environment (less competition for food and more rapid growth) but conditions may not be favorable when smolts enter the estuary. There is a complex interaction of selective forces throughout the life cycle created by the multiple habitats utilized, the seasonal variation in individual states of these habitats, and the interrelationships in states among major habitats arising from major climatic cycles.

Shifts in genetic traits within a population take generations to occur. Adaptations can lead to speciation. The significant distinguishing features of a species or family (e.g., Salmonidae), such as temperature tolerance, by which they are classified as coldwater, coolwater, or warmwater organisms (see Magnuson et al. 1979) have arisen over the evolutionary history of these groups. Significant divergence in temperature tolerance within a species or a family would not be likely without other major changes in the organisms. Evolutionary adaptations as significant as temperature adaptation, with all its physiological implications, likely limit evolutionary pathways (see Ricklefs 1973).

## INCIPIENT LETHAL TEMPERATURE VS. CRITICAL THERMAL MAXIMUM

Temperature tolerance of fish is evaluated by one of two principal methods. One can measure the **incipient lethal temperature (ILT)** by acclimating the fish to one temperature and then subjecting them instantaneously to another temperature (e.g., see Fry et al. 1946, Hart 1947, 1952, and Brett 1952). The ILT method assesses the temperature needed to produce 50% mortality in 1000 min (Bjornn and Reiser 1991) although Elliott (1981) and Elliott and Elliott (1995) indicate that a 7-d period is usually standard. With the **critical thermal maximum (CTM)** method (see Becker and Genoway 1979), fish acclimated to one temperature are subjected to uniform rates of temperature change until loss of equilibrium occurs. CTM is calculated as the arithmetic mean of the temperatures at which individual test fish lose equilibrium **(LE)** or die **(D)** given a prescribed rate of heating from an acclimation temperature that allows deep body temperature to track environmental temperature without significant lag time. If heating is too fast relative to the size of the test organism, the observed temperature of the water bath will be higher than the body core temperature producing the physiological response (Kilgour and McCauley 1986). The CTM is found at the upper boundary of the resistance zone. Survival above this level is essentially nil (Jobling 1981).

Becker and Genoway (1979) noted that Fry (1967) and Hutchinson (1976) considered the ILT method more physiologically meaningful than the CTM method. The abrupt transfer method provides important information on extent of the resistance zone (Kilgour and McCauley 1986). However, the CTM method provides more rapid analysis and requires fewer test organisms and offers the ability of not having to sacrifice organisms to produce test results, provided that they are held in warm water only to the LE-point and then revived immediately. However, both methods have disadvantages. The ILT method subjects fish to handling stress when they are placed into a higher or lower temperature tank. The ILT method requires a greater number of exposure chambers and more time to complete an experiment (e.g., 96 h) (Becker and Genoway 1979). Also, the exposure temperature constitutes a thermal shock with a magnitude dependent upon the difference between the exposure and acclimation temperatures. The CTM method eliminates handling and transfer to a new tank, but it has been determined that the rate of change in temperatures can affect the results (Elliott and Elliott 1995). Another disadvantage of the CTM method is that the result is dependent on acclimation history (Jobling 1981).

Becker and Genoway (1979) recommended use of a heating rate of 18°C/h for the CTM method after evaluating rates of 1 to 60°C/h. An advantage of this high rate of heating is that fish are not given time to partially acclimate to temperatures above their initial acclimation temperature, thereby avoiding confusing the relationship between acclimation and exposure temperature. If the heating rate is very low, it may be possible for fish to acclimate to a temperature toward the upper end of the tolerance range or to an indeterminate, intermediate acclimation temperature (Kilgour and McCauley 1986). However, if the heating rate is high, any error in assessing the point at which a fish reaches LE or death equates to error in determining the corresponding temperature. Also, the temperature lag effect for a fish's body in relation to the changing experimental water temperature increases with body mass. In the field, fish body temperature is highly correlated with temperature preference (McCauley et al. 1977), indicating that presence of an adult in warm water does not indicate its preference for warm water. Under field conditions, body temperature would be a better indicator of preference, provided a wide range of temperatures within the optimum range are equally available because body temperature integrates time spent under various thermal conditions. Elliott and Elliott (1995), in a comparison of a wide range of heating rates (0.01 to 18°C/h), found that a high heating rate was not suitable for determining CTM on Atlantic salmon and brown trout. They recommended a heating rate of 1°C/h to provide the highest precision. In addition, it is not possible to revive fish that have reached the LE-point before they proceed to the D-point when the heating rate is high (Elliott and Elliott 1995).

Results from the ILT and CTM methods can be related despite the apparent differences in approach (Kilgour and McCauley 1986). CTM increases with rate of heating to an asymptote ($T_{max}$) that corresponds to UULT determined by the ILT method (Elliott and Elliott 1995). The UULT (upper ultimate lethal temperature) is the temperature that fish (50% of the test group) cannot tolerate for more than 10 min. The lethal temperature that produces 50% mortality at a heating rate approaching 0°C/h (i.e., a very slow heating rate allowing full acclimation) corresponds to the UUILT (Kilgour and McCauley 1986). Kilgour and McCauley (1986) recommend use of CTM with a slow rate of heating (i.e., ≤1°C/d) as a means to predict UUILT. With a very slow heating rate, the fish can continue to acclimate up to the maximum temperature possible for the species. Elliott and Elliott (1995) used an array of heating rates from 0.01°C/h to 18°C/h to determine the behavior of the CTM value. The asymptotic curve showing the increase in CTM with heating rate is described by the formula $T = T_{max} - a \exp(-br)$ where $T_{max}$ approximates UULT, T is the upper critical temperature or CTM, r is the heating rate, and $a$ and $b$ are coefficients. When the curve is extrapolated to a 0°C/h heating rate, the CTM calculated approximates UILT (Elliott and Elliott 1995). When $r = 0$, $T = T_{max} - a$. For example, at a high heating rate (18°C/h) for brown trout (1+ age) they found a $T_{max}$ of 30.0°C. With an extremely low heating rate (0.01°C/h), T = 24.8°C, which approximates UUILT.

Fields et al. (1987) distinguished determinations of critical thermal maximum (CTM) and the chronic thermal maximum in their rates of heating to the D-point. Their CTM was determined with a heating rate of 12°C/h starting from a variety of acclimation temperatures while the chronic thermal maximum was determined using 0.04°C/h. The chronic thermal maximum would appear to yield a value similar to the UUILT considering results in Elliott and Elliott (1995). Fields et al. (1987) used the difference between the chronic thermal maximum and the field temperature as an index to the relative amount of sublethal stress; the smaller the difference in these values, the greater the sublethal stress. Long-term exposure to high temperatures leads to reduced growth rates, reduced reproductive rates, and stress-related mortality.

The observed CTM increases with rate of heating, but the exact value also depends upon whether the chosen endpoint is the LE- or D-point. With juvenile coho acclimated to 15°C, the CTM (measured to the LE-point) varied from 27.7°C to 29.6°C over a rate of heating of 1°C/h to 60°C/h (Becker and Genoway 1979). The mean D-temperature at which a CTM is expressed for a 15°C acclimation temperature varies with rate of temperature increase. Becker and Genoway (1979) reported a mean D-temperature of 29.7°C at 18°C/h heating rate, but the D-temperature varied from 27.6°C at 1°C/h to 31.1°C at 60°C/h. That is, when temperature was increased at a rapid constant rate, the mean temperature at death was higher than when increase in temperature was slower. At the high rate of heating, coho reached the mean D-temperature in 0.27 h.

The lethal temperature as indicated by either CTM or UILT methods is highly correlated with the optimum growth temperature (Jobling 1981). An equation describing this relationship is $Y = 0.76X + 13.81$ ($N=22$, $r=0.87$). In this equation Y is the lethal temperature and X is the growth optimum . Regressions of final preference on lethal temperature were also made by Jobling (1981). The CTM, determined using a standard rate of heating for various acclimation temperatures, describes a line parallel to and at some distance above the UILT line, but whose exact meaning is not as clearly defined as is a lethal limit derived by the UILT method, owing to the dependence of CTM on heating rate (Jobling 1981, Elliott and Elliott 1995).

## GROWTH ZONE

The growth zone is an area defined in relation to pairs of acclimation and exposure temperatures for which growth is positive. Combinations of acclimation and exposure temperatures not defined by this area may be in the tolerance or resistance zones but will not produce conditions in which feeding will take place or if it does, energy expenditures will exceed energy assimilated; consequently, negative growth or death take place outside the growth zone. The growth optimum is the temperature at which growth rate is maximal under a certain level of energy intake (ration level). For any salmon species the zone of adequate activity (Brett et al. 1958) is defined by a polygon in X-Y space for exposure vs. acclimation temperatures. The upper bound to this polygon is the loading level and the lower bound is the inhibiting level. Within this activity zone a cruising speed corresponds to each exposure/acclimation temperature combination. Loading stress increases with temperature above the positive growth zone, but it also increases with reduction in food availability because this serves to shrink the growth zone.

The most complete understandings of bioenergetic responses to temperature are available for sockeye (Brett 1971) and brown trout (Elliott 1981, 1994). For brown trout, growth occurs over the range 4-19°C when fed at maximum rations (4000 cal/d for a 50 g fish); when ration is decreased to 500 cal/d the growth zone shrinks to 4-8°C (Elliott 1981). Under maximum ration a water temperature of 13-14°C provides the optimum growth rate for brown trout. Between 13°C and 19°C respiration loss becomes great, requiring an increasing percentage of the daily energy intake (Elliott 1994). As ration decreases, optimum growth temperature and growth range both decrease (Elliott 1981). For sockeye feeding to satiation, 15°C was the optimum growth temperature for both 5-7 and 7-12 month-old juveniles, but for the younger age group the rate of decline in specific growth rate (%/d) on each side of the optimum was much steeper (Brett et al. 1969). Reduced oxygen concentration and other factors can accentuate thermal stress (Wedemeyer and McLeay 1981) even under temperatures within the growth zone. Such factors can also lower the optimum growth temperature.

In laboratory experiments it is generally considered that maximum ration can be taken in two feedings to satiation (Elliott 1975a). In the field if food is limiting, temperatures that might normally be considered to provide positive growth conditions can instead lead to growth loss. This can be true if either food abundance is low in microhabitats where feeding takes place or if the quality is not adequate to provide needed energy intake. Shifts in species composition of the food base can reduce quality. If rearing temperatures are near the growth limits so that growth rates are ≤80% of the maximum growth, growth stress can lead to disease and increased mortality (Armour 1990). If food supplies are limited in summer, leading to poor deposition of fat for fish about to enter the winter period, energy demands during winter can be severe enough to cause mortality. This is especially true in females undergoing ovogenesis. If body fat declines to <2.2% during winter, death ensues (Newsome and LeDuc 1975).

Growth rate may be considered a highly sensitive and integrative index to environmental conditions. Growth rate is a function of water temperature on fish physiology and the physiological performance mediates behavior and ecological interactions. Water temperature also influences the production of fish populations and algal communities and species composition of the fish community and underlying trophic levels (Graynoth 1979). Growth rate integrates food availability and quality as well as other factors such as competitive advantage in species interactions and bioenergetic suitability of the environment. Stream reach types provide varying types of feeding environments for fish populations due to temperature regime, stream gradient, flow variation, and food abundance and quality that interact to influence the ability of a species to inhabit the reach and to grow there. Growth rates may reflect environmental conditions more sensitively than observed mortality rates (Beamish et al. 1975, as cited by Rodgers and Griffiths 1983). Further, growth rates can be a predictor to later fish survival (Blaxter 1969, as cited by Rodgers and Griffiths 1983).

## PHYSIOLOGICAL OPTIMUM TEMPERATURE

The physiological optimum is the temperature under which a number of physiological functions, including growth, swimming, spawning, and heart performance, are optimized. When physiological optimum temperature is not known, it can be estimated as the average of growth optimum and final preferendum (Armour 1990).

## PRODUCTION

Laboratory experiments that determine effect of temperature on adult salmonids using ILT or CTM methods do not account for reduction in gamete production or growth rates caused by sublethal high temperatures. In addition, temperatures that may allow positive individual growth may be so high, given sufficient food resources, that mortality rate in the population increases. This effect can lead to poor production and low fecundity. Linkages among population survival under temperature stress, mean growth rates of various age classes, and production of these age classes make it important to consider production dynamics.

Production is the elaboration of tissue by a population over a specified period of time, regardless 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, etc. Under conditions of satiation feeding, as long as water temperature for a given time interval is within the bounds defining zero growth, individual growth rate will be positive and, consequently, a positive increment of production is likely in the time interval because survival rates would also be high. If temperature approaches the upper growth limit, growth rate will still be positive but population mortality rate may increase, resulting in a sharp decline in stock number and consequently, stock biomass over a time interval. This loss in population biomass represents a loss of tissue elaborated (production) in previous time intervals. This loss may not be compensated by production during the time interval in which temperature is approaching the growth limit because growth rate is so low and mean biomass has been reduced. This situation was well revealed by Hokanson et al. (1977). They demonstrated on rainbow trout that the upper temperature for positive growth was higher than the temperature that resulted in zero net biomass gain for the population (i.e., biomass remained constant for 40 d).

## TEMPERATURE REGIME

The term temperature regime is used frequently in this report. Temperature regime is a term that can carry considerable underlying meaning. It is used here in various contexts. In one sense, it can represent the ambient conditions in a stream. The regime can be specified on any temporal or spatial basis. That is, it can be a daily, monthly, seasonal, annual, decadal regime in which the temperatures of interest to explain a biological response could be as simple as a series of annual maximum temperatures or as complicated as a daily pattern of maximum and minimum temperatures superimposed on a long-term trend in daily mean temperature for a 10-year period. Spatially, the regime could be a frequency distribution of daily maximum and minimum temperatures for a pool, a stream reach, or the distribution of such local regimes throughout an entire stream network. In the latter sense, one might want to explain the chinook production from an entire stream network in relation to the temperature regimes experienced by adults, eggs, juveniles, and smolts in all identified holding, incubation, and rearing areas and the spatial linkages among these habitats, considering that there will be intrabasin migration during development. The temperature regime then would be the complete thermal experience of a segment of the population or the entire population.

The temperature regime is what we take to be the actual thermal experience of an organism during its complete developmental process or some significant life stage. For salmon we can be concerned about marine, estuarine, and freshwater regimes for the entire life cycle, or we can isolate the freshwater phase as a management or scientific problem and try to characterize the regime for the egg, juvenile, smolt, and adult phases. Monitoring of field conditions and establishment of laboratory developmental conditions both require decisions about how to abstract the concept of the regime. Taking the egg stage as an example, we can study egg development under a constant temperature for the entire stage (fertilization to fry emergence), subject the eggs to a stepped increase or decrease in constant temperatures at intervals during egg development (steps coincide with significant egg developmental stages), a pattern of daily sine wave cycles between a fixed minimum and maximum representing normally experienced diel fluctuation in the field, or a more random diel cycle with a varying daily mean and diel amplitude. Acclimation and exposure of test organisms can be accomplished under any combination of these thermal conditions. In the laboratory there is value in knowing how to statistically characterize the acclimation and exposure temperatures so that the biological response can be extrapolated to field conditions. Conditions in the field, however, might not follow experimental temperature regimes fully, so there arises a question of how to apply laboratory work. Questions about how to relate laboratory and field work using various statistics for temperature regime can be explored by extensively evaluating the literature. Likewise, a better appreciation of the influence of constant temperatures vs. fluctuating temperatures on biological response can be had by evaluation of all available studies, using all variations of temperature regimes as mentioned above in acclimation and exposure phases. Constant and fluctuating temperature effects can be evaluated in survival, growth, development, disease resistance, or other studies of performance.

# EGG/ALEVIN LIFE STAGE

## CHINOOK

### Constant Temperature

*Survival*

Chinook spawn during the fall when stream temperatures begin to decline. The optimal temperature for holding chinook broodstock in hatchery ponds is considered to be 6-14°C (Leitritz and Lewis 1976, Piper et al. 1982). Holding females at 3.3°C totally inhibits maturation and results in complete mortality prior to spawning (Leitritz and Lewis 1976). Even before eggs are deposited in gravels, exposure of adult females holding ripe eggs to temperatures above 14°C can cause egg mortality and delayed inhibition of alevin development (Rice 1960, Leitritz and Lewis 1976). For eggs incubated at 16°C, mortality occurring post emergence can be much more severe than that occurring prior to emergence because of physiological difficulty in completing yolk absorption (Jewett 1970, as cited by CDWR 1988).

Reiser and Bjornn (1979) listed recommended incubation temperatures as 5.0-14.4°C. Water temperature of 14.4°C was cited as the upper limit of the optimum water temperature range for incubation of salmon eggs (Bell 1991). A maximum temperature of 12.8°C was also recommended by Snyder et al. (1966) (as cited by EPA and NMFS 1971, p. 46) in their survey of literature available. The CDWR (1988, p. 4) identified the temperature range of 12.8-14.2°C as one that produces only 50% egg survival from egg to sac-fry stage owing to abnormal physiological development and yolk coagulation. Percentage of American River fall chinook reaching eye-up stage was ≤55% when river temperatures exceeded 15.5°C (Hinze et al. 1956, as cited by Marine 1992). Numerous authors cited poor egg survival when incubation temperatures fall within the range 13.3-17.2°C (Leitritz 1962, as cited by Parker and Krenkel 1969, p. A-19; Seymour 1954, as cited by Parker and Krenkel 1969, A-21; Slater 1963; EPA and NMFS 1971, p. 46; Healey 1979; Jewett 1970, as cited by CDWR 1988, p. 27). Seymour (1956) (as cited by Alderdice and Velsen 1978) observed 50% survival from fertilization to 50% hatching at 16.0°C. In a Sacramento River chinook study, mortality of eggs incubated at 15.6-16.1°C was <20% to the fingerling stage, leading to the conclusion that this chinook stock was no more resistant than other chinook stocks (Healey 1979).

A study of survival from fertilization to hatching showed that there was no significant difference between egg batches incubated at 9.9 and 11.4°C (49 and 50% survival, respectively) but those incubated at 15.0°C had a markedly reduced survival rate (23% survival) (Garling and Masterson 1985). A similar effect was measured during incubation from hatching to swim-up. Survival was 98-99% at the two lower temperatures but was 74% at 15.0°C. Consequently, survival from fertilization to swim-up at 15°C was 17% while that at the two lower constant temperatures was about 49%. A laboratory study of Sacramento River winter-run chinook, which normally spawn from April into July, showed that starting from an initial number of eggs in May, survival of initial egg lot was 88.5, 50.9, and 2.4%, respectively, in months May, June, and July, during which mean water temperatures were 13.6, 15.4, and 17.4°C (Slater 1963). During this period, development in the laboratory proceeded from egg to early fry stages. The author concluded that this winter-run chinook could survive only where tributaries were available with May-August temperatures in the range 5.8-14.2°C. This study clearly reveals the influence of environmental conditions in selecting portions of a run or appropriate life histories.

Murray and McPhail (1988) measured survival of chinook embryos from fertilization to hatching at 2, 5, 8, 11, and 14°C. Survival at 5, 8, and 11°C was uniformly high (>83%) but declined drastically at 2 and 14°C (survival of 14% and 48%, respectively). Combs and Burrows (1957), in their study of Entiat River chinook, observed poor embryo survival at temperatures above 16.1°C. They recommended 14.2-15.6°C as the upper temperature for chinook egg incubation. Heming (1982) recommended temperatures of 6-10°C as the optimal temperature range for chinook embryos and alevins based on a study of Campbell River chinook, Vancouver Island. Survival rates (fertilization to emergence) at temperatures of 6 and 8°C were >91% but declined to 76% at 12°C and fry were smaller due to less efficient use of yolk in growth by alevins.

Egg incubation at low temperatures can seriously affect survival. The minimum initial incubation temperature at which survival is not reduced is 5.8°C (Burrows 1954; Combs and Burrows 1957; Combs 1965; Snyder et al. 1966, as cited by EPA and NMFS 1971, p. 46). Seymour (1956) (as cited by Alderdice and Velsen 1978) measured a 50% survival rate from fertilization to 50% hatching at about 2.5-3.0°C. Survival was 0% for eggs incubated at 1.1°C (Seymour 1956, as cited by CDWR 1988), but if eggs were first incubated for 3 weeks at 12.8°C followed by incubation at 1.1°C, survival was 97% (Seymour 1956, as cited by Andrew and Geen 1960). A similar finding was made by Combs (1965), who reported that survival was only 8% when chinook eggs were incubated continuously at 1.7°C from fertilization. However, after 6 d incubation at 5.8°C, eggs could withstand transfer to 1.7°C with minor mortality. Combs and Burrows (1957) observed that temperatures as low as 0.6°C could be tolerated for several weeks without significant mortality, provided that eggs were initially incubated for 1 month at ≥5.6°C. Murray and McPhail (1988) measured survival from fertilization to hatching at 2°C of 14%; survival was especially impaired during the stage from fertilization to epiboly. At 3°C survival was only 50% for embryos but was >80% for alevins at temperatures from 2°C to 16°C (Beacham and Murray 1990).

### *Growth and Development*

A significant effect of temperature on egg/alevin development can be generated during the pre-spawning phase. Berman (1990) (also reported in Berman and Quinn 1990) determined that holding temperatures of 17.5-19°C caused females to produce smaller alevins than females held at 14°C. The higher adult holding temperatures also produced abnormalities during egg developmental stages. Alevin and fry size can also be controlled by temperatures experienced during incubation. Chinook alevins required a greater time period to achieve 50% emergence at 2 and 5°C than did coho, sockeye, chum, or pink salmon (Murray and McPhail 1988, Beacham and Murray 1990). At 5°C incubation temperature chinook achieved a greater fry length than at other temperatures (i.e., 2, 8, 11, or 14°C). The smallest alevins were produced at 14°C (Murray and McPhail 1988). At a constant incubation temperature of 5°C, chinook development time to emergence is greater than at higher temperatures and is longer than for the other four salmon species. Low temperature incubation produces delayed emergence but also greater fry length. The benefit of emerging at larger size may not always outweigh disadvantages of late emergence. Late emergence in the spring might be an advantage in avoiding high spring flows, ice breakup, or low food abundance, but early emergence in chinook races that must overwinter (e.g., spring or summer races) could offer increased duration of fry rearing prior to winter, thereby providing greater opportunity to reach a large size having high overwinter survival and chance of emigration in the first spring period. An early emerging chinook would emerge at a lower than optimum size and could be subject to competitive disadvantage relative to other early emerging salmonids. The selective pressure ensuring emergence during a specific time period in spring could operate via the increased swimming capability of large fry allowing greater food gathering, predator avoidance, and competition for space (Murray and McPhail 1988).

The egg incubation period is a very biologically sensitive developmental period requiring accumulation of specific degree-days for proper hatching and emergence timing (Alderdice and Velsen 1978, Crisp 1981, Beacham and Murray 1990). Too low a cumulative degree-day total, even if egg incubation occurs within the zone providing high egg survival rates, would result in delayed fry emergence. Likewise, too high a cumulative degree-day total would result in early emergence, which could lead to fry having to cope with adverse flow conditions (Hartman et al. 1984).

Alderdice and Velsen (1978) contrasted the abilities of the unmodified thermal sums and the log-inverse Bělehrádek models to accurately describe available data on egg development rate from fertilization to 50% hatching. The unmodified thermal sums model is based upon accumulation of thermal units or degree-days (days x temperature) above 0°C. At temperatures >4°C either model provides accurate prediction of development time, but below 4°C the unmodified thermal sums model increasingly overestimates time to 50% hatch. At 1°C constant temperature incubation the thermal sums and Bělehrádek models estimate 468 and 268 d, respectively, from incubation to 50% hatch. Beacham and Murray (1990) obtained good results using a modified thermal sums model that accumulated degree-days above a temperature threshold unique for each species.

Beacham and Murray (1990) examined the accuracy of ten models for predicting mean time to hatching and to emergence as related to temperature for five species of Pacific salmon. One of these models (model 4), of the form $\ln D = \ln a + b \ln(T-c)$, was relatively simple and accurate. This was also the preferred model of the ten models investigated by Alderdice and Velsen (1978). Model parameters for this log-inverse Bělehrádek model included: *D* as observed hatching or emergence time after fertilization; *T* as observed mean temperature (°C), and the fitted coefficients *a*, *b*, and *c*. For chinook the equation used to predict emergence time is:

Chinook $\ln D = 10.404 + (-2.043)\ln(T-[-7.575])$ $r^2 = 0.970$

This equation allows one to plot days to emergence as a function of constant incubation temperature. At 2°C incubation temperature chinook require approximately 325 d from fertilization to emergence. This decreases to approximately 50 d at 16°C **(Fig. 3)**. Taking the difference between the number of days to emergence at temperature T°C from the days at (T+1)°C, allows one to plot the effect of 1°C increases in temperature from a base temperature. For chinook, as in the other salmon species, the effect of a 1°C warming of stream water is most dramatic at low base temperatures. For example, when the base temperature is 2°C, warming the water by 1°C results in a shortening of time to emergence by 60 days for chinook **(Fig. 4)**. If winter incubation temperature were a constant 6°C, a warming to 7°C would result in a reduction of time to emergence by 22 d. This indicates that emergence timing and, therefore, possibly population survival can be influenced substantially from climatic or anthropogenic alterations to winter incubation regime acting on embryo development.

First feeding chinook fry do not develop normally at temperatures above 12.8°C (Burrows 1954, as cited by Parker and Krenkel 1969, p. A-22). The period of first feeding is a delicate transition point for fry (Brett 1952). In addition, fingerlings have a preference for temperatures in the range 12-14°C (Brett 1952). At swim-up, alevins have yolk reserves that enable them to survive for some time before needing to initiate feeding (Peterson and Martin-Robichaud 1989). Given the variation in thermal history that can occur during incubation, fry at emergence can have variable amounts of yolk available to them. This food reserve provides a cushion for emergent fry seeking to establish first feeding. There is uncertainty too in the ability of alevins to feed in the gravel before emergence. Due to these uncertainties, it appears to be desirable to moderate temperatures during fry emergence so that fry can properly initiate feeding and growth.

### Varying Temperature

Fluctuating temperature effects on salmonid eggs have been investigated for regimes changing in a stepped fashion throughout the incubation period (a series of different constant temperatures during incubation phases) and also for dielly fluctuating regimes.

#### *Survival*

In a test of survival of spring chinook salmon from South Santiam Hatchery, mean daily temperatures ranging from 10°C to 11.9°C (maximum diel variation ±1.1°C) during the first month of incubation resulted in 72.8% survival to the eyed stage versus eggs incubated in a regime with mean daily temperatures declining from 18.3°C (maximum diel variation ±3.9°C) to 12.8°C in which survival was 51.2% (Johnson and Brice 1953). Despite the fact that temperatures continued to decline, additional mortality occurred into the fry stage attributable to the early egg exposure history. This mortality was attributed to yolk coagulation. Fall chinook eggs from the Little White Salmon Hatchery incubated for a 1-month period in which water temperature declined from a mean daily temperature of 18.9°C to 16.7°C had 0% survival to the eyed stage. In a temperature regime where mean daily temperature declined from 12.8°C to 7.2°C, survival was 96.4% (Johnson and Brice 1953).

Olson and Foster (1955) measured survival of Hanford Reach fall chinook from the Columbia River in the laboratory under a natural seasonal temperature regime during incubation from November to May. In addition to the control under an ambient temperature regime, other egg lots were incubated at 2.0°C below and 1.1, 2.2, and 4.4°C above ambient. They found low (21%) survival under initial temperatures of 18.4°C, but when initial incubation temperatures were ≤16°C survival was ≥90%. Interestingly, under initial incubation temperatures of 18.4°C in the seasonally declining ambient regime, hatching success was high, but the high mortality occurred soon after fry first feeding began. This indicates a delayed effect of embryo damage.

Murray and Beacham (1987) studied survival and development of chinook embryos and alevins at 4, 8, and 12°C in which embryos were transferred from the initial temperature at completion of epiboly (early transfer) or complete eye pigmentation (late transfer) to the same or a different temperature (i.e., one of the three test temperatures). Test temperatures at various developmental stages were denoted as $T_1$, $T_2$, and $T_3$ (see **Table 1**). $T_1$ was the temperature from initial incubation to completion of epiboly; $T_2$ was the temperature from completion of epiboly to completion of eye pigmentation; $T_3$ was the temperature from completion of eye pigmentation to emergence. Embryos initially incubated at 8 or 12°C had higher embryo and alevin survival rates than those incubated at 4°C. However, for chinook embryos initially incubated at 4°C followed by early or late transfer to 8 or 12°C, survival rate was less than for embryos incubated continuously at 4°C. Alevin survival rate for a chinook early transfer from 4 to 12°C was 86%. A $T_1$ of 8 or 12°C produced significantly higher embryo survival rates from fertilization to hatching than did a $T_1$ of 4°C. The $T_1$ temperature experienced during incubation had a far greater effect on embryo survival than did $T_2$ or $T_3$. After the period from fertilization to epiboly, the direction or magnitude of temperature change had little effect on embryo or alevin survival within the range 4 to 12°C. A temperature regime that simulates the natural regime for the stock (i.e., gradually decreasing, no extreme shifts, minimum temperature above 4°C) results in high chinook survival.

**Table 1.** Studies of effect of varying temperatures during chinook egg incubation, indicating exposure temperatures during developmental stages.

| Reference | $T_1$ | $T_2$ | $T_3$ |
|---|---|---|---|
| Murray and Beacham (1987) | initial incubation to completion of epiboly | from completion of epiboly to completion of eye pigmentation | from completion of eye pigmentation to emergence |

*Growth and Development*

Alderdice and Velsen (1978) reported for Oncorhynchus tshawytscha) that egg development rate at a constant temperature <6°C-7°C was less than at ambient temperatures having the same mean but varying dielly and also decreasing during the incubation period from fertilization to 50% hatch. They considered a constant temperature to be a regime that was confined to the mean ±1°C. In contrast to these findings, Murray and Beacham (1987) found that the hatching and emergence times for chinook were similar at a given mean temperature under either increasing or decreasing temperature regimes (i.e., constant temperature incubation with stepped change; the three temperature periods were $T_1$, $T_2$, and $T_3$).

A decreasing temperature regime that simulates natural incubation conditions yields larger alevins and fry than increasing temperature regimes. The experimental temperature regime used by Murray and Beacham (1987) to study chinook embryo and alevin development was a series of three constant temperature periods (**Table 1**). A decrease from a $T_1$ of 8 or 12°C to a $T_2$ and $T_3$ of 4 or 8°C resulted in increased chinook alevin and fry size. Similar results were found for other salmonids by Peterson et al. (1977), Murray (1980), and Murray and Beacham (1986) (as cited by Murray and Beacham 1987). Increasing or decreasing temperature regimes, within the range 4°C to 12°C, having the same mean temperature over development resulted in similar times to hatching and emergence (Murray and Beacham 1987).

Winter egg incubation and alevin rearing temperatures in the field vary daily and seasonally during this developmental phase. Temperatures tend to vary daily in a manner simulated by a sine function. If one assumes a mean daily temperature of 5°C, with temperature varying according to a perfect sine wave by a ±3°C amplitude, the expected developmental time to emergence at this varying temperature regime can be compared to that at a constant mean temperature by summing development by increments of temperature change (see Alderdice and Velsen 1978). The full range of temperature variation for a day was represented as 5°C ± (3°C x sin(deg)) in which each 12-h period was divided into 180 equal time intervals (i.e., sin(0 degrees) to sin(90 degrees) in 1 degree increments above and below the mean temperature of 5°C). Development time to emergence on the varying temperature regime was then estimated as the mean of 180 individual development times by entering the temperature at each time increment into the development time-constant temperature model. Development time to emergence for the 5°C ± 3°C diel regime was estimated by this summation method, using the Bělehrádek equation of Beacham and Murray (1990) for chinook at each temperature increment, to be 205.0 d. Development at a constant temperature of 5°C would require 187.1 days.

The comparison of chinook egg developmental rates conducted by Alderdice and Velsen (1978) showed that eggs subjected early to constant (range about the mean <2°C) temperatures less than 6-7°C developed more slowly than under ambient conditions having the same mean. The much slower developmental rates of incubating eggs at very low temperatures appeared to be a major cause for a great divergence in accuracy of models in predicting development time to 50% hatching over the full range of normal incubation temperatures. It is possible that the discrepancy in theoretical development times predicted from application of the best model of Beacham and Murray (1990) above to the diel sine wave pattern and to the constant temperature, both having the same mean, can be attributed to the difficulty of applying a model based on constant incubation temperature to a diel cycle. It may be that physiological processes in egg development do not respond instantaneously to each temperature change in a sine wave pattern but develop at a rate related to some effective acclimation temperature defined by thermal exposure history. In the theoretical example above, it appears that the effective temperature in a 5°C ± 3°C diel regime is not 5°C but is slightly lower, resulting in longer development times. This might result from the Bělehrádek equation predicting slower egg development rates toward the lower extent of this diel cycle, a phenomenon noted by Alderdice and Velsen (1978). These authors indicated that initial egg development at constant low temperatures may impair early cell division. If the developmental equation used in this comparison incorporates such response at low temperatures, it might be that a better comparison of constant vs. cyclic temperature effects on development time should be made after early stages of egg development. Whichever approach is taken, it appears that development times may be different under constant vs. cyclic temperature regimes.

Winter water temperatures were recorded using continuous thermographs in the mainstem John Day (RK 422), Middle Fork (RK 103), North Fork (RK 97), and in Granite Creek. Temperatures for the mainstem, Middle Fork, and North Fork were recorded during the two winter periods of 1980-81 and 1982-83 (Lindsay et al. 1986, p. 17, 39-40). Original data were converted to cumulative thermal units plotted against days from peak spawning. Thermal units were calculated as the cumulative summation of days x mean daily temperature as degrees above 0°C **(Fig. 5)**.

Peak spawning commences about 2 weeks earlier in the mainstem than in the North Fork and Middle Fork. Maximum redd counts can be observed typically in the Mainstem by about September 10, the Middle Fork by September 18, and the upper North Fork by September 16 (spawning in the lower North Fork peaks approximately 4 d after that in the upper section). Annual variation in date of occurrence of maximum redd count was about 6 d in Granite Creek and 18 d in the upper North Fork. With emergence peaking between March 15 to June 15 in most years throughout the subbasin (maximum range February 25 to July 7), the median egg/alevin incubation period was approximately 228 d. However, the end of emergence in 1981 occurred by April 30 on the Mainstem and by June 14 in the North Fork. These dates on the North Fork and Mainstem corresponded to 231 and 277 days, respectively, after peak spawning on the Mainstem **(see Fig. 5)**. Because peak spawning commenced approximately 14 days later on the North Fork than the Middle Fork, 231 days from peak spawning to end of emergence were required for 1980-1981 eggs in the Mainstem and 263 days in the North Fork.

During the winter 1980-1981 incubation period approximately 1528 and 1211 Celsius thermal units (days x degrees above 0°C) were required from egg deposition to emergence for chinook in the Mainstem and the North Fork, respectively **(Fig. 5)**. Mean temperatures for the entire incubation period of the Mainstem and North Fork populations were 5.8°C and 4.1°C, respectively, as estimated from temperature recorders located in the Mainstem at RK 422 and in the North Fork at RK 97. Beacham and Murray (1990) noted such compensation in rate of development is typical of Pacific salmon. That is, more thermal units are required for completion of development from egg to emergence when incubation occurs at high temperatures than at low temperatures. This mechanism moderates development rate at high temperatures and tends to stabilize emergence dates under annual temperature variations. However, even with this stabilizing mechanism, emergence on the North Fork required 32 d additional development time.

The thermal sums model (cumulative degree-days above 0°C) applied to the example based on data of the Lindsay et al. (1986) study was found by Beacham and Murray (1990) to be a relatively weak predictor of emergence time compared with 9 other models. Peterson et al. (1977) showed that the "degree-days" required at various stages of egg development for Atlantic salmon (Salmo salar) varied with temperature regime during incubation. For example, they found that various combinations of temperatures during two distinct incubation phases can result in hatching on the same day with different degree-day accumulations. For hatching at 75-d incubation, between 400 and 550 degree days are required depending on $T_1$ and $T_2$. Hatching can occur with 500 degree days with 50 to 125 d-incubation depending on the combinations of $T_1$ and $T_2$. Along any time-to-hatching isopleth, alevin length increases with degree days required. The developmental phases studied were fertilization to eye pigment development, eye pigmentation to 50% hatching, and hatching to complete yolk absorption.

An improved variant of the thermal sums model incorporating degree days above some physiological meaningful temperature for chinook provided better accuracy. However, as noted above, their log-inverse model provided relatively high accuracy and was employed below in an attempt to predict time to peak emergence from bi-weekly mean field temperature in the North Fork John Day. By subtracting the cumulative thermal units reported by Lindsay et al. (1986) at period 1 from those at period 2 and dividing by 14 (the number of days between these periods), the mean temperature (°C) for the 14-day intervals was calculated. Mean temperatures throughout the winter incubation for 1980-1981 were then plotted for the Mainstem at RK 422 and the North Fork at RK 97 **(Fig. 6)**. By entering mean temperatures for successive incubation periods in the Mainstem and North Fork into model 4 (the log-inverse Bělehrádek model) from Beacham and Murray (1990), total time to emergence was computed. For example, if the mean temperature during the first 14-day period of the winter 1980-1981 incubation were 11°C, application of model 4 predicts that 84.3 d are required at a constant temperature of 11°C from egg to emergence. In this 14-d period, 16.6% of total development can be accomplished. When temperatures drop during the next interval, a smaller percentage of development is accumulated (this is the method expressed by Alderdice and Velsen 1978). Carrying out this procedure on the North Fork starting from peak spawning indicated that at 231 days after peak spawning on the North Fork (231 d after peak spawning on the North Fork or 245 d after peak spawning on the Mainstem) emergence should be complete **(Fig. 6)**. That is, development model 4 predicted that 245 d after peak spawning on the Mainstem emergence should be complete on the North Fork at RK 97 because 100% of the necessary development increments were accumulated. Instead, emergence was complete at 263 d after peak spawning on the North Fork. This 32-d discrepancy in emergence dates between observed and predicted on the North Fork might be misidentification of the spawning peak and/or a very broad peak, resulting in continued emergence after t=231 d was reached. Also, because emergence in the North Fork in 1981 spanned 75 d from beginning to end, the peak easily could have been 32 d prior to the end. The ending tail of the distribution might have been minor and not have represented a significant portion of the spawning population. Another weakness in this model estimation was that mean incubation temperatures under the declining seasonal regime were estimated for 2-wk intervals and not as even a daily mean for a diel cycle. Considering the sources of error, the utility of the standard developmental model for chinook appears to be reasonably good.

The discrepancy might also be attributable to the possibility that intra-gravel water temperature may not be well reflected by the surface water thermograph. However, one would have to conclude that intra-gravel water temperature was lower than surface water temperature. It is common for there to be a ±10% variation around the mean in incubation time within a species (Crisp 1981), but applying constant temperature incubation models to fluctuating field temperature exposure also adds to the variation. Spatial variation in temperature distribution in a stream reach is also common, so the thermograph may not perfectly represent the incubation temperatures for all eggs in the reach (B. McIntosh, Oregon State University, Corvallis, OR, pers. comm.). Nonetheless, it appears that model 4 is probably a reasonable method for projecting emergence date under a winter temperature regime in the field or estimating the shift in emergence date given an alteration in the temperature regime.

## ASSOCIATED COLDWATER SPECIES

### Constant Temperature

#### *Survival*

After the occurrence of ovulation in females and sperm maturation in males, the effect of elevated water temperature on rainbow trout egg and sperm viability becomes of concern

(Billard 1985). Holding temperatures of 20°C experienced for 70 h caused reduction in viability of eggs held in the body cavity, compared with females holding at 10°C (Billard and Breton 1977, as cited by Billard 1985). To promote female maturation and development of highest quality eggs, holding at temperatures from 5.6-13.3°C is essential (Leitritz and Lewis 1976).

### UILT experiments

Murray and McPhail (1988) studied embryo and alevin survival at incubation temperatures of 2, 5, 8, 11, and 14°C for coho, sockeye, chum, pink, and chinook salmon. For coho, embryo survival from fertilization to hatching was high at 5, 8, and 11°C, but was markedly less at 2°C and 14°C. Coho alevin survival at 14°C was lower than at the other incubation temperatures. At low temperature incubation (2°C), embryo survival to hatching was high and greater than for either sockeye or chinook. Even at 1.5°C coho embryo survival rates remained high and were much higher than for the other four species (Beacham and Murray 1990). Embryo survival for coho reached 50% at 1°C. For odd-year pink, even-year pink, chinook, chum, and sockeye this survival rate was reached at 4.5, 3.5,, 3.0, 2.5, and 1°C.

The effect of constant temperature egg and alevin incubation was also studied by Tang et al. (1987) on two coho stocks (the University of Washington hatchery stock and a stock from the Dungeness River). It was considered that the UW coho stock originated from a stream that was warmer than the Dungeness River stock. From information provided in this paper it is not possible to infer whether differences in thermal regimes of these two streams were culturally derived or how long the differences had existed. Evidence provided in the Genetic Effects section (see 117) indicates that adaptation to a significant degree to such shifts in thermal regime does not happen in such short times. Nonetheless, differences in response by the two stocks observed could reflect inherent stock differences. The UW stock had high egg survival to hatching between 1.3 and 12.4°C. Survival at high (17.0°C) and low (0.6°C) extremes was 0%. Even at 14.4°C survival was only 15%. Alevin survival to emergence was also high (91-100%) between 1.3-12.4°C but was 65-80% at 14.4°C. The Dungeness stock, which was more coldwater tolerant, had lower egg and alevin survival at 12.5°C (74% and 41% survival, respectively). At 14.4°C egg and alevin survival rates for the Dungeness stock were 1% and 0%, respectively. Survival at 1.3°C for the Dungeness stock was 90%, but unfortunately this stock was not tested at 0.6°C. These data appear to indicate stock differences in response of embryos and alevins to temperature. A temperature of 12.5C could be considered safe for the UW stock but of concern for Dungeness based on this short-term experiment. However, a small increase in temperature above 12.5°C produced increased impact to both stocks at egg and alevin stages. This indicates a narrow threshold for safety. Additional factors (e.g., disease could make this unsuitable for longer term incubation.

In sockeye highest embryo survival occurred at 8°C. Survival declined markedly toward 14°C and somewhat less so toward 2°C. Much of the mortality at 2°C occurred from fertilization to epiboly (Murray and McPhail 1988). Embryo survival up to 15.6°C was found to be high by Mead and Woodall (1968) and Withler and Morley (1970), both as cited by

Murray and McPhail (1988). Andrew and Geen (1960) reported severe mortality on sockeye (Cultus Lake, British Columbia) eggs incubated at ≥15.6°C. They also reported optimal survival at 12.8°C for incubation of Raft River sockeye but greatly reduced survival at 14.4°C. Combs (1965) found that sockeye survival at temperatures <4.4-5.8°C was low, whereas it was high between this lower threshold and 12.8°C. Between 12.8 and 16.9°C survival of sockeye eggs declined drastically from 86 to 17%.

In chum and pink salmon, embryo survival was highest at 11 and 8°C, respectively. However, at 14°C there was a slight decline in survival for chum and a major decline in survival for pink. Embryo survival for both species was 0% at 2°C. This mortality occurred immediately after fertilization (Murray and McPhail 1988). Pink salmon embryos had the lowest survival among the five species under incubation temperatures <4°C (Murray and McPhail 1988, Beacham and Murray 1990). Chum and pink had the greatest variation in survival among temperatures (i.e., given the temperature range 2 to 14°C) and chinook the lowest (Murray and McPhail 1988). Beacham and Murray (1986a, 1987b, as cited by Murray and Beacham 1987) found that chum survival rates at 8°C were higher than at either 4°C or 12°C. Except for one of the seven chum stocks studied, survival from fertilization to hatching at 4°C was only slightly less than at 8°C (Beacham and Murray 1986). The variability in survival rates for chum among stocks and family groups within stocks could be high (14% to 100%) and was greater at 4°C than at other test temperatures.

In their study of chum salmon, Beacham and Murray (1985) reported that the reduction in survival rate from incubation at 4°C mostly occurred from fertilization to hatching, not during post-hatch. Survival at 4°C to hatching was 74-84%, depending upon female size. After the critical initial incubation stage, survival from hatching to emergence was 100% at 4°C at all female size classes. Survival at both 4 and 12°C to hatching (74-88%) was lower than survival at 8°C (>96%), and varied with female size. Survival from hatching to emergence was high (97-100%) at 4 and 8°C for all three female size classes, but was low (69-76%) at 12°C.

Chum egg survival rates from fertilization to 50% hatching were high (≥96%) at 8°C for eggs from all three female size classes tested (Beacham and Murray 1985). However, when incubation temperatures during this developmental period were 12°C, the survival rate of eggs from large females (77%) was less than that of small females (88%). When incubation temperatures from hatching to emergence were 12°C, the survival rate of eggs of large females (69%) was again less than that of small females (76%). The difference in survival from egg fertilization to fry emergence between large and small female size classes was greatest at 12°C. Considering the entire incubation period from fertilization to emergence, eggs from large and small females had survival rates of 53% and 67%, respectively, at 12°C while survival was >94% for both size classes at 8°C.

Female size class is important in determining survival rate of eggs during incubation. Females of larger body length have greater fecundity (Beacham 1982, as cited by Beacham and Murray 1985). Egg size increases with body length (Beacham and Murray 1985). In addition to this study on chum, survival rate has also been shown to be greater for eggs of small females than for large females of coho, chinook, and rainbow trout (see references in Beacham and Murray 1985). Larger eggs have smaller surface area to volume ratios so may suffer oxygen deficiency to a greater degree than smaller eggs due to the control on diffusion at the egg boundary (Daykin 1965). Increases in water velocity improve oxygen transport to the vicinity of the egg boundary layer, but if DO is <8 mg/l at 10°C, increased velocity over steelhead eggs cannot prevent initiation of oxygen deprivation (Daykin 1965). High levels of fine sediments in egg pockets reduce intragravel water velocity and thereby intensify synergistic effects of temperature and dissolved oxygen. These observations may mean that larger eggs would have lower survival rates at higher temperatures and at lower percentage oxygen saturation. Also, while large females may have higher fecundity than small females, this may be balanced to some degree by a lower survival rate during incubation at any given temperature. Greater depth of egg incubation, however, by large females results in a different risk level than found in small females due to scouring effects (DeVries 1997), subsurface temperature regime, and the risk of subsequent "dig-up" by other large females (van den Berghe and Gross 1989). Confirmation of many of these relationships in the field was made by van den Berghe and Gross (1989) for coho spawning in tributaries to the Skykomish River, Washington. Largest females had as many as seven times more eggs as smallest females. Large females were able to occupy highest quality spawning gravel and to more successfully defend completed redds. However, smaller females produced smaller eggs that had a greater percentage survival in poor quality gravel than larger females, thereby compensating somewhat for lower fecundity and gravel quality in their territories (van den Berghe and Gross 1989).

Embryo survival was at a uniformly high level at 8°C incubation temperature for coho, sockeye, chum, pink, and chinook salmon. In addition, variation in embryo survival among these species was lower at 8°C than at any other test temperature (Murray and McPhail 1988). Considering these five Pacific salmon species, coho, sockeye, chum, pink (even-year), pink (odd-year), and chinook, the high temperature producing 50% embryo survival was 13.5, 15.5, >16, >15, 15.5, and 16°C, respectively. The low temperature producing 50% embryo survival was 1, 1, 2.5, 3.5, 4.5, and 3.0°C, respectively. Egg fertilization in salmon spawning in autumn may coincide with water temperatures of 15°C or more. Temperatures in this range may incur considerable mortality.

Bull trout (Salvelinus confluentus) have temperature requirements that are narrower than for chinook. Bull trout spawn in Oregon streams as early as August. Dolly varden (S. malma) require temperatures below 9°C (McPhail and Murray 1979, as cited by Taylor and Barton 1992) to initiate spawning. Egg mortality occurs at temperatures above 8°C (McPhail and Murray 1979, as cited by Taylor and Barton 1992).

In west-slope cutthroat trout (Oncorhynchus clarki lewisi), a spring-spawning species, temperatures <10°C are required for normal oogenesis and ovulation to occur. When broodstock were held at temperatures >10°C during gamete maturation, egg and fry survival were both approximately 40% (Smith et al. 1983, as cited by Marine 1992).

A significant effect of pre-spawning temperature exposure on brook trout broodstock was measured by Hokanson et al. (1973). When brook trout were spawned at 10.4°C or at 13.2°C and subsequently reared at 10°C, percentage of normal hatching was 65% and 38%, respectively. When brook trout were spawned at 10.4°C or at 13.2°C and subsequently reared at 16°C, percentage of normal hatching was 0% in each case. Percentage of normal hatching was >90% at constant incubation temperatures of 6°C to 8°C and declines steadily to 0% at 16°C. This temperature range (6-16°C) may represent the right portion of a bell-shaped survival curve. This study provides important evidence that adult holding water temperatures are as important as incubation temperature in determining egg viability.

Hatching success of rainbow trout eggs reaches its maximum (90%) at 10-12°C. The curve relating hatching success to temperature is bell-shaped and declines to 0% survival at 3°C and 18.5°C (Matighofen 1983, as cited by Humpesch 1985). Kwain (1975) measured a low survival rate (≥10%) of rainbow trout embryos to hatching at 15°C at all pH levels studied between pH 4.5-6.9 in egg mortality experiments at 5, 10, and 15°C. At a pH of 6.9, the highest survival rate (86%) occurred at 10°C. Grayling, another spring-spawning species, also had a relatively high optimum temperature for hatching (7-11°C) (Humpesch 1985). The temperature zone in which brown trout hatching success is high (i.e., >90%) is broad (1-10°C). However, as constant temperature of incubation is increased above 10°C, survival to hatching declines to 0% at 15°C. Brook trout have very similar percentage survival to hatching as with brown trout. Hatching success is 80-85% in the range 1.5-9.0°C, above which it steadily declines to 0% at 15°C (Humpesch 1985), a result similar to that shown by Hokanson et al. (1973). For Arctic char, survival to hatching is approximately 85% in the temperature range 1.5-5.0°C. Above 5°C, survival steadily declined until reaching 0% survival at 12.5°C. The lower limit for hatching in brown trout, Arctic char, and brook trout was <1°C (Humpesch 1985). These three species are winter-spawning species and are able to tolerate cold water during incubation. In rainbow trout and grayling the lower limit for hatching was 3°C (Humpesch 1985). Such information shows, particularly for high temperature effects, that relatively small temperature increases beyond the optimum survival zone results in a steady decline in survival to 0%.

Newly hatched brook trout alevins acclimated to 12.0°C have a 1-d $TL_{50}$ of 22.5°C. For newly hatched alevins acclimated to constant temperatures in the range 2.5-12.0°C, the 7-d $TL_{50}$ ranged from 19.4-20.4°C (McCormick et al. 1972). This result indicates that newly hatched brook trout alevins do not have the physiological mechanism for temperature acclimation; however, swim-up alevins do have increasing temperature tolerance with increasing acclimation temperatures in the range 7.5-12°C. A similar lack of acclimatory ability was also found in pre-swim-up Atlantic salmon and brown trout by Bishai (1960) (as cited by McCormick et al. 1972). Increasing the exposure time from 1 d to 7 d results in a 2.5°C lowering of the temperature that would produce 50% mortality. Swim-up alevins have a thermal tolerance that exceeded that of newly hatched alevins by 2.0-4.5°C, depending upon acclimation temperature. At 12.0°C acclimation temperature the $TL_{50}$ of swim-up alevins was 24.8°C (95% confidence interval was 22.8-26.9°C). The UUILT (ultimate 7-d $TL_{50}$ of newly hatched alevins) was 20.1°C. The UUILT (ultimate 7-d $TL_{50}$ of swim-up alevins) was 24.5°C

(McCormick et al. 1972). This compares favorably with the UUILT for young brook trout (25.3°C) found by Fry et al. (1946) (as cited by McCormick et al. 1972). Newly hatched alevins are considerably more temperature sensitive than swim-up alevins.

Thermal shock

The effects of constant temperature incubation on survival to 50% hatching and emergence and an abrupt temperature shift (increase or decrease) followed by return to initial temperature during four different stages of development prior to hatching were illuminated by Tang et al. (1987) on coho eggs from the University of Washington hatchery stock. Survival to 50% hatching and 100% yolk absorption were studied on eggs incubated at constant temperatures ranging from 0.1°C to 17.0°C. In a separate experiment, an 8-h exposure to a shock temperature was administered to eggs incubating at 1.5, 3.5, 4.0, 6.1, and 10.2°C. After holding eggs at the shock temperatures, temperature was restored to the initial constant incubation temperature. Eggs incubating at 10.2°C that were transferred to 17.0°C (a ∆+6.8°C) had a 67% survival to hatching when shocked at development period 1 (the 1.7-mm embryo stage) and 77% survival to hatch when shocked at developmental period 2 (the 35-somite embryo stage). Egg survival at a 17°C constant incubation temperature was 0%, while at constant temperatures ranging from 2.5 to 10.2°C egg survival was >81% and alevin survival was >95%. The 8-h shock exposure to 17.0°C upon transfer from 10.2°C was not enough exposure time to result in total mortality but had significant negative consequences. A temperature reduction from 10.2°C to 4°C incubation (i.e., a ∆-6.2°C) at developmental period 2 resulted in 62% survival to 50% hatching. Because survival during incubation to 50% hatching at constant temperatures approximating 4°C was >94%, it appears that there was a significant cold shock effect by transfer from 10.2°C during period 2. Shock magnitudes of ∆+6.8°C from a 10.2°C constant temperature caused a reduction in survival of egg batches to 50% hatching stage, exceeding that expected from constant temperature incubation at 10.2°C, but the same magnitude of shock given to eggs at any developmental period incubating at constant temperatures from 1.5°C to 6.1°C did not cause unusual mortality. This implies that a ∆+6.8°C is not necessarily harmful by itself unless accompanied by exposure of eggs to resistance temperatures (i.e., ≥17.0°C). This interpretation is reinforced by evidence that by applying, in any developmental period, a ∆+6.8°C to eggs incubating at 4.0°C, survival was >94%.

### *Growth and Development*

Murray and McPhail (1988) studied the time to hatching and emergence and alevin and fry size for five species of Pacific salmon at five incubation temperatures (2, 5, 8, 11, and 14°C). Hatching and emergence times were inversely dependent upon incubation temperature. For all test temperatures, coho had the shortest hatching and emergence times. At 2, 5, and 8°C, the longest hatching time was observed in sockeye. At 2 and 5°C, the longest time to reach 50% emergence was observed in chinook. At 8, 11, and 14°C, the longest time to reach 50% emergence was observed for pink salmon alevins. Similar relationships between temperature and hatching and emergence times were obtained by Beacham and Murray (1990).

Given the constant incubation temperatures 2, 5, 8, 11, and 14°C, coho and sockeye alevins at hatching were largest at 2°C. At 5°C pink salmon alevins achieved their largest standard length, while at 8°C chinook and chum alevin length was the greatest for these species. In terms of fry standard length, coho achieved their maximum length at 2°C, chinook and chum at 5°C, and sockeye and pink salmon at 8°C (Murray and McPhail 1988).

Incubation of chum eggs from fertilization to emergence provided greatest survival rates at a constant temperature of 8°C. At a constant temperature of 12°C, survival was 88% to hatching and 76% from hatching to emergence. However, at 12°C the influence of female size class became important. Larger chum females produced larger eggs (this relationship, though, is not universal, see review in Beacham and Murray 1985). There was also significant variation in egg diameter among family groups within size classes. Bigger eggs provide a greater amount of yolk reserves for alevins and thereby allow greater conversion to body tissue. Conversion efficiency is dependent upon incubation temperature (Marr 1966, Heming 1982). The largest female size class produced the longest and heaviest fry. The longest alevins were produced at 4°C; the heaviest, but shortest, alevins at hatching were produced at 12°C. Despite the larger size of alevins from large size females, eggs from small size females had a greater viability. Regardless of female size, length of emergent fry was smaller at lower incubation temperatures and weight of emergent fry increased up to 12°C. The lower survival rate of eggs to emergence from large females may be compensated by the increased survival rate of larger size fry produced by these females. Larger chum fry emigrate rapidly to the ocean, so large size is an advantage. For other species, such as coho or chinook, which have prolonged freshwater residency, emergence at larger relative size by a specific date is probably an advantage. Early emergence at any size may be a disadvantage if emergence coincides with high flows or poor food availability. However, early emergence at greater relative size (possibly due to larger female size and larger egg size) could at least partially compensate for high flows.

Beacham and Murray (1990) examined available data for mean time to hatching and to emergence for five species of Pacific salmon. Their log-inverse regression model (model 4), of the form $\ln D = \ln a + b\ln(T-c)$, was simple and accurate relative to other models. Model parameters include: $D$ as observed hatching or emergence time after fertilization; $T$ as observed mean temperature (°C), and the coefficients $a$, $b$, and $c$. For coho and sockeye the equations used to predict emergence time were:

| | | |
|---|---|---|
| Coho | $\ln D = 7.018 + (-1.069)\ln(T-[-2.062])$ | $r^2=0.979$ |
| Sockeye | $\ln D = 7.647 + (-1.134)\ln(T-[-3.514])$ | $r^2=0.969$ |

Coho require fewer days from fertilization to emergence than either chinook or sockeye at any temperature between 2 and 16°, but the magnitude of the difference between these species is greatest at temperatures below 8°C. As few as 50 days are required for emergence at a constant temperature of 16°C while low temperatures of 2°C lengthen time to emergence to approximately 250 days in coho and 300 in sockeye **(Fig. 3)**. Taking the difference between the number of days to emergence at temperature T°C from the days at (T+1)°C, allows one to plot the effect of 1°C changes in temperature from a base temperature. For the three salmon species, the effect of a 1°C warming of stream water is most dramatic at low base temperatures. For example, when the base temperature is 2°C, warming the water by 1°C results in a shortening of time to emergence by approximately 53 d for both coho and sockeye **(Fig. 4)**.

For rainbow trout eggs incubating at 10°C, Humpesch (1985) noted that 32-34 d were required to achieve 50% hatching success. However, five other studies of rainbow trout hatching success provided a maximum range of 19-43 d required to achieve 50% hatching (references as cited by Humpesch 1985). These differences could be attributable to a combination of stock differences or differences in experimental conditions. Three of these studies, though, provided results that were very similar to those of Humpesch (1985). Developmental rate can also be influenced by oxygen level and light intensity (see references as cited by Humpesch 1985).

Rainbow trout and cutthroat trout, introduced into Emerald Lake, Colorado approximately 100 years ago, formed a hybridized population that has had 20-25 generations in the lake system. These hybrids spawn in an inlet and an outlet stream to the lake (Van Velson 1985, as cited by Behnke 1992). The outlet stream has a warmer temperature regime that allows twice the accumulation of temperature units between spawning and emergence as the inlet stream. Nonetheless, hybrid trout from each location, when taken to a hatchery, required 330 temperature units (i.e., units above 0°C) to reach hatching at a constant temperature of 12°C (Behnke 1992). Another 300 units were needed to reach emergence. These data indicate that 27.5 days are required at 12°C to reach hatching. Hatching time for trout at 12°C in these Colorado lake populations was approximately 5.5 d less than for rainbow trout at 10°C reported by Humpesch (1985).

Instantaneous rates of growth, mortality, and net biomass gain were studied on newly hatched brook trout alevins (McCormick et al. 1972) at 7.1, 9.8, 12.4, 15.4, 17.9, and 19.5°C. Conditions for growth and survival from the alevin through juvenile stages were suitable between 9.8°C to 15.4°C (McCormick et al. 1972). Under conditions where food was not limiting, the optimum growth temperature from the alevin through juvenile stages was 12.4-15.4°C. If food is limiting, optimum growth temperatures decrease (Elliott 1981, 1994). Net population biomass gain was calculated for 2-wk growth periods by subtracting weight lost due to mortality from weight gained by each lot of alevins. At 19.5°C the instantaneous rate of net biomass gain was -2.78%/d, meaning that loss of biomass from mortality exceeded biomass gained by survivors. Temperatures ≥18°C are considered detrimental except for brief periods (McCormick et al. 1972). It is worth noting that the upper temperature linked to the downstream distribution limit of brook trout (19°C) (Burton and Odum 1945), is similar to the temperature range in which instantaneous rate of net biomass gain declines to 0%/d (i.e., 17.9-19.5°C).

## Varying Temperature

### *Survival*

Under field conditions eggs fertilized at one temperature generally are subsequently exposed to either higher or lower temperatures. Temperatures during the autumn spawning periods of salmon in the Columbia Basin have a smaller diel range than during summer periods as well as a slowly declining mean temperature during the season. High temperatures during fertilization are of concern, as are the magnitude and sequences of temperatures from spawning through the incubation period.

Murray and Beacham (1986) studied effects of varying temperatures during development of pink salmon (Oncorhynchus gorbuscha). Temperatures regimes were designated as those experienced by eggs at three phases of development: fertilization, 50% hatching, and 50% emergence for egg lots tested in 1977 and 1981 (**Table 2**). Temperatures were changed stepwise by 0.5°C every three days until the temperature regime for the phase was reached. The $T_1$ temperature for these egg lots was the temperature at fertilization, and the $T_2$ and $T_3$ temperatures were destination temperatures at 50% hatching and 50% emergence. When $T_2$ and $T_3$ temperatures included 2 or 4°C, egg and alevin survival was significantly lower than at the higher temperatures studied (5°C to 15°C). Survival from fertilization to emergence under these conditions was decreased by a maximum of 7 to 18% for egg lots in 1977 and 1981 from the highest survival rates. No effect of either increasing or decreasing the temperature regime on survival was noted except when temperatures of 2°C-4°C were included. Transfer of eggs of all five pink salmon stocks studied in 1983 from incubation at 8°C and 12°C at all stages of development to 1°C resulted in high survival to 50% hatching (>88%). For five of six stocks studied, incubation at 12°C and transfer to 1°C at hatching resulted in a low alevin survival (37.9%-60.3%). Only the most northerly stock (the Keogh River stock) studied had a lesser impact of transfer. Murray and Beacham (1986) suggested that this indicated a stock difference enabling the northerly stock to withstand greater temperature reduction during incubation.

Survival of pink salmon from a southeast Alaska stock were studied in the laboratory under ambient conditions and at mean temperatures of 4.5, 3.0, and 2.0°C (Bailey and Evans 1971). The ambient regime varied from 6.9-8.7°C in the first 37 d and then declined to 4.0°C. The other experimental regimes fluctuated as much as ±2°C in 1 d but showed no trend over the entire exposure period (103 d). Egg survival was high (97%) under the ambient regime but declined from 90% at 4.5°C to 0% at 2.0°C. Initial incubation temperatures >4.5°C were necessary prior to declines to 4.0°C to prevent excess mortality and spinal abnormalities.

Murray and Beacham (1987) studied survival and development of chum embryos and alevins at 4, 8, and 12°C in which embryos were transferred from the initial temperature at completion of epiboly (early transfer) or complete eye pigmentation (late transfer) to the same or a different temperature (i.e., one of the three test temperatures). Test temperatures at various developmental stages were denoted as $T_1$, $T_2$, and $T_3$ (see **Table 2**). A $T_1$ of 8°C or

12°C produced significantly higher embryo survival rates from fertilization to hatching than did a $T_1$ of 4°C. The $T_1$ temperature experienced during chum egg incubation had a far greater effect on embryo survival than did $T_2$ or $T_3$. Based on constant temperature experiments, chum survival rates were higher at 8°C than at 4 or 12°C (Beacham and Murray 1986a, 1987b as cited by Murray and Beacham 1987). Also survival rates of embryos and alevins were poor at 2°C and moderate at 14°C (Murray 1980, as cited by Murray and Beacham 1987). After the period from fertilization to epiboly, the direction or magnitude of temperature change had little effect on embryo or alevin survival within the range 4°C to 12°C. A temperature regime that simulates the natural regime (i.e., gradually decreasing, no extreme shifts, minimum temperature above 4°C) for the stock resulted in high chum survival (Murray and Beacham 1987).

Peterson et al. (1977) studied the effect of a sequence of three constant temperatures ($T_1$, $T_2$, and $T_3$) on Atlantic salmon, where temperatures were 2, 4, 6, 8, 10, and 12°C, for incubation phases of fertilization to eye pigmentation, pigmentation to 50% hatching, and hatching to complete yolk absorption (see **Table 2**). Mean survival for eggs reared at $T_1$ between 4 and 8°C was 95%. Eggs reared at $T_1$ <4°C had a survival of 78%. For egg lots held at a constant 2°C temperature until hatching, survival (as low as 69%) was significantly less than that at all other temperatures. When $T_1$ was 10°C and 12°C, survival was 87% and 89%, respectively, which might have been related to fungal infection.

In a study of cutthroat trout eggs fertilized at 7°C and then cooled at a rate of 1°C/h to a constant temperature of 3°C in ≤11 d from fertilization, the survival of embryos that were cooled was significantly less than of control embryos (held at a constant 7°C) (Hubert and Gern 1995). However, after 13 d from fertilization, when embryos reached a stage of development in which the neural tube had closed, survival of cooled embryos was the same as that of control embryos (Hubert and Gern 1995). Embryos cooled from 7°C to 3°C after fertilization had low survival to hatching (36%) and swim-up (20%). Embryos incubated continuously at 7°C had a survival rate of 79% whereas those transferred to 3°C at 15 d had a higher survival rate (94%) (Hubert et al. 1994). However, Hubert and Gern (1995) did not find a higher survival rate in embryos similarly transferred to 3°C at 15 d. Closure of the neural tube is a developmental stage common to all salmonids. Temperature sensitivity of eggs soon after fertilization is commonly observed (Peterson et al. 1977). Hokanson et al. (1973) observed that development of brook trout eggs to the stage of eye pigmentation confers a greater relative temperature resistance to the embryo.

**Table 2.** Incubation temperatures used at various developmental periods in the literature exploring the effects of temperature change on survival and development.

| Reference | $T_1$ | $T_2$ | $T_3$ |
|---|---|---|---|
| Murray and Beacham (1986) | temperature at fertilization (used in the 1977 and 1981 egg lots)<br>a 36-d period for 5 stocks; a 20-d period for 2 stocks; starting at fertilization (used in the 1983 egg lots) | final temperature reached at 50% hatching, with temperature increased by 0.5°C every 3 d from temperature at fertilization<br>transfer to 1°C until termination of experiment; transfer for 5 stocks occurred near hatching ($T_1$ = 12°C) or at operculum growth onset ($T_1$ = 8°C); transfer for 2 stocks occurred near eye pigmentation ($T_1$ = 12°C) or yolk plug closure ($T_1$ = 8°C). | temperature at 50% emergence with temperature increased by 0.5°C every 3 d from temperature at hatching. |
| Murray and Beacham (1987) | initial incubation to completion of epiboly | from completion of epiboly to completion of eye pigmentation; transfer to $T_2$ at completion of epiboly was "early transfer" | from completion of eye pigmentation to emergence; transfer to $T_3$ at completion of eye pigmentation was "late transfer" |
| Peterson et al. (1977) | fertilization to eye pigmentation | eye pigmentation to 50% hatching | hatching to complete yolk absorption |
| Marten (1992) | mean temperature from fertilization to 100% of embryos with eye pigmentation | mean temperature from eye pigmentation to 50% hatching | |

A similar study on cutthroat trout, brown trout, and rainbow trout of temperature reduction during early egg incubation (Stonecypher et al. 1994) emphasized the significance of embryo sensitivity to cold temperatures soon after water hardening. Four stocks were studied: Snake River cutthroat (mid-May to mid-June spawning), Soda Lake brown trout (fall spawning), Eagle Lake rainbow trout (spring spawning), and hatchery rainbow trout from Hot Creek stock (fall-spawning). Fertilization and water hardening at 7°C, followed in 2 h by continued incubation at 7°C resulted in 94-100% survival among the four stocks to the eyed stage and 85-98% to the swim-up stage. When the initial 7°C incubation was followed by acclimation to 2°C, survival of the above four stocks to the eyed stage was 26, 54, 53, and 14%, respectively. To the swim-up stage, survival of these four stocks was 6, 49, 40, and 9%, respectively. At 2°C most of the mortality that occurred over a 140-d incubation period occurred within the first 40 d. These authors found no significant difference in survival of any stock to the eyed stage or to swim-up according to acclimation rate (i.e., in a comparison of 0.25, 1, 5, and 20°C/h rate of temperature adjustment). These data indicated that a cold thermal shock of $\Delta$5°C (i.e., from 7 to 2°C) administered at a rate of 20°C/h was no worse than one provided at a slower rate (0.25°C/h). However, the low final incubation temperature itself caused high mortality, mostly experienced up to the eyed stage.

Brook trout egg survival and development was studied at $T_1$ temperatures of 3, 5, and 8°C and $T_2$ temperatures of 2, 3, 5, 8, and 12°C (Marten 1992). $T_1$ was the temperature up to the point where 100% of viable eggs developed eye pigmentation (see **Table 2**); $T_2$ was the temperature from eye pigmentation to 50% hatching. Survival of eggs to hatching was dependent only upon $T_1$. During the period from the eyed stage to hatching, embryo survival was not dependent upon either $T_1$ or $T_2$. Survival to the eyed stage (E) was expressed by the equation $E = 52.7 + 10.1T_1 - 0.682T_1^2$. After the eyed stage was reached, survival was ≥85% at any $T_2$ used in the study (i.e., from 2 to 12°C).

*Growth and Development*

Murray and Beacham (1986) studied the effect of a series of constant incubation temperatures (i.e., stepped variation of temperature during development) on rate of development and alevin and fry size of pink salmon. Transfer of eggs from 8°C or 12°C late in development (i.e., near or just prior to hatching) had no significant effect on alevin length. However, transfer early in development (i.e., on or before onset of eye pigmentation) reduced alevin length. Bailey and Evans (1971) determined that early egg incubation at 3°C caused a reduction in alevin length compared with alevins incubated at ambient temperatures. A temperature regime simulating one naturally experienced by pink salmon eggs and alevins (i.e., initially high temperature, decreasing to a low level at hatching, and increasing to a high level) yielded larger alevins and fry than other regimes.

Time to hatching for pink salmon was greater at a constant temperature than under a decreasing temperature having the same mean (Murray and Beacham 1986). At a constant temperature of 5.1°C time to hatching was 96.6 d, but under a decreasing regime from 11 to 2°C (mean 5.2°C), hatching time was 87.7 d (a difference of 8.9 d). The time to 50% hatching under an increasing regime (5°C to 14°C) was 3.5 d greater than under a decreasing regime (14°C to 5°C) with similar mean. Time to 50% fry emergence under an increasing regime (5-14-14°C) was 1.9 days greater than under a regime of 15-6-15°C) with similar mean.

Within the range of test temperatures studied by Murray and Beacham (1987) (4, 8, and 12°C), chum hatching and emergence were delayed by increasing temperatures during development, especially when the initial $T_1$ temperature was 4°C. A constant 8°C incubation temperature regime or an early (i.e., at completion of epiboly) or late (i.e., at completion of eye pigmentation) transfer to 8°C (i.e., at $T_2$ or $T_3$) resulted in longer and heavier chum alevins and fry (Murray and Beacham 1987). The same study involving chinook embryos showed that chinook alevins and fry attained larger size when subjected to a decreasing temperature regime (i.e., transfer from $T_1$ of 8 or 12°C to a $T_2$ or $T_3$ of 4 or 8°C).

Peterson et al. (1977) studied the effect of a sequence of three constant temperatures ($T_1$, $T_2$, and $T_3$) on Atlantic salmon, where temperatures were 2, 4, 6, 8, 10, and 12°C, for incubation phases of fertilization to eye pigmentation, pigmentation to 50% hatching, and hatching to complete yolk absorption. When incubated at constant temperatures, lengths at hatching for two stocks of Atlantic salmon declined with increasing temperature between 4 and 12°C.

Peterson et al. (1977) reported an interaction between $T_1$ and $T_2$ in their effects on size at hatching. A $T_1$ >6°C produced alevins that were smaller at hatching for a given $T_2$. However, size at hatching was more influenced by $T_2$ than by $T_1$. The greatest development rate to hatching occurred with $T_2$ = 12°C, but at $T_2$ >8°C egg mortality owing to fungal infection became significant. By reducing $T_2$ to 2°C, maximum alevin size was achieved. A $T_1 = T_2$ = 6°C produced an alevin of moderately large size with high survival in a moderate amount of time. Increasing $T_1$ and $T_2$ temperatures in a hatchery to 8-12°C resulted in more rapid development but smaller size at hatching. The opportunity to provide early feeding and growth to fry can be advantageous prior to release. However, for alevins reared under a natural temperature regime in New Brunswick streams, where $T_1$ = 0.5-1.0°C and $T_2$ = 3-4°C, development time was longer but alevin length was greater at hatching than for alevins incubated at constant temperatures from 6 to 12°C. The large size at hatching under incubation temperatures <6°C translates to large emergent fry. A temperature of 6-7°C was noted as an optimum incubation temperature producing relatively large alevins in a relatively short time to hatching.

Prediction of development time to hatching is inexact based upon mean temperatures during the incubation period because of the separate regressions of temperature on development during growth periods between fertilization and hatching (i.e. periods governed by $T_1$ and $T_2$, see **Table 2**) (Peterson et al. 1977, Marten 1992). Degree-days (i.e., cumulative temperature x time) required from fertilization to hatching in Atlantic salmon can vary from 400 to 550 degree days (Peterson et al. 1977). An accumulation of 450 degree-days over a 100-d period or 500 degree-days accumulated over a 50-d period can produce the same size alevin. Mean daily temperatures for the 100- and 50-d periods, respectively, would be 4.5 and 10.0°C if development were at a constant temperature from fertilization to hatching. That is, very similar overall degree-day accumulation rates were found in separate cases of development to hatching requiring developmental times varying by a factor of two. If development time can be reduced from 100 to 50 d, keeping alevin size constant and involving just a small increase in degree-day accumulation (i.e., 450 to 500), one can see the importance of the precise combination of $T_1$ and $T_2$, because higher $T_2$ temperatures produce smaller alevins. Because a greater number of degree-days are required at a higher mean temperature, there appears to be a compensatory reduction in development rate to limit the variation in development time with temperature. Alderdice and Velson (1978) illustrated a similar type of compensation by modeling chinook egg development rate (%/d) as a function of temperature. For temperatures <4°C the thermal sums model estimated increasingly lower development rates than did the more realistic log-inverse model. For temperatures >4°C the thermal sums model estimated increasingly greater development rates than the log-inverse model. Thermal compensation invalidates the assumption of temperature x days being a fixed value within the range of normal development temperatures for a species. The conclusion that compensation occurred in the case of Atlantic salmon was based on developmental rates measured under stepped temperature variation during incubation rather than the combination of diel cycles and seasonal trends in mean temperature that would be expected in the field (Peterson et al.

1977).

Alevin size is also influenced by the temperature variations prior to hatching. A 75-d period from fertilization to hatching is required for development of alevins under both a [$T_1$]:[$T_2$] combination of [8]:[6]°C and [4]:[12]°C. However, the former temperature regime yielded alevins that were 2 mm longer (Peterson et al. 1977).

In a study of cutthroat trout egg incubation, when embryos were initially incubated at 7°C and then transferred to 3°C at 13 d following fertilization, time to hatching was 95-97 d (Hubert and Gern 1995). Hubert et al. (1994) similarly found that when cutthroat embryos were transferred from 7°C to 3°C at 15 d after fertilization, time to hatching was increased by 31 d compared to embryos incubated at a constant 7°C. Embryos incubated at constant temperatures of 3°C and 7°C required 97 d and 45 d, respectively, from fertilization to hatching (Hubert et al. 1994).

Time of development of brook trout eggs from fertilization to 50% hatching is dependent upon the mean temperatures experienced from fertilization to the eyed stage and from the eyed stage to 50% hatching ($T_1$ and $T_2$, respectively) (Marten 1992). Regressions of development time required for each of the two development periods on mean temperature for each period explained >99% of the variability. The mean number of days from the eyed stage to 50% hatching was explained fully by $T_2$. $T_1$ had no effect on development rate in the subsequent developmental period. Development rates in each period were independent. Higher mean incubation temperatures resulted in more rapid development to hatching but also produced smaller brook trout alevins. Earlier hatching at a smaller size may be compensated by ability to begin feeding and growth at an earlier time.

# JUVENILE LIFE STAGE:  FRY, FINGERLING, PARR

## CHINOOK

### Constant Temperature

*Survival*

UILT experiments

The upper incipient lethal temperature (UILT) is the upper temperature at which 50% mortality is observed for a given acclimation temperature.  By increasing the acclimation temperature, the UILT is increased to a point beyond which no further increase is possible (i.e., the UUILT or ultimate upper incipient lethal temperature).  At this combination of acclimation and exposure temperatures, 50% mortality of the population is observed in a 1000-min period (approx. 17 h) according to methods in Brett (1952) or simply 24 h (Armour 1990).  Extending exposure beyond 24 h results in a greater percentage mortality; reducing exposure below 24 h decreases percentage mortality.  Increasing the exposure temperature beyond the UUILT, holding exposure time constant at 24 h, results in greater percentage mortality.  Also, increasing exposure to temperature levels above the UUILT results in 50% mortality in progressively shorter time periods **(Fig. 7)**.  Mortality is a function of both exposure time and temperature, given a certain acclimation temperature.

The upper incipient lethal temperature (UILT) is a function of acclimation temperature.  For spring chinook juveniles acclimated to 20°C, the upper incipient lethal temperature is 25.1°C (**Table 3**) (Brett 1952).  This is the temperature at which 50% mortality is observed within a 1000-min period.  If acclimation temperature is increased to 24°C, the constant exposure temperature required to produce 50% mortality is 25.1°C.  This temperature is the upper incipient lethal temperature for fish acclimated to 24°C.  This is also the highest acclimation temperature for which UILT continues to increase.  Consequently, 25.1°C is the ultimate upper incipient lethal temperature (the highest temperature at which tolerance does not continue to increase with increasing acclimation temperature).  As temperature continues to increase, mortality increases rapidly with exposure.  Brett's (1952) studies on the Dungeness Hatchery spring chinook population indicated that for juveniles acclimated to 24°C, the median resistance time at 27.5°C was only 5.5 h.  Decreasing exposure temperature to 27°C resulted in a median resistance time of 10.9 h.  At temperatures >25°C resistance time decreases rapidly.  If juveniles were acclimated to a temperature of 20°C instead of 24°C, median resistance time at 27°C was only 3.9 h.  At high exposure temperatures, common to streams of the interior Columbia River, mortality is extremely sensitive to small changes in exposure time as well as acclimation temperature.  This makes use of a UUILT value as a sole index to a temperature standard hazardous because it can be uncertain what the effective acclimation temperature actually is.

**Table 3.** Upper incipient lethal temperature of chinook salmon.

| Species | Common Name | Author(s) | Acclimation temperature (°C) | UILT (°C) ±2SE |
|---|---|---|---|---|
| *Oncorhynchus tshawytscha* | chinook | Brett (1952) | 20<br>24 | 25.1±0.1<br>25.1±0.1 |

If maximum temperatures are contained within the 15.6°C upper boundary **(see Figs. 2 and 7)** for purposes of ensuring proper chinook growth, and if the acclimation temperature could be considered to be approximately 15.6°C, the associated UILT is 24.8°C. Using the formula of Coutant (1972) (see Armour 1990) to estimate that temperature that would result in 100% survival with an acclimation temperature of 15°C, one calculates that juveniles exposed to 22, 23, 24, and 25°C can tolerate these temperatures for 62.2, 18.1, 5.3 and 1.5 hours, respectively. Again, the higher the temperatures above 15.6°C, the higher the risk of disease mortalities and the greater the loading stress. Thermal stress can act in a cumulative manner between the feeding limit (temperature at which feeding ceases, slightly beyond the chinook growth limit of 19.1°C) and the UILT (Elliott 1981). Within this zone the combined effects of limiting stresses such as food limitation, low oxygen concentration, high turbidity, and competition for space plus loading stress of temperature can result in mortalities (Elliott 1981, Wedemeyer and McLeay 1981). This zone is the so-called tolerance zone, identified by Elliott as the area of the exposure/acclimation temperature graph **(see Fig. 7)** bounded by the UILT for 7-day exposure.

Studies by Brett (1952) have been considered authoritative for decades on UILT values for chinook. New studies show that Brett's estimates are still appropriate, or possibly that they represent the high end of the range for some populations. The temperature tolerance of ocean-type chinook from a southern British Columbia hatchery population (Robertson Creek) was compared with that of a stream-type chinook from a northern British Columbia wild population (Bear River) (Beacham and Withler 1991). Twenty families were produced from adult collections made of the ocean-type chinook and 32 families from the river-type population. Juveniles were marked by family and their holding tanks adjusted from the 14°C ambient temperature to the test temperature in 2 d. The ocean-type population was tested at 22°C and the stream-type population was tested at temperatures including 21.6 and 22.4°C. For the northern stream-type families held at 22.4°C, 87% mortality occurred in 1.9 d. Cumulative percentage mortality at 21.5°C reached about 60% in 3 d, followed by a reduced mortality rate. After 16 d cumulative mortality reached about 80%. For the southern, stream-type chinook, only 3% mortality occurred within the first 8 d, but cumulative mortality was 74% in 18 d at 22°C. 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, they are better adapted to short-term exposure to high water temperature than the stream-type population.

These authors speculated that the UILT for salmonids may vary by population, depending on their history of adaptation to temperature regimes. However, for the ocean-type population they saw little remaining additive genetic variation that would enable selection for increased temperature tolerance. This study appears to demonstrate that the more southern Dungeness Hatchery population studied by Brett (1952) had a higher UILT than did the two British Columbia populations. Brett reported a UILT of 24.3°C with acclimation at 10°C and a UILT of 25.0°C at 15°C acclimation. In both British Columbia populations (ocean- and stream-type) there was <10% mortality at all test temperatures up to the maximum exposure temperature of 22.4°C (acclimation temperature of 14°C). That is, it would require higher temperatures than 22.4°C to produce 50% mortality within 1000 min even in the British Columbia populations. Mortality in the British Columbia populations was cumulated for up to 18 d instead of only 1000 min as in Brett (1952). Nonetheless, it appears that resistance to high temperatures is somewhat less in the British Columbia populations than the Washington population. It is interesting that despite the differences in response to temperature within the first few days, the British Columbia populations had similar cumulative mortalities over a 16- to 18-d period. It is also noteworthy that prolonged exposure to temperatures that might be considered to be in the safety zone based on use of the Brett (1952) and Coutant's formula (see Armour 1990) were lethal.

### Thermal shock

Rapid shifts in temperature, either upward or downward (feasible primarily through point-source releases) can induce acute temperature shocks, producing a high mortality rate. The severity of the shock depends on effective acclimation temperature at the time of the temperature shift, the magnitude of the temperature shift, and the exposure time (Tang et al. 1987). This conclusion is supported by Hart (1947, 1952) (as cited by Hokanson et al 1977), who found that most fish species can tolerate temperature shifts of 15°C-18°C provided the exposure temperature is within the tolerance range.

Even if fish can withstand temperature shocks of considerable $\Delta T$, the ecological consequences can be significant. Chinook juveniles acclimated at 15°C and shocked by instantaneous transfer to constant temperature baths in the range 26 to 30°C for exposure times equivalent to 10% of the median time to loss of equilibrium (LE) for those temperatures were subject to a significantly greater predation rate than were unshocked controls (Coutant 1973). When a 0.5 h recovery period was allowed after the high temperature shock and return to the initial 15°C holding temperature, increased predation was demonstrated for any shocks to exposure times of ≥20% of mean time to LE. In this experimental design, recovery involved a second shock from a high exposure temperature to the lower holding temperature.

### *Growth and Development*

The preferred temperature range for fingerlings was 12°C-13°C (based on determination of mean of the distribution) when acclimated to temperatures ranging from 10°C to 24°C (Brett 1952). Increasing stream temperatures do not necessarily lead to increases in abundance of the foods normally comprising the diet of salmonids (i.e., drifting macroinvertebrates). Increased temperatures result in increased metabolic demand, can increase competition over a limited food base, and can lead to displacement of rearing juveniles to habitats in which they are more exposed to warm-water tolerant predators or competitors. Increased stream temperatures have been shown to result in decreased food availability and salmonid growth rates. Production in a model stream at 12.0°C was 65% higher than that at 16°C (Bisson and Davis 1976, as cited by CDWR 1988, p. 31). An optimum growth temperature of 15°C was recommended by Banks et al. (1971) (as cited by Garling and Masterson 1985). Brett et al. (1982) recommended 14.8°C as the growth optimum for juvenile chinook feeding on ration of 60% of the maximum (assumed to be a typical level in the field). Marine and Cech (1998) determined that growth rates of fall chinook under sublethal rearing temperatures (21-24°C) were substantially reduced from growth rates exhibited at 13-16°C. Wilson et al. (1987) recommended 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 14.6°C (Reiser and Bjornn 1979). If growth temperatures are maintained between 10°C and 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 and 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 15.6°C significantly increase the risk of mortality due to warmwater diseases. A synthesis of this evidence leads to a recommended optimum production temperature zone of 10.0-15.6°C.

The optimal growth zone of 10.0-15.6°C is found within the bounds for positive growth at 4.5°C (lower limit) and 19.1°C (upper limit) (see Armour 1990). The 4.1°C 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 21.4°C. If chinook were to have unlimited rations, the optimum growth temperature would be approximately 19°C (Brett et al. 1982). Under these conditions they are able to feed in temperatures as high as 23°C, but feeding declines between 23°C and 25°C to nil (Brett et al. 1982). The more conservative growth limits recommended in Armour (1990) are probably a better reflection of the influence of temperature on the population. At temperatures above the growth boundaries, growth becomes increasingly negative because feeding declines toward zero and respiration rate increases rapidly. Below the lower growth limit juveniles also typically cease feeding and seek cover. Metabolic inhibition can occur below 4.5°C (Elliott 1981, p. 232). If food becomes limiting, 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). Elliott found for brown trout that the temperature at which growth is zero drops from 19°C to 8°C when food rations are reduced from maximum to 12.5% of maximum. Because the growth optimum falls within 10.0°C-15.6°C and because diseases become a significant mortality risk beyond this upper optimum growth level, it is necessary to manage stream water temperatures on a stream network level from headwaters to mainstem, major salmon-rearing reaches so that temperatures can be maintained below 15.6°C within the historic rearing area. With the added concern that food rations under field conditions are typically less than satiation levels, a reduced growth zone expands the upper temperature zone causing loading stresses. This argues additionally for keeping temperatures no higher than the growth optimum range.

#### *Feeding*

Brett et al. (1982) observed feeding behavior of juvenile chinook from the Nechako River, British Columbia and the Big Qualicum River, Vancouver Island. They reported good feeding response to unlimited food supply at temperatures of 22°C, but feeding became more sporadic between 23°C and 25°C, at which point it ceased. Food conversion efficiency was maximal for both stocks at 19.6°C-19.8°C. Maximum conversion efficiency was 30.9% for the Big Qualicum hatchery chinook and 25.1% for the Nechako wild chinook. Conversion efficiency declined to 5% at approximately 24.8°C in both stocks.

### Varying Temperature

The effects of temperature have been measured on survival, growth and development, and feeding of fish at constant temperatures in the laboratory, but temperature regimes in freshwater habitats generally vary considerably during the day and from season to season. Diel variation is cyclic with a mid-afternoon high and an early morning low and has been approximated in the laboratory as a sinusoidal-pattern variation with either a smooth or stepped increase and decrease. Mean daily temperatures increase to a maximum during summertime in the northern hemisphere. Daily amplitude of variation is also greatest at this time. Seasonal effects of temperature on biotic response are partially a function of seasonal progression of average daily temperatures (or possibly shift in daily maxima), but they may also be related to other environmental cues such as photoperiod, diet, food supply (Fry 1957), and light intensity. In addition, a large amplitude of diel variation is frequently considered to be a threat to health of the fish community. Streamside vegetation removal or stream channel widening leads to increases in daily maxima and amplitude of daily variation. Reaches having their canopies removed experience elevated high temperatures in summer (as much as a Δ+10°C to 15°C from canopy removal on a 100-m reach) and decreased minima in winter and generally < 1°C-2°C increase in minima in summer (Beschta et al. 1987). Diel increases or decreases in temperature (e.g., variation from diel minimum to maximum) can be approximated in laboratory experiments as a CTM test with a "slow" heating rate, assuming the maximum is in the resistance zone. With a diel temperature range of 10°C, for example, the heating rate over a 12-h period would be 0.8°C/h, a rate generally considered to be a slow heating rate in CTM tests.

In studies of the effect of elevated temperatures on fish, it is known from constant temperature experiments that the response depends upon the exposure temperature, duration of exposure to that temperature, and also the previous acclimation temperature. Acclimation in constant temperature experiments is generally allowed for a period of 2-3 d to 2 wk as a minimum necessary to achieve consistency in response to temperature increases. However, in the field, fish are acclimated to a thermal history whose characteristics are poorly defined and exposure is to temperatures that may increase from the tolerance zone into the resistance zone and back. Effect of exposure to increasing temperatures within the upper resistance zone may then be assumed to be an integration of all exposure temperature-duration pairs in conjunction with preceding acclimation history. It is often hypothesized that acclimatization in the field is either to a temperature equal to a mean daily temperature, maximum daily temperature, or a temperature between these values. Acclimatization may also be attuned to one or more antecedent days of temperature cycles. An objective of this review is to examine evidence for properly interpreting the influence of temperature cycles on fish response (survival, growth and development, and feeding).

### *Survival*

#### Diel cycle:

Tests of survival of 0+ age migrants were conducted in liveboxes in the Grande Ronde River, Oregon in early August (Burck 1994). With a diel temperature regime of 25.6°C to 16.1°C (mean 20.9°C), survival was 0% in 24 h. In a 4-d test where maxima were 23.9°C-25.6°C and minima were 11.1°C to 13.3°C, survival was 20%. Increased survival appeared to be attributable to lower minima, lower mean temperatures, or also less time spent at temperatures above 23°C. At another site where 4-d tests were performed and daily maxima ranged from 19.4°C to 22.2°C, survival was 100% in most tests (one test indicated 50% survival). Survival in liveboxes under ambient field conditions can be attributed primarily to exposure and acclimation temperatures but may also be influenced by stress from the experimental chamber. If stress from holding in the chamber is involved, it appears that this is not a significant factor at maximum temperatures below 22°C. As in all laboratory or field short-term survival tests, high survival in the short term might not be representative of longer term probability of survival.

### *Growth and Development*

There appears to be little information available on the growth optima for chinook under a fluctuating temperature regime in the laboratory or field. More investigation of available data sources needs to be done.

### *Feeding*

There appears to be little information available on feeding rates of chinook under fluctuating temperature regimes.

# ASSOCIATED COLDWATER SPECIES

## Constant Temperature

### *Survival*

#### UILT experiments:

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 a great deal of consistency among species (**Table 4**). Taking only those tests in which acclimation temperature was ≥20°C so that one might assume the UILT to be approximately equal to the UUILT, the range in UILT values found was 23°C to 27°C. Redband trout tend to be the most heat resistant of the salmonids. The range in measured UILT values for all species excluding redband trout was 23°C-26°C.

**Table 4.** Upper incipient lethal temperature of various salmonids and other associated, coldwater fish species.

| **Species** | **Common Name** | **Origin (River/ Lake)** | **Author(s)** | **Accl. Temp (°C)** | **UILT (°C)** |
|---|---|---|---|---|---|
| *Oncorhynchus kisutch* | coho salmon | Nile Cr. Hatchery, British Columbia | Brett (1952) | 20<br>23 | 25.0<br>25.0 |
| *Oncorhynchus nerka* | sockeye salmon | Issaquah Hatchery, WA | McConnell and Blahm (1970) (as cited by Coutant 1972)<br>Brett (1952) | 20<br>20<br>23 | 23.5<br>24.8<br>24.3 |
| *Oncorhynchus keta* | chum salmon | Nile Cr. Hatchery, British Columbia | Brett (1952) | 20<br>23 | 23.7<br>23.8 |
| *Oncorhynchus gorbuscha* | pink | Dungeness Hatchery, WA | Brett (1952) | 20<br>24 | 23.9<br>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<br>Ennis Hatchery<br>Winthrop Hatchery | Kaya (1978) | 24.5<br>24.5<br>24.5 | 26.2<br>26.2<br>26.2 |
| | redband trout | Parsnip Reservoir, Oregon | Sonski (1983a) | 20<br>23 | 27.4<br>26.8 |
| | | Parsnip Reservoir, Oregon | Sonski (1984) | 20<br>23 | 26.2<br>26.2 |
| | | Firehole River, Wyoming | | 20<br>23 | 27.2<br>26.3 |
| | | Wytheville rainbow | | 20<br>23 | 26.8<br>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<br>24 | 25.3<br>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 |
| *Lampetra planeri* | lamprey | England | Potter and Beamish (1975) | 25 | 29 |

Although field observations of thermal limits to distribution for most salmonids appear to indicate a threshold of approximately 22°C-24°C, some laboratory tests with coldwater species indicate tolerance to temperatures of 24°C. For example, Lohr et al. (1996) reported that Arctic grayling from Montana, when acclimated to 20°C were able to survive a 1 wk exposure to 24.0°C water. However, survival was 0% at 25°C. Similarly, Dwyer and Kramer (1975) reported that cutthroat trout (acclimated at 17°C and adjusted to test temperatures at a rate of 1°C/d) survived 24°C water for more than 2 wk but consumed little or no food at this high temperature, which was just below upper lethal temperatures. As will be seen in a more extensive review of field distribution of salmonids relative to temperature (see p. 87) , the upper field distribution limit appears to be 2°C to 3°C less than the UUILT.

### Thermal shock

Thermal shock is typically encountered as juvenile fish are entrained in power plant cooling systems or exposed to heated effluent. It can also occur at the confluence of streams of different temperatures or at the thermocline in lakes, such as those used by rearing sockeye salmon. The exposure temperature (i.e., shock temperature) is an instantaneous increase in temperature from the acclimation temperature. In a similar manner as chinook, rainbow trout subjected to a $\Delta T$ of considerable magnitude but at exposure times far less than those needed to produce loss of equilibrium (LE), can suffer significantly increased predation effects. Rainbow juveniles acclimated at 15°C and shocked by instantaneous transfer to constant temperature baths of 26, 28, or 30°C for any exposure times equivalent to ≥30% of the median time-to-LE at those temperatures were subject to a significantly greater predation rate than were unshocked controls (Coutant 1973). These data allow projection of the exposure time needed to initiate an increasing predation rate. Any exposure in excess of 18% of median time to LE caused predation to increase relative to unshocked control fish. When 0.5 h recovery period was included upon transfer to the 15°C holding temperature bath after the high temperature shock, an exposure of ≥80% of the median time-to-LE was needed to produce significantly increased predation rates at these shock temperatures. Exposure times for rainbow trout of as little as 10 min at 26.7°C after acclimation to 15°C are sufficient to produce an increased predation rate.

The median resistance time for rainbow trout acclimated to 18°C and subjected to 30°C instantaneously was only 25.9 min. When these fish were acclimated to a temperature of 12°C, the increased shock upon transfer to 30°C resulted in a median resistance time of 8.6 min (Stauffer et al. 1984). It may be unusual for fish to experience thermal shocks of high magnitude under naturally occurring field conditions. However, fish attempting to move about within a stream reach during low flow, high temperature periods during the summer may experience relatively rapid shifts in temperature among microhabitats. If fish are concentrated in coldwater refugia to escape lethal conditions, but must enter warmwater zones to feed they can be subject to shock upon entering the warm zone and also upon returning to the refuge.

A sublethal temperature increase from 10°C to an elevated temperature of 20°C was imposed on juvenile coho and steelhead in laboratory tests to determine physiological changes that accompany thermal shock. Both species exhibited hyperglycemia, hypocholestorolemia, increased blood hemoglobin, and decreased blood sugar regulatory precision. Coho suffered greater metabolic dysfunction than steelhead (Wedemeyer 1973). Multiple stresses can load or limit physiological systems, reduce growth rates, initiate disease, reduce osmoregulatory ability, and result in death when the physiological tolerance is overwhelmed (Wedemeyer and McLeay 1981).

Shock methodology is better able to provide predictive models of fish survival under entrainment than CTM studies (Hartwell and Hoss 1979). Studies of shock effects after acclimation to cyclic temperatures are not common in salmonids. Hartwell and Hoss (1979) studied shock resistance effects in juvenile spot (Leiostomus xanthurus). They found no significant difference among treatments (constant temperature and cyclic temperature acclimation) in which spot acclimated to a constant temperature 15, 20, or 25°C (or fluctuating regimes win means equal to those constant temperatures ±2°C or ±4°C) and then were exposed to shocks from 0°C to 20°C above mean acclimation temperature. Median lethal shock temperatures declined from approximately Δ18°C to Δ11°C as mean acclimation temperature increased from 15°C to 25°C.

Tests of cold shock have also been conducted on rainbow trout in the laboratory. Rainbow trout (7-16 cm fork length) acclimated to 10, 15, and 20°C had 96-h $TL_m$ values of 0.5, 1.4, and 3.3°C, respectively (Becker et al. 1977). The 96-h $TL_m$ represented the cold shock temperature, given a prior temperature acclimation, required to cause 50% mortality in a 4-d period. This cold shock was an abrupt transfer to cold temperature water. With acclimation to 20°C, there was complete loss of equilibrium (LE-point) when fish were plunged into 3.5°C temperature water, but no loss of equilibrium for cold shocks down to a temperature of 5.0°C. At the three acclimation temperatures (10, 15, and 20°C) abrupt transfers to cold temperatures of 1.2, 2.0, and 4.4°C, respectively, could be administered and still have >90% survival. These data indicate that from an acclimation temperature of 20°C a substantial instantaneous thermal decrease (Δ15°C) can be withstood for a 4-d period with no mortality.

Fish in these tests, however, did not receive the reverse shock back to the initial temperature because temperatures were held at the low shock temperature continuously for 4 d. Mortalities that did occur in this 4-d period occurred mostly in the first 24 h. As with high temperature exposure, mortality under abrupt cold shock is a result of temperature and exposure time (Becker et al. 1977).

### *Growth and Development*

Temperature preference by fish in a thermal gradient 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,

Juvenile sockeye had a positive growth response between 4°C and 21°C in laboratory experiments with feeding to satiation once per day (Donaldson and Foster 1941). Growth rate was negative at 22.8°C and at this temperature mortality was significant. Good growth with low mortality occurred at 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. Sockeye (7-12 months old) feeding at satiation (>6% dry wt/d) had a growth rate optimum at approximately 15°C. Growth rates declined at both higher and lower temperatures. Growth rates reached zero at approximately 24°C under satiation feeding. When feeding rate was lowered to 1.5%/d, the optimum growth temperature declined drastically to 5°C. At this feeding rate, growth rate (%/d) was zero at approximately 15°C (Brett et al. 1969). Feeding rates of Skaha Lake sockeye at 16.7°C were 2.3-3.2%/d (fresh weight; based on a sample of the 2-wk periods having mean temperatures of 16.7°C). Feeding rates were approximately 2.2%/d at 10°C, but the optimum growth occurred at this low temperature (Donaldson and Foster 1941). The lower optimum temperature in this experiment compared to that of Brett et al. (1982) feeding at 60% of satiation was probably attributable to shortage of food.

Redband trout reach their maximum growth rate at 20°C. Growth rates are less at both 15°C and 22.8°C (Sonski 1982, as cited by Sonski 1983b). By contrast, brown trout growth can be high in the temperature range 7-19°C, but growth is poor above 20°C (Frost and Brown 1967).

### *Feeding*

Fingerling sockeye begin losing appetite at 23.3°C and cease feeding at 24°C. Maximum feeding rate was measured as 8% dry body wt/d at 20°C. Optimum growth temperature was

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

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 25.5°C-27.0°C. In his comparison of thermal tolerance by three rainbow trout species, Sonski (1984) found that no redband trout or Wytheville rainbow fed at temperatures >26.0°C. The Firehole River stock would not feed beyond 26.7°C. Apache trout began to refuse feeding at temperatures of 20°C and at 21.2°C stopped feeding totally (Alcorn 1976).

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 acclimated to 15°C was 19.1°C ± 0.27 (SE). When fish were acclimated to 20°C, no feeding took place. Under cold temperature regimes, when brown trout were acclimated to water at 10°C, normal feeding occurred when fish were subjected to 2.9°C ± 0.27. When acclimated to even lower temperature (5°C), normal feeding occurred at 0.4°C ± 0.21. Similarly, Frost and Brown (1967) determined that feeding rate declined sharply above 19°C in brown trout.

## Varying Temperature

### *Survival*

#### CTM experiments:

Becker and Genoway (1979) recommend the use of a temperature increase rate of 18°C/h. They subjected coho (O. kisutch) to an acclimation temperature of 15°C for 2 wk and then a rate of heating of 18°C/h. The LE-temperature was 28.70°C and the D-temperature was 29.7°C. This is greater than the value of 26.0°C incipient lethal temperature (ILT) recorded by Brett (1952) for this species with 20°C acclimation. However, the ILT method assesses the temperature needed to produce 50% mortality in 1000 min (Bjornn and Reiser 1991). The CTM method is the arithmetic mean of the temperature at the LE-point or D-point.

If the mean D-temperature for coho is considered, this point is reached in 0.82 h at a rate of heating of 18°C/h. When applying the ILT method and the coefficients (*a* and *b*) provided by Armour (1990) for spring chinook acclimated at 15°C and subjected to exposure at 29.72°C, one calculates a median survival time of 3.2 min (0.05 h). Using the coefficients for coho derived by Brett (1952), one calculates a median survival time of 2.8 min (0.047 h) at 29.7°C. The CTM and ILT methods for evaluating thermal tolerance provide somewhat different interpretations. On the one hand, starting at 15°C acclimation temperature, coho subjected to a constant rate of temperature increase (18°C/h) can survive on average 0.82 h until death. Juvenile coho acclimated to 15°C and subjected instantaneously to a temperature of 29.7°C have a median time to death of 0.047 h. Obviously, the ILT method is sensitive to the magnitude of difference between acclimation and exposure temperature. If juvenile coho are acclimated to a higher temperature (23°C) and then subjected to an exposure temperature of 29.7°C, estimated median survival time is 12.7 min (0.21 h) using formula number 8 in Armour (1990) and the coefficients (*a* and *b*) for 23°C acclimation in Brett (1952) (see Coutant 1972).

The mean D-temperature at which a CTM is expressed for a 15°C acclimation temperature varies with rate of temperature increase. Becker and Genoway (1979) reported a mean D-temperature of 29.7°C at 18°C/h heating rate, but the D-temperature varied from 27.6°C at 1°C/h to 31.1°C at 60°C/h. That is when temperature was increased at a rapid constant rate, the mean temperature at death was higher than when increase in temperature was slower. At the high rate of heating, coho reached the mean D-temperature in 0.27 h. With slow rates of heating, a portion of the time that fish are exposed to test temperatures is spent at temperatures within the tolerance range. Also, slow heating rates can result in some degree of acclimation as temperature increases. This would tend to make the results of the two methods somewhat different.

Cold shock resistance was measured in rainbow trout in Columbia River water by Becker et al. (1977) using a similar series of declining temperature rates (1, 3, 5, 10, and 18°C/h). When rainbow trout were acclimated to 20°C and then subjected to the declining temperature regimes, it was found that $LE_{50}$ values (temperatures required for 50% of the test group to reach the LE-point) reached lower temperatures as cooling rates decreased. This implies that with more gradual cooling rates, partial acclimation can be more complete. The most rapid cooling rate (18°C/h) resulted in a 2.1°C $LE_{50}$, while the slowest cooling rate (1°C/h) resulted in the lowest, 0.9°C $LE_{50}$. The most rapid cooling rate was able to change water bath temperature from the 20°C acclimation temperature to the $LE_{50}$ point (2.1°C) in approximately 1 h. Abrupt transfer, on the other hand, from the acclimation temperature to 3.5°C caused 100% of the test group to reach the LE-point. Another experiment testing abrupt transfer to 3.3°C resulted in 50% survival in a 96-h test (i.e., there was a 50% mortality caused by a temperature decline of only 0.2°C from the LE-point). Starting from a 15°C acclimation temperature, the LE point was reached at <0.1°C under similar decline rates. These data show that there is survival value in reducing the rate of cooling to avoid thermal cold shock, loss of equilibrium, or mortality. They also show that very small changes in temperature can result in massive changes in population health. Although trout can withstand significant downward changes in temperature in the short term, disease outbreaks have frequently been experienced with salmonids in the longer term upon abrupt transfers to cold water. In addition, other factors, such as starvation or nutritional status can reduce the response thresholds.

A wide variety of studies were tabulated showing CTM values (**Table 5**) achieved after acclimation to temperatures of generally 15 to 20°C followed by heating at various rates from slow (0.04 to 1.0°C/h) to fast (18-24°C/h). CTM values varied from approximately 26°C to 30°C for these salmonids. CTM values generally are 1°C to 4°C higher than corresponding UILT values. CTM studies indicate the water temperature achieved under a fixed rate of

**Table 5.** Critical thermal maxima for various salmonids as reported in the literature.

| Species | Common Name | Origin (River/ Lake) | Author(s) | Accl. Temp (°C) | Heating Rate (°C/h) | CTM (°C) |
|---|---|---|---|---|---|---|
| *Oncorhynchus kisutch* | coho salmon | n.r.; | Becker and Genoway (1979) | 15 | 1 | 27.65[a]<br>27.56[b] |
| | | | | | 18 | 28.70[a]<br>29.72[b] |
| | | | | | 60 | 29.63[a]<br>31.15[b] |
| | | 6 British Columbia hatcheries; stock from Capilano, Chehalis, Chilliwack, Quinsam and Eagle Rivers, Tenderfoot Creek | McGeer et al. (1991) | 6 | 1 | 23.8-24.4[a or b] |
| | | Bingham Cr., WA<br>Bockman Cr., WA<br>Snow Cr., WA | Konecki et al. (1993) and Konecki et al. (1995a) | 11.5[c]<br>16.6[c]<br>14.6[c] | 20<br>20<br>20 | 28.2<br>29.1<br>29.2 |
| | | Bingham Cr., WA<br>Snow Cr., WA | Konecki et al. (1993) and Konecki et al. (1995a) | 11±1<br>11±1 | 20<br>20 | 27.6<br>27.9 |
| *Oncorhynchus mykiss* | steelhead | | | | | |
| | rainbow trout | n.r.; (2-3 months old) | Grande and Anderson (1991) | 17 | 0.04-0.08 | 26.3 |
| | rainbow | USFWS Williams Cr. NFH, Arizona | Lee and Rinne (1980)[e] | 20 | 1.2 | 29.35 (±0.58)[a] |
| | redband trout | | | | | |
| *Salmo salar* | Atlantic salmon | age 0+ and 1+ combined | Elliott and Elliott (1995) | 20 | 0.01<br>1.0<br>18 | 27.74 (±1.20)[d]<br>32.63 (±0.38)<br>32.83 (±0.83) |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | n.r.; (2-3 mo.) | Grande and Anderson (1991) | 17 | 0.04-0.08 | 28.7-29.2 |
|  |  | n.r.; (3-4 mo) | Grande and Anderson (1991) | 17 | 0.08 | 29.2 |
| *Salmo apache* | Arizona trout | Arizona | Alcorn (1976) | 15.6 | 0.04-0.06 | 21.2-22.3[a] |
|  |  | Big Bonita Cr., Arizona? | Lee and Rinne (1980)[e] | 20 | 1.2 | 29.40 (±0.21)[a] |
| *Salmo trutta* | brown trout | age 1+ and 2+ combined | Elliott and Elliott (1995) | 20 | 0.01<br>1.0<br>18 | 24.80 (±1.56)[d]<br>29.58 (±0.63)<br>29.98 (±1.44) |
|  |  | Ord Creek, Fort Apache Indian Res., Arizona | Lee and Rinne (1980)[e] | 20 | 1.2 | 29.85 (±0.58)[a] |
| *Salmo gilae* | Gila trout | Main Diamond Cr., McKnight Cr., Gila NF, New Mexico | Lee and Rinne (1980)[e] | 20 | 1.2 | 29.57 (±0.31)[a] |
| *Salmo clarki* | cutthroat | Oregon, wild | Golden (1976) | 23<br>13-23 cycle | ? | 30.57<br>29.82 |
| *Salvelinus fontinalis* | brook trout | n.r.; (3-4 months old) | Grande and Anderson (1991) | 17 | 0.08 | 27.2 |
|  |  | Ord Creek, Fort Apache Indian Res., Arizona | Lee and Rinne (1980)[e] | 20 | 1.2 | 29.76 (±0.35)[a] |
| *Salvelinus namaycush* | lake trout | n.r.; (2-3 months old) | Grande and Anderson (1991) | 17 | 0.04-0.08 | 25.9[b] |
|  |  | n.r.; (3-4 months old) | Grande and Anderson (1991) | 17 | 0.08 | 25.9[b] |
| *Thymallus arcticus* | Arctic grayling | Big Hole River, Montana | Lohr et al. (1996) | 20 | 24 | 29.3 |

Key:
a-- CTM determined to LE-temperature (i.e., loss of equilibrium)
b-- CTM determined to D-temperature (i.e., death)
c--mean ambient field temperature
d--95% confidence limits
e--test fish reported to be adult, but size was only 15-20 cm total length
n.r.--origin of test fish "not reported"

heating or cooling at the point where the LE- or D-temperature was reached. For species having a CTM of 26°C, for example, total exposure time between 25°C and 26°C can be short at a high heating rate. For example, at a heating rate of 18°C/h, only 0.05 h exposure time to elevated temperatures occurs during this 1°C temperature rise.

Stepped variation (daily)

Resistance to daily stepped temperature increases was studied on Lahontan cutthroat trout by Vigg and Kock (1980) (**Table 6**). Although temperature increases were very slow after reaching a temperature of 20°C, measured CTM values were similar for the two contrasted stocks and these values were also similar to CTMs for many other stocks tested by conventional techniques.

**Table 6.** Critical thermal maximum of salmonids resulting from daily stepped temperature increases.

| **Species** | **Common Name** | **Origin (River/ Lake)** | **Author(s)** | **Alkalinity (mg/l)** | **Accl. Temp (°C)** | **ΔT every X days (°C; d)** | **CTM (°C)** |
|---|---|---|---|---|---|---|---|
| *Salmo clarki henshawi* | Lahontan cutthroat trout | Marble Bluff strain--Pyramid Lake population | Vigg and Koch (1980) | 69 | 16 | 1°C@1d to 20°C then 1°C @ 4d | 22.3[a] ±0.2[b] |
| | | | | 357 | | | 20.9 ±0.1 |
| | | | | 1487 | | | 19.4 ±0.3 |
| | | Summit Lake strain--Pyramid Lake population | | 69 | | | 22.6 ±0.2 |
| | | | | 357 | | | 21.0 ±0.05 |
| | | | | 1487 | | | 19.9 ±0.1 |

Key:
a-- CTM determined to D-temperature (i.e., death)
b--95% confidence limits

Diel cycle:

Diel temperature fluctuations can present a serious threat to survival of juvenile salmonids in terms of maximum temperature experienced and cumulative exposure to temperatures within the resistance zone. Fluctuating temperature regimes become exaggerated in magnitude and can achieve higher maxima and lower minima when riparian vegetation is removed than if old growth vegetation is maintained. Even in southeast Alaska, daily maxima can reach 29°C (Thomas et al. 1986). In Oregon daily maxima of 30°C are not uncommon in denuded streams. In southeast Alaska, diel fluctuations in old growth streams may be only 4.8°C while temperature fluctuations in clearcut streams are typically 9°C. Martin et al. (1986) determined a relationship between diel temperature fluctuation and percentage summer mortality of juvenile coho in several streams on Mount St. Helens, Washington that represented extremes in vegetation cover. Summer mortality was described over the range of diel temperature fluctuation from 4 to 16°C by y = -0.330 + 0.082x, where x is diel fluctuation (in °C) and y is percentage mortality. Bear Creek had a diel fluctuation of >16°C, which equates to 98% mortality. Bear Creek had maximum summer water temperatures exceeding 25°C for 10 d in one year and 30 d the next.

A biologically serious consequence of the influence of riparian vegetation removal is that daily mean temperatures may rise only 1.2°C but the magnitude of diel fluctuation and daily maxima can be much greater than under old growth conditions. This is worrisome because the risks of thermal exposure are often calculated in terms of maximum weekly average temperature (MWAT) (see NAS 1972). Actual risk of cumulative exposure to elevated daily maxima may not be well represented by this method.

Shifts in fluctuating temperature regimes can be in terms of increased mean temperature, increased range or both. Impacts to individual survival and population density and size can be inferred from upward shifts in temperature regimes due to climatic warming. Meisner (1990) modeled effects of a 4.1°C increase in mean July and August air temperatures on summer thermal habitat for brook trout. Air temperature increases produced a comparable increase in groundwater temperature. Brook trout are limited in distribution by a 24°C thermal barrier. The increased air temperature resulted in a 30-42% decrease in available summer habitat in two southern Ontario streams. Elliott (1994, p. 230) demonstrated by use of his brown trout growth model that a 4°C water temperature increase resulted in a markedly smaller smolt size in brown trout, which would lead to a reduced survival. Growth rates are governed by water temperature and initial size of trout in populations of different densities and in a variety of stream types.

Based on laboratory studies on juvenile coho, blackside dace, and sculpin, DeHart (1975) showed that predicted times to 100% mortality from fractions of lethal doses, calculated from constant temperature UILT studies, accumulated over a 2-day period of cyclic temperature fluctuation were very similar to observed mortality rates. A model for additive mortification under a fluctuating temperature regime was also demonstrated in laboratory work of Fry et al. (1946) (as cited by Kilgour and McCauley 1986).

In a test on wild coastal cutthroat trout under fluctuating regimes, fish acclimated to a 13-23°C cyclic regime and subjected to a 13-27.5°C regime required 1.25 cycles for 50% mortality and 1.75 cycles for 80% mortality (Golden 1976). Fish acclimated to a constant 23°C acclimation temperature followed by the same cyclic regime, required 1.5 diel cycles for 50% mortality and 1.75 cycles for 90% mortality. In two tests on wild cutthroat acclimated to the fluctuating temperature regime where the experimental exposure temperature regime was increased to 13-28°C, 0.75 diel cycles were required for 100% mortality. For those fish acclimated to a constant 23°C regime followed by exposure to the cyclic regime, 0.75 diel cycles were required for 50% mortality and 1.00 diel cycles for 90% mortality (Golden 1976). This study indicates that mortality can be a cumulative response to thermal exposure history as did the work of DeHart (1975). The acclimation temperature regime selected by Golden

(1976) fluctuated from 13 to 23°C (note: 23°C is near the critical threshold to distribution of many salmonids as suggested in the Distribution section). Only 1.25 cycles of the 13-27.5°C regime were required to produce 50% mortality. In addition, further exposure to this cyclic regime increased cumulative mortality. Acclimation to the maximum temperature (i.e., 23°C) of the acclimation cycle improved survival somewhat over that achieved in a fluctuating temperature acclimation regime. This indicates that degree of acclimation in a cyclic regime tends to be equivalent to that provided by a constant temperature that is less than that produced by the maximum of the cyclic regime. This is not unexpected because the rate of acclimation to high temperatures is greater than that to low temperatures (Brett 1946). Also, Brett (1946) noted a relatively slow loss of heat-tolerance under declining temperatures compared with the rate of acclimation to a temperature. It is probable that the equivalent acclimation temperature in a fluctuating regime with stationary minimum and maximum would continue to increase toward some intermediate asymptote during several days of acclimation. The number of days to achieve relative stability of the effective acclimation temperature in a cyclic regime has not been studied to any extent. However, time needed to fully acclimate to an increase of 8-10°C magnitude from one constant temperature to another was 1 to 3 d for several fish studied (Brett 1946). One of the clearest and most recent demonstrations of this effect was done recently or channel catfish (Bennett et al. 1998). These authors showed that the rate of accruement of heat tolerance, as demonstrated by the rate of increase in CTM values with acclimation time, was greater under an increase in acclimation temperature than the rate of attrition of heat tolerance under the reciprocal reduction in acclimation temperature. Acclimation rates were a function of the direction of change in acclimation temperatures (increase or decrease), magnitude of the final acclimation temperature, and the absolute amount of temperature change. Rate of acclimation was faster at higher temperatures.

Cutthroat trout (Salmo clarki) appear to acclimate in a fluctuating temperature environment to an acclimation temperature equivalent to that produced by a constant temperature acclimation to $T_{min}+0.75(T_{max}-T_{min})$ (Golden and Schreck, unpublished ms) although Heath (1963) reported that sea-run cutthroat trout appeared to acclimate to the maximum temperature rather than mean for temperatures cycled between 10 and 20°C. This was conclusion was based upon the CTM under the thermocycle (29.8°C) being equivalent to that under a constant 20°C acclimation (29.9°C). If in Golden's (1975) experiments on cutthroat, fish were acclimated to a cyclic regime of 13-23°C, the equivalent constant temperature would be $T_{min}+0.75(T_{max}-T_{min})$ or 20.5°C. With a diel temperature fluctuation of 14.5°C (i.e., a regime of 13 to 27.5°C), the average rate of change would be (27.5-13°C)/12h or 1.2°C/h. This is the approximate rate of heating recommended by Elliott and Elliott (1995) in CTM experiments. Also, this magnitude of diel fluctuation is very close to that used by Thomas et al. (1986) to represent the diel temperature regime created by clearcut logging of riparian zones in southeastern Alaska. At this rate of heating Lee and Rinne (1980) measured CTM values of approximately 29.5°C for 5 species of trout acclimated to constant temperatures of 20°C. This was also similar to Golden's (1975) CTM for cutthroat trout. Even though cutthroat trout acclimated to a 13-23°C cycle were heated to a peak of only 27.5°C (Golden and Schreck, unpubl. ms) and not 29.5°C (i.e., the LE-temperature of Lee and Rinne 1980), mortality was produced from cumulative exposure to the diel cycles (13-27.5°C) even when maximum daily temperature did not exceed the LE-temperature. In addition, increasing the peak of the cycle to 28.5°C substantially reduced the mean number of cycles to death.

Thomas et al. (1986) tested the effect of fluctuating temperatures on survival of 0+ and 2+ age coho salmon relative to fish acclimated to a constant temperature. Fish acclimated to either a constant temperature of 11°C or a fluctuating temperature of 10°C-13°C were subjected to a fluctuating regime produced by increasing daily maximum by 2°C and decreasing minimum by 1°C every 2 d. For fish acclimated to a constant temperature (11°C), an $LT_{50}$ was produced for both age groups at a peak temperature of 24°C in the diel cycle. That is, 50% mortality was reached during the time periods when diel fluctuations shifted from 5°C-23°C to 4°C-25°C. For fish acclimated to the fluctuating temperature cycle, an $LT_{50}$ of 28°C was observed in 0+ coho and 26°C in 2+ coho. All fish survived the 5°C-23°C cycle and none survived the 2°C-29°C cycle. It is interesting that survival was high when maximum temperatures did not exceed 23°C but mortality became significant when maximum diel temperature reached 24°C for coho acclimated to a constant 11°C. In the 3°C-27°C diel cycle the mean heating rate would be 2°C/h, corresponding to rates commonly used in CTM experiments. It is interesting that 50% mortality was achieved in cycles including either 26°C or 28°C as maxima for the two age classes. Becker and Genoway's (1979) study on coho using a high heating rate indicated a CTM of 28.7°C, but McGeer et al. (1991), using a lower heating rate, determined that CTM was considerably lower (maximum of 24.4°C). The CTM from McGeer et al. corresponds to the $LT_{50}$ of Thomas et al. (1986) for coho acclimated at constant temperature. It is difficult to compare results from all these experiments. For example, the high heating rate used by Becker and Genoway could have resulted in significant overshooting of the temperature needed to produce loss of equilibrium or death. Also, in the study of Thomas et al. (1986) diel fluctuations and a slow widening of the diel range were studied simultaneously. Fish that succumbed in a 4°C-25°C cycle had previously experienced a 2-d exposure to a 5°C-23°C cycle. The cumulative effect of prior thermal history could have enhanced the impact of the 4°C-25°C cycle. As maximum temperatures rise gradually over the course of the experiment, fish can become acclimated to higher temperatures. The higher rate of acclimation to elevated than to decreased temperature probably means that effective acclimation during the testing tended to increase gradually and be more in tune with the trend in daily maxima than with the means. Another complicating factor is that Thomas et al. (1986) noted that a diel cycle of 10°C-13°C represents conditions in a typical southeastern Alaska old growth forest while 6.5°C-20°C represents a clearcut. Maximum temperatures at those latitudes can reach 29°C, so the high temperatures producing mortality in tests (e.g., 24°C-28°C) are significant relative to observed field conditions, but the diel range used in laboratory tests may have been too great. There are several potentially confounding effects in this test: the large diel amplitude of fluctuation that causes its own stress and which is greater in magnitude than experienced in typical field situations; the ability of fish to continue to acclimate to higher temperatures as maxima increase every 2 d; that as maxima increase, the mimina decrease, meaning that the daily time period of exposure to increasingly lethal temperatures increases but may be compensated to some extent by more time spent at cooler temperatures also; and the cumulative effects from prior exposure cycles.

In the field, there is not apt to be the large decrease in minimum diel temperatures as used in the laboratory tests, so fish in the field would be exposed daily to longer periods where temperatures exceed thermal limits.

Lee and Rinne (1980) studied effects of diel temperature fluctuations on five trout species (reported to be adults, but whose total lengths ranged only from 15-20 cm) and avoided some of the confounding factors in the Thomas et al. (1986) study. Lee and Rinne (1980) acclimated fish to 10°C; Thomas et al. acclimated them to 11°C. Lee and Rinne increased maximum temperature 1°C every 2 d rather than 2°C every 2 d. They also increased minimum temperature 1°C every 2 d rather than decrease it every 2 d. This resulted in diel fluctuation being a constant 6°C. The initial exposure cycle of Lee and Rinne was 15-21°C. Loss of equilibrium was reached in brown trout, rainbow trout, Arizona trout and Gila trout in a cycle of 21-27°C. Brook trout required a cycle of 22-28°C to reach the LE-point. This means that when fish exhibited loss of equilibrium in a 21-27°C cycle, they had been exposed for 2 d each to cycles of 15-21, 16-22, 17-23, 18-24, 19-25, and 20-26°C. It would be interesting in such an experiment to also determine how many cycles at 20-26°C or 21-27°C would be necessary to produce loss of equilibrium. This might aid in removing the effect of 10-12 d of prior exposure history during which possibly the latter 4-6 d (i.e., the latter 2-3 cycles) could have produced a cumulative mortality load. The mean heating rate in Lee and Rinne's fluctuating temperature experiment was 0.5°C/h. The heating rate in their CTM tests was very similar (1.2°C/h). They found that loss of equilibrium was reached at approximately 28.5°C for all five species in the CTM tests in which initial acclimation temperature was 10°C and was approximately 29.5°C at 20°C acclimation temperature. This experiment indicates that even though rate of heating was similar in the CTM test and the fluctuating temperature test, loss of equilibrium could be produced at a maximum temperature 1.5-2.5°C lower under a diel cycle than that observed in the CTM experiments. Further, fish in the fluctuating temperature experiments were able to continue to acclimate to increasing temperatures during the 10-12-d course of the experiment. Because this ability to increase acclimation to higher temperatures should have given them an advantage when subjected to the next higher diel cycle, it is even more significant that the LE-temperature is as low as 27°C in a diel cycle. However, it is possible that continued exposure to a 19-25°C or a 20-26°C cycle could have eventually resulted in loss of equilibrium if continued, assuming that these cycles created a portion of the cumulative thermal load that led up to the 21-27°C cycle causing loss of equilibrium.

Threader and Houston (1983) studied the effect of acclimation to a diel temperature cycle relative to constant temperature acclimation. Rainbow trout acclimated to a diel cycle of 8°C-16°C and then subjected to constant high temperatures exhibited a 24-h $LT_{50}$ of 25.6°C. However, when juvenile rainbow were conditioned to acclimation temperatures of 12, 16, or 20°C, 24-h $LT_{50}$ values were 24.6, 25.4, and 25.9°C, respectively. There was very little difference in terms of lethal temperature. However, the fluctuating acclimation temperatures provided increased median resistance times relative to constant temperature acclimation. Rainbow trout acclimated to a constant 12°C temperature vs. 12±4°C had median resistance times of 3.3 h vs. 10.1 h when exposed to a constant temperature of 26°C. However, one can assume from the test results and those of other studies reported here that when temperature fluctuation is 8°C-16°C, the effective acclimation temperature would be greater than the mean acclimation temperature. Juveniles acclimated to a 16°C constant temperature and then exposed to 26°C had a median resistance time of 8 h. This implies that acclimation to a fluctuating temperature confers greater resistance to high temperatures than would be achieved even by acclimation to the maximum temperature in the diel cycle.

Rearing temperatures fluctuating in the range 18.4°C-26°C (i.e., 22.2 ± 3.8°C) can result in significant population mortality rates in rainbow trout. Hokanson et al. (1977) reported that rainbow trout, acclimated at 16°C and reared under a fluctuating temperature regime of 22.2 ± 3.8°C in the laboratory, had a specific growth rate of zero and a mortality rate of 42.8%/d for the first 7 days of exposure, whereas mortality for trout held under optimal temperatures was only 0.36%/d. Optimal growth temperature range was 17.2°C-18.6°C (constant temperature regime) or 15.5°C to 17.3°C ±3.8°C (fluctuating temperature regime). A constant temperature of 26°C was similar to that level indicated by Threader and Houston (1983) needed to produce $LT_{50}$ after acclimation to 16°C.

### *Growth and Development*

#### Diel cycles: Laboratory Evidence

Hokanson et al. (1977) studied growth and survival of rainbow trout, Oncorhynchus mykiss, juveniles reared on maximum rations under fluctuating temperatures (T°C ±3.8°C) vs. that at constant temperatures. The physiological optimum (PO) temperature of rainbow trout is 16°C-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°C) vs. a fluctuating temperature regime (T°C ±3.8°C). In this temperature zone, a constant temperature of T+1.5°C provided comparable specific growth rate to juveniles reared at T°C ±3.8°C. However, specific growth rate at mean temperatures greater than PO was higher under a given mean temperature at constant temperature rather than under a fluctuating temperature regime of the same mean temperature. This result indicates that when water temperature under field conditions is greater than PO, it is not safe to assume that a mean of a diel temperature fluctuation is protective, even if it is known from constant temperature experiments that this mean is not injurious. The negative influence of the diel cycle appears to come from exposure to temperatures that are higher than the mean.

Hokanson et al. (1977) found that rainbow trout specific growth rate at a fluctuating temperature of 22.2 ±3.8°C was zero. Population production involves a balance between mean individual growth and mortality rate of the population. Hokanson et al. (1977) determined that a rainbow trout population would exhibit zero increase (maintenance) over a 40-d period at a constant temperature of 23°C and a fluctuating temperature of 21°C ±3.8°C because under these temperature conditions, specific growth rate balances specific mortality rate. With this laboratory information on constant and fluctuating temperatures and corroborating field information, Hokanson et al. (1977) recommended a mean weekly temperature of 17±2°C for rainbow trout so that maximum yield is not reduced more than 27% when trout are subjected to normal fluctuating temperature regimes.

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 diel temperature cycles of 12°C-20°C and 16°C-20°C relative to constant temperatures of 16°C and 20°C and could find no differences. Thomas et al. (1986) measured growth of juvenile coho for 40-d periods under constant 11°C temperature vs. diel temperature cycles of 10-13, 9-15, 8-17, and 6.5-20°C, all of which averaged 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 is cause for the greater efficiency in use of assimilated energy in growth. Konstantinov and Zdanovich (1986) (as cited by Behnke 1992) measured greater growth rates on several fish species under fluctuating rather than constant temperature regimes. Konstantinov et al. (1989) summarized several of their studies on effect of fluctuating thermal regimes on fish, stating 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 upon food ration. Under zooplankton rations equal to 4.0%-6.9% dry body weight/d and a fluctuating temperature regime similar to that experienced in the field in diel migrations, sockeye grew as well or more rapidly than under constant temperatures of 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 5°C-9°C and the epilimnion, with 12°C-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 ration, food conversion efficiency and growth were greater in a constant temperature regime than under fluctuating conditions such as found during diel vertical migrations in the field.

Clarke (1978) measured growth rates of juvenile sockeye in the laboratory at constant and fluctuating temperatures. At constant temperatures ranging from 7.5°C to 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 7.5°C growth rate was approximately 0.2%/d and at 17.5°C it was approximately 0.8%/d. At a constant 10°C regime, growth rate was 0.35%/d (estimated by regression for all constant temperature growth experiments), but under fluctuating regimes of 7°C-13°C and 5°C-15°C (mean daily temperatures of 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 7°C-13°C was equivalent to that observed at a constant temperature of 11.4°C. Under the diel regime with great amplitude (5°C-15°C), growth was equivalent to that observed at a constant temperature of 13.9°C. This indicates that under diel fluctuating regimes, there was an acclimation to an equivalent temperature found between the mean and the maximum temperature. This acclimation effect in terms of growth rates was similar to that observed in terms of survival under thermal stress with prior acclimation in cyclic diel temperature regimes.

As might be inferred from the work of Hokanson et al. (1977), if a diel temperature cycle has a mean greater than the physiological optimum and a maximum in the resistance zone, growth rate might be less than that found under a constant temperature equal to the mean of the cycle. A likely cause is that at temperature extremes feeding inhibition might occur, thereby limiting daily food intake. As food intake rate declines, the critical temperature providing positive growth and the optimum growth temperature decline (Elliott 1981, 1995, Kovacs and Leduc 1982). It must be determined whether feeding to satiation under a cyclic regime providing critically high temperatures that limit feeding can provide the same food intake as that gained under a constant temperature equal to the cycle. If feeding rate (as mediated by photoperiod, competition, or other factors) is correlated with temperature and responds instantaneously to temperature changes during diel cycles so that feeding rate can be maximized on a daily basis, the inability to feed during certain extreme portions of the cycle or during metabolic stress might be compensated to some degree by feeding during benign temperature periods. The colder portions of the diel cycle would tend to occur at night when feeding by sight feeding salmonids tends to be reduced. Growth rates are probably the most relevant and sensitive indicator and integrator of effects during diel cycles..

Wurtsbaugh and Davis (1977) studied growth of steelhead trout in laboratory streams under three fluctuating temperature regimes (i.e., natural cycle, natural +3°C, and natural +6°C) in all four seasons and found that trout growth could be enhanced by temperature increases up to 16.5°C. During the summer season the control temperature (natural cycle) was 16.2°C (mean) and the elevated temperatures averaged 19.5°C and 22.5°C. The average diel temperature range for the summer growth period was about 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 22.5°C) growth rate was zero at a food consumption rate of 7%/d. Gross food conversion efficiency decreased as temperatures increased from 16.2°C to 22.5°C. Maintenance rations increased by a factor of three over the temperature range 6.9°C to 22.5°C. This study revealed that trout growth was improve by increasing temperatures up to a maximum of 16.5°C, but that this threshold applies to the field only under satiation feeding. Because they measured field growth rates in an Oregon coastal stream indicating food limitation, they concluded that temperatures less than 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 13°C to 24°C over this summer period. A water treatment facility resulted in increasing control temperatures by 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 15°C-26°C. A comparison of the day 0 to day 30 initial growth period with the day 60 to day 90 growth period is revealing. The initial period had daily control temperatures varying from 13°C to 18°C; the final period had temperature variation from 19°C to 24°C. The treatment temperature regime was equal to the daily control temperatures +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 21°C-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 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 (17.7-21.7°C, mean 19.7°C), ambient-2.2°C, and ambient+2.2°C. Growth rate under the reduced temperature condition was 44% greater than under the ambient condition, even though mortality rates associated with columnaris disease in the two conditions were comparable.

In another study on Oncorhynchus 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 8, 15, and 18°C for 2- and 8-week periods. Best steelhead growth occurred at 15°C. By contrast, instantaneous growth rate under the fluctuating temperature as 11% less (Grabowski 1973). The thermocycle was sinusoidal, so a mean temperature of 13°C can be inferred. Growth at constant temperatures of 8 and 18°C were 36 and 29% less than at 15°C (Grabowski 1973).. These data allow one to hypothesize that the effective growth temperature for the 8-18°C cycle was close to 15°C, but it is not possible to determine whether it was slightly above or below 15°C.

### Diel cycles: Field Evidence

From Elliott's (1975a, 1975b) studies of brown trout growth under constant temperatures, the ability to model brown trout growth in the laboratory and field under fluctuating temperatures arose. This growth model has often been found equally capable of predicting growth under constant as well as fluctuating temperatures (Elliott 1994). Elliott (1975a) found that growth rates in the laboratory over 42-d periods in which temperature fluctuated as much as ±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 6.8°C in March to 12.1°C in June; in another, temperature decreased from 12.9°C in August to 7.2°C in November. Estimates of growth in the field made by entering the mean weekly temperatures (calculated as the mean of 7 daily mean temperatures) into the growth model revealed a 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 upon mean monthly temperatures were ≤2% different from computations based upon temperatures taken every 4 h. Likewise, Preall and Ringler (1989) developed a computer model of brown trout growth based upon Elliott's work and predicted potential growth for populations in three central New York streams based upon initial weight, condition factor, and weekly mean temperature regime. These authors measured actual growth under fluctuating temperature conditions 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 the explanation for growth rates exceeding laboratory-derived maxima under constant temperatures and satiation feeding was either inter-population genetic differences or the ability of fish in the field, under fluctuating temperature regimes, to feed at rates greater than under constant temperatures. It is also possible that the ability to assess the temperatures actually experienced by fish in the field is poor and not well represented by mean reach temperature. Jensen (1990) noted that in two streams observed growth was predicted best by using the 75% temperature (the median between the mean and maximum) and for another stream, growth was best predicted using mean temperature. Assuming that Jensen was able to measure the diel cycle actually experienced by brown trout in these streams, the similarity in application of the 75% temperature in predicting growth to its use in estimating equivalent acclimation temperatures in UILT tests is interesting. It appears that physiological conditioning of fish in fluctuating temperature regimes 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 under fluctuating temperatures is that food quality in the field is better than that provided in laboratory experiments. Also, fat content of selected prey items of salmonids could be higher than for the average of prey available in the benthos and provide a diet of high caloric content. Food quantity, however, is often considered to be 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 10.0, 6.9, 9.4, and 16.2°C in autumn, winter, spring, and summer, respectively) when fish were fed to satiation. Feeding to satiation at a frequency of 3 to 5 times/d (typical for most growth experiments) is considered to provide growth rates comparable to those under continuous feeding with excess food. In the field an increase in water temperature, when produced by canopy removal, can lead to increased primary production. A greater level of primary and secondary production increases food availability to fish (Murphy and Hall 1981, Hawkins et al. 1983) provided that substrate sedimentation does not increase simultaneously 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, 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 is maintained at a high level with increasing temperature, feeding rate and growth decline beyond the optimum temperature.

Mean instantaneous growth rates for 0+ and 1+ age Atlantic salmon over a 10-year period in the Miramichi and Restigouche Rivers were 2.33 and 1.23, respectively (Randall and Chadwick 1986, as cited by Power and Power 1994). Mean annual instantaneous growth rates for 1+ age parr of anadromous brown trout from 12 Norwegian rivers varied from 1.14-1.94 g/g/y (Jensen 1990). These mean growth rates were 76-136% of the maximum computed from laboratory growth rates at constant temperatures corresponding to the mean temperature in the field for 10-d increments over the growing season.

### Effect of Seasonal Temperature Trends

Field studies of salmonid growth under the combination of diel fluctuating temperatures and increasing or decreasing seasonal temperature trends have been documented by several authors (see Jensen 1990 for review). 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 on growth rates has been observed in brown trout and Atlantic salmon by various 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.

Growth rates of sockeye fry (Babine Lake, B.C. stock) were measured at satiation feeding (3 times/d) from March to mid-May under three temperature regimes: constant 10°C, declining 13 to 7°C, and an increasing 7 to 13°C. Mean temperature was 10°C in each treatment. Rate of temperature change in the declining or increasing treatments was 1°C/wk over a 56-d period. Growth rates were not significantly different among treatments. A photoperiod increasing from 12 to 16 h light/d at a rate of 30 min/wk (typical of the geographic latitude for the stock) produced a significant increase in growth rate under all three temperature regimes compared to growth rates under a 12 h photoperiod (Clarke et al. 1978).

### *Feeding*

#### Increasing Diel Temperature

In CTM experiments in which the heating rate was 2°C/d, five species of juvenile salmonids were observed feeding up to temperatures that were 1-2°C less than the $LT_{50}$ (Grande and Anderson 1991). Lake trout, brook trout, brown trout, rainbow trout, and Atlantic salmon were observed feeding at temperatures of 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 1.0-1.5°C/d showed that fish began refusing food at 20°C and totally ceased feeding at 21.2°C. In northern California streams, juvenile steelhead were seen actively feeding in water temperatures as high as 24°C (Nielsen et al. 1994). However, once temperatures reached 22°C, rate of foraging began to decline.

#### Diel cycles: Field Evidence

Coho in the field feed under temperatures as low as 2.5°C and display aggressive interactions in coastal British Columbia streams (McMahon and Hartman 1989).

# SMOLT LIFE STAGE

## SMOLTIFICATION IN SALMONIDS

The rate of silvering during the smoltification process is related to temperature, pre-smolt size, migration timing, and photoperiod (McMahon and Hartman 1988). Up to a point, increased temperatures result in increased rate of silvering (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). 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). Salinity tolerance is best accompanied by tests of plasma $Na^+$ within 24 h of the saltwater challenge. A promising physiological indicator of smoltification is the sharp increase in thyroxine (T4) in blood plasma (Wedemeyer et al. 1980), but numerous other physiological tests are available to index the degree of stress on fish health (Wedemeyer 1980). Among these are measures of plasma glucose and cortisol as indices of acute or chronic stress (Wedemeyer 1980).

Variations in migration timing can be influenced by temperature regime. Most of the variation in emigration date observed in chum and coho in Carnation Creek, British Columbia, was attributed to mean stream temperatures between peak spawning and emergence (Holtby et al. 1989). Chum stocks from the Fraser River return to home streams consistently during specific time periods. Early spawning stocks of chum are larger and older than late-spawning stocks. The early spawning stocks produce larger eggs and emerge later than the late spawning stock. Their larger egg size also produces fry of larger size (Beacham and Murray 1986). This adaptation to home stream conditions allows smolt migration to be timed so that smolts from all stocks descend within a narrow window. 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 subsequent survival in the marine environment (Thedinga and Koski 1984, Holtby et al. 1989). From application of laboratory studies on smoltification in relation to temperature, it would appear that an accelerated temperature regime during springtime would either result in earlier emigration or less success in smoltification (see Zaugg and Wagner 1973). Laboratory tests clearly showed that a high constant temperature regime (20°C) during the emigration period of coho caused a very restricted peak in gill ATPase activity compared to a normal (10°C) temperature regime. Under the elevated temperature regime, ATPase activity plummeted prior to ocean entry (Zaugg and McLain 1976).

Transformation from parr to smolt during seaward migration can be blocked by temperatures in the range 15°C-20°C (Adams et al. 1973). Temperatures of >17-20°C place smolts under either lethal or loading stresses that can impair metabolic activity, reduce swimming performance of lead to death (Brett 1958).  For example, in subyearling fall chinook in the Columbia River, temperatures of 18°C-20°C inhibit feeding.  After exposure to 20°C for several hours heat shock proteins are produced (Sauter and Maule 1997).

In smolting steelhead trout, rearing temperatures >13°C prevent increases in ATPase activity (Hoar 1988).  The smolt transformation in steelhead rearing in water >11.3°C was inhibited (Adams et al. 1975).  This inhibitory effect on steelhead is stronger than on coho, chinook, or Atlantic salmon (Adams et al. 1975).  Temperatures >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 12.3°C is nearly the upper limit for smolting (Zaugg and Wagner 1973).  When temperatures exceeded 13°C, gill Na-K-ATPase activity declined in fish that had already begun the smoltification process 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 due to inhibition of migratory ability.

Some physiological processes in smoltification of salmonids are greatly retarded by water temperatures >13°C and in some Pacific salmonids smolt stage cannot be attained at temperatures reaching 16°C (see references as cited by Johnston and Saunders 1981).  It is recommended for chinook and coho that a maximum temperature of approximately 12°C exist to maintain the migratory response and seawater adaptation in juveniles (Wedemeyer et al. 1980, CDWR 1988, p. 4 ).  Temperatures must be maintained at <12°C to prevent premature smolting (Zaugg and McLain 1976, as cited by Hoar 1988; Wedemeyer et al. 1980).  An apparent exception to this rule is that temperatures as high as 15°C have been used to increase growth rate and onset of smolting in coho.  However, the rate of desmoltification is also high in this temperature range.  Fall chinook undergo an even greater desmoltification rate than coho in this temperature range (Wedemeyer et al. 1980).  Yearling steelhead held at 6.5°C and transferred to 15°C had a marked reduction in gill ATP-ase activity, indicating a reversal of some smolting changes.

Aside from physiological impairment to smolts caused by elevated temperatures during migration, direct mortality has been reported.  Over a 48-km distance in the lower Sacramento River there was a 50% mortality at 23.01 ± 1.08°C, a temperature considered to be the UILT with 95% confidence interval (Baker et al. 1995).  This estimate was based on 15 smolt releases in May or June from 1983 through 1990.  Average weight of smolts was 5.15 to 9.40 g.  This field based estimate agrees well with laboratory measurements of Brett (1952) for chinook acclimated to 20°C (i.e., 25.1 ± 0.1°C).

Wedemeyer et al. (1980) offered several recommendations for hatchery culture of salmonids during winter and spring, preceding development to the smolt stage.  Their recommendations are relevant to achieving proper physiological development during the smoltification process, timing of saltwater entry, and consequently high marine survival.  They recommended that water temperatures kept below 12°C would protect the smoltification process for chinook, coho, and steelhead.  Sockeye terminate their downstream migration if water temperature exceeds 12-14°C (Brett et al. 1958), although coho are able to withstand some further increases before impeding migration. The influence on the smoltification process, though, may be common to both species.

Wedemeyer et al. (1980) recommended that temperature follow a natural seasonal pattern. For example, varying temperatures were found to be more stimulating to steelhead smoltification than constant temperatures (Wagner 1974, Zaugg and Wagner 1973). The mainstem Columbia River reservoirs provide environmental conditions that are cause for considerable concern for the smoltification process. That is, the large thermal inertia due to the volume of stored water alters the seasonal thermal regime. During late summer the warm water that fills the reservoirs such as in the lower Snake River is very slowly displaced by the gradually cooling tributary waters entering the mainstem. Although the majority of the smolt migration occurs earlier in the spring in the Columbia Basin, the elevated summer and autumn reservoir temperatures would seriously interfere with or prevent late smolt migration, thereby reducing life history diversity. Reservoirs also cause a dampening in diel temperature fluctuation that might somewhat inhibit smoltification. Superimposed on this physical template, there has been an increase in mean Columbia River mainstem temperature over the past 50 years that may be caused by a combination of climatic warming, cumulative land use, and river flow management practices (Quinn and Adams 1996).

The coupling of mainstem thermal regimes with those in natal tributaries may also be of concern for maintaining timing and success of smoltification and emigration, and optimum marine survival. That is, land use practices in tributary watersheds have led to more rapid temperature increases in spring and summer. This causes temperatures to exceed 12°C (a critical temperature for initiating smoltification) earlier in the season. Smolting salmonids would either be forced to emigrate earlier than historically to escape warmwater conditions in spring or would revert to the parr stage and be forced to migrate headward to rear in cool waters and then overwinter a second year. A rapid warming to the 12°C smoltification threshold could result in less time available for 0+ fall chinook to achieve sufficient size prior to smolting. Small size at smolting in coho results in a lower percentage adult return (Thedinga and Koski 1984). It is possible that pre-smolts having low body lipid content or condition factor due to small size at threshold temperatures cannot sustain further reductions in these factors that would accompany smolt transformation (see Folmar et al. 1982)

As revealed in studies on Rogue River spring chinook, the increase in gill Na-K-ATPase activity was greatest for juveniles >10-12 cm fork length (Ewing et al. 1979). These authors hypothesized that juveniles must be >8 cm fork length by the September-October for smoltification to be successful. Up to 85% of the returning adults emigrate during this time period, whereas the remainder emigrate the following May. Poor juvenile growth in a particular year could result in poor adult return due to the influence on timing of smoltification. For spring chinook and steelhead, an extra overwintering would likely result in high mortality (see Rhodes et al. 1994 for review of overwinter survival). Early emigration from tributaries may actually be advantageous if it results in avoidance of severe winter conditions (e.g., ice, high flows, scour, low temperatures), the possibility of some winter growth in downstream reaches under more moderate temperature conditions, and earlier downstream migration from the mainstem. However, delays in passage through the reservoirs could still subject smolts to temperatures that could cause desmoltification. Late smolt releases from upriver hatcheries are also apt to result in increased desmoltification. Such practices are sometimes used in the Columbia River to decrease competition between hatchery and wild components of a stock. For example, in the Hanford Reach of the Columbia River, downstream migration of naturally produced 0+ age fall chinook peaks in early June. Hatchery releases of fall chinook into the Hanford Reach occur from approximately June 15-July 1, although at a considerably larger size. Even in 1942 maximum temperatures during May and June were 11.7 and 17.2°C, respectively while maximum July temperatures were 21.1°C at river kilometer 228 near Warrendale (USGS 1968). It is easy to see that there would be an advantage to early migration with respect to temperatures conducive to smolting. Wedemeyer et al. (1980) recommended that smolt releases from hatcheries coincide with historic migration times.

Survival of smolts upon reaching the marine environment depends heavily upon 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). Two of the most important factors regulating these measures of seawater adaptability are freshwater rearing temperature and time of transfer to seawater. The relative growth rate of fall chinook in sea water was greatest after rearing in freshwater in a temperature range of 8-14°C, followed by transfer to 13-14.5°C in early May to early June. Freshwater rearing at 16°C resulted in seawater growth rates at 14°C that were approximately 70% of those with a 10°C freshwater rearing phase. Best plasma sodium regulation occurred under the freshwater-saltwater temperatures of 13.8 and 10.2°C, respectively. This study indicated that the higher the freshwater rearing temperature relative to the seawater rearing temperature, the lower would be the relative growth rate in seawater during the second through fourth weeks in seawater (Clarke and Shelbourn 1985). In years having mainstem Columbia River temperatures that are especially high relative to the ocean, the lowered growth rates could possibly decrease survival. When coho smolts enter saltwater prior to complete smoltification, cannot maintain a critical size prior to saltwater entry, or enter saltwater as smolts but then fail to maintain the necessary size, they frequently undergo desmoltification and become parr-revertants (Mahnken and Waknitz 1979, Folmar et al. 1982). It is possible that the freshwater-saltwater temperature combinations described above for fall chinook could be influential in defining saltwater growth potential. Low initial saltwater growth may be followed by desmoltification, parr-reversion, and return to freshwater to await ocean entry the following year. This process likely entails higher juvenile mortality. A higher incidence of parr-reversion and/or death in early saltwater rearing due to osmoregulatory dysfunction might then be a consequence of mainstem river vs. ocean thermal regimes.

Smolts that are released with subclinical infections will be apt to suffer delayed mortality in the marine environment. Many low grade infections by freshwater disease organisms are activated by stresses of migration and acclimation to saltwater (Wedemeyer et al. 1980) and the mortalities produced by these diseases go largely unnoticed. Smolts may contract these diseases in natural rearing environments, in hatcheries, and diseases in the mainstem may be spread especially through crowding in fish passage facilities or on barges. Other diseases classified as marine (e.g., viral erythrocytic necrosis) can be contracted in the estuary or ocean. It is important to control the stressors in the estuarine environment that can activate marine disease vectors (Wedemeyer et al. 1980). Preventing culturally based water temperature increases in the estuary is an important measure for controlling latent mortality from diseases. In addition, numerous chemical contaminants, which are typically concentrated in estuarine environments, such as herbicides, have been shown to inhibit smolt function and migratory behavior (Wedemeyer et al. 1980) and require careful control and monitoring. Combined effects of temperature and chemical contaminants frequently are shown to have synergistic effects (see Multiple Factor Effects section, p. 152).

# ADULT LIFE STAGE

## CHINOOK

### Constant Temperature

*Migration or Holding Survival*

Laboratory tests confirm that temperatures above 21°C equal or exceed incipient lethal temperatures for Columbia River chinook stocks migrating during the summer season. For example, Becker (1973) identified the thermal tolerance of chinook jacks to be 21°C-22°C based on a 168 hr TLM test. Coutant (1970) identified the incipient lethal temperature for chinook jacks as 22°C with prior acclimation to 19°C (estimated from ambient river temperatures). It is significant that given the few studies on lethal limits for salmon adults, that existing evidence indicates that these levels appear to be significantly below juvenile tolerance limits.

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 27°C-30°C. The GMST for adult sockeye was 1000 min at 24°C with acclimation at 15.8°C-18.3°C. Survival time at 26°C was only 100 min. Time to loss of equilibrium of adults was plotted vs. exposure temperature on the same graph as that showing survival times vs. exposure temperature. 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 than the time to death relationship. Furthermore, because sockeye exposed to temperatures of approximately 18°C-21°C become highly susceptible to Flexibacter columnaris, they took this temperature range as a greater thermal threat to continued stock survival.

Berman (1990) studied survival of Yakima River adult spring chinook held for 1.5 months at 14°C (control) and 19°C (treatment). Holding for this time period caused nearly total mortality at 19°C from columnaris infection. No mortality occurred in the control group.

In a continuation of her experiments, Berman (1990) subjected adults to elevated temperature holding conditions (17.5-19°C) for a 2-wk period prior to spawning. Control fish were held at 14-15.5°C. Progeny of the elevated treatment group had higher pre-hatch 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 observed in the elevated treatment 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.

**Varying Temperature**

*Migration: timing, normal migration temperatures, delay*

It is common for water temperatures in the Columbia River to exceed the upper migration limit of 21°C during August (USGS 1968) and for temperatures in the Snake to be even higher (≥25°C) (Thompson 1974, Karr et al. 1992). As an example of the problem posed for fall chinook migration, the 1990 water temperatures in Lower Granite Reservoir peaked on approximately August 13 at 25°C and gradually declined to about 21°C by September 16 (Karr et al. 1992). There is very little stratification in the reservoirs on many days during summer (Bennett et al. 1997) that can provide cooler water for migrating adults. For example, on August 8, 1991 adults migrating between Ice Harbor Dam and Lower Granite Dam had available to them very limited bottom area in only the deepest pools with temperatures of 20-21.1°C. All other parts of the water column were >21.1°C throughout the reservoirs (Karr et al. 1998).

As difficult as the thermal challenge to migration has been in the past, the situation seems to be getting gradually worse. Over the past at least 55 years there has been a trend in water temperature below Bonneville Dam for warmer condition. The trend in the date when late spring-early summertime water temperature on the Columbia mainstem below Bonneville Dam exceeded 15.5°C since 1938 shows that this temperature was reached on approximately July 1 in 1938 but was reached by June 1 in 1993 (Quinn and Adams 1996). Also, since 1949 there has been a significant increase of 1.8°C in annual maximum temperature in the lower Columbia River. Upstream at McNary Dam the mean June-July temperature increased by 1.5°C and the maximum temperature increased by 1.2°C since 1954. Further upstream on the Columbia River at Priest Rapids Dam the mean temperature did not change significantly from 1975 to 1994 but the maximum temperature increased by 3°C. At Ice Harbor Dam on the Snake River mean temperature autumn cooling to 15.5°C has been delayed 11 d from 1962 to 1994 (Quinn et al. 1997). Sockeye salmon have shifted their emigration timing to 6 d earlier since 1949. Despite this degree of plasticity in run timing to compensate for the trend of increasing lower river temperatures, the sockeye run has experienced an increase in mean temperatures between 1949 and 1993 from 16°C to 18.5°C at Bonneville Dam (Quinn and Adams 1996).

Spring chinook destined for the Grande Ronde River have a migration peak at Bonneville Dam on approximately April 15 and a spawning peak near September 5. Migration up the Grande Ronde River occurs in May. If temperatures in Snake River reservoirs or the lower Grande Ronde River were to exceed 21°C in May, it is likely that a critical window of opportunity to migrate up the mainstem Grande Ronde would disappear. Judging from scroll case temperatures at Lower Granite dam, temperatures in the Snake River are <12.8°C up to mid-June (Karr et al. 1992) but increasing temperatures in the Lower Grande Ronde may pose a problem to late migrants. Summer chinook bound for the South Fork Salmon River have a migration peak at Bonneville Dam on June 15 and spawning peak on September 1. Passage through the Snake River reservoirs occurs during July. The summer chinook immigration period coincides with a period of increasing temperatures in Lower Granite Reservoir in which temperatures rise from approximately 13.9°C to 25°C. This stock in the Snake River may be subject to thermal blockages having substantial implication to productivity because temperatures in the latter half of the migration period can be continuously in the range 21°C-25°C (Karr et al. 1992). Fall chinook historically entered the Snake River from late August through November with a peak in September (Snake River Subbasin Plan 1990). The adult fall chinook migration period commences at approximately the same time that the peak temperatures are reached. At Ice Harbor Reservoir during 1990, water temperatures were 23°C on August 15 but they had declined to only 22°C by September 16 (Karr et al. 1992). Currently, the run extends to mid-December. Peak spawning at the Lyons Ferry hatchery occurs in late November. Because of the large volume of warm water retained in Snake River reservoirs, elevated temperatures can present prolonged thermal barriers to fall chinook. These temperatures reveal that fall chinook in the Columbia River in late August ready to enter the Snake River could have to delay their upstream migration by 4 weeks until suitable temperatures exist for passage. Even then, high temperatures can lead to metabolic stress or disease.

On the Tucannon River, Washington, a radiotracking study on spring chinook revealed that when maximum temperatures of 21.1°C were reached, a thermal barrier to migration was established (Bumgarner et al. 1997). In 1996 this threshold was reached on June 24 in the lower Tucannon River, after which maximum daily temperatures did not decline below 21.1°C until September 8. One radiotracked spring chinook was apparently forced to remain in the Snake River until late September because it was finally detected migrating upstream in the Tucannon River at RK 12.3 on September 20 (Bumgarner et al. 1997). Because spawning typically occurs between late August and late September and because this adult might have experienced prolonged adverse temperatures in the Snake River, the probability of successful spawning of such delayed individual fish is apt to be low.

The temperature range under which the entire chinook run migrates upstream is 3.3°C-20°C. Normal migration temperatures of individual chinook races are narrower. Spring, summer, and fall chinook tend to migrate within the temperature ranges 3.3-13.3, 13.9-20.0, and 10.6-19.4°C, respectively (Bell 1991). In general, migration blockages become important when temperatures exceed 21°C. It is likely that the upper physiologically or behaviorally determined migration temperature listed for spring chinook represents customarily observed water temperatures during the genetically-determined migration period rather than a physiological limit to migration. With no contrary evidence, it will be assumed that a water temperature of 21°C represents the upper migration limit for all races. However, ability to withstand prolonged bioenergetic stress may be less in the smaller spring chinook than in the other races.

When salmon migration is blocked by adverse temperatures in the mainstem Columbia River, adults have been observed taking thermal refuge in small tributaries. For example, in an extreme temperature year (1941), chinook, sockeye, and steelhead were observed congregating in small, cold creeks near Bonneville and Rock Island Dams when temperatures in the Columbia rose to 21.7°C to 23.9°C (Fish and Hanavan 1948). Average monthly water temperatures were 21°C on July, 1941 at Bonneville Dam and 20.3°C on August, 1941 at Rock Island Dam (Sylvester 1958). Thermal blockage to adult fall chinook migration was reported at a temperature of 21°C in the Sacramento-San Joaquin River delta, but even temperatures as low as 19°C caused a partial blockage (Hallock et al. 1970). In this river system, no migration occurred until DO was >4.2-5.0 mg/l; migration blockages are controlled by threshold DO and temperature conditions. Temperatures of >21°C in the mainstem Clearwater River, Idaho caused spring chinook migration to suspend migration and hold in the cooler North Fork Clearwater until temperatures declined. This blockage occurred in late July and early August as determined by following radio-tagged spring chinook (Stabler 1981).

### *Migration survival*

Temperatures in a stream or river generally fluctuate on a diel basis. It is often assumed by optimistic biologists that survival is high if temperature excursions into incipient lethal zones are brief. However, studies of adult salmon subject to fluctuating temperatures illustrate the increased mortality risk with increasing temperatures. Of 3241 adults returning to Lyons Ferry hatchery in 1987, pre-spawning mortality was 32% at the hatchery alone.

Delays caused by an unfavorable migration environment may contribute to reproductive failure. Adults, which fast during a long upstream journey (≥1 month), exhaust virtually all energy reserves prior to spawning and death (Idler and Clemens 1959; Gilhousen 1980). High temperatures can increase the rate at which limited energy is consumed for standard metabolism (Fry 1971). Delays of as little as 3-4 d at migration barriers have been associated with premature mortalities (Andrew and Geen 1960), as has unusual exertion (DeLacy et al. 1956, Paulik 1960, Gilhousen 1990). The Stuart Lake sockeye in the Fraser River system travel at a rate of 42.4 km/d and reach their spawning grounds in 27 d (Idler and Clemens 1959). Males lose 14% of total body weight, 91% of initial fat reserves, and 32% of initial protein. Females lose 34% of total body weight, 96% of initial body fat, and 53% of initial body protein at the point of death. Body water content changed from 64% at initiation of migration to 83% at death. Absolute body fat content over this period declined from 14.8% to 1.3%. This run migrates 1152 km total distance in-river to the spawning grounds and climbs 678 m in elevation. The average river water temperature for the majority of the migration period reached a maximum of approximately 15.6°C-16.9°C based upon two years' data. Given that water temperatures reach a maximum in Lower Granite Reservoir on the Snake River of 19.4°C by July 1 (based on 1990 data, Karr et al. 1992) and the Stanley Basin sockeye run has even greater distances and elevations to traverse, plus more dams to pass, it is easy to understand their low migration success. These higher water temperatures would incur much greater metabolic expenditures and stress in burst swimming.

A radiotracking study of spring chinook migrating upstream in the Willamette River above Willamette Falls detected many negative consequences of migrating in water temperatures in the range 21-25°C. Mortality rates of adults prior to spawning were high. Some adults avoid high Willamette River temperatures by entering the Santiam River, but many others moved back downstream and never reached spawning grounds. Mortality rates were reported as high as 50-60% in some years due to the combination of disease and inability to migrate (Schreck et al. 1994).

### *Holding*

Streams that have become degraded from cumulative effects of management practices may have elevated water temperatures, reduced cover from large woody debris, and reduced resting pool area due to pool filling by sediments eroded from streambanks or upland areas (Rhodes et al. 1994). Reduction in volume and depth of large resting pools reduces availability of cold thermal refugia. This effect can be aggravated by withdrawal of cool groundwater for irrigation from aquifers linked hydrologically to surface stream flows. Thermal effects on adults lead to increased mortality. Among these effects are depletion of energy reserves owing to increased respiratory demands at warmer water temperature, protein coagulation, enzyme inhibition, and other effects. Thermal effects on eggs held by maturing females can produce subsequent mortalities during incubation. In addition to acute effects, many of the diseases that commonly affect chinook become highly infectious and virulent above 15.5°C. Both the percentage survival and time to death decrease as temperatures increase beyond this threshold. These diseases affect adults and juveniles alike. (See Disease section for more detail, see p. 104).

Prespawning mortality may occur during migration or holding. Mortality from disease effects is common during these periods, especially as temperatures increase, but is difficult to predict. Susceptibility to disease varies by stock. Some stocks are genetically more resistant to disease. The disease organism must be present for disease to occur and generally the frequency of infection increases with concentration of the disease organism. Even in a stock with a relatively fixed genetic makeup, there is annual variability in prespawning survival that can be a function of occurrence of the disease organism, annual virulence of the organism, abundance of the target fish and other fish species that may also be a host, annual condition of the fish that predisposes it to infection, and water temperature, which partially controls the infection rate and time to death.

When ripe adult females are exposed to temperatures beyond the range 13.3°C-15.6°C, pre-spawning adult mortality becomes pronounced and the survival of eggs to the eyed stage decreases. In addition to direct effects on adults, pre-spawning adults exposed to prolonged temperatures of 15.6°C-16.7°C , had survival of eggs to the eyed stage of 70% when then incubated at 12.7°C-13.3°C and a survival of 50% when incubated at 15.6°C-16.7°C. Adults exposed to 12.8°C-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 survival of eggs to the eyed stage taken from adults held at 11.7°C-12.2°C was highest (95%) (Hinze, Culver, and Rice 1956, as cited by CDWR 1988). Eggs taken from chinook when held at constant temperatures >13-15°C have poor viability (Hinze et al. 1956, as cited by Marine 1992, Rice 1960, Leitritz and Lewis 1976) .

Leitritz and Lewis (1976) and Piper et al. (1982) recommended chinook broodstock holding temperatures of 6°C-14°C. Conventional salmon hatchery practice is to consider chinook broodstock to be thermally stressed at temperatures >15°C; survival declines dramatically in holding ponds when temperatures exceed 17°C (Marine 1992). Raleigh et al. (1986) summarized the suitability of pre-spawning temperatures for adult chinook as maximal in the range 8.0°C to 12.5°C, but declining to zero at 24°C. A study by Fish (1944) revealed that adult chinook survival under fluctuating temperature regimes of 9.4°C-23.3°C (x=16°C) was only 36% but under a temperature regime of 11.1°C-15.6°C (x=11.9°C) 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 coldwater 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 rate in natural habitats 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 in these years 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 1977-1981. 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 18°C to 21°C (M. Everson, ODFW, pers. comm., as cited by Marine 1992).

### *Spawning*

Median dates of spawning migrations are known to be related to latitude, with earlier migrations at progressively higher latitude (Godin 1981). This life history trait appears to be designed to provide sufficient accumulated degree days during egg incubation so that timing of entry to the ocean occurs when oceanic temperatures and food availability are optimal or attainment of sufficient juvenile size occurs to allow adequate overwinter survival in freshwater habitat. Burger et al. (1985) hypothesized that individual stocks have adapted in run timing so that adult spawning occurs at an optimal time to promote fry survival. Run timing appears to be related to the unique thermal regimes presented by various water bodies. For example, lake outlet streams provide warmer conditions in autumn that appear to have selected for a late-spawning chinook run that is unique for the high latitudes of Alaska (Burger et al. 1985). Temperature preferences by adults during the spawning season are instrumental in determining spawn timing and location (Murray and Beacham 1987).

Temperatures observed at spawning time in the field probably reflect a combination of the genetically determined life history traits specifying optimum temperatures for various portions of the life cycle. Given the inherent temperature optima for any stock for its various life stages, population survival throughout the life cycle involves certain adjustments given the annual climatic variations. Compensation can occur to a limited extent in the egg stage during incubation (Alderdice and Velsen 1978). Also through behavior, adult fish express a degree of flexibility in adjusting location of holding or time of spawning to optimize their thermal regime to the extent feasible under annual conditions and their own bioenergetic constraints. 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, alevin, or fry survival. For this reason, judgment by fish habitat managers needs to be exercised in selecting suitable spawning temperatures. There is some plasticity in timing of life stage events relative to annual climatic patterns, 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.

Observed spawning of chinook in a wide variety of locations was reported for a composite temperature range of 2.2°C-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) were 5.6°C-13.9°C in their literature review. These limits were extracted from Bell (1986). EPA and NMFS (1971) recommended a maximum temperature of 12.8°C. Bell (1991) gave a range of 5.6°C-14.2°C as the preferred spawning zone, with 11°C as a preferred temperature based on an extensive summary of literature. 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 12.5°C and the maximum weekly temperature was 14°C (Dauble and Watson 1997). Because 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 12.5-14°C, a spawning temperature range of 5.6°C-12.8°C appears to be a reasonable recommendation, suitable for the Columbia Basin, unless colder thermal regimes are natural in any tributary.

It has been reported that spawning is initiated under a declining temperature regime. Chambers 1956 (as cited by Raleigh et al. 1986) found that spring chinook normally spawn as water temperature declines from 12.8°C to 4.5°C and fall chinook under a 13.4°C to 5.0°C decline. It appears that the critical temperature threshold of approximately 12.8°C and a declining temperature regime is one that is associated with ability to complete the spawning act, maximum long-term viability of eggs and alevins, and good and improving 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 at present how to separate disease and bioenergetic stress effects.

Chinook females spend from 4-25 d defending their redds after spawning commences from observations on a number of streams in British Columbia (Neilson and Geen 1981, Neilson and Banford 1983, both as cited by Healey 1991). On the Kamchatka River chinook spend 10-23d guarding their redds, starting from initiation of redd digging through redd closure and subsequently being swept away by the currents (Vronskiy 1972). The cooler water temperatures in these streams may, however, allow fairly lengthy periods of nest guarding. Coho survived 4-15 d (mean 11 d) in an Oregon stream after spawning (Willis 1954, as cited by Sandercock 1991). In an Sashin Creek, Alaska, coho females survived a mean of 11 and 13 d from initiation of spawning in two different years of study, respectively (Crone and Bond 1976). The range in female redd life for both these years was 3-24 d. Mean redd life in two Oregon coastal streams was approximately 13 d (Koski 1966, as cited by Crone and Bond 1976). Completing the act of spawning requires a great amount of stored energy and any excess might allow the adult to survive additional time. Ability to guard the redd may provide a fitness advantage if adult competition for spawning gravel is high. If an adult is delayed in spawning for a period of greater than 24 days (chinook) or 13 d (coho) by any combination of possible factors such as migration difficulties at dams, migration blockages by temperatures of approximately 21°C or greater, or by tributary water temperatures that continue to exceed spawning thresholds (approx. 12.8°C) , it can be assumed that 100% of the adults will not survive to initiate spawning. This method of calculation is based on the bioenergetic assumption that after completing the migration and possibly holding under "normal" thermal regimes, adult females have a limited energy reserve allowing it to excavate a redd and then live a certain number of extra days to guard the redd. Post-spawning redd guarding behavior has fitness value in protecting eggs from being displaced by other spawners (van den Berghe and Gross 1989), but the days (and energy) required for this activity would not be as critical as those devoted to redd digging. In chinook 5-14 d are required for redd digging (Vronskiy 1972), so delays in spawning of greater than this magnitude could be of concern if males or females are prevented from reaching spawning grounds (for stocks that spawn soon after reaching spawning ground) or commencing spawning for this number of days or more. If the migration delay subjects females to high holding temperatures in waiting for the blockage to be relieved or in retreating downstream to cooler tributary mouths, valuable energy needed later in spawning is lost at a minimum.

Given the available studies it appears that temperatures greater than 12.8°C can be assumed to begin inhibiting the spawning act. At temperatures greater than approximately 16°C we can assume that spawning will not occur. If spawning time for each individual reaching the spawning grounds in the early portion of the spawning period is delayed by 3 or more days, survival to the egg deposition stage should begin to decrease. If the delay is greater than 24 days for these same fish, survival to egg deposition should be very low.

## ASSOCIATED COLDWATER SPECIES

### Constant Temperature

#### *Rearing:Preference*

Adult salmonids in general have preferences for lower water temperatures than juveniles of the same species (McCauley and Huggins 1979, as cited by Spigarelli et al. 1983). Laboratory studies demonstrated a 24-h mean preferendum of 12.2°C for adult brown trout (Reynolds and Casterlin 1979c). Juveniles, on the other hand, have final preferenda of 17.4-17.6°C (references as cited by Spigarelli et al. 1983).

#### *Migration or holding survival*

Studies of lethal limits under constant or fluctuating high temperature are rare for adult salmonids. However, Columbia River steelhead, acclimated to river temperature of 19°C had a lethal threshold of 21°C (Coutant 1970). These lethal limits are 5.5°C lower than for juvenile rainbow acclimated to 18°C (Alabaster and Welcomme 1962, as cited by Coutant 1972). It appears that adults are much more sensitive to thermal extremes than are juveniles.

#### *Spawning*

In female brook trout the maximum temperature for maturation and ovulation is 16°C-19°C. Males can achieve functional maturity at temperatures as high as 19°C (Hokanson et al. 1973). However, at 19°C development of ova becomes inhibited and ova can be resorbed. Similar effects on egg survival during egg development have been studied in rainbow trout. Post-ovulation survival of eggs in the body cavity of rainbow trout females held at >13°C was much lower than at lower holding temperatures (Billard and Gillet 1981, as cited by Billard 1985).

In the laboratory, brook trout spawning was typically initiated at 10°C but occurred under temperatures as high as 16°C. The highest percentage of viable eggs per female was found at 8°C. When brook trout were spawned at 16°C, percentage viable eggs per female declined to 0% of the maximum observed at 8°C. An increase in spawning temperature from 10°C to 16°C resulted in a steady decline in spawnings per female, viable eggs per female, and total eggs per female to values approaching zero. A spawning temperature of 11.7°C provided the upper mean $ET_{50}$ or the median effective temperature representing the sublethal response for production of viable eggs per female. This study points out clearly that the mere ability of the fish to mature under holding temperatures does not indicate that spawning success will be normal or that eggs will be viable. Hokanson et al. (1973) recommended that for the month prior to spawning, maximum water temperature should be <19°C and mean temperature should be <16°C. During the breeding season maximum water temperature should be <12°C. Optimal conditions would be provided by mean spawning temperatures <9°C for optimal spawning activity, gamete viability, and embryo survival.

## Varying Temperature

### *Global and Regional Effects on Production*

Scarnecchia et al. (1989) analyzed data for yields of Atlantic salmon from 59 Icelandic rivers using data on streamflows and sea and air temperature. They determined that rivers on the northeast and northern coast had significantly greater variation in yields of grilse and 2-sea fish than did the western rivers. Greater variation in yields was correlated with a greater annual variation in spring-summer sea temperatures. This is the period of smolt migration and initiation of feeding in the ocean. Also, rivers having highly variable seasonal streamflows had highly variable 2-sea salmon yields. Streamflow variation is a commonly used predictor of fish biomass and density in freshwater environments (Binns and Eiserman 1979, Poff and Ward 1989).

The variation in production caused by the combination of seasonal streamflow variation and oceanic temperature variation frequently act in concert in the Pacific Northwest. The El Niño/La Niña weather patterns on the California to British Columbia coast related to cyclic variation in ocean temperatures induces patterns of climatic events in coastal and interior streams of the Pacific Northwest, producing variation in winter rainfall or snowpack, summer rainfall, channel scouring events, and summer air and water temperatures. Reduced winter snowpacks caused by more moderate winter air temperatures result in lower summer streamflows. Extreme highs or lows in seasonal streamflows and water temperature conditions can be very damaging to fish production and stressful to salmonids. Even though salmonids of the Pacific Northwest utilize streams that inherently are highly variable, normal and anthropogenically accentuated variability can lead to periods of low population survival. Under favorable climatic conditions, salmonids are capable of rapid population recovery, assuming that habitat quality is good.

Most climatologists studying global warming predict increases in air temperature of approximately 1°C-2.8°C within 20 years. Air temperature increases of this magnitude would elevate maximum summertime water temperatures and cause regional impacts to fish distribution and abundance. These impacts would be especially significant at the southern extremes to a species' distribution (Meisner et al. 1988, Jowett 1990, Lattenmaier and Gan 1990, Meisner 1990, Neitzel et al. 1991, Keleher and Rahel 1996). Because of the tendency for water temperature to reach equilibrium with air temperature (Dingman 1972, Crisp and Howson 1982, Stefan and Preud'homme 1993, Sullivan 1990), and for equilibrium to be more rapidly achieved with reduced summer streamflows and reduced canopy cover, it will become increasingly important to restore canopy cover on entire stream systems and also to restore channel morphology as a means to increase suitable summer rearing area (Theurer et al. 1985). Even though little may be done to ameliorate ocean conditions and improve adult salmon growth short of controlling global warming, mortality in the adult and juvenile freshwater phases can be reduced by numerous improvements in land use practices that would reduce anthropogenically accentuated variability in seasonal streamflows and water temperatures.

*Migration: timing, normal migration temperatures, delay:*

Migration delays caused by high temperatures have often been observed, particularly where tributary temperatures exceed those of the mainstem Columbia River (Major and Mighell 1967). Strickland (1967) (as cited by Stabler 1981) determined from analysis of dam passage data that steelhead do not begin migrating up the Snake River from the Columbia River until Snake River temperatures fall below 21°C. Adult sockeye spawning migrations were blocked at temperatures exceeding 21.0°C (Major and Mighell 1967). During the period in which sockeye have been observed passing Ice Harbor Dam (June 14-October 26) most sockeye passed at temperatures near 20°C and few passed the dam at ≥22.2°C (Quinn et al. 1997). Hatch et al. (1993) reported that as water temperature reached 22.8°C in the Okanogan River, sockeye passage upstream to Lake Osoyoos terminated. During the migratory period, sockeye did not migrate from the Columbia River staging area upstream on the Okanogan River until temperatures dipped below 22.8°C. Even though Hatch et al. (1993) observed renewed migration activity below 22.8°C, it appears likely that the optimal migration temperature is about 14.4°C, the temperature at which the sockeye cruising speed is maximum (see Bell 1991).

*Holding*

A study by Fish (1944) revealed that sockeye survival was 51% when adults were subjected to fluctuating temperatures of 9.4°C-23.3°C (x=16°C) but was 96% at 11.1°C-15.6°C (x=11.9°C). 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 coldwater holding particularly necessary to inhibit pathogens.

In addition to the effects on egg viability caused by maturing adult female salmon holding in pools with elevated water temperature (>15°C-16°C), warm water can also lower viability of eggs of non-anadromous salmonid adults by influencing their nutritional status during their feeding period (see Hokanson 1977). A lowered food intake during the season when growth is normally rapid, leading up to egg deposition, 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 egg quality of rainbow trout within the body cavity of females after ovulation has been reported at holding temperatures of 13-15°C by numerous authors (see citations in Flett et al. 1996, Billard 1985, Smith et al. 1983). Holding cutthroat females at temperatures fluctuating from 2-10°C produced eggs of significantly higher quality than when females were held at 10°C (Smith et al. 1983).

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

Bouck et al. (1975) studied survival of sockeye, acclimated to 13°C and adjusted to test temperatures at a rate of 2°C/d. Adults holding at a test temperature of 22°C died after 3.2 d from thermal effects. Holding for 11.7 d at 20°C resulted in 100% mortality via indirect thermal effects stemming from infection by columnaris. Fish held at 16.5°C had lower health and reproductive indices than fish held at 10°C. Among these indices were the absence of fat reserves at 16.5°C vs. the abundant reserves at 10°C, the doubling of weight loss, enlarged liver, and reduced egg size at the higher temperature. The non-infectious pathology at 16.5°C occurs precisely during the major period of reproductive development in the Columbia River. For these reasons, Bouck et al. (1975) concluded that 10°C was more favorable for maturing sockeye than 16.5°C, and in addition, does not subject these fish to the greater risk of thermal death and disease that is associated with 16 and 20°C holding.

### *Rearing: Preference*

In field situations adult brown trout temperature preferences vary seasonally. Adults with radiotransmitters and internal thermistors, in the vicinity of a thermal plume in Lake Michigan ranging up to ≥22°C, had median internal body temperatures of 10.9, 14.6, 11.9, and 10.0°C in spring, summer, autumn, and winter, respectively (Spigarelli et al. 1983). The overall median body temperature of adults in the plume area was 11.7°C. This is similar to the optimum growth temperature of approximately 13°C reported by Elliott (1994, p. 87) and the 24-h mean preferendum of 12.2°C (Reynolds and Casterlin 1979c). The annual modal body core temperature for both males and females was 12°C, similar to the median. However, on a monthly or seasonal basis, there were differences in preference between males and females. For example, in August males had a modal preference of 14°C-15°C and females 18°C. In October males had a modal preference of 18°C and females 12°C. Skewness in preferences for males or females during a month was reflected in differences between medians and modes.

Among the majority of females, the distribution in core temperatures was positively skewed in October but negatively skewed in June and August. For all males the August core temperature distribution was positively skewed. Dispersion of body temperatures was less than that for ambient temperatures, indicating a selection by adults that defined their niche breadth within the available temperature regime. The dispersion (±34% interval) around median temperatures experienced was greatest at low ambient temperatures and decreased to near zero dispersion at ambient temperatures of 16°C.

### *Spawning*

Fall chinook, sockeye, and coho were all reported to spawn on falling temperatures starting at peak temperatures of 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 14.4-16.1°C. On the Fraser River, spawning temperatures >12.8°C were associated with an increasing number of females that died without spawning (Andrew and Geen 1960). Temperatures >12°C can inhibit or delay spawning by Atlantic salmon (Beall and Marty 1983, as cited by deGaudemar and Beall 1998). Spawning of brook trout begins to occur after the weekly mean temperature falls below 13°C (approximately early October). During the spawning period water temperatures steadily decline from approximately 12.8°C to 7.1°C (Hokanson et al. 1973). Based on a survey of effects of temperature on all aspects of spawning in fall-spawning salmonids, it appears that spawning temperatures in the spring and fall chinook spawning habitats having a 12.8°C peak and a declining trend would satisfy biological requirements.

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 causes a reduction in egg viability and an increase in egg retention and egg malformation. As little as a 1-wk delay in spawning after full maturation causes a marked reduction in egg quality (deGaudemar and Beall 1998).

### *Feeding*

#### Diel cycles: Laboratory Evidence

Daily food intake in adult brown trout (Wild Rose Hatchery, Wisconsin) can be approximately 50% greater in fluctuating temperature environments than under constant temperature conditions equivalent to the mean of the diel cycle (Spigarelli et al. 1982). The diel cycle in laboratory tests was 9°C-18°C (mean 12.5°C). This was compared with feeding at a constant 12.9°C and an arrhythmically fluctuating regime with a range of 4°C-11°C (mean 7.7°C). The latter regime was the natural regime (ambient) of inshore Lake Michigan water. Mean daily food consumption rate was 3.3% of wet body weight in the cyclic regime and approximately 2.1% in the other regimes. Under the "ambient" regime the predicted feeding rate for a mean temperature of 7.7°C was <50% of that for a constant temperature of 12.9°C, based upon Elliott's (1975a) equation. However, observed feeding rates were nearly identical. This suggests a stimulatory effect of fluctuating temperatures.

Of the food intake under each treatment, gross conversion efficiency (percentage converted to growth) was no different under the fluctuating regime than under the constant or ambient (lake conditions) regimes. However, of the weight gained under each treatment, 48% was attributable to lipid deposition under the ambient regime, 30% under the cyclic regime, and 20% under the constant regime. The higher fat deposition rates appear to be attributable to daily variation in temperature (Spigarelli et al. 1982).

## *Growth and Development*

### Diel cycles

Daily growth rate in adult anadromous brown trout can be >50% greater in fluctuating temperature environments than under constant temperature conditions equivalent to the mean of the diel cycle (Spigarelli et al. 1982). The diel cycle in laboratory tests was 9°C-18°C (mean 12.5°C). This was compared with growth at a constant 12.9°C and an arrhythmically fluctuating (ambient) regime with a range of 4°C-11°C (mean 7.7°C). Over a 57-d growth period, mean growth rate under the cyclic regime was 0.74%/d. Under the constant and ambient regimes, growth rates were 0.48%/d and 0.42%/d, respectively. Under the cyclic temperature regime, predicted growth rates for the mean temperature of the cycle, based upon equations from Elliott's laboratory work (1975a) were only 50% of those observed. Observed growth rates indicated that the apparent acclimation rate was >18°C. In addition, it is interesting that at the "ambient" temperature, which also fluctuated and had a mean of 7.7°C, the observed brown trout growth rate was approximately the same as under a constant temperature of 12.9°C. Spigarelli et al. (1982) noted that the growth enhancement observed might not occur under field conditions where food is limiting or when the mean of a diel cycle exceeds the optimum metabolic temperature of the species (see Hokanson et al. 1977).

### Effect of Seasonal Temperature Trends

Brown (1946) (as cited by Spigarelli et al. 1982) measured growth rate of brown trout under slowly rising and falling temperatures (0.14°C-0.21°C/d rate of change) superimposed on a diel amplitude in fluctuation of 1°C-3°C. The long-term range in temperatures was 4°C-18°C (mean of 11°C). Growth rates under the fluctuating regime were no different than at a constant temperature of 11°C.

# DISTRIBUTION RELATIVE TO TEMPERATURE

## PROBLEMS IN WEIGHING THE EVIDENCE FROM LABORATORY AND FIELD

Data on observed distribution of fish in their native habitats provide useful information to compare with laboratory data. Field data provide insights on thermal requirements that integrate many different kinds of effects. For example, distribution of adults or juvenile fish at any point in time is caused by a combination of factors, such as direct thermal mortality, preference and avoidance, ability to feed and grow in selected locations during extended periods (e.g., 1-2 weeks), disease tolerance and resistance, competitive interactions with other species having the same or different temperature tolerance, predation. These factors are strongly mediated by short-term temperatures or thermal regimes (daily, weekly, or seasonal). Besides thermal control, numerous other habitat factors can be responsible for fish distribution such as pH, dissolved oxygen (DO), suitable stream gradient, suitable substrate for spawning, food availability, flood frequency and magnitude. These factors, though potentially of major significance, do not necessarily operate simultaneously in any set of streams. Stream gradient controls the ability of adults to immigrate to points within the watershed and the ability of juveniles to migrate during the rearing period. Fish utilizing habitat that is marginal with respect to any non-thermal factor will be at increased disadvantage (i.e., will suffer higher mortality, lower growth rate, lower fecundity and reproduction success, and lower production) if subjected additionally to thermal stress. However, adverse thermal conditions, either natural or man-caused, generally are accompanied by other habitat conditions that negatively affect survival (see Rhodes et al. 1994). Combinations of factors outside the optimum range for any species can be expected to operate cumulatively or synergistically.

Most laboratory studies assess response to primarily one variable (e.g., elevated temperature) at a time. Even with greater control on independent variables, results can be biased by experimental conditions as well as ability of the scientist to interpret results. For example, studies of temperature preference sometimes vary when conducted in vertical vs. horizontal temperature gradients. Confinement in experimental containers can itself cause stress. Conclusions also depend on interpretation of data from different kinds of methods. For example, the ILT method gives different insights to temperature tolerance than the CTM method. Despite the drawbacks that exist with laboratory results, field data are not free from bias either. Observations that fish inhabit streams with high maximum temperatures measured in mid-stream may lead to the faulty conclusion that a species tolerates temperatures of this magnitude unless the temperature in the immediate environment of the fish is measured. Even these local measurements can be misleading, though, unless one determines a daily time budget for individuals and the population in different temperature zones or unless internal body temperatures are tracked in relation to ambient temperatures (e.g., Spigarelli et al. 1983, Berman and Quinn 1991). Selection of temperatures within a thermal gradient cannot be averaged simply based upon time spent in each thermal environment because the rate of equilibration of a fish's internal body temperature to a warm water bath was faster than equilibration to a cold water bath (Berman and Quinn 1991). That is, rate of heat loss was slower than rate of heat gain when a fish was presented with temperature differentials of equal magnitude. Also, more time was required for a large sized fish to equilibrate to warm water than a small fish. These laboratory results indicate that in the field adults could tolerate a water temperature increment (provided that the resultant temperature is < UILT) for a longer time than for a juvenile before internal body temperature reached equilibrium with the environment because of their larger body mass. And in any population, there is always some degree of variation in temperature tolerance that may allow members at the extremes of the distribution to withstand temperatures different from the majority of the population. Because fish with limited choices tend to choose a thermal environment that most closely matches its requirements, the temperature selected may not represent suitable conditions. Conditions may simply be the best available locally, the best that the fish can find given energetic constraints (time and energy available for searching), or the best that can be occupied given constraints imposed by competition or predation. Conversely, absence from zones of warmer waters may not indicate absolute inability to survive in those waters, but may reflect a combination of predation, competition, or avoidance effects. And temperatures tolerated for a few days may not be indicative of temperatures providing sustainable fisheries because of longer-term effects of disease, growth, competition, and other factors. Field observations can be difficult to interpret because one is never sure whether the response (i.e., presence/absence, density, community composition, condition factor, growth rate, survival), if controlled by temperature, is a function of maximum, minimum, or mean temperature, diel temperature variation, thermal regime experienced over a period of ≥ 1 d, delayed effects from thermal experience in an previous life stage, etc.

The combination of laboratory data on temperature tolerance and field data on distribution relative to temperature, though, provides powerful corroborative evidence. Laboratory data provide evidence for effects of constant or fluctuating temperatures without the influence of most extraneous factors. Those that may exist can be examined for significance if they are suspected. Field data are likely to give a conservative estimate of the upper limits to thermal tolerance, except in those cases where cold refuges sustain a species in the midst of adverse average ambient conditions.

## CHINOOK

### Juveniles

#### *Presence/Absence*

Lindsay et al. (1986) recorded the observed lowest extent of chinook juvenile distribution on the North Fork and Middle Fork John Day Rivers in Oregon from June 15 to September 15 for the years 1980-1984. On the North Fork a continuous thermograph installed at river kilometer 71 (RK 71) (a point which is also 21 km downstream of the lower extent of spawning) provided data used to plot downstream extension of juveniles relative to mean maximum water temperature (°C) **(Fig. 8)**. This relationship can be expressed by a regression $Y = -26.8 + 4.31X$ ($R^2 = 0.62$, $p<0.001$), where X is mean maximum water temperature (°C) and Y is the lower distribution in terms of river kilometer (RK) above the mouth of the North Fork. This regression indicates that when the mean maximum water temperature was 22.7°C for a one-week period at a point location in the North Fork (i.e., at the recorder), no juveniles were found to be rearing below that point. A similar analysis of the Middle Fork data reveals that when mean maximum water temperature was 19.5°C at a point on the mainstem of the Middle Fork for a one-week period prior to sampling juveniles that no juveniles were found below this point (see Lindsay et al. 1986, p. 41). Burck et al. (1980) had previously reported studies of juvenile chinook distribution on the John Day River. They found that chinook juveniles were not found in any areas on the Middle Fork or North Fork, John Day River, Oregon, having mean weekly water temperatures of 21°C-22°C.

In the neighboring Grande Ronde River, Oregon, Burck (1994) studied spring chinook outmigration from Lookingglass Creek (a coldwater stream) into the Grande Ronde River. Between July 3-August 9, 1968, 565 0+ age chinook migrants were caught leaving Lookingglass Creek entering the roadless canyon of the Grande Ronde River. Even though fish were caught downstream of Lookingglass Creek in the Grande Ronde River above the confluence with the Wallowa River, very few were caught in the canyon in 9 nights of sampling. During the July 2-August 7 study period maximum temperatures ranged from 21.6°C to 26.1°C in the reach of the Grande Ronde River above the confluence with the Wallowa River. More than half of the Lookingglass 0+ migrants left their home stream by the end of August. Faced with temperature extremes as high as 26.1°C, it appears likely that high juvenile mortality would have occurred. Burck (1994) conducted livebox survival tests on groups of 10 fish each in the Grande Ronde River above the mouth of Lookingglass Creek during early August 1969. Mortality was 100% in 24 h under a diel fluctuation of 16.1°C to 25.6°C (mean 20.9°C). Under a fluctuating diel temperature regime of 9.4°C-12.2°C (minima) to 20.6°C-22.2°C (maxima) for a 4-d period in late August, mortality ranged from 0% to 50%.

On the North Fork John Day, no juveniles were found in reaches where temperatures exceeded 22.8°C (Lindsay et al. 1986). Theurer et al. (1985) estimated that spring chinook production on the Tucannon River, Washington would be zero for all stream reaches having average maximum daily July water temperature greater than 23.9°C (or average mean daily temperature of 20°C). According to data of Theurer et al. these conditions were present for all stream reaches downstream of RK 40. Based on actual field observations of Bugert et al. (1992) on the Tucannon River, no juvenile spring chinook were observed in the July-August, 1990 period in the Marengo section, representing RK 18.0-42.1. Although water temperature data are not available for 1990, water temperature data for August 1991 indicate that daily maxima as high as 27.2°C were observed in this section (measured at RK 41). Although no observations were made for the lower 18 km, one would expect this section to be devoid of chinook in the summer months also. The mean daily temperature for July 1991 was 21.8°C and the mean maximum temperature was 24.6°C at Marengo. In August these indices were

22.4°C and 24.8°C, respectively. Field observations on juvenile distribution and temperatures (Bugert et al. 1992) are consistent with Theurer et al.'s (1985) temperature and production modeling.

In Alaska two stocks were challenged with high water temperatures, an ocean-type chinook from a southern stream (Robertson Creek) and a stream type chinook from a northern stream (Bear River) (Beacham and Withler 1991). After 3-d exposure at 20.3°C-21.5°C, the cumulative percentage mortality reached about 60% for the northern stock. In 16 d cumulative mortality was 80%. Cumulative mortality for the southern stock was similar after an 18-d exposure (i.e., 74%), but this stock suffered little mortality in the first 8 d. Although this study did not record field distribution relative to temperature, prolonged exposure to temperatures similar to those considered to represent distributional limits did result in high levels of mortality for both chinook stocks. This laboratory test appears to confirm field evidence.

In the Sixes River system in south coastal Oregon, chinook juveniles were typically absent from river reaches having maximum temperatures exceeding 23°C (Frissell et al. 1992).

*Density*

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. Laboratory studies on steelhead fry indicated that density was twice as great in an experimental channel under a diel cycle of 8°C-19°C as in a channel having a constant temperature of 18.5°C. Fry density was reduced about 50% as temperatures increased from a constant 8.5°C to 13.5°C and again to a constant 18.5°C (Hahn 1977). In an Idaho tributary to the Lochsa River that fluctuated from a minimum of approximately 8°C-12°C to a maximum of 24°C, juvenile chinook salmon and steelhead were found to have high densities and normal growth (Bjornn 1978, as cited by Bjornn and Reiser 1991). In the lower mainstem Lochsa River, August maximum and minimum temperatures are approximately 26°C and 11.5°C, respectively. Densities of juvenile chinook in this reach of the mainstem are very low in August, while densities in upper Lochsa tributaries, such as Post Office Creek, tend to be much higher. Maximum temperatures of tributaries such as Post Office and Weir Creeks were 18 and 20°C, respectively, during the same period (Mabbott 1982). This study indicates the inhospitable summer rearing conditions in the mainstem as opposed many of the tributaries.

**Adults**

Hallock et al. (1970) concluded that fall chinook avoided DO <5 mg/l and water temperature >18.9°C during upstream migration in the San Joaquin Delta. A high DO did not compensate for high migration temperatures. In the Willamette River, 25% of the spring chinook migrated when the DO was ≥3.5 and the water temperature was ≤21°C. No fish migrated when DO was 3.3 mg/l and the temperature was 22.4°C, although migration blockage was associated with temperatures as high as 23.4°C at nearly equal DO values (Alabaster 1988, 1989).

Adult spring chinook are able to enter warm water zones briefly without harm because their large mass helps regulate internal body temperature. However, implanted thermistors revealed that they sought out cool refuge areas created by groundwater or subsurface seepage in a canyon providing adult holding habitat in the Yakima River. This behavioral thermoregulation allowed spring chinook adults to maintain internal body temperatures an average 2.5°C cooler than the ambient 12°C-19°C temperatures of the river in holding areas (Berman and Quinn 1991). Spring chinook in Sacramento and San Joaquin River tributaries held in deep pools that rarely exceeded 21°C-25°C (Moyle 1976).

In the John Day River system, primary spawning areas are limited to the Middle Fork, North Fork, and Upper Mainstem. The Middle Fork watershed has been heavily affected by grazing and logging. This has led to loss of riparian vegetation, and alterations in channel condition (bank degradation). The Middle Fork John Day River temperature for 1994, recorded from June through September had daily maximum water temperatures that peaked at 30°C in late July. The summer of 1994 was hot and dry. In 1995, a cool, wet year, daily maximum temperatures peaked at 27°C (McIntosh et al. 1995a). The upper portion of the North Fork watershed is located in wilderness and, consequently, has greater riparian cover than the Middle Fork. In the North Fork, almost all chinook holding and spawning occurs in the wilderness reach. This reach supports more than twice the number of spawners per kilometer as the Middle Fork, which averages 18 chinook spawners/km. In the Middle Fork, adults held in widely scattered coolwater patches (predominantly pools with groundwater inflow) that were 1°C-3°C cooler than surrounding habitat. Aerial videography and thermal radiometers indicated that surface water temperatures in the vicinity of holding adults was 22.0°C-23.4°C when average temperatures in well-mixed riffle areas nearby were 23.5°C-25.5°C. It is possible that water temperature near the streambed was cooler than surface temperature because inflowing groundwater would tend less to mix vertically in a deep pool than in riffle areas. The North Fork wilderness reach averaged 5°C-7°C cooler than the Middle Fork. Rather than having coolwater habitats as small, widely scattered patches, the North Fork was uniformly cool (Torgerson et al. 1995). Because of the uniformly cool waters in the North Fork, chinook were able to hold in riffle as well as pool habitats. Such observations aid in explaining the distribution of adults at the scale of the tributary as well as within tributaries at the riffle/pool scale. These observations emphasize the importance of maintaining channel structural features such as bank stability and large woody debris and minimizing pool infilling by fine sediments as means to preserve fine-scale habitat diversity that provides thermal refugia and the importance of riparian cover in preserving macroscale control on rate of thermal loading longitudinally in a stream.

## ASSOCIATED SPECIES

### Juveniles

*Presence/Absence*

Relatively abundant information exists on the effects of high temperature on the distribution of salmonids. Dimick and Merryfield (1945) reported that no salmonids occurred in the Willamette River where water temperatures exceeded 22.8°C and that the majority of salmonids were associated with water temperatures from 12.8°C to 15.5°C. Such observations imply a continual decrease in salmonid density as temperatures increase from 15.5°C to 22.8°C. Sockeye in the field are not generally observed in waters >18°C, despite having tolerance to temperatures as high as 24°C (Brett 1971). Mantelman (1960) reported that rainbow trout were found in the temperature range of 13°C-19°C and avoided temperatures >22°C. Reeves et al. (1987) found steelhead to be dominant in steelhead/shiner interactions when water temperatures ranged from 12-15°C, but that shiners were dominant when water temperatures were 19°C-22°C. This study indicated that negative competitive interactions reduce the ability of salmonids to maintain feeding stations and grow in streams with temperatures above this threshold. This effect may also be coupled with lethal effects that become prominent above 22°C. It is known that fish operating outside their optimum temperature zone have reduced feeding rate or feeding inhibition, difficulty defending territories, lethargy, etc.

Upper temperature distributional limits for self-sustaining brook trout populations in southern Ontario streams were reported as a 3-wk mean of maximum temperatures equal to 22°C (corresponds to 25.6°C instantaneous maximum) (Barton et al. 1985). Brook trout in an Ontario lake were most often found at temperatures ≤21°C in July when temperatures as high as 27°C were available (Biro 1998). Ricker (1934), MacCrimmon and Campbell (1969), both as cited by Meisner (1990), Bowlby and Roff (1986), and Meisner (1990) found upper temperature limits to brook trout distribution ranging from 22°C-24°C maximum temperature in Ontario streams. Burton and Odum (1945) reported a general 19°C distribution limit in Virginia streams, although brook trout were infrequently observed at temperatures >20°C. Rainbow trout (Salmo gairdneri irideus) was found in waters >19°C and gradients >0.02 (Burton and Odum 1945). It is possible that temperature and gradient distributions acted to segregate these species.

Kaya et al. (1977) observed that rainbow trout and brown trout (juvenile to large adult age classes) in the Firehole River moved into Sentinel Creek when mean daily temperature exceeded 24°C or a daily maximum of 25°C. The upper avoidance temperature for these two species was measured as 20°C-22°C (Coutant 1975, as cited by Kaya et al. 1977). In a northern California stream, summer steelhead migrated to coldwater areas (stratified pools with groundwater input) when water temperature exceeded 23°C (Nielsen et al. 1994). In a southern California stream (Sespe Creek, Ventura County) rainbow trout tolerated summer water temperature distribution in a pool from 21.5°C at the bottom to 28.9C° at the surface for 4 d before either moving out or dying. Rainbow trout tended to congregate in a pool having bottom temperatures of 17.5-21°C and surface temperatures of 27.9°C. Trout selected a mean temperature of 18.3°C in this environment (Matthews and Berg 1997). Water temperatures >22°C were associated with diminishing food intake. Elson (1942) and Fry (1951) (as cited by Gibson 1966) reported trout moving into coolwater zones when water temperature exceeded 20°C . Gibson (1966) similarly observed salmon parr entering a spring seepage with water temperatures of 17°C when the river temperature exceeded 22°C. Bisson et al. (1988) observed coho juveniles aggregating in the vicinity of groundwater inflow to a stream in Washington when ambient water temperatures exceeded 22°C. Scott and Poynter (1991) reported the distribution limit of rainbow trout, transplanted from California to New Zealand, to extend to maximum temperatures of 22.5°C. Numerous other authors have reported upper thermal distribution limits for rainbow trout as between 21°C and 23°C (Hokanson et al. 1977, Cech et al. 1990). In the Sixes River system in south coastal Oregon, coho juveniles were absent or very rare in any stream segment having maximum temperatures exceeding 21°C, while cutthroat trout were totally absent where maximum temperature exceeded 21°C. Rainbow trout were rare but still present in stream segments reaching maximum temperatures of 24°C (Frissell et al. 1992).

Rainbow trout and brown trout occupied the upper fish zone on Deer Creek in California (Moyle and Baltz 1985). The summer water temperature range for this zone was 13°C-18°C. In the middle stream zone, summer temperatures ranged from 14°C-20°C. Rainbow trout comprised 86% of the fish abundance in the upper zone, but only 39% in the middle zone. Brown trout were absent in the middle zone. Smallmouth bass were present in the lower zone, having summer temperatures of 19°C-32°C, but were absent in the middle zone. Speckled dace were common in the lower two zones. In addition to thermal regime, fish zonation and overlap in distribution was governed by channel gradient, substrate, and presence of riffle/run vs. pool habitat (Moyle and Baltz 1985). This study implicates 20°C as a critical upper limit to trout distribution, but reduction in overlap with warmwater fish of the lower zone is also linked to other habitat factors. Trout are able to occupy low gradient stream reaches provided cold water is available.

The Arizona trout (Salmo apache) begins to refuse food at 20°C and stops feeding totally at 21.2°C in laboratory tests. Loss of equilibrium occurs in the temperature range 21.2°C to 22.3°C and death at 23°C (Alcorn 1976). No data are available on field temperatures limiting distribution but the threshold temperature for equilibrium loss and death is similar to upper distribution limits for many salmonids. Trout were found to cease feeding within the temperature range of 22°C-25°C (Dickson and Kramer 1971, Kaya 1978). However, Behnke (1992) reported redband trout feeding at 28°C in Oregon's Catlow Valley.

Eaton et al. (1995) used the method of Biesinger et al. (1979) to estimate the maximum temperature tolerated in the field by a wide variety of fish species. Using a large national data base on fish presence/absence and weekly mean temperatures at the points of collection, they calculated the 95th percentile weekly mean temperature for any species having at least 1000 correlated measurements. They eliminated the upper 5% of the observations from consideration to provide a more conservative estimate of upper thermal tolerance. For salmonids reported, the 95th percentile maximum weekly mean temperatures were 19.8, 21.0, 22.3, 23.2, 23.4, 24.0, 24.0, 24.1°C for chum salmon, pink salmon, brook trout, cutthroat trout, coho salmon, rainbow trout, chinook salmon, and brown trout, respectively. For these species, these upper limits to field distribution (weekly mean temperatures) were from 1°C to 3°C lower than upper thermal tolerance limits measured in laboratory experiments and reported in the literature (except for chum, which was 5°C lower). By inference from this data base one would conclude that most salmon and trout would be eliminated in stream reaches with weekly mean temperatures of 21°C to 24°C.

Geographic distribution of salmonids is correlated with optimum temperature ranges for normal feeding and growth. Arctic char and Atlantic salmon are found as far south as 65°N and 41°N latitude, respectively, with brown trout being intermediate. The optimum growth range temperatures are 11°C-14°C, 16°C-17°C, and 13°C for Arctic char, Atlantic salmon, and brown trout, respectively (Jensen et al. 1989).

Magnuson et al. (1979) proposed a classification of fishes into thermal guilds. The coldwater, coolwater, and warmwater guilds have optimal temperatures in the ranges 11°C-15°C, 21°C-25°C, and 27°C-31°C, respectively. Lyons et al. (1996) developed a coldwater index of biological integrity applicable solely on coldwater fish communities. Their designation of coldwater, coolwater, and warmwater stream communities were those having maximum daily mean temperature of <22°C, 22°C-24°C, and >24°C, respectively. They found that high quality coldwater streams have predominantly salmonids and cottids and a few cyprinids or catastomids, while the warmwater streams have numerous species, dominated by cyprinids, catostomids, centrarchids, and percids. Frissell et al. (1992) noted a continual decrease in coldwater species diversity in the fish communities of the Sixes River, Oregon as water temperatures ranged from 17°C to 25°C. Laboratory studies on competitive abilities of brook trout, brown trout, and creek chub with a size range of 107-165 mm fork length in constant temperature environments ranging from 3 to 26°C detected a transition in competitive ability of trout at 22-24°C that reflected the replacement of trout by creek chubs (Semotilus atromaculatus) (Taniguichi et al. 1998).

Fish species distribution within a stream system is frequently found to be arrayed longitudinally in thermal guilds. Rahel and Hubert (1991) documented shifts in fish community composition in a Rocky Mountain stream from an elevation of 2234 m to 1230 m. The headwater zone supported coldwater fishes: brook trout, brown trout, longnose dace, and white suckers. The coldwater assemblage was replaced by a minnow-sucker assemblage below 2000 m. The downstream reach had an assemblage consisting of carp, quillback, green sunfish, and largemouth bass. Maximum water temperatures in the headwater and downstream sites were 15-18°C and 22-27°C, respectively. In a northern California stream, brook trout were found at headwater sites and three trout species, sculpin, suckers, whitefish, and two minnow species were found downstream (Gard and Flittner 1974). This stream had a coldwater thermal regime along its entire length. The species replacements that were observed were caused by downstream additions of microhabitat types preferred by those species.

*Density*

Li et al. (1992) reported a decline in steelhead biomass from 18 $g/m^2$ at a maximum summer water temperature of 16°C in tributaries of the John Day River to 0 $g/m^2$ at a maximum temperature of 28°C. The sharp reduction in biomass with increasing temperature is an indication of either progressive mortality or emigration from zones exceeding temperature preferenda. When fish spend significant proportions of a day at temperatures in the "resistance" zone (see Elliott 1981), lethal temperature doses are more clearly a function of exposure time to high temperatures and acclimation temperature. Hokanson et al. (1977) reported that rainbow trout reared under a fluctuating temperature regime of 22 ± 3.8°C had a specific growth rate of zero and a mortality rate of 42.8%/d, whereas mortality for trout held under optimal temperatures was only 0.36%/d. They recommended a mean weekly temperature no greater than 17 ± 2°C for trout experiencing fluctuating temperatures in the field. However, even this recommendation was estimated to result in a 27% reduction from maximum yield of the population over that in optimal conditions. Optimal growth conditions under constant temperatures occurred at 17.2°C-18.6°C but in a fluctuating (±3.8°C) temperature regime, optimum growth conditions occurred at mean temperatures of 15.5°C-17.3°C. The maximum specific growth rate in the optimum range for constant and fluctuating temperatures was 5.12 and 5.24%/d, respectively . A fluctuating regime with a mean of 21°C resulted in zero net biomass gain (i.e., specific growth rate equals specific mortality rate of the population).

Frissell et al. (1992) reported the effect of maximum temperature on density of coho, cutthroat, and rainbow trout in the Sixes River system of south coastal Oregon. Coho (0+ age), cutthroat (1+ and 2+ age), and rainbow (1+ age) had linearly decreasing densities as maximum temperatures increased from 17°C. Coho declined to virtually zero density at 21°C, although they remained in rare occurrence at temperatures as high as 24°C. Rainbow trout (1+) declined to zero density as maximum temperatures reached 24.5°C. Age 0+ rainbow declined in density precipitously from 17°C to approximately 20°C, but then maintained very low densities in waters up to approximately 24.5°C. Age 2+ rainbow had possibly a more clear threshold temperature (approximately 21°C) causing a sharp decline in density. This age group was absent at temperatures higher than 22°C. The response to temperature of total salmonid density was best described by a logarithmic declining curve, primarily because of the sharp decrease in densities of coho and cutthroat in the temperature range 21°C-23°C. Age 1+ steelhead was the least sensitive to thermal increases of the four salmonids in the fish community (chinook, coho, cutthroat, and rainbow) of the Sixes River while cutthroat was the most sensitive.

Highest densities of bull trout were found in Montana streams at temperatures <12°C, and density declined steadily to zero as temperatures reached 19°C (Shepard et al. 1984). Brook trout (YOY) selected bottom temperatures of 20°C in June in a littoral area of a lake in central Ontario when cooler temperatures were available nearby, but further from shore. In

July when surface water temperatures ranged peaked at 25°C near shore, brook trout selected the coldest available temperatures (18-20°C) (Biro 1998). Trout shifted in position from 2 m from shore in June to 3-7 m from shore in July in order to thermoregulate. This behavior might be due to changing thermal preferences with age of the YOY or to predation risk from older fish requiring colder, deeper water. Nonetheless, a positive linear relationship ($R^2$ = 0.87) existed between YOY density (no./$m^2$) and groundwater flow rate (ml/$m^2$/min) (Biro 1998). High groundwater flow was associated with cooler bottom habitat.

### Adults

*Presence/Absence*

Steelhead found holding in deep pools in the New River, California experienced a temperature range of 16.8 to 24.6°C over a 27-d period during late July-early August (Nakamoto 1994). Unoccupied pools differed from occupied pools by having maximum temperatures about 1°C higher. The diel temperature variation for unoccupied pools, though was 1.5-9.8°C while that of occupied pools was 1.7-5.8°C.

Adult brown trout in Lake Michigan selected temperatures of 16-17°C, as measured by implanted radiotransmitters, when temperatures in a warmwater plume were >22°C (Spigarelli et al. 1983). Upper avoidance temperature of brown trout as measured in the laboratory was 20°C (Alabaster and Downing 1966, as cited by Spigarelli et al. 1983). Self-sustaining populations of brook trout tend to be limited to stream zones with temperatures <19-20°C (see references cited by Hokanson et al. 1973). Cutthroat populations cannot be sustained in stream zones experiencing temperature maxima consistently greater than 22°C (Hickman and Raleigh 1982, as cited by Taylor and Barton (1992). An acute daily maximum recommended for cutthroat would then be 22°C; for rainbow this value is 24°C (Taylor and Barton 1992). In a tributary to the Yellowstone River, cutthroat were excluded from stream reaches having water temperatures exceeding 22°C (Gresswell 1995). Bull trout are essentially limited in their distribution to streams with temperature maxima of <15°C (Pratt 1984). Similarly, the rough sculpin is found in large spring-fed streams having maximum daily temperatures that rarely exceed 15°C (Brown 1989). With acclimation temperatures of 10, 15, and 20°C, the acute preferred temperatures of marbled, rough, and Pit sculpin ranged from 11.1-14.7, 13.3-14.4, and 9.9-16.4°C, respectively (Brown 1989).

*Density*

In southern Ontario streams the fish species composition and abundance of salmonids within the community is dependent upon maximum temperature during the summer (Stoneman and Jones 1996). Cold-, cool-, and warmwater streams had trout and cottids, cyprinids, percids, and catostomids, and cyprinids and percids as dominant species, respectively. Even though all three stream types experienced maximum air temperatures >32°C, the cold-, cool-, and warmwater streams had maximum water temperatures of 16-17, 23, and 28°C, respectively. Salmonid abundance was low in the coolwater streams and was rare to absent from warmwater streams.

Abundance of the rough sculpin displays an inverse relation to water temperature (Moyle and Daniels 1982, as cited by Brown 1989).

## SYNTHESIS OF DISTRIBUTION DATA

Field studies reviewed for chinook, steelhead, and rainbow trout indicate that the distributional limit of these salmonids corresponds approximately to a mean daily water temperature of 20°C and a maximum daily water temperature of 22°C-24°C. This distributional limit is a point at which biomass approaches zero. Conditions for growth and survival immediately upstream from this boundary are apt to be marginal. Zero net growth of a chinook juvenile population occurs at 19.1°C (see Armour 1990) but positive growth may occur up to a temperature limit of 21.4°C at 60% satiation feeding (Brett et al. 1982), a typical level of feeding in the field. Laboratory studies on a wide variety of salmonids indicate an ultimate upper incipient lethal limit of 22.8°C-25.6°C. The similarity in critical temperature indices from field and laboratory research suggests that laboratory studies on growth and survival at elevated temperatures can be used to explain distribution of the species in the field. However, as Hokanson et al. (1977) pointed out, even if a species such as chinook might continue to feed and grow up to a temperature limit of 21.4°C (as reported by Brett et al. 1982), the juvenile population eventually reaches a temperature threshold (the ZNG temperature, or 19.1°C for chinook) at which mortality balances growth rate (Ricker 1958, as cited by Hokanson 1977). Because many prominent salmon diseases become virulent above 15.6°C, the impact to population production is potentially even more severe as temperatures rise toward the limits to growth because of increases in mortality rate. This could cause the temperature for ZNG to be even lower (i.e., the balance between growth and mortality would occur at lower temperatures). The upper zero net biomass gain temperature for the population is useful as an index to the population distributional limits (Hokanson 1977).

## TEMPERATURE PREFERENCES OF SALMONIDS

Data available on fish distribution in relation to temperature maxima or more complex indices of temperature regime experienced recently in a stream reach are the product of factors such as preference, avoidance, behavioral thermoregulation, mortality, bioenergetics, ability to migrate, competition, predation, disease, and other factors. The upper temperature limit to distribution in the field is a good conservative index to maximum temperature that would cause complete absence of a species. This index should be reliable so long as the presence of coldwater refugia does not bias perceived relationships between fish distribution and general longitudinal water temperature patterns.

Some good reviews of temperature preference by fishes are available in the literature (Ferguson 1958, Coutant 1977, Jobling 1981). In general, salmonid juveniles appear to have final preferenda in the range 11.7°C to 14.7°C. Rainbow trout, a common coldwater species in the Columbia Basin, is frequently considered to be among the least sensitive to thermal stress. However, several studies would attribute a final preferendum to it of approximately 14.7°C (see Stauffer et al. 1984), although these authors cited two references indicating higher preferenda. Reynolds and Casterlin (1979a) summarized results of ten studies of rainbow trout temperature preference. They reported that juvenile and adult rainbow had final preferenda of approximately 19°C and 13.5°C, respectively.

Laboratory studies on temperature preference indicate short-term response to a range of temperatures, and consequently provide a significant portion of the explanation for observed distribution in the field, provided that fish in the field have the ability to freely migrate and escape adverse temperatures or have a wide range of temperatures available (Hokanson 1977, Stauffer 1980). There is reason to believe that juveniles are less capable of escape from adverse thermal conditions than adults (see Stauffer 1980). Adults have a greater swimming speed and are capable of migrating upstream over higher barriers or against swifter current speeds to seek cooler water than juveniles. However, if cooler waters become available only in high gradient streams (>4%) both juveniles and adults of salmon species would be precluded from using these drainages. Most trout are limited to stream zones with gradients of <10% to 15% (Fausch 1989). Chinook juveniles in the John Day River migrate downstream during spring after emergence and then back upstream to avoid increasing water temperatures of summertime (Lindsay et al. 1986). Headward escape could easily become precluded by high gradient reaches or relatively small barriers (e.g., water surface drops over logs or falls).

There are some important considerations in evaluating laboratory temperature preference data. First, there are reported differences in preference with species, sex, life stage, age, and season (see Hokanson 1977, Spigarelli et al. 1983). There are also variations among individuals during a season, from day to day for individual fish (Spigarelli et al. 1983), and from day to night (Brett 1971). Other factors that probably influence preference that are not well studied are photoperiod, reproductive status, nutritional status, health, and presence of chemical agents (pesticides, heavy metals, etc.) (Reynolds and Casterlin 1979a). Acclimation history can influence preference. Some authors have reported different preferences depending upon prior acclimation in rising vs. falling field temperatures (Cherry et al. 1977, Stauffer 1980). However, as pointed out by Mathur and Silver (1980) the studies by Cherry et al. (1975, 1977) on preference in several warmwater fish species inflated the number of degrees of freedom in their tests of significance by their practice of taking all observations of preference in a experimental gradients as independent measures. They cautioned that only the central tendency for a single test should be considered as representing preference because consecutive observations are correlated. Other common mistakes in estimating preference involve recording the frequency distribution of several individuals per tank because movements are not independent. Accuracy of a fish in selecting temperatures in laboratory experiments may depend upon whether a fluctuating acclimation temperature regime was used. Reduced accuracy in temperature selection has been attributed to acclimation at constant temperatures (Stauffer 1980).

Interpretation of laboratory preference data or field studies in which radiotransmitters were used to monitor temperatures selected must take into consideration the degree of temperature variation known to occur as well as the accepted correspondence between preference and physiological limits. These relationships can be illustrated with selected species. For example, brown trout adults have reported final preferenda of 16°C (Spigarelli et al. 1983) and 12.2°C (Reynolds and Casterlin 1979c). Final preference of brown trout juveniles was reported as 17.4°C (Cherry et al. 1977). Brown trout adults selected 14°C in spring, 16°C in late summer and fall, and 18°C-19°C in winter (see Spigarelli et al. 1983). In late summer there can be differentiation by sex in temperatures selected, with females selecting 18°C and males 14°C-15°C. Distribution of thermal preference by sex during summer was negatively skewed in females and positively in males. The skewness shifted to negative in winter months for both males and females (Spigarelli et al. 1983). Upper avoidance temperatures cited in the literature for adults and juveniles were 20°C and 25°C, respectively (see Spigarelli et al. 1983).

Temperature preference measured in the laboratory or field is sometimes an inaccurate reflection of physiologically suitable temperatures. For example, yellow perch demonstrate considerable variation in preference because of their imprecise response to temperature (see Hokanson 1977). They have been reported to enter temperature zones exceeding their UILT and then die for lack of sufficient avoidance response. Rainbow trout acclimated to 24°C exhibited avoidance to a temperature of 27°C, which is above the UUILT for this species (Stauffer et al. 1984). Fish with low thermal responsiveness can become stressed at high temperatures so that they are unable to escape lethal conditions (Reynolds and Casterlin 1979a, 1979b, Mathur et al. 1981, Stauffer et al. 1984). For the most part, though, direct fish kills at high temperature are rare unless fish are unable to escape or migrate to cooler water. Despite the observation of Stauffer et al. (1984) of fish entering temperature zones above the UUILT as measured in the laboratory, distribution in the field has been described as always limited by temperatures that are less than the UILT (Hokanson 1977).

Temperatures preferred in laboratory experiments are generally highly consistent with field temperature preferences, especially when data are collected from the same populations (Ferguson 1958, Brown 1989, Stauffer et al. 1976, Stauffer 1980). 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 measured preferred temperatures 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). Swimming speed is highest at the preferred temperature (Kelsh 1996).

Rainbow and brook trout, acclimated to temperatures in the range 15°C-18°C, selected temperatures that approximated acclimation temperature. The final preferendum identified for these species by Cherry et al. (1975) was, then, about 15°C-18°C. Final preferenda for rainbow trout were 13.6°C (Garside and Tait 1958, as cited by Ferguson 1958) and for brook trout were 14°C-16°C (Graham 1958, Fisher and Elson 1950, both as cited by Ferguson 1958). When rainbow were acclimated to 24°C, they avoided temperatures of 25°C-26°C (Cherry et al. 1975, Cherry et al. 1977). Brown and brook trout, acclimated to 24°C, avoided temperatures of >25°C and 26°C, respectively, as well as temperatures <17°C and 18°C. These salmonids avoided temperatures that were greater than the 7-d UILT, when acclimated to temperatures near the final preferendum. The final preferenda of rainbow, brown, and brook trout as measured by Cherry et al. (1977) were 19.7, 17.4, and 16.0°C. Their tendency to be repelled by temperatures as high as those exceeding the 7-d UILT exposes these salmonids to temperatures that result in accumulating a lethal dose (Cherry et al. 1977). The preferred temperature of chinook fingerlings is 12°C-13°C (Brett 1952), based on means for the distributions of fish acclimated to temperatures ranging from 10°C to 24°C. The modes of the distributions of fingerlings in temperature gradients for acclimation temperatures between 10°C and 24°C ranged from 0.5°C to 1.5°C higher than the means.

Final preferenda of rainbow trout decreased from approximately 19°C in the first month to about 13°C for yearlings (Kwain and McCauley 1978). These preferenda are also well supported by other research (see Kwain and McCauley 1978). These other sources indicate that final preferenda of 1+ and 2+ rainbow are the same. It is common for final preferenda to decrease with age in many fish species (Kwain and McCauley 1978). In the field, observation of young-of-year (YOY) in downstream warmwater zones might appear to be advantageous for early growth, but as temperatures increase during the summer period, the YOY would also be those fish least capable of avoiding increasing temperatures by migrating upstream. However, to the extent that cooler microhabitats exist in interstitial spaces in the streambed substrate, the YOY are more able to exploit these habitats but feeding would be restricted in these thermal refuges. For steelhead and rainbow, which reach maturity after at least two summers of juvenile growth, population production is dependent upon the survival of the most temperature sensitive growth stage, which from literature reviewed, may be the parr or pre-smolt stages.

# JUVENILE MIGRATION AND DISPERSAL

## CHINOOK

As an example of seasonal chinook migration and dispersal within a subbasin, data from Lindsay et al. (1986) on the John Day River provide an interesting case history. Distribution of chinook fingerlings extends from the three primary spawning areas (North Fork, Middle Fork, and upper Mainstem) downstream after emergence to varying distances. From the spawning areas in the North Fork, fingerlings extend their distribution downstream as far as 24 km below the North Fork mouth. By July as water temperatures begin to warm up, juveniles begin to migrate back upstream. From the mouth of the North Fork, the furthest upstream that juvenile rearing was observed to retreat was to RK 114 by August in 1978, based upon observations spanning the years 1978-1984 (Lindsay et al. 1986, p. 38 and Appendix B) **(Fig. 9)**. (Note: Lindsay et al. reported distribution in river kilometers (RK); the maps of OWRD indicate river miles). Among years, the lower limit to distribution in August varied from RK 55 to RK 114, a variation of 59 river kilometers that are available to support chinook production under a recent range of conditions imposed by climatic variation and with respect to level of watershed development. The upper limit to juvenile rearing was at RK 168 in the North Fork. In the Middle Fork juvenile rearing occurs from the mouth of the Middle Fork upstream to RK 118 **(Fig. 9)**. Among the seven years in which the lower limit to distribution of 0+ age spring chinook was recorded in the Middle Fork, the furthest headward retreat in August was to RK 77. The same pattern of juvenile movement downstream after emergence, followed by a return movement upstream during July-August that was observed in the North Fork also occurred in the Middle Fork.

Juveniles that could migrate downstream in the spring after emergence and then upstream the distances involved (e.g., 122 km from the lowest extent of spawning on the North Fork to Spray, Oregon on the mainstem John Day River) appeared to alternately take advantage of habitat with suitable rearing temperatures during springtime and then escape the increasingly warm and adverse rearing temperatures in these stream reaches during summer. During the period of return juvenile upstream migration, juveniles were found in many years in the lower few kilometers of several tributaries of the North Fork, upper mainstem, and Middle Fork beyond the time when juveniles in the mainstem of each of these major forks had migrated upstream to avoid adverse water temperatures. For example, in the North Fork John Day, short sections (0.1-4.0 km) of various tributaries such as Rudio, Deer, Wall, Potamus, Mallory, Camas, and Desolation Creeks were used for rearing in occasional years (years in which sampling was conducted included 1978, 1979, 1982-84 (Lindsay et al. 1986, p. 43)). However, even a small stream such as Wall Creek has temperature suitable for steelhead rearing in its headwaters but has very severe mid-summer water temperature problems recorded in its midsection. This is likely to cause chinook juveniles rearing in the lower zones of these tributaries in June to be cut off from retreat up the mainstem as the critical temperature threshold shifts upstream and later temperatures in the tributary become lethal for coldwater species. The current extreme temperatures found in most tributaries of the major John Day River forks owing to substantial land alterations make these near-mouth rearing zones traps which juveniles probably do not long survive.

In 1980, 1982, and 1984 chinook juveniles were sampled in tributaries of the upper mainstem and were found rearing in the lower 1-3 km above the mouths of Beech, Indian, Dixie, and Dads Creeks. No juveniles were noted in Fields, Riley, Canyon, Reynolds, Deardorff, or Rail Creeks, as examples. For the 1979-1984 period in the Middle Fork, juveniles were noted in generally the 1-4 km section above the mouth of a number of tributaries, such as Granite Boulder, Indian, Big, Clear, Squaw, and Big Boulder Creeks, although they were noted up to 12 km above the mouth of Camp Creek.

Studies conducted on smolts outmigrating between the North Fork trap and Spray, Oregon showed that mean migration rates increased from 2.8 to 8.5 km/d during the migration period in this portion of the migration range (Lindsay et al. 1986, p. 28). For smolts migrating between Spray and John Day Dam, mean migration rate during 1982-1984 was 15.5-17.9 km/d. The smolt migration past Spray extended from mid-February through mid-May with a peak in most years on approximately April 1. From Spray to John Day Dam is 282 km. At a mean migration rate of 15.5-17.9 km/d (Lindsay et al. 1986, p. 30) it would require from 16 to 18 d to reach the Columbia River. With large percentages of the smolt migration passing Spray in May in some years, it is possible that an 18-d migration period through warming lower reaches of the John Day mainstem during springtime would pose a problem for smolts. Evaluation of temperature regimes in the lower John Day during the migration period in relation to smolt physiological tolerances needs to be conducted.

## ASSOCIATED SPECIES

The tendency for resident salmonids to undertake intrabasin migrations has become increasingly well recognized. Migrations of 130 km or more have been observed in subadult and adult fluvial westslope cutthroat in Idaho (Bjornn and Mallet 1964), with a typical pattern of upstream movement in spring and downstream movement in fall. Upstream and downstream movement distances of several kilometers by Colorado River cutthroat trout were reported by Fausch and Young (1995). Brown trout migration distances are also substantial (Clapp et al. 1990, Young 1994). These migrations are typically seasonal, occurring in spring and fall. Outmigration in the fall can be a response to lack of pools used in overwintering (Thurow and Bjornn 1978, as cited by McIntyre and Reiman 1995; also see references in Rhodes et al. 1994 to overwintering fish needs). This is a mechanism for insuring survival in streams that may be unstable (i.e., having high sediment loads that fill pools, lacking LWD, or that may become excessively cold and prone to icing or ice flows). Migration is also a mechanism to increase dispersion to take advantage of spawning or rearing opportunities in nearby streams. However, open stream canopies that may provide good growth conditions (e.g., high food production, optimum temperature conditions) in spring may become excessively warm as summer progresses (see Clapp et al. 1990, Lindsay et al. 1986).

Dispersal into these habitats in spring to exploit food resources may be only a temporary advantage. If routes for upstream retreat or sufficient coldwater refugia are not available for these seasonal migrants, the colonizing individuals would likely perish.

# DISEASE

## OVERVIEW OF COMMON FRESHWATER DISEASES

The influence of water temperature on susceptibility to freshwater diseases and control on median resistance time of fish exposed to disease pathogens has been well documented in fish pathology literature. Field evidence of the frequency of mortality from infectious warmwater diseases is also available from the literature. Nonetheless, despite the greatly increasing risk of massive salmonid mortalities in freshwater environments having temperatures above 15.6°C, far too little attention has been placed on the importance of stream temperature control to limit warmwater diseases. Part of the explanation for this is that mortality from disease generally requires several days. Juveniles that become infected prior to emigrating from natal habitat to the ocean may die in mainstem Columbia River reservoirs or in the ocean as the disease progresses and this mortality source may be overlooked (Ratliff 1981, 1983). Also, diseased fish probably are more susceptible to predation and less able to perform essential functions, such as feeding, swimming, and defending territories.
Certain freshwater diseases are known to be more prevalent in cold water. The so-called "cold water disease" is produced in salmonids by the myxobacterium Cytophaga psychrophila at temperatures of 5°C-10°C (Snieszko 1974). Infectious hematopoietic necrosis (IHN) is a viral disease that is most common at 8°C-10°C. It is generally thought that this disease is avoided by rearing salmonids at 15°C (Snieszko 1974). However, there is conflicting evidence for temperature control on IHN. Hetrick et al. (1979) found that pathogenicity of IHN was enhanced at higher temperatures. Bacterial kidney disease (BKD), caused by Renibacterium salmoninarum or a gram-positive diplobacillus, Corynebacterium, has been shown to have an optimum temperature for infection below 15°C (Sanders et al. 1978). However, the incidence of many other freshwater diseases is greater at temperatures above 15°C.

The myxosporidian parasite Ceratomyxa shasta is capable of killing juvenile salmonids with as little as one infectious unit (Ratliff 1983). Ceratomyxa is an important cause of pre-spawning and juvenile mortality among spring chinook, coho, sockeye, Atlantic salmon, brook trout, rainbow trout, brown trout, and cutthroat trout (Margolis and Evelyn 1975). A number of bacterial diseases are prevalent in warm waters. Bacterial gill disease is caused by Myxobacteria spp. and is stimulated by low oxygen concentrations (Wedemeyer and McLeay 1981). Flexibacter columnaris causes the disease, commonly named columnaris, that infects the liver. F. columnaris and Chondrococcus columnaris are synonymous (Servizi and Jensen 1977). Aeromonas liquefaciens, A. punctata, and A. hydrophila are common bacterial pathogens whose occurrence is linked to organic pollution (Snieszko 1974) and high water temperatures (Groberg et al. 1978). A. hydrophila causes a motile aeromonas septicemia in salmonids (Groberg et al. 1978). These pathogens infect the gills and peritoneal cavity (Snieszko 1974). Aeromonas salmonicida is the infective agent for furunculosis, which has been observed in chinook, chum, sockeye, pink, coho, and Atlantic salmon, and rainbow trout. This obligate fish pathogen can be highly infectious in either freshwater or the estuary. It produces a general septicemia and massive tissue destruction (Beacham and Evelyn 1992). Aeromonas, Pseudomonas, and myxobacteria are continuously present in the majority of stream environments (Wedemeyer and McLeay 1981). Vibrio is caused by the marine bacterium Vibrio anguillarum. This bacterial infection produces a hemorrhagic septicemia that has optimum growth conditions in waters above 15°C. Although this is primarily a saltwater disease, there is concern for its occurrence in the estuary.

It is sometimes argued that with some freshwater diseases having optimum conditions for infecting fish in cold water and some in warmer water, there is no preference in temperature regulation regarding disease. However, in the case of bacterial coldwater disease, it flourishes at temperatures up to 10°C but appears to be controlled at 12.8°C (Rucker et al. 1953, as cited by Pacha and Ordal 1970). Most warmwater diseases begin to become serious threats above 15°C. With respect to freshwater diseases, temperatures in the range 12.8-15°C appear to be least problematic for salmonids in resisting both broad classes of disease.

## FIELD OBSERVATIONS

### Chinook

In the Deschutes River during 1973 and 1974 infection frequencies by Ceratomyxa of juvenile chinook averaged 47% and 77%, respectively, for all groups sampled. Infection was as high as 90% in wild chinook in July 1979 (Ratliff 1981). Mortality was as high as 56% in 1978 and 90% in 1979 in the Deschutes River from ceratomyxosis. Pre-spawning mortality of adult spring chinook passing above the Warm Springs National Fish Hatchery from 1977-1986 ranged from 36% to 75%, based upon differences between females passing the hatchery and redd counts. Much of this mortality may be attributed to BKD, which was documented in 1980 and 1981 at the hatchery. In these years mortality was 73% and 75% in the Warm Springs River. In the late-run (mid-June to mid-July) Willamette River spring chinook, migrating in river temperatures of 21-25°C, there is frequently a mere 40-50% survival of adults enroute to spawning grounds after passing Willamette Falls. This high loss rate is probably attributable to warmwater disease and inability to migrate further under high water temperatures (Schreck et al. 1994).

Ceratomyxa has been reported as common among wild, prespawning chinook in the Fraser River. Infections in emigrating chinook juveniles near the Fraser River mouth have also been reported (Margolis et al. 1992). Annual percentages of juveniles infected in the Fraser River ranged from 1.8%-4.7% (Margolis et al. 1992) but reported infection rates for the Columbia River are higher (8.9%-14.0%) (Fryer 1984, 1985, both as cited by Margolis et al. 1992). Chinook stocks have widely varying susceptibilities to infection (Zinn et al. 1977; Ching and Parker 1989, as cited by Margolis et al. 1992). Temperatures >10°C are generally associated with infectivity by Ceratomyxa in salmonids (Udey et al. 1975), but infections have also been reported at colder temperatures. However, progression of the disease and consequent mortality are more rapid at higher temperatures (Margolis et al. 1992).

Infection frequency appears to be linked to warm water temperatures but is also related to flow rates. The low flow rate of the North Arm of the Fraser River appears to be responsible for the higher infection rate of emigrating chinook (6.8%) as compared with the Main Arm (2.1%). A low rate of flow is likely linked to a higher density of infective units of C. shasta (Margolis et al. 1992) and a greater probability of infection. High infection frequency is associated with reduced time to death. With a low infection frequency, it may take up to 100 d at 10°C to observe death (Ratliff 1983). Low flow rates typical of Columbia River reservoirs and prolonged exposure to disease organisms during migration through reservoirs periods may be a significant cause of increased infectivity in the Columbia River (see Ratliff 1981) relative to the Fraser River. Although upriver stocks have been considered to be relatively resistant to C. shasta, this conclusion has been based primarily on exposure tests of 5 d. At the typical migration rate of yearling salmon and steelhead (18 and 35 km/d) in the Columbia River, total exposure times of 53 and 27 d, respectively, during migration from Oxbow Dam to the ocean might substantially increase the rate of infection (Hoffmaster et al. 1988).

Temperatures of 20°C were reported to result in 100% mortality of chinook during columnaris outbreaks (Ordal and Pacha 1963). These authors found that strains of low virulence initiated infection at water temperatures ≥20°C but highly virulent strains were infective with temperatures as low as 12.8°C. They considered temperature-induced columnaris as a major factor responsible for declines of Columbia River chinook. The system of reservoirs has been credited with the major increase in columnaris disease in the Columbia River (Snieszko 1964). Fujihara et al. (1971) and Fujihara and Nakatani (1970) reported that columnaris is associated with temperatures ≥15°C in the Columbia River. Fujihara and Nakatani (1970) observed greatest incidence of columnaris in the Columbia River as temperatures sharply increased in early July to >17.2°C. As determined by surveys of antibody titers in 1964-65 and 1969-70, the peak yearly infection rates in the Columbia River with columnaris are 70-80% in adults (Fujihara and Hungate 1970). Mortality in chinook exposed to columnaris appeared to be age or size dependent with younger and smaller individuals being more susceptible (Fujihara et al. 1971). The median time to death of 10-month old chinook exposed to columnaris was only 28 h at 20°C. Time to death increased with temperature in the range 10 to 20°C. Even though peak temperatures were not necessarily associated with peak incidence of the disease (Fujihara and Nakatani 1970), death is more rapid at higher temperature. Fish that contracted the disease and did not die frequently acquired some disease resistance, but deliberate infection to impart an antibody titer would come at a high cost in population mortality (Bouck et al. 1975).

In the Rogue River pre-spawning mortality from furunculosis and columnaris averaged 12% for wild and 36% for hatchery spring chinook from 1977 through 1981 (Cramer et al. 1985, as cited by Lindsay et al. 1989). In the summer of 1977 as temperatures exceeded 17°C an outbreak of bacterial gill disease caused the loss of 458 thousand spring chinook from a rearing pond for the Rapid River hatchery (Parrish 1978). Of the adult fish held for spawning, 11% died of the gill disease; 5.5% of the fish that died also had kidney disease. The overall mortality rates from bacterial gill disease in the previous year for ponded fish was 14.5%.

The problems with columnaris disease in the Columbia River were heavily documented in numerous studies conducted from the 1940s to early 1970s. In the Fraser River columnaris is of continual concern because of the very noticeable impacts to adult sockeye on spawning grounds. In the Columbia River columnaris has not continued to receive the attention that it probably deserves, possibly because of so many other critical problems in fish survival. In addition, because the Columbia River is impounded and because there are fewer fish than in the Fraser, death of adults in the reservoirs from columnaris might be less noticeable. When individual fish are radiotracked on a continual basis, it is rare to find a carcass even when it is washed ashore (Schreck et al. 1994). Frequency of infection by columnaris has been observed in fall chinook in small-scale surveys that were conducted in recent years on the Columbia River. After the large fish kill detected at McNary Dam on July 16, 1994, 125 juvenile fall chinook were collected at John Day Dam and held at the Lower Columbia River Fish Health Laboratory at the USFWS facility in Cook, Washington. In a 4-d period 94% of these fish died with a columnaris infection considered to be a low virulence strain (Tiffan et al. 1996). In mid-July, 1998 there were three consecutive days of high fall chinook mortality detected at McNary Dam due to high water temperatures. Of 25 fish sampled from the Juvenile Fish Facility at McNary Dam that were distressed (swimming on their sides) during this high water temperature period, it was determined that 88% had columnaris infection. Although the fish were near death, there were no visible external signs of disease (Tiffan, USFWS, Cook, WA).

### Associated Species

Chondrococcus columnaris infection in sockeye was implicated in high sockeye mortalities in the Columbia River (Fish 1948). Columnaris becomes increasingly active above 15.6°C (Colgrove and Wood 1966). The near obliteration of the run of 1941 at Bonneville Dam occurred when temperatures reached a high of 23.6°C and average of 20.3°C (Fish 1948). Bouck et al. (1970) (as cited by EPA and NMFS 1971) did not observe sockeye mortalities from columnaris at 16.7°C but did note frequent lesions and death at 20°C. For adult sockeye on Fraser River spawning grounds, mortality of females ranged from 5%-86% from bacterial gill infections at temperatures of 22°C (International Pacific Salmon Fisheries Commission 1962, as cited by Parker and Krenkel 1969) In 1970 there was a columnaris epidemic in the Hanford Reach and in the Wenatchee portion of the mainstem Columbia River in which it appeared that coarsefish passed the disease to adult sockeye during their migration (Fujihara et al. 1971).

Columnaris has been isolated from throughout the mainstem Columbia River and in numerous tributaries: Okanogan, Wenatchee, John Day, Umatilla, Yakima, Snake, and Similkameen Rivers. It is carried by all species of Pacific salmon, and also in carp, sucker, chub, bass, northern pikeminnow, chiselmouth, and catfish (Colgrove and Wood 1966). Many strains are of high virulence and can kill within 12-24 h. Contagion of the disease has been suspected during passage of salmon through fish ladders (Pacha 1961) and increased incidence may be a result of creation of the slow moving reservoirs (Snieszko 1964). Warm sloughs may also harbor the disease organism in coarsefish that can then infect salmonids migrating in warmed reservoirs (Fujihara et al. 1970).

Prespawning survival rates among adult sockeye in the Fraser River spawning areas were as low as 10% (as found in the Chilko stock) in the early 1960s. In experiments on the Horsefly spawning grounds, it was found that adult sockeye held at a mean temperature of 15.6°C had survival rates of only 19%-37%. However, when held at mean temperatures of 12.8°C and a maximum <13.9°C, the sockeye did not die and gill lesions from columnaris infection began to heal (Colgrove and Wood 1966). A mean of 12.8°C and a maximum of <13.9°C is, then, a recommended holding temperature on spawning grounds. Given that river temperatures enroute to spawning grounds for the Chilko and Stuart Lake Runs averaged 16.7°C during 1956 (Idler and Clemens 1959), it appears that if fish can survive migration through these adverse temperatures, it would be essential to find suitable temperatures on spawning grounds. Unfortunately, during other years temperatures at Hell's Gate during the Horsefly sockeye migration can be even higher (up to 19.3°C) (Williams et al. 1977).

Degree of resistance to disease is an inherited trait. Skamania summer steelhead were highly resistant to Aeromonas salmonicida and A. liquefaciens when water temperature exceeded 17°C but Siletz and Umpqua stocks were not. The Deschutes River, Oregon, and Clearwater River, Idaho, stocks of summer steelhead were resistant to ceratomyxosis but the Umpqua stock was not. Exposure of pure stocks and their crosses to Willamette River water for week-long periods in early October at temperatures of 15°C-16°C and 12°C-14°C, followed by transfer to pathogen-free water at 12°C indicated that pure stocks of Skamania, Umpqua, and Siletz summer steelhead had survival rates of 97-100%, 1-2%, and 3%, respectively, in 105 d. Crosses of the Skamania stock with the other two less resistant stocks resulted in survival rates of 32%-90% under these same conditions (Wade 1986).

Presence of the infective stage C. shasta was demonstrated in many locations in the Columbia and Snake Rivers by holding disease-susceptible rainbow trout in liveboxes for 7 or 14 d at various locations (Hoffmaster et al. 1988). Infection frequency was generally <20% in reservoirs near many of the mainstem dams. However, in June 1984 infection frequency was 52% at the Dalles Dam and in July 1986 at Hells Canyon and Oxbow Dams was 96% and 95%, respectively, at these dams (Hoffmaster et al. 1988). In 1967 and 1968, coho placed in live-boxes in the Columbia River at Bonneville Dam had infection rates of 53 and 60%, respectively. At the Dalles Dam in 1967, rainbow trout in live-boxes exhibited a 13% infection rate. C. shasta is also a serious disease problem on the Sandy River and the Willamette River where 92% and 62%, respectively, of fish that died before spawning were infected with the disease. The disease appears to be controlled by water temperatures <10°C (Sanders et al. 1970).

## LABORATORY OBSERVATIONS

### Chinook

Juvenile spring chinook infection with Chondrococcus columnaris at temperatures of ≤12.2°C was negligible, but between 15°C and 23.3°C the percentage infected of the fish exposed to the disease rose steadily with temperature from 27% to 80% (Fryer and Pilcher 1974). Percentage infected is a value calculated by multiplying the percentage mortality at each temperature by the percentage of all dead fish for the experimental group that were found to be infected with C. columnaris. It is assumed in this calculation that fish not dead at termination of the experiment were not infected. Rates of survival from columnaris infection in spring chinook were found to decrease between temperatures of 3.9°C and 23.3°C (Fryer and Pilcher 1974) (**Table 7**). Survival was ≤30% for temperatures of 20.6°C or greater. Time to death from the point of infection was reduced from 7 to 2.5 d as temperatures increased from 15°C to 23.3°C (**Table 8**). Columnaris was completely suppressed at temperatures ≤9.4°C (Fryer and Pilcher 1974, Holt et al. 1975).

Juvenile spring chinook infected with Aeromonas salmonicida and then held at constant temperatures from 3.9°C to 20.5°C had survival rates of 74-92% at 3.9°C-6.7°C within 12 to 23 d. However, at 20.5°C survival was only 7% within 2-3 d, results that were very similar to those with steelhead and coho (Groberg et al. 1978). Infection by A. hydrophila (formerly known as A. liquefaciens) resulted in survival of only 32% at 20.5°C. Survivals were very high at 3.9°C-9.4°C. The threshold for stimulation of this disease appears to be at approximately 12.2°C, at which point survival was 62% (Groberg et al. 1978).

Infection of juvenile chinook with Aeromonas salmonicida and Aeromonas liquefaciens resulted in similar survival rates upon exposure to temperatures ranging from 3.9°C to 23.3°C (Fryer et al. 1976) (**Table 7**). Survival in each case declined as temperatures increased. Survival at temperatures of 20.6°C or greater were lower for A. salmonicida (≤7%) than for A. liquefaciens (≤32%) infection. Time to death required one to several days at 15°C for these Aeromonas species and was substantially decreased as temperatures increased to 22.2°C (**Table 8**).

**Table 7.** Effect of water temperature on survival of juvenile spring chinook infected with Chondrococcus columnaris, Aeromonas salmonicida, and Aeromonas liquefaciens. Data from for C. columnaris are from Fryer and Pilcher (1974); data for Aeromonas spp. are from Fryer et al. (1976)

| Water temperature (°C) | Chondrococcus columnaris | Aeromonas salmonicida | Aeromonas liquefaciens |
|---|---|---|---|
| | % survival | | |
| 23.3[a] or 22.2[b] | 8 | 2 | 22 |
| 20.6 | 30 | 7 | 32 |
| 17.8 | 48 | 26 | 38 |
| 15.0 | 69 | 44 | 44 |
| 12.2 | 80 | 30 | 62 |
| 9.4 | 94 | 52 | 100 |
| 6.7 | 94 | 74 | 86 |
| 3.9 | 98 | 92 | 88 |

[a] C. columnaris,
[b] Aeromonas spp.

**Table 8.** Mean time to death (days) for juvenile chinook estimated by regression from studies conducted between 3.9°C and 23.3°C for two selected temperatures (15°C and 23.3°C or 22.2°C) for exposure to Chondrococcus columnaris, Aeromonas salmonicida, and Aeromonas liquefaciens. Data for C. columnaris are from Fryer and Pilcher (1974) and data for Aeromonas spp.are from Fryer et al. (1976)

| Disease | Chinook |
|---|---|
| | Mean time to death (days) at 15 °C (23.3°C[a] or 22.2°C[b]) |
| Chondrococcus columnaris | 7.0(2.5) |
| Aeromonas salmonicida | 5.9(2.2) |
| Aeromonas liquefaciens | 1.3(0.9) |

[a] C. columnaris,
[b] Aeromonas spp.

**Associated Species**

Fryer and Pilcher (1974), Holt et al. (1975), and Fryer et al. (1976) provided a wealth of information regarding survival of salmonids exposed to a variety of infectious diseases and held at temperatures between 3.9°C to 23.3°C. These authors studied Chondrococcus columnaris infection in juvenile rainbow trout, coho, and spring chinook salmon; Flexibacter columnaris in steelhead; Aeromonas salmonicida infection in coho, steelhead, and spring chinook; and Aeromonas liquefaciens infection in steelhead trout and spring chinook (**Tables 9 and 10**). In all cases survival rates were low at 17.8°C-23.3°C, moderate at 12.2°C-15°C, and very high at 3.9°C-9.4°C. Survival of control groups (groups not exposed to disease) was generally 90%-100%, except as noted below. Progress of the infections was accelerated at higher temperatures and was progressively inhibited as temperature levels decreased.

Coho salmon and rainbow trout exposed to Chondrococcus columnaris had a rapidly increasing rate of infection with increase in temperatures above 12.2°C (Fryer and Pilcher 1974). For coho and rainbow, infection frequency of the experimental group was low at 12.2°C (3%-8%) but was 49% and 40%, respectively, at 15°C, and rapidly jumped to 100% at temperatures ≥20.6°C. Infection of fish after exposure to disease organisms is the first stage in progression of disease. Percentage survival of coho after exposure was very low for temperatures ≥17.8°C. A temperature of 12.2°C appears to be the threshold for initiating significant mortalities in coho. Below this temperature survival was near 100% (**Table 9**). In rainbow trout survival was ≤8% for temperatures above 17.8°C. As with coho, the threshold for initiating significant mortality in rainbow occurred at ≥12.2°C. The mean time to death in relation to temperature after exposure for both species was nearly the same (Table 11). Time to death decreased at higher temperatures. Fujihara et al. (1971) found that in a fluctuating temperature regime (17.7°C-21.7°C; mean 19.7°C) in troughs using Columbia River water, juvenile rainbow under crowded conditions, had survival rates of 81%. By increasing mean ambient temperatures by 2.2°C, the survival rate declined to 33%. Approximately 50% of the mortalities reported were associated with columnaris infection under the ambient and ambient+2°C tests.

Experiments with steelhead infected with Flexibacter columnaris, a columnaris strain of intermediate virulence, showed that percentage survival was very high in the temperature range 3.9°C-12.2°C but decreased from 44% to 0% as temperatures rose from 15°C to 23.3°C (Holt et al. 1975). At 15°C, 5.6 d were required to kill juvenile steelhead after exposure to infection, but only 1 d was required to kill juvenile fish at 23.3°C.

The impact of columnaris disease on fish populations is related to the virulence of the strain, water temperature, and degree of aggregation of fish (Pacha and Ordal 1970). Many of the published reports on survival of columnaris disease were based on exposure of fish to the disease in the laboratory. Questions then arise about the natural frequency of infection, because if the disease vector is not present and the fish do not become infected, elevated temperature can then not influence rate of progression of the disease or survival with the disease. Also, the manner of inducing infection in test organisms might be criticized. For example, is there a difference between contact exposure and injection into muscle or peritoneum? These questions require evaluation of observed disease frequencies and ability to become infected and succumb under various exposure routes.

Surveys of infection frequency of sockeye and chinook in the Snake River in July and early August of 1955-1957 revealed 28-75% of fish infected when water temperature was >21.1°C (Ordal and Pacha 1963, as cited by Pacha and Ordal 1970). During this same period the disease was widespread in the Yakima and Okanogan Rivers. In 1958 high percentages of salmon were infected based on samples taken at several mainstem Columbia River dams from Rock Island to Bonneville, as well as on the Yakima, Wenatchee, and Okanogan River. In 1958 water temperatures in the Okanogan were so warm that the run was vastly damaged by columnaris. Thousands of adults left the Okanogan to seek the cooler temperatures of a tributary (the Similkameen River), only to die there from columnaris infection (Pacha and Ordal 1970). Over the years 1955 to 1959 the sockeye run to Redfish Lake, Idaho declined by an order of magnitude, coincident with a large increase in Columbia River water temperatures. In 1955 and 1956 the frequency of infected sockeye was 34 and 50%, respectively, in samples taken at Clarkston, Washington (Pacha 1961). Even though these infection frequencies were high, it is likely that they became higher as the fish migrated toward their spawning grounds. Pacha (1961) reported that Anacker (1956) sequentially sampled the sockeye run into the Okanogan River, finding that columnaris frequency rose from 6.3% in August at Rock Island to 23.8% and then 38% in 9 and 15 d further along in the migration. At the termination of the run the disease incidence was 55% (Pacha and Ordal 1970).

The infection rate and time to death are related to the virulence of the columnaris strain, the condition of the fish, and the method of infection. With highly virulent log phase cells, the contact method is the most effective method of infection. The contact method is least effective as a means for infection in low virulence strains (Pacha 1961). However, Fish and Rucker (1943) showed that uninjured sockeye fingerlings exposed to columnaris became infected and died within only 48 h. Injured fish required 72 h to die. Temperatures <15.6°C prevented infection, but higher temperatures led to rapid death. Temperatures of 21°C allow the bacteria to easily penetrate the mucus coating of skin and gills, and between 15.6 and 21°C it can invade the body through cuts and abrasions (Fish 1948). The perils of adult migration through fish ladders and over sharp rocks and descaling and abrasion of juveniles on fish screens are but a few means for opening routes of infection. Prespawning mortality can be minimized by holding adults in water temperatures ≤10°C to allow abrasions to heal (Fish 1944).

Studies of survival of coho salmon and rainbow trout exposed to Ceratomyxa shasta were conducted by exposing fish to Willamette River water in a livebox (Fryer and Pilcher 1974). Coho were exposed for 72 h at a mean river temperature of 15.2°C and rainbow were exposed for 48 h at a mean river temperature of 15.9°C. All fish were then held at 12.2°C briefly. Experimental and control fish were then rapidly equilibrated to their experimental temperatures. Coho infected with C. shasta exhibited low survival at ≥20.6°C, high survival at 9.4°C-15°C, and very high survival at 3.9°C-9.4°C. For rainbow trout infected with C. shasta, survival was high at 3.9°C but was low at all other temperatures. The disease progressed most rapidly at higher temperatures, and became progressively slower as temperature decreased. That is, when fish were infected, life expectancy was extended as temperatures decreased. The mean life expectancy for juvenile rainbow was 42 days after exposure to C. shasta followed by holding under test conditions at 15°C. At 23.3°C the mean life expectancy was reduced to 15 days. Time to death in rainbow varied greatly, from 157 d at 6.7°C to 15 d at 23.3°C. Time to death in coho was very similar. The percentage of juvenile coho infected after exposure to the disease organism appeared to have a threshold at 12.2°C; a very small percentage of test groups exposed at temperatures of ≤9.4°C became infected. In rainbow, frequency of infection was uniformly high at all temperatures ≥6.7°C. Fryer and Pilcher (1974) concluded that their experiments on survival of coho and steelhead after exposure to C. shasta for 48 or 72 hr reflected maximum estimates of survival under field conditions because these species under natural conditions are exposed for longer periods to infectious organisms.

Juvenile steelhead, coho, and spring chinook salmon infected with Aeromonas salmonicida and then held at constant experimental temperatures ranging from 3.9°C to 20.5°C had high survival (74%-98%) at 3.9°C to 6.7°C within 12 to 23 d. However, at 20.5°C survival was 0%-7% within only 2-3 d (Groberg et al. 1978). In both species, fatal infections were progressively enhanced at temperatures from 12.2°C to 20.6°C. A. hydrophila (formerly known as A. liquefaciens) infection in juvenile steelhead resulted in 60% survival at 12.2°C, declining to survivals of approximately 35% at temperatures from 17.8°C to 20.5°C (Groberg et al. 1978). Data reported by Groberg et al. (1978) for coho and steelhead infected with Aeromonas salmonicida were the same as reported by Fryer and Pilcher (1974) for coho and Fryer et al. (1976) for steelhead.

Implications of these results for survival to spawning are interesting. The temperature regime, the genetic susceptibility to the disease, virulence of the disease organism, and other stressors determine the infection rate, the percentage survival, and the mean time to death. With a disease such as C. shasta, having such a large range of times to death at temperatures from 3.9°C to 23.3°C, the ability of an adult that became infected during upstream migration to live long enough to spawn depends highly on the temperature regime. Contraction of diseases during migration through warm water reaches may not result in pre-spawning mortality, provided the bulk of the migration and holding period is spent in cold water. However, spring or summer chinook, which hold for extended periods, may succumb to disease prior to spawning if inadequate holding water temperature is available. This is especially probable for diseases studied by Fryer and Pilcher (1974) and Fryer et al. (1976) other than C. shasta. For these diseases, the relatively short durations between exposure and death, regardless of temperature, make it unlikely that adults that are exposed and infected during migration at high temperatures or holding under high temperatures could survive sufficient time despite the disease so that they could still complete spawning, given the generally lengthy migration and holding periods for most salmon.

**Table 9.** Effect of water temperature on survival of juvenile coho infected with Chondrococcus columnaris, Aeromonas salmonicida, Aeromonas liquefaciens, and Ceratomyxa shasta. Data for C. columnaris, A. salmonicida, and C. shasta are from Fryer and Pilcher (1974) and data for A. liquefaciens are from Fryer et al. (1976).

| Water temperature (°C) | Chondrococcus columnaris | Aeromonas salmonicida | Aeromonas liquefaciens | Ceratomyxa shasta |
|---|---|---|---|---|
| | % survival | | | |
| 23.3 | 0 | [a]0 | 0 | 4 |
| 20.6 | 0 | 0 | 0 | 8 |
| 17.8 | 1 | 6 | 0 | 42 |
| 15.0 | 49 | 30 | 3 | 78 |
| 12.2 | 96 | 58 | 59 | 76 |
| 9.4 | 100 | 54 | 97 | 98 |
| 6.7 | 100 | 88 | 100 | 100 |
| 3.9 | 100 | 86 | 100 | 100 |

[a] survival was equal to control survival rate; mortality probably associated with high exposure temperature

**Table 10.** Effect of water temperature on survival of juvenile Oncorhynchus mykiss infected with Chondrococcus columnaris, Flexibacter columnaris, Aeromonas salmonicida, Aeromonas liquefaciens and Ceratomyxa shasta. Data for C. columnaris, A. liquefaciens, and C. shasta are from Fryer and Pilcher (1974) and data for F. columnaris and A. salmonicida are from Fryer et al. (1976). Key: [a] tested on rainbow; [b] tested on steelhead.

| Water temperature (°C) | Chondrococcus columnaris [a] | Flexibacter columnaris [b] | Aeromonas salmonicida [b] | Aeromonas liquefaciens [b] | Ceratomyxa shasta [a] |
|---|---|---|---|---|---|
| | % survival | | | | |
| 23.3 | 0 | 0[c] | 4[c] | 18 | 0 |
| 20.6 | 0 | 0 | 4 | 36 | 2 |
| 17.8 | 8 | 8 | 16 | 33 | - |
| 15.0 | 60 | 44 | 46 | 61 | 8 |
| 12.2 | 92 | 84 | 70 | 60 | 4 |
| 9.4 | 100 | 100 | 72 | 100 | 20 |

| | | | | | |
|---|---|---|---|---|---|
| 6.7 | - | 98 | 90 | 100 | 23 |
| 3.9 | | 100 | 98 | 100 | 100 |

[c] survival of control group also was equally low; mortality probably a result of high exposure temperature

**Table 11.** Mean time to death (days) for juvenile coho and rainbow/steelhead from studies conducted between 3.9°C and 23.3°C for two selected temperatures (15 °C/23.3°C) for various freshwater diseases. Data from Fryer and Pilcher (1974) and Fryer et al. (1976).

| Disease | Coho | Steelhead/rainbow |
|---|---|---|
| | % survival at 15°C/23.3°C | |
| Chondrococcus columnaris | 4.3(1.4) | 4.2(0.9) |
| Flexibacter columnaris | | 5.8(1.2) |
| Aeromonas salmonicida | 7(2.6) | 4.9(2.6) |
| Aeromonas liquefaciens | 2.3(1) | 2.1(1.7) |
| Ceratomyxa shasta | 40(12) | 42(15) |

Juvenile coho experimentally infected with Vibrio anguillarum and held at constant temperatures from 3°C to 21°C had reduced rates of survival with increasing temperatures above 12°C (Groberg et al. 1983). The relationship between temperature and mortality was similar to that found by Groberg et al. (1978).

BKD infection was studied on juvenile coho, sockeye, and steelhead by Sanders et al. (1978). Juveniles of these three test species were infected with the bacterium causing BKD and held at constant experimental temperatures between 3.9°C and 20.5°C. For coho and steelhead, percentage survival was 0%-22% in the temperature range 6.7°C-12.2°C. Survival increased above 12.2°C until it reached 86%-92% at 20.5°C. Sockeye, which were highly susceptible to BKD, had nearly 100% mortality in the temperature range 6.7°C-20.5°C. Mean time from infection to death in coho decreased from 81 d at 3.9°C to 23 d at 20.5°C. Mean times to death for steelhead at these two test temperatures were 81 and 14 d, respectively; for sockeye, mean times to death were 109 and 20 d, respectively. This study did not involve determination of incidence of infection when exposed to the disease organism in water. Outbreaks in the field generally occur in spring and autumn when water temperatures are ≤10°C (Sanders et al. 1978). However, after fish are infected at low temperatures, death would be reached in >80 d if the fish continued to be held at the low temperatures. But once temperatures rise to 20.5°C, time to death decreases considerably. Warm temperatures

(17.8°C to 20.5°C) might suppress incidence of infection, but once these salmonids are infected at low temperatures, an increase in temperature simply hastens time to death.

IHN infection in rainbow trout responds in a similar manner to temperature as does BKD infection (i.e., shorter survival time with higher temperatures after infection occurs). It is generally reported that IHN does not occur in the field above about 15°C (Hetrick et al. 1979). However, if juvenile rainbow trout are infected at temperatures below 15°C and then transferred to warmer temperatures, the course of the disease to death is faster. Although Amend (1970, as cited by Hetrick et al. 1979) reported that IHN was prevented in juvenile sockeye when held at temperatures >18°C, Hetrick et al. (1979) found that fingerling rainbow trout infection occurred at temperatures from 3°C to 18°C. At 12°C infected rainbow experienced only 30% survival with a mean time to death of 10.7 d; at 15°C survival was 48%; at 18°C survival from IHN was ≤54% (after subtracting mortalities of the control group) and mean time to death was reduced to 7.4 d. Because rainbow trout can become infected at temperatures up to 18°C, it appears that elevated temperatures are not a safety mechanism when confronted with IHN.

Proliferative kidney disease (PKD) was studied in juvenile rainbow trout in northern Ireland (Ferguson 1981). It was found that temperatures of 16°C stimulated full development of the disease, but that declining temperatures were linked to inability of the disease to develop. PKD has been shown to affect chinook, steelhead, coho, brook trout, brown trout, and Atlantic salmon (Hedrick et al. 1984). It is caused by a protozoan that becomes activated at temperatures ≥15.6°C and causes enlargement of the kidney. PKD has been found in Idaho, California, and Vancouver Island.

# GENETIC VARIATION IN RESPONSE TO THERMAL ENVIRONMENT

## FAMILY-LEVEL VARIATION

### Juvenile Survival and Preference

When comparing the temperature optima of major families of freshwater fishes found in the Columbia River drainage, a large degree of overlap is apparent. The family Salmonidae (salmon and trout) has temperature optima ranging from 5°C to 22°C. The other two major coldwater groups, the Coregonidae and Thymallidae, in North American freshwaters have very similar ranges for temperature optima, 8°C-15°C and 4°C-18°C, respectively (Elliott 1981). Chinook and the other Pacific salmon inhabit waters with a more restricted temperature range than exhibited by Salmonidae in general, have optima as high as 16°C. A very meaningful, though infrequently used, indicator of thermal tolerance is the thermal polygon (Elliott 1981). This index is computed as $(°C)^2$ by determining the area bounded by the upper and lower lethal limits on the acclimation-thermal exposure graph. Interestingly, despite the low tolerance demonstrated by coldwater stenotherms, they have relatively high resistance to thermal stress compared to warmwater eurytherms, which tend to behave in the inverse manner (Elliott 1981). Brett (1956) showed that the five species of North American Oncorhynchus have extremely low values ($450\text{-}529°C^2$), even compared with brook trout ($625°C^2$) and brown trout ($583°C^2$). Goldfish, by contrast, have a value of $1220°C^2$. Most cyprinids (e.g., shiners, dace, northern pikeminnow, except carp) have temperature optima ranging from 15°C-32°C) (Elliott 1981) and thermal tolerance indices ranging from approximately 750 to $900°C^2$ (Brett 1956). Centrarchids (e.g., bass) have temperature optima much like the cyprinids. For example, smallmouth bass prefer temperatures of 21.4°C and have an upper lethal limit of 35°C (Scott and Crossman 1985). The optimum growth temperature for juveniles is 26°C (Horning and Pearson 1973).

Temperature preferences are a very good indicator of physiological temperature optima (Brett 1971). Temperature preferences for various representatives of Salmonidae, Cyprinidae, and Centrarchidae, and other groups were compiled by Coutant (1977). A brief summary of ultimate preferenda (means of all the references provided, sorted by age, and considering only summer preference when given) is provided in **Table 12**. This table is not comprehensive for all currently available literature but does provide a rapid view of the major differences among fish families using a readily accessible review. Not all species listed of the Cyprinidae, and Centrarchidae have been introduced into the Pacific Northwest, but these species adequately represent other members of the family for purposes here.

**Table 12.** Ultimate temperature preferenda for various representative Salmonidae, Cyprinidae, and Centrarchidae. Values are means computed from tabulated values in Coutant (1977), considering only summer preference when seasonal data are provided. In cases where multiple estimates were made on similar size fish by a single investigator, all those values were averaged and attributed to only one reference.

| Species | Common Name | References | Ultimate preferendum (°C) |
|---|---|---|---|
| **Salmonidae** | | | |
| Oncorhynchus tshawytscha | chinook salmon | Brett (1952)<br>Spigarelli (1975) | 11.7 (young)<br>17.3 (adult) |
| Oncorhynchus nerka | sockeye salmon | Horak and Tanner (1964) | 11.7 |
| Salmo gairdneri | rainbow trout | McCauley and Pond (1971)<br>Horak and Tanner (1964), Garside and Tait (1958), Spigarelli (1975), Cherry et al. (1975) | 18.5 (fingerling)<br>16.9 (adult) |
| **Cyprinidae** | | | |
| Notropis atherinoides | emerald shiner | Barans and Tubb (1973)<br>Barans and Tubb (1973) | 22.5 (YOY)<br>23 (adult) |
| Notemigonus crysoleucas | golden shiner | Reutter and Herdendorf (1974) | 22.3 (adult) |
| Pimephales promelas | fathead minnow | Jones and Irwin (1965)<br>Cherry et al. (1975) | 23.4 (<74 mm)<br>29 (adult) |
| Pimephales notatus | bluntnose minnow | Cherry et al. (1975) | 29 (adult) |
| **Centrarchidae** | | | |
| Micropterus salmoides | largemouth bass | Dendy (1948), Clugston (1973), Neill (1971), Coutant (1975), Ferguson (1958), Reynolds et al. (1976), Reynolds and Casterlin (1976), | 28.8 (all sizes) |
| Micropterus dolomieui | smallmouth bass | Barans and Tubb (1973)<br>Barans and Tubb (1973) | 31 (YOY)<br>29 (adult) |

| | | | |
|---|---|---|---|
| Lepomis gibbosus | pumpkinseed | Neill (1971), Reutter and Herdendorf (1974), Reynolds, unpubl. | 28.6 (small to adult) |
| Lepomis macrochirus | bluegill | Neill (1971), Ferguson (1958), Beittinger (1974), Reynolds and Casterlin (1976), Reynolds et al. (1976)<br>Cherry et al. (1975) | 31.7 (53-155 mm+young)<br>32 (adult) |

The UUILT is not always identified precisely in the literature but a small increase in upper incipient lethal limit with substantial increase in acclimation temperature is a good indication that the ultimate incipient level is reached. Given the data compilation for Salmonidae in this report (**Tables 3 and 4**) and the compilation by Coutant (1972), one can infer a range of UUILT for the families Salmonidae, Cyprinidae, and Centrarchidae, to be 23°C-25.6°C (Tables 3 and 4), 29°C-33°C (Table 13), and 33°C-37°C (Table 14), respectively. This range in UUILT values mentioned for Salmonidae accounts for the response of the species chinook, coho, sockeye, chum, and pink salmon, steelhead, Atlantic salmon, 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.

**Table 13.** UILT values for various Cyprinidae--dace, minnows, chubs, shiners, (except carp) from the literature as representative for the family. Values taken from Coutant (1972).

| Species | Common Name | References | Acclimation Temperature (°C) | Exposure Temperature (°C) |
|---|---|---|---|---|
| Rhinichthys atratulus | blacknose dace | Hart (1947) | 20<br>25 | 29.3<br>29.3 |
| Notropis atherinoides | emerald shiner | Hart (1947) | 20<br>25 | 30.7<br>30.7 |
| Notropis cornutus | common shiner | Hart (1952) | 20<br>25 | 31.0<br>31.0 |
| Semotilus atromaculatus | creek chub | Hart (1952) | 20<br>25 | 30.3<br>31.5 |
| Notemigonus crysoleucas | golden shiner | Hart (1952) | 20<br>25<br>30 | 32.0<br>33.5<br>34.5 |
| Pimephales promelas | fathead minnow | Hart (1952) | 20<br>30 | 31.7<br>33.2 |

| | | | | |
|---|---|---|---|---|
| Pimephales notatus | bluntnose minnow | Hart (1952) | 20<br>25 | 31.7<br>33.3 |

**Table 14.** UILT values for various Centrarchidae from the literature as representative for the family. Values taken from Coutant (1972) and Brungs and Jones (1977).

| Species | Common Name | References | Acclimation Temperature (°C) | Exposure Temperature (°C) |
|---|---|---|---|---|
| Micropterus salmoides | largemouth bass | Hart (1952) | 20<br>30 | 32<br>33.7 |
| Lepomis megalotis | longear sunfish | Neill, Strawn, and Dunn (1966) | 30 | 36.8 |
| Lepomis macrochirus | bluegill | Hart (1952) | 20<br>30 | 32<br>33.8 |

* acclimation temperature not given

## SPECIES-LEVEL VARIATION

### Egg/Alevin Survival and Development

Murray and McPhail (1988) provided a very detailed investigation of effects of incubation temperature on five species of Pacific salmon (chinook, coho, sockeye, chum, and pink salmon). They measured effects of five incubation temperatures (2, 5, 8, 11, and 14°C) on fertilization-to-hatching and hatching-to-emergence stages. These species appear to be adapted to different spawning times and temperatures (Murray and McPhail 1988); consequently, by selection of spawning time the incubation temperature regime can be matched to the species' needs so that high survival is likely. High survival during incubation involves avoidance of high intragravel temperatures immediately after spawning (in autumn spawning species) and avoidance of extremely low temperatures during winter. Temperatures low enough to be lethal may occur in high altitude spawning zones (e.g., spring chinook or steelhead reaches) or in low gradient reaches dominated by glacial- or snowmelt. Lethal low temperatures are also more likely where riparian cover has been removed in regions dominated by continental air masses and clear skies. High survival at emergence is a function of avoiding instantaneous temperature extremes (high and low) and accumulating the necessary thermal units so that emergence is timed to correspond to moderate discharge regimes. Emergence timing also influences the potential for growth to a size class capable of emigrating. For example, early emergence by coho allows them to grow for a longer period before their first winter than other salmon that do not emerge early. Size at emigration is directly related to smolt-to-adult survival rate. If multiple years of freshwater rearing are necessary because of slow growth rate, percentage mortality increases with overwinter rearing in natal habitats but may be somewhat compensated by higher survival of resulting larger smolts.

Murray and McPhail (1988) found important variation among salmon species in their early development. When incubated at the high temperature (14°C), chum, pink, and chinook survived better than coho and sockeye. All five species suffered reduction in alevin and fry size when incubated at 14°C. When incubated at the lowest temperature (2°C), no pink or chum embryos survived. Chinook survival rate was lower than that of coho or sockeye. The largest fry of coho, chinook, chum, pink, and sockeye were produced by constant incubation temperatures of 2, 5, 5, 8, and 8°C, respectively. Coho hatched and emerged sooner at all temperatures than the other species. The time from fertilization to 50% emergence in pink salmon at 8, 11, and 14°C was greater than the other species. But when incubated at 2°C and 5°C, chinook required the most time to reach 50% emergence. At 8°C embryos of all five species had their highest survival rates. Variation among species in embryo survival rate was also lowest at 8°C but increased at the extremes of incubation temperatures used (i.e., at 2 and 14°C). Beacham and Murray (1990) found significant differences among these same five species of Pacific salmon in response of alevin length, weight, yolk weight, and tissue weight to incubation temperature. They determined that 60% of total variance was accounted for by species. These authors also found variation among species in development rate, embryo and alevin survival, and fry size at various incubation temperatures. For example, coho is adapted to late autumn to early winter spawning and low water temperatures. It also has the fastest development rate to hatching and emergence, highest embryo survival rate and largest alevin and fry at incubation temperatures <4°C (Beacham and Murray 1990). Its greater rate of development at low temperatures compensates for late spawning.

Inter-specific hatching success was studied in various coldwater species by Humpesch (1985). He found highest hatching success (>90%) for all species incubated within their optimum temperature range. Hatching success was >90% for each species at their optimum temperatures. Optimum temperature varied from 5°C for brown trout, Arctic char, and brook trout, 8°C for Danube salmon, to 7°C-11°C for rainbow and grayling. Within temperature ranges given in **Table 15** he measured high hatching success (>80%), which dropped off at temperatures higher and lower than the ranges specified. This relationship was described by a bell-shaped curve for each species. Upper hatching limits (i.e., the upper temperature at which hatching success reached 0%) varied from 12.5 to 18.5°C. Lower hatching limits (i.e., the lower temperature at which hatching success reaches 0%) varied from <1 to 3°C. Time to hatching at 10°C incubation temperature varied among species. Of the five species in **Table 15**, rainbow hatched most rapidly at 10°C while brook trout, Arctic char, and grayling all required up to about 53 d to reach 50% hatching. There is variation among researchers in days to 50% hatching success within a species that reflects intra-specific variation but also research technique to an unknown extent. Given these sources of variation, the actual variation is actually small. Within the well-studied species, Salmo gairdneri, Humpesch's review indicated a range in days to 50% hatch at 10°C of 31 to 36 d. At 5°C incubation Humpesch (1985) measured 71-75 d to 50% hatch. Including the data from five other authors expands this range to 52-91 d. Given the four stocks of brown trout studied by Humpesch, 38-42 d were required to 50% hatching at 10°C, indicating little intra-specific variation. Adding the data from four other authors expands this range to 38-52 d.

**Table 15.** Interspecific variation in hatching temperatures and days to 50% hatching in several coldwater fish species. Data from Humpesch (1985).

| Species | Temperature range for >80% hatching success (°C) | Upper hatching limit (°C) | Lower hatching limit (°C) | Time to 50% hatching at 10°C (d) |
|---|---|---|---|---|
| Salvelinus fontinalis | 1.5-9 | 15 | <1 | 37-53 |
| Salvelinus alpinus | 1.5-5 | 12.5 | <1 | 46-53 |
| Salmo gairdneri | 10-12 | 18.5 | 3 | 32-34 |
| Salmo trutta | 1-10 | 15 | <1 | 38-42 |
| Thymallus thymallus | 7-12 | 18.5 | 3 | 48-54 |

### Juvenile Survival and Preference

Temperature preferences in salmonids are thought to reflect physiological optima (Brett 1971). In addition, final preference tends to be a good index to optimum growth temperature (Jobling 1981)

Peterson et al. (1979) studied the temperature preferences of several species of salmonids including rainbow trout (Oncorhynchus mykiss), anadromous and landlocked Atlantic salmon (Salmo salar), brook trout (Salvelinus fontinalis), lake trout (Salvelinus namaycush), and Arctic char (Salvelinus alpinus) (**Table 16**). Because fry were allowed 1 h and fingerlings 2 h for adjustment to test conditions, followed by a 64-min determination of frequency distribution at 2-min intervals in a horizontal temperature gradient tank, this test should be considered to be an acute preference test. Acronyms for these species are Om, Ss, Sf, Sn, and Sa, respectively. Hybrids of these species were also tested. Fry of the species tested preferred different temperature ranges. The Oncorhynchus/Salmo group selected temperatures of 13.6°C to 14.3°C. Within the Salvelinus genus preferred temperatures of fry were 8.7°C to

9.9°C. The Salvelinus hybrids preferred temperatures ranging from 9.2 to 10.5°C. There was a very small difference between anadromous and landlocked salmon fry.

Oncorhynchus mykiss and Salvelinus namaycush fingerlings preferred similar temperatures as fry. However, fingerlings of Salvelinus fontinalis and the (Sf ♀ x Sn ♂) and (Sn ♀ x Sf ♂) hybrids preferred higher temperatures than the corresponding fry. The hybrids of the fingerlings were also intermediate between the pure strains. Genetic differences were detected between genera and between hybrids and the pure parent strains. However, there were no differences within a species in the case of anadromous and landlocked forms of Salmo salar and very little difference in preference among fry of the three Salvelinus species tested.

**Table 16.** Results of thermal preference tests of Peterson et al. (1979) for fry and fingerlings of several species and hybrids of salmonids. Oncorhynchus mykiss, Salmo salar, Salvelinus fontinalis, Salvelinus namaycush, and Salvelinus alpinus are symbolized as Om, Ss, Sf, Sn, and Sa, respectively..

| Species or hybrid | fry* | fingerlings** |
|---|---|---|
| Om | 14.3 | 14.7 |
| Ss (anadromous) | 13.8 | |
| Ss (landlocked) | 13.6 | |
| Sf | 8.7 | 17.5 |
| Sa | 9.2 | |
| Sn | 9.9 | 10.8 |
| Sa ♀ x Sf ♂ | 9.2 | |
| Sf ♀ x Sa ♂ | 10.5 | |
| Sf ♀ x Sn ♂ | 9.4 | 14.7 |
| Sn ♀ x Sf ♂ | 10.1 | 14.4 |

* acclimation temperature of fry was 12.7°C

** acclimation temperature of fingerlings was 12.1°C

Goddard and Tait (1976) measured the preferred temperatures of yearling $F_3$ to $F_5$ hybrids from an original $F_1$ created from a Sn♀ x Sf ♂ cross. Progeny of the $F_1$ were subjected to selection for early maturity in succeeding generations. Between the $F_3$ and $F_5$ generations, final preferred temperatures of hybrids acclimated to 12°C decreased from 16.3°C ($F_3$) to 14.8°C ($F_5$). Goddard and Tait noted a reduction in temperature preference with each successive generation from one typical of brook trout toward that of lake trout (near 11.7°C).

The $F_5$ hybrid temperature preference with 12°C acclimation is similar to that reported by Peterson et al. (1979) for their fingerling $F_1$ hybrid from a Sn ♀ x Sf ♂ cross acclimated to 12.1°C. The mean length of the $F_5$ hybrids of Goddard and Tait was 137.2 mm; that of the fingerling $F_1$ hybrid of Peterson et al. was 61.7 mm. It is possible that the size difference of the $F_1$ hybrids tested was partially responsible for the differences in preference observed. Even though Goddard and Tait were able to breed hybrid strains with varying degrees of temperature preference, the preference of the hybrid was confined by the temperature ranges of the parent species. Peterson et al. (1979) also found that the $F_1$ hybrids preferred temperatures intermediate between that of the parent species.

In a study evaluating the relationship between acute temperature preference and acclimation temperature within three families (Cyprinidae, Ictaluridae, and Centrarchidae), Mathur et al. (1981) noted that less than 2% of total variance in temperature preference among species within a family was accounted for by the species effect. Most of the variation among species within a family (64%-81%) was due to acclimation temperature and less than 2% was attributable to species. Even though the species effect was statistically significant in the case of the Cyprinidae and Ictaluridae, Mathur et al. (1981) concluded that this effect was biologically trivial. They considered that a biologically significant effect would be more than barely discernible with a large sample size, but should be related to magnitude of the difference. Hart (1952) also considered that the effect of acclimation temperature may completely obscure differences at the species or racial level. In addition, he noted that differences in age, size, water chemistry, and season must also be controlled when comparing populations because these factors also lead to variation in response. Variability in acute preference is great enough within a population that geographic variation would be difficult to demonstrate (Mathur et al. 1981).

A portion of the variation in temperature preferences or UUILT or CTM values reported in the literature is attributable to variation in methodology and unique test conditions applied by the experimenter (Mathur et al. 1981). As typical with all experimental work, sources of interspecific variation among literature on temperature effects include genetic differences among the test organisms; differences among species linked to acclimation, nutritional or health status, life stage, etc. of the test groups; uncontrolled environmental variation from one test period to another or among test groups or sites; and measurement error. One means of reducing variation associated with species effects is to evaluate a single published study on a variety of species in which a common laboratory protocol was applied to each species.

Cherry et al. (1977) studied preferred and lethal temperatures for several species of salmonids, cyprinids, and centrarchids. Final temperature preferences for representatives of these families were <19, >24, and >29°C, respectively. The 7-d UUILT for these groups, respectively, was 23-25, 26-36, and 35°C-36°C. Within the salmonids, rainbow trout, brown trout, and brook trout avoided temperatures outside the bounds 15-26, 17-25, and 18°C-26°C, respectively. The 7-d UUILT values for these three salmonids, respectively, were 25, 23, and 24°C.

Brett (1952) measured UUILT on several salmon species (Oncorhynchus 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. He found that among species of Pacific salmon the UUILT values varied only from 23.8°C-25.1°C. Brett's detailed studies, reported in several publications, is rivaled only by Elliott's work on brown trout (Elliott 1975a, 1975b, Elliott 1994).

Lee and Rinne (1980) studied the critical thermal maxima (CTM) to loss of equilibrium (LE-temperature of Becker and Genoway 1979) of five species of trout (15-20 cm total length and described as adults) collected in the southwestern U.S. Rainbow trout (formerly Salmo gairdneri, currently O. mykiss), brown trout (Salmo trutta), and brook trout (Salvelinus fontinalis) were introduced species; Gila trout (Salmo gilae) and Arizona trout (Salmo apache) are native. These five species had CTM values for 20°C acclimation and 1.2°C/h temperature increase of 29.4, 29.9, 29.8, 29.6, and 29.4°C, respectively. The LE-temperature for coho acclimated at 15°C and subjected to an equivalent temperature rise to that used by Lee and Rinne (1°C/h) was 27.7°C (Becker and Genoway 1979). A higher acclimation temperature for coho would likely have made the coho CTM value even more similar to those of the trout species. The similarity in CTM values for these six salmonids from different genetic backgrounds and environments makes it seem unlikely to expect broad levels of adaptation within a species that are not seen among species.

### Juvenile Growth

Sadler et al. (1986) studied variation in fingerling growth rate among species (brook trout, lake trout and rainbow trout) at two constant temperatures. At 10°C the rank of specific growth rate from low to high was brook trout, lake trout, and rainbow trout. At 16°C ranking from low to high was lake trout, rainbow trout, and brook trout. Only lake trout had no difference in specific growth rate at these two temperatures. A lake trout x brook trout hybrid tested had a growth rate that was intermediate between that of the parents. Brook trout, rainbow trout, and splake (Sn ♀ x Sf ♂) were significantly higher at 16°C than at 10°C. The preferred temperatures of lake trout and brook trout, respectively were 11.7°C (McCauley and Tait 1970) and 17°C (McCauley and Casselman 1981) (both as cited by Sadler et al. 1986). Rainbow trout fingerlings, provided a temperature gradient from 12 to 28°C in vertical and horizontal gradient laboratory tanks, preferred a mean of 18.4°C in both tanks (McCauley and Pond 1971). Temperature preference appeared to be related to the optimum range for growth. Also, in lake trout their food conversion efficiency declined significantly when rearing at the higher temperature.

## STOCK-LEVEL VARIATION

### Egg/Alevin Survival and Development

Murray and Beacham (1986) studied the survival and rate of development of pink salmon (Oncorhynchus gorbuscha) eggs from five different British Columbia stocks under various temperature regimes. For their pink salmon studies in which stock differences were examined, the incubation temperature regime used was a transfer from initial high temperatures (either 8°C or 12°C) to 1°C at various stages of embryo development. Eggs of all stocks were fertilized at 8°C and then held at either 8°C or 12°C for 36 d. The eggs held at 8°C reached stage 26 (onset of operculum growth) and those incubated at 12°C reached developmental stage 29 (near hatching) in this 36-d period. Embryos were then transferred to a 1°C bath. Egg survival was more variable among stocks than among families within stocks from the point of transfer to 1°C to termination (day 133 to 150 of development). For three stocks, egg survival rates were similar when made at stages 26 or 29. The other two stocks each had significant differences in survival between transfers at these two stages. Under any given temperature regime there was no stock difference in time to 50% hatching. Survival to hatching was uniformly high (>88%) among all five stocks surveyed in transfers from 8°C or 12°C to 1°C. Alevin survival was low (38%-60%) for all stocks studied after hatching, except for the most northerly stock (Keogh River), when eggs incubated at 12°C were transferred to 1°C at hatching. The authors suggest that more northerly stocks may be better adapted to greater temperature reduction later in embryo development.

Survival can be partially a function of egg size and size of alevin at hatching or size of emergent fry (a function of egg size and incubation temperature). A portion of this survival is expressed in development to emergence (e.g., ability of fry to emerge from a gravelbed), but egg size and temperature conditions resulting in larger emergent fry also can lead to greater early ocean survival. Temperature regime is governed by a combination of the inherent climatic and hydrologic regime for the stock and land management influences on the vegetative cover in the watershed (especially the riparian zone). Egg size is determined firstly by species effects and secondarily by stock effect, size and age of female, season, and nutritional status. Beacham et al. (1988) measured morphometric differences in pink salmon among stocks within broodlines (i.e., even- and odd-year) and also between broodlines. They found that morphometric characters (adult size, head size, caudal peduncle thickness, fin size) varied more among stocks within broodlines than between broodlines. However, on the basis of allelic frequencies, variation between broodlines was greater than variation among stocks within a broodline. The morphometric variation among stocks or differences between broodlines could indicate adaptation to the natal river conditions (Beacham 1985, as cited by Beacham et al. 1988). Fish spawning in larger rivers within the geographic range surveyed (British Columbia) were larger in all morphometric characters measured than in smaller rivers. Odd-year stocks typically have larger eggs than even-year stocks for equivalent body lengths, even when both stocks originate from the same river (Bilton and Smith 1973). This egg size advantage, such as observed in the Babine odd-year pink run, is translated to larger fry and also larger adults (Bilton and Smith 1973). Also, within a stock, the mean length of males and females and the weight of eggs increased as the spawning season progressed (Beacham et al. 1988).

There are great variations in migration distances among stocks of both chinook and sockeye in British Columbia as well as the Columbia River. Sockeye migration distances vary from the coastal area to 700 km upriver in the Fraser River and chinook migrate distances ranging from the coastal area to >1000 km upriver. These different spawning environments result in the interior-spawning stocks (ISS) being adapted to cold winter climates and the coastal-spawning stocks (CSS) adapting to mild winter conditions. Interior stocks of both species had smaller eggs than the coastal stocks and had higher embryo survival rates at lower incubation temperatures (Beacham and Murray 1989). The smaller egg size (and lower fecundity) of ISS stocks may be caused by the need to convert available energy to swimming greater distances rather than egg production. In sockeye studied, among stock variation in egg diameter accounted for 82% of total egg diameter variation, while differences among females accounted for 10% of the variation. In chinook, among stock variation accounted for 37% of total egg diameter variation, whereas differences among females accounted for 42% of egg diameter variation. No significant differences in egg size were detected between red-fleshed and white-fleshed chinook.

Beacham and Murray (1989) studied survival and development of two sockeye stocks (1 ISS and 1 CSS stock) and three chinook stocks (1 ISS and 2 CSS). When the eggs of ISS and CSS sockeye and chinook stocks were incubated under constant temperatures of 2, 4, 8, 12, and 15°C, the ISS developmental rates to hatching and emergence were faster than those of CSS. This implies that ISS stocks were more efficient in metabolizing yolk at low temperatures than were CSS stocks (Beacham and Murray 1989). Survival rates of ISS to hatching and emergence were higher than for CSS at low incubation temperatures, which could indicate their adaptation to colder thermal conditions. At 2°C the survival rates of the CSS and ISS sockeye stocks were 33% and 91%, respectively, from fertilization to hatching. Subsequent survival from hatching to emergence was high for each stock (>95%). No chinook embryos of either stock group (CSS or ISS) survived at 2°C incubation to hatching. However, the CSS and ISS stocks compared in the study by Beacham and Murray (1989) were from southern British Columbia. A northern British Columbia chinook ISS stock (Babine River) studied by Murray and McPhail (1988) had 14% survival from fertilization to emergence at 2°C. Beacham and Murray (1989) concluded, on the basis of their data and that of Alderdice and Velsen (1978), that an incubation temperature of 3°C results in a 50% chinook embryo mortality. In sockeye 50% mortality was produced at incubation temperatures of 1°C to 3°C, depending upon stock. Alevin survival rates were different among sockeye stocks and among chinook stocks only at 15°C. In sockeye, survival for the CSS stock was higher than for the ISS stock at 15°C; in chinook one CSS stock had relatively low survival at 15°C (56%) compared to the ISS stock (90%) and the other CSS stock (87%). Beacham and Murray (1989) attributed the better performance of CSS sockeye at 15°C to their greater degree of adaptation to milder climates. However, by this reasoning it is difficult to explain the low survival of the CSS chinook stock.

Sockeye alevins of all stocks were longest when incubated at either 4°C or 8°C and shortest at 15°C (Beacham and Murray 1989). Chinook alevins were longest at 4°C. Both sockeye and chinook alevins were heaviest at 8°C and had the greatest amount of yolk at 15°C. Sockeye fry were longest at 4°C whereas chinook fry were longest at 8°C. Both sockeye and chinook fry were lightest at 15°C incubation. Fry of sockeye and chinook both had the greatest amount of yolk remaining at emergence when incubated at 15°C. However, in converting yolk to tissue, the ISS sockeye stock had better growth (conversion of yolk to tissue) at 2°C relative to that at 8°C than the CSS sockeye stock. The authors hypothesized that this reflects a greater adaptation of the ISS stock to low incubation temperature. Stock differences were observed in alevin and fry length, total weight, yolk weight, and tissue weight in both sockeye and chinook. However, these differences were related to initial egg size of the stock. For both sockeye and chinook, adult females of the CSS and ISS stocks were similar in length, but the ISS stocks of each species had significantly smaller eggs than the CSS stocks. In sockeye, stocks accounted for 82% of total variance in egg diameter and females within stocks accounted for only 9% of egg diameter variance. In chinook comparable assignment of variance was 37% and 42%, respectively.

Two forms of chinook were also compared by Beacham and Murray (1989), red-fleshed and white-fleshed forms from the Quesnel River. Red-fleshed chinook incubated at 15°C had significantly higher embryo survival rates than the white-fleshed variety, although the comparative differences were small (98% vs. 92%). Carotenoids in the eggs of red-fleshed chinook may improve oxygen uptake by eggs at higher temperatures, improve percentage survival to hatching, and may also aid in egg respiration when held in the body cavity of overripe females waiting to spawn (Craik 1985). The environment of loose eggs in the abdominal cavity of overripe females holding in warm water conditions is one of low oxygen (Flett et al. 1996, Craik 1985, de Gaudemar and Beall 1998).

With the species odd-year pink, chum, and sockeye salmon, the variation in alevin hatching and fry emergence times is related to time of spawning. Those populations with early spawning time also have late alevin hatching and late fry emergence. Hatching time of even-year pink alevins was later than for odd-year alevins at all test temperatures (Beacham and Murray 1990).

Populations of kokanee from Hill and Mackenzie Creeks flowing into the northeastern side of Upper Arrow Lake in southeastern British Columbia were found to have similar embryo and alevin survival rates for all temperatures tested between 2°C and 10°C (Murray et al. 1989). Embryo survival was >80% at temperatures from 4°C to 10°C, but was only 60% at 2°C for the two populations. Embryo mortality at 2°C occurred in epiboly. Alevin survival was homogeneously >90% at all temperatures from 2°C-10°C. Days to 50% hatching and 50% emergence for these two populations were also similar and varied inversely with mean incubation temperature.

One of the most extensive studies ever conducted on the influence of parental stock and temperature on egg/alevin survival and development was that of Murray et al. (1990) on 13 stocks of coho in British Columbia. These stocks spanned a wide geographic region that incorporated effects of northern vs. southern stocks (i.e., latitudinal effects) and island vs. mainland (i.e., moderate coastal climate vs. cold winter mainland climate). Coho gametes were collected from 13 different stocks. Eggs from single females were fertilized with sperm from single males, producing 5 full-sib families per stock. Eggs were incubated in temperature baths of 2, 5, 8, 11, and 14°C. There were significant differences among stocks in egg diameter and weight that were related to female postorbital-hypural length. Stock effect accounted for 74% of total variance in egg weight and female length accounted for 23% of the total variance in egg weight.

In the stage from fertilization to hatching, survival of embryos for most of the 13 coho stocks was highest at 4°C or 5°C and were >85% at 2, 4, 5, and 8°C (Murray et al. 1990). Of the three island stocks, two of them (i.e., Pallant Creek and Roberstson Creek) had low embryo survival rates (approximately 65%) at 1.5°C. Complete mortality occurred at 14°C and 15°C in all stocks (except for two families of the Coho Creek stock in 1979). For alevins, survival rates in the 1976-1979 studies were not significantly different among stocks for a given temperature, except at 2°C. At this temperature stocks from Coho Creek and Salmon River (two of the ten mainland stocks) had significantly higher survival rates than the other stocks. However, in 1986 alevin survival rates to emergence were significantly different among stocks within temperatures 1.5, 2, 8, and 12°C, but not 4°C. Over the entire period from fertilization to 50% emergence, there were significant differences in development time among stocks and among temperatures. However, stocks that hatched early at one temperature were not consistently early at all other temperatures (i.e., there was an interaction effect of stocks and temperature in the ANOVA design).

For the 13 coho stocks surveyed in 1976-1979 no significant difference existed among stocks in alevin standard length or total wet weight, but differences among stocks were found among incubation temperatures (Murray et al. 1990). Alevin length and weight were typically highest at low incubation temperatures and decreased with increasing temperature. Alevin length was shortest at 12°C. In the 1976-1979 surveys there were no significant differences among stocks in fry standard length or total weight, but incubation temperature produced a significant effect. The longest and heaviest fry developed at 5°C. In the 1986 survey the longest fry and greatest weight at emergence developed at 4°C and 8°C and the shortest and lightest at 1.5°C.

Regional differences among stocks were apparent in the studies on coho by Murray et al. (1990). Northern stocks were more efficient at converting yolk to either alevin or fry tissue at 1.5°C than were southern stocks. At this same temperature mainland stocks were more efficient than island stocks. The converse was true at a warmer temperature (8°C) in these two regional comparisons. This implies that there are significant genetic adaptations relative to temperature that improve the efficiency, and presumably fitness, of stocks to cope with their environments. However, if fry total weight at emergence is also a good index to fitness at a given temperature, there was no stock difference observed in fry total weight in the 1976-1979 surveys. Another unifying principle in this stock comparison is that across all stocks surveyed, 14°C was the upper threshold for normal development and 0.6°C-1.3°C was the lower threshold. However, within these bounds there were significant effects of incubation temperature that can vary the survival or developmental rates to hatching and emergence and the yolk conversion efficiencies.

Beacham (1988) studied the genetic differences between two stocks of pink and two stocks of chum salmon from Alaska. Chum from the Kshwan and Bella Coola Rivers and pink salmon from the Quinsam and Harrison Rivers provided the comparisons . A total of 25 families, produced from adults sampled from each river, were the basis for calculating mean survival rates. Survival rates of chum eggs were tested at constant temperatures of 3.1, 8.0, and 15.1°C; pink eggs were tested at 4.1, 8.0, and 15.9°C. For chum, only at the low temperature were embryo survival rates different between stocks (70.1 and 93.9%, respectively). In pink salmon, alevin survival rates were significantly different at the high temperature (45.7 and 87.8%, respectively) and embryo survival rates were significantly different at the low temperature (38.4 and 47.0%, respectively). In both species there was a significant difference between stocks in the hatching and button-up times at the lowest incubation temperature.

Cutthroat and rainbow trout introduced into Emerald Lake, Colorado in 1888-1890 (Lentsch 1985, Van Velson 1985) (as cited by Behnke 1992) have had 20-25 generations in the lake and have formed a hybridized population. The outlet stream accumulates twice the number of temperature units as the inlet stream during the incubation period of these species (i.e., spawning to emergence). At a 12°C incubation temperature, both inlet and outlet spawners hatched at 330 temperature units. This study implies that there has been no selection for development rate in the two stocks originating from the original planting despite their substantially different incubation environments. Unfortunately, in this study development rates were not tested at the low temperatures experienced in the inlet stream (minimum of 2°C in June, maximum of 6°C during summer) to assess whether the low temperature inlet population performs better at 2°C than the outlet population.

Humpesch (1985) studied inter- and intra-specific variation in hatching success and embryonic development of five salmonid species (brook trout, Salvelinus fontinalis; Arctic char, Salvelinus alpinus; rainbow trout, Salmo gairdneri; brown trout, Salmo trutta; Danube salmon, Hucho hucho; and grayling, Thymallus thymallus). Brown trout were collected from a lake outlet stream, a summer-cool lowland stream, a summer-cool upland stream, and an alpine lake. Grayling stocks were collected from two summer-cool rivers in a mountainous area. Humpesch considered these various habitats for these species to be thermally distinct. The regressions of hatching success on incubation temperature provided regression coefficients *a* and *b*. These were not significantly different among stocks within the species studied.

Variation in egg and embryo response to elevated temperatures was studied in two geographically distant stocks of largemouth bass, Micropterus salmoides salmoides (a northern stock from Minnesota and Wisconsin and a southern stock from Tennessee) (McCormick and Wegner 1981). The median temperature tolerance limits ($TL_{50}$) for 0-3-d-old hatched larvae averaged 32.1°C and 32.6°C for the northern and southern stocks, respectively, for larvae acclimated to 20, 24, 27, and 30°C. There was very little difference in $TL_{50}$ values at all these acclimation temperatures, allowing them to be averaged. When acclimated to 22°C, newly hatched larvae had 24-h $TL_{50}$ values of 31.0°C and 30.6°C for the northern and southern stocks, respectively. Differences between stocks in all but one of the temperature challenges were ≤0.5°C. Despite the great difference in geographic latitude between the stocks compared, they were homogeneous in response to thermal stress within this subspecies.

## Juvenile Survival and Preference

McCauley (1958) indicated that tests of the upper lethal temperatures for two races (not recognized as separate subspecies) of Salvelinus fontinalis failed to reveal any difference in response. The geometric mean resistance at 1000 min exposure occurred at 26°C with 20°C acclimation. However, McCauley reported a difference in response between two subspecies of Salvelinus alpinus (i.e., S. a. willughbii and S. a. alpinus). However, the geometric mean resistance at 1000 min exposure occurred at approximately 24.7°C with S. a. willughbii and at 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.

Elliott (1981) pointed out how genetic differences that are often assumed between different populations of a species are frequently found not to be significant. He reported an example in which brown and rainbow trout living in a stream with daily maximum temperatures of 28.8°C did not have greater thermal tolerances when compared with trout from two hatcheries (Kaya 1978). Brett (1956) reported that what is taken as geographical variation is often nothing more that variability owing to experimental method and acclimation temperatures. Konecki et al. (1995a) measured CTM values at streamside of three coho populations in Washington coastal streams that varied in thermal regime and found apparent differences. However, after providing approximately a 3-month acclimation at a constant temperature, the CTM values were not significantly different. Mathur and Silver (1980) showed that the reported statistically different preference temperatures measured by Hall et al. (1978) for three white perch populations (from North Carolina, Maryland, and New Jersey) were actually non-significant when the correct number of degrees of freedom were applied to the statistical analysis. Repeated recording of the temperature selected by an individual fish in a gradient produces a set of highly correlated observations, inflating the degrees of freedom. Also, if many fish are tested in an apparatus at the same time, preferences are affected by behavioral interactions (Mathur and Silver 1980).

Beacham and Withler (1991) studied the survival of ocean-type and stream-type juvenile chinook to 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. Fifteen juveniles from each of the families were tested separately at high temperature rearing conditions. The stream-type population, rearing at 21.5°C, had a total mortality of 79% after 16 d. The ocean-type population, rearing at 22°C, had a total mortality of 74% after 18 d. These populations responded very similarly to high temperature (approximately 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.

Genetic selection for disease resistance has been shown to vary among populations or strains of salmonids. For example, susceptibility to furunculosis and vibriosis infection varies among populations (see citations in Beacham and Evelyn 1992). Survival and mean time to death of fish having these diseases depends upon temperature exposure. A population highly resistant to one disease may not be equally resistant to another disease. Additive genetic variation allows selection for some degree of resistance to diseases.

The UILTs of four widely dispersed rainbow trout populations from four Great Lakes watersheds were determined on fry acclimated to 15°C at a rate of 1°C/d (Bidgood and Berst 1969). Fry were tested at 25, 26, 27, 28, 29, and 30°C. Fry were able to tolerate 25°C for 4 d but the UILT was between 25 and 26°C. This species had been introduced to Lake Superior in 1895 but no differences in UILT were determined among these populations. Either the populations were all using similar environments or a 100-year period is not sufficient for differences in UILT to appear.

CTM was studied in two strains of Lahontan cutthroat trout (Salvelinus clarki henshawi) by Vigg and Koch (1980). These two strains were the Summit Lake strain, which may be descended from the Pyramid Lake strain, and the Marble Bluff strain, taken from the Truckee River mouth. CTM was determined by raising water temperature by 1°C/d, starting from an acclimation temperature of 16°C. After 20°C was reached, temperatures were raised by 1°C every 4 d. In Truckee River water, the Summit Lake and Marble Bluff strains reached the D-temperature (see Becker and Genoway 1979) at 22.6°C and 22.3°C, respectively. Mean survival times were 321 and 381 h, respectively. In Pyramid Lake water, the D-temperatures were 19.9°C and 19.4°C, respectively. Mean survival times were 112.0 and 78.6 h, respectively. The differences observed in the two water sources was attributed to alkalinity, with Pyramid Lake having high alkalinity (1487 mg/l) and the Truckee River low alkalinity (69 mg/l). Although the Summit Lake strain was slightly more resistant to thermal death than the Marble Bluff strain, the absolute differences between strains varied only from 0.1°C to 0.5°C, depending upon water source. The variation due to water source was 2.7°C for the Summit Lake strain and 2.9°C for the Marble Bluff strain.

Coho fry collected from a cool groundwater-fed stream and a heterothermal stream in Washington state were tested for preferred temperatures (Konecki et al. 1993, Konecki et al. 1995b). Mean summer temperatures (and ranges) were 11°C (5°C) and 12.5°C (10°C), respectively. Fry originating from the groundwater-fed stream selected modal temperatures ranging from 6°C-16°C while those from the heterothermal environment selected temperatures in the range 7°C-21°C. Mean preferred temperatures of these two populations were 9.9°C and 11.6°C, respectively. Fry from the heterothermal stream had more variable and slightly higher thermal preferences than did fry from the stable, groundwater fed stream. The fact that fry were reared in the laboratory at 10°C ±1°C from gametes collected from natal streams until testing might infer a genetic difference between streams. However, no difference could be confirmed from CTM tests when acclimatization effects were eliminated (i.e., by lengthy acclimation at identical temperatures). Although it is considered that salmon stocks become locally adapted to their natal stream environments (Beacham and Murray 1989, Taylor 1991), Konecki et al. (1993) could find no evidence of this in their study of coho. It is possible in this study that the variation in mean water temperature among streams was a recent phenomenon attributable to land management practices and insufficient time has elapsed for selection of thermal tolerance to occur.

Konecki et al. (1993) determined the temperature units needed to produce first hatching in six coho populations (based upon 4 to 13 separately measured families per population) from coastal Washington streams. Incubation at 6°C required from 327 to 447 temperature units (TU) to initiate first hatch in the six populations. Salmon embryos are able to adjust development rate as incubation temperature varies. For example, with increasing incubation temperature, if more temperature units are required to initiate first hatch it is possible for the stock to somewhat delay hatching so that the center of the hatching distribution occurs at a time favorable for the stock (Beacham and Murray 1990). Although there appeared to be stream-specific variation in mean temperature units required to produce first hatching at 6°C, the upper boundary of TUs required varied only from 414 to 486.

In a comparison of thermal resistance among 3 stocks of rainbow trout (redband trout, Firehole River rainbow, and Wytheville rainbow) Sonski (1984) found very little difference. He measured UILT values for subyearling trout acclimated at 23°C of 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 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 highly tolerant of elevated water temperatures.

Warmwater fishes tend to have a different range of responses to temperature increases. Data on biological response to temperature increase among four genetic stocks of juvenile largemouth bass (northern largemouth bass, Florida largemouth bass and the two reciprocal $F_1$ hybrids) provide additional illumination regarding the significance of stock variation (Fields et al. 1987). CTM values (determined by using a rate of temperature increase of 12°C/h and acclimation temperatures of 8, 16, 24, and 32°C) for the northern largemouth bass (NLMB) and the Florida largemouth bass (FLMB) were 40.9°C ± 0.4 and 41.8°C ± 0.4 (±SD), respectively, at the maximum acclimation temperature (32°C). When tested at a heating rate of 0.04°C/h, the chronic thermal maxima for these two stocks were 37.3°C ± 0.60 (SD) and 39.2°C ± 0.64, respectively, at the maximum acclimation temperature (32°C). At 32°C acclimation temperature (as well as at 24°C) the CTM and also the chronic thermal maximum were statistically different between the NLMB and FLMB stocks. The differences in thermal response between these two stocks became apparent only at the higher acclimation temperatures. Both $F_1$ hybrids had CTM and chronic thermal maximum values, respectively, that were very similar to those of the FLMB stock. Although the NLMB stock had a significantly lower tolerance to temperature increase, Fields et al. (1987) questioned whether this response was biologically meaningful. They also noted that CTM may not be a reliable indicator of adaptation to sublethal temperatures. Fields et al. (1987) suggested that the chronic thermal maximum, however, may be a relevant indicator of thermal stress. This is determined by slow heating tests (0.04°C/h) for fish acclimated to 32°C (cf. Elliott and Elliott 1995). The degree of sublethal stress, if predicted by the difference between field temperatures and the chronic thermal maximum, should be reflected in growth rates. This should give the FLMB a selective advantage over NLMB in field situations where thermal stress is high.

One of the most extensive evaluations of geographic variation in ILT 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 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. Hart (1952) 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. Any species tends to occupy similar thermal regimes across the extent of its range (Hart 1952). Anthropogenic temperature increases then would be considered to limit the local extent of the distribution within its overall range, thereby making it more patchy.

In tests on ammocoetes of Lampetra planeri Potter and Beamish (1975) found that UILT was identical for two populations of this lamprey species with acclimation at 25°C. However, they did detect a slight seasonal variation in the stocks evaluated. L. planeri collected in the spring had a UILT of 29.2°C while those collected in summer had a UILT of 29.4°C. The seasonal effect was more apparent at lower acclimation temperatures.

## Juvenile Growth

Differentiation within chinook salmon into fall and spring chinook stocks is associated with a broad segregation in geographic range. The ocean type (fall) chinook are predominant in coastal populations and the stream type (spring) chinook are predominant in inland populations. In addition, ocean type chinook are more abundant in chinook coastal populations south of 56°N latitude. This geographic difference in distribution is associated with a difference in temperature regime, with coastal populations experiencing much more moderate thermal regimes. Coincident with inherent thermal regimes in their native habitats, the growth opportunities are markedly different. These differences in growth environments are linked to significant aspects of life history differentiation among these stocks, such as number of years spent in freshwater rearing and adult size (Taylor 1990).

Growth is a good indicator of performance of a species at various temperatures. When fed to satiation, chinook achieved maximum growth rates at 19°C. 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). 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.

Wangila and Dick (1988) studied the growth response of two strains of rainbow trout (Oncorhynchus mykiss) and their hybrid at 7°C 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 was divided into four groups of 75 individuals each, two of which were tested at 7°C and the other two at 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 to 4.5 g) and October 15 (ending weights 10.5 to 13.9g). Growth was modeled with the equation $\log_e G = a + b \log_e W$. Pooling growth rates of all families for the two strains and hybrid, the *a* (intercept) and *b* (slope) coefficients for the regression are shown in **Table 17**.

**Table 17.** Regression coefficients for the equation $\log_e G = a + b \log_e W$, where $G$ is specific growth rate (g/d), $W$ is body weight (g), a is the intercept and $b$ is the regression slope. Values reported are the combined growth rates of 4 families of the LAS strain, 3 families of the TAG strain, and 4 families of the hybrid of rainbow trout. Data taken from Wangila and Dick (1988).

| | Growth at 7°C | | | Growth at 15°C | | |
|---|---|---|---|---|---|---|
| Strain | $a$±SE | $b$±SE | $r^2$ | $a$±SE | $b$±SE | $r^2$ |
| LAS | 0.89±0.16 | -0.44±0.01 | 40 | 1.83±0.05 | -0.38±0.02 | 91 |
| TAG | 0.53±0.38 | -0.23±0.20 | 9 | 1.72±0.12 | -0.33±0.05 | 71 |
| LAS x TAG | 0.42±0.21 | -0.15±0.11 | 5 | 1.65±0.07 | -0.31±0.03 | 79 |
| All | 0.65±0.12 | -0.29±0.07 | 19 | 1.74±0.04 | -0.34±0.02 | 81 |

Slopes for the regression of specific growth rate on mean weight were significantly different among the two strains and hybrid at 7°C but not at 15°C. The high degree of heterogeneity of slopes at 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.

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 10°C and 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 to the "N" strain derived from wild stock from a river in Ontario.

McCormick and Wegner (1981) studied the growth rates of two stocks of largemouth bass that were widely separated geographically. They found that the maximum rate of net biomass gain occurred at 32°C in both the northern and southern populations. This temperature was considered to be the optimum. However, the temperature producing zero net growth was 34.8°C and 35.3°C for these two stocks, respectively. Using the formula MWAT = T(Op) + [UILT-T(Op)]⁄3, one would calculate a maximum weekly average temperature of 33.5°C for both stocks. Mortality became significant in these two stocks at 35°C and 36°C, respectively. From this analysis, it was clear that these two stocks did not differ significantly in thermal response despite the great differences in latitude. Also, there was very little temperature difference (3°C-4°C) between that producing optimum growth conditions and that resulting in zero net growth or rapidly escalating mortality. For this reason it appears to be risky to depend upon MWAT calculations to safeguard largemouth bass stocks. Horning and Pearson (1973) measured growth rate for smallmouth bass from a Missouri stock. Highest instantaneous growth rate (%/d) was achieved at 26°C (i.e., 1.23%/d) under satiation feeding, but growth rate declined rapidly from 29°C (1.02%/d) to 35°C (-0.08%/d). These authors considered 29°C as the maximum safe limit for smallmouth bass. Similar concerns about application of MWAT in bass need to be applied to salmonids.

## FAMILY GROUP VARIATION WITHIN STOCKS

### Egg/Alevin Survival and Development

Beacham and Murray (1989) studied survival and development rates of interior-spawning stocks (ISS) relative to coastal-spawning stocks (CSS) of sockeye and chinook in British Columbia. Ten full-sib families were produced per sockeye stock from crossing single males and single females within one sockeye ISS stock and one sockeye CSS stock, and five full-sib families per stock from one chinook ISS stock, and two CSS stocks. Of the 10 families in the CSS sockeye stock, embryo survival rates at 2°C were <40% for 7 of the 10 families but were <40% for only 1 of 10 families in the ISS stock. However, at temperatures above 2°C there were no significant differences in embryo survival rates. At 15°C all 10 families of the sockeye CSS stock had alevin survival rates >90%, but only 5 of 10 families of the ISS stock had alevin survival rates >90%. Beacham and Murray (1989) cited this result as evidence of adaptation to thermal conditions experienced by the stocks in their natal habitats.

In chinook studied by Beacham and Murray (1989), embryo survival rates were significantly different among ISS and CSS stocks (i.e., the ISS stock had higher survival than CSS stocks) only at 4°C and alevin survival rates were significantly different among stocks only at 15°C (one of the two CSS stocks was significantly lower than the other CSS and the ISS stock). However, significant differences among families within stocks were found at 2, 4, and 15°C. At 4°C, 4 of 5 families of one CSS stock had embryo survival rates <60%, but 7 of 8 families of an ISS stock had survival rates >97%. Again, this appears to provide evidence of adaptation to colder water conditions in the ISS stock.

Danzmann and Ferguson (1988a, 1988b) randomly crossed gametes of ≥50 males and 50 females of the Arlee strain of rainbow trout of Montana and examined survival from hatching to yolk sac resorption of embryos at 5, 8, and 12°C. Fish in the middle of the hatching at all temperatures studied had a higher average heterozygosity (based on allozymic variation in 8 alleles) and greater survival rate, and therefore greater fitness than less heterozygous individuals (those tending to hatch in the tails of the hatching distribution). Heterozygous embryos also developed more rapidly to hatching and produced larger juveniles. Although not dealing with variation among family groups, this study reveals the survival advantages attributable to allozymic variation within a stock.

Konecki et al. (1993) determined the temperature units needed to produce first hatching in six coho populations (based upon 4 to 13 separately measured families per population) from coastal Washington streams. Based upon the three stocks in which 10-13 families per stock were measured for temperature units (TU) to first hatch with incubation at 6°C, the standard deviation was 5.2%-7.7% of the mean.

In one of the most extensive surveys available on effect of incubation temperature on early development of Pacific salmon, Murray et al. (1990) surveyed 13 coho stocks from British Columbia, allowing geographic comparisons of island vs. mainland stocks and northern vs. southern stocks. Murray et al. (1990) collected gametes from these 13 stocks and produced 5 full-sib families per stock (in most stocks) from matings of single male-female pairs and tested survival to 50% hatching and survival to emergence at 2, 5, 8, 11, and 14°C. In addition, they measured development times to 50% emergence and alevin and fry length and weights at the various constant incubation temperatures. The greatest differences among families in embryo survival rates to 50% hatching occurred at the extreme temperatures within the temperature range studied. For example, in the 1976-1979 surveys, embryo survival rates at 11°C ranged from 73%-95% for three families of the Elk Creek stock (a mainland stock). At 1.5°C five families of the Robertson Creek stock (an island stock) had embryo survival rates of 16%-94%. It is interesting that even within a stock, families had considerable variation in their survival at a given incubation temperature. Differences in alevin survival rates, as with embryo survival rates, were most significant among families within stocks at extreme temperatures for the temperature range studied. For example, the Robertson Creek stock had alevin survival rates varying from 50%-97% among families at 1.5°C. The Chehalis stock (a mainland stock) had families exhibiting survival rates from 70%-95% at 12°C. Inter-family variation within any stock in either embryo or alevin survival rates was typically of a magnitude difference of only 2%-10% survival at temperatures of 4°C and 8°C.

In terms of coho alevin length and weight, there was significant variation among families within stocks (Murray et al. 1990). However, this variation appeared to be attributable to egg size within stocks. Also, for coho fry standard length and total weight, there were significant differences among families within stocks in the 1976-1979 surveys.

### Juvenile Survival and Preference

Beacham and Withler (1991) studied the survival of southern ocean-type and northern stream-type juvenile chinook at high water temperatures. 20 separate families of the ocean-type (hatchery) and 32 families of the stream-type chinook (wild) were produced from gamete collections and matings of 1 male with each of 2 females. 10-15 juveniles from each of the 20 ocean-type (Robertson Creek) families were placed into each of 2 test tanks; 15 juveniles from each of the 32 stream type (Bear River) families were placed into each of 5 test tanks for experimentation. Fish were individually marked to identify their family of origin. At 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 22.0°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.

Variation within family groups was demonstrated for one population each of three species, chinook, coho, and chum salmon (Beacham and Evelyn 1992). Heritibility of mortality rate and time to death given exposure to vibriosis, furunculosis, and BKD was studied in these three populations. Heritibility rates varied among species. Among family groups within a population there was a positive correlation in these heritibility factors for resistance to Vibrio and Aeromonas salmonicida.

### Juvenile Growth

Growth rates of individual families were measured by Wangila and Dick (1979) for two strains of rainbow trout and one hybrid produced from these strains. Regressions were derived for specific growth rate on mean weight. Specific growth rates generally declined as fish weight increased. Heterogeneity in slopes of the regression for families within stocks were apparent by plotting $\log_e G$ against $\log_e W$. At 7°C there was a large amount of heterogeneity among slopes for families within each stock. At 15°C the level of heterogeneity was substantially reduced among families within stocks. It appears that most families had similar growth rates when reared at temperatures near their growth optimum but growth rates were far more variable among families within stocks when reared at suboptimal temperatures. Although the growth rate determinations made by Wangila and Dick (1979) within families of two strains and hybrid of rainbow trout were computed upon adequate numbers of individuals per family, it appears that the small number of families tested for each of the three stocks made it difficult to generalize about the mean growth rates of the entire population for any stock. This study points out the importance of evaluating the temperature response of a population comprised of many families. In addition, it reveals that when comparing growth rates among stocks or when the growth rates pertain to test groups of different sizes, it may not be appropriate to apply a standard regression of $\log_e G$ against $\log_e W$. This would be especially dangerous when applied at growth temperatures in the suboptimal zone.

Variation exists among families in temperature units required to produce first hatching at a constant incubation temperature (Konecki et al. 1993). However, information on the TUs required to produce median hatch for a family is probably far more ecologically meaningful. Assuming that significant variation occurs in median hatch dates among families, there would be an associated variation in time of first feeding. Early emergence and first feeding can lead to a longer growth period, larger size at a particular date and social dominance that can further enhance ability to preferentially feed and grow rapidly (Metcalfe and Thorpe 1992). Greater ability to grow during the summer rearing period also stimulates growth during the winter period. Even a 1 week delay in first feeding can mean that emigration requires an additional year of freshwater rearing compared to early-feeding fry. The benefits to early emergence are dependent upon food being available at an early date and hydrologic conditions being favorable. Early emergence in coho can result in larger size entering the winter rearing period, which typically allows greater overwinter survival. It can also result in early emigration (i.e., if fewer growing seasons are required prior to smoltification) and elimination of an overwinter rearing period in freshwater. However, too early an entry to the marine environment may result in adequate food resources not being available (Holtby 1988, Holtby and Scrivener 1989). Variation among and within families in median emergence time may cause fitness to vary annually in relation to environmental conditions. Variation among stocks in median emergence time, if significant, must be considered in any supplementation program in which a stock from one stream must be transplanted to another stream. Such a program might be required if an indigenous stock has been extirpated or so weak that natural rebuilding before extirpation is not likely.

## CONCLUSION FROM SURVEY OF GENETIC VARIATION

Based upon thermal tolerance literature there appears to be little justification for assuming large genetic adaptation on a regional basis to temperature regimes. For example, prior to adoption of the revised water temperature standards for Oregon streams in 1996, there were separate water temperature standards assigned to salmon habitat in the western vs. the eastern portions of the state. Salmon-bearing streams in the western Cascades and Coast Range were assigned a standard of 14.4°C but salmon-bearing streams in northeastern Oregon had a standard of 20.0°C, largely on the assumption that they would be adapted to the warmer air temperature regimes of the region. The large (5.6°C) difference in adaptation that would be required, however, is not supportable by any known literature. Rather than the salmon in northeastern Oregon being adapted to maximum temperatures found in the lower limits of major subbasins to the Columbia River, they are confined to those streamzones providing the cold water they need, primarily headwater areas. Unfortunately, the progressive headward shift in the lower limit to the coldwater zone that has accompanied watershed development has allowed displacement of salmon from many of their former habitats by encroachment of warmwater zones (and warmwater fish) into the headwater areas. The zones in which major salmon production capacity was lost tended to be the wide, low gradient areas typical of streams at these positions in the longitudinal channel profiles where low gradients and natural channel widening occur. Starting from a pristine condition, increments of temperature result, in this general case, in greatest losses in useful spawning and rearing area in the initial stages of anthropogenic temperature increase. Because salmon are coldwater fish with limited intra-specific variability in thermal tolerance, chinook are highly dependent on preservation of all remaining coldwater sources. Restoration of salmon production in these areas cannot proceed without restoration of riparian cover, channel morphology, and overall watershed condition (factors contributing to sediment and water yield and storage) on a systemic basis.

# BIOENERGETIC CONSIDERATIONS
# SCOPE FOR ACTIVITY

The scope for activity is a region bounded by two curves--one showing the relationship of active metabolic rate (AMR) (also known as the aerobic metabolic rate) as a function of temperature and the other, standard metabolic rate (SMR) as a function of temperature. The greatest distance between the two curves defines the maximum scope (MS) for activity and occurs at a temperature (TMS) that is predicted to be the preferred temperature (Warren 1971, Kelsch and Neill 1990). Swimming performance can increase substantially when metabolism involves a combination of aerobic and anaerobic processes. However, under such conditions, subtraction of the SMR from oxygen consumption during swimming does not accurately represent the oxygen demand of the swimming activity itself (Beamish 1978). Preferred temperature is a function of acclimation history; therefore, available scope is also a function of acclimation history. The scope for activity (MS) at any exposure temperature can change in value as acclimation temperature changes because of shifts in the values of AMR and SMR that occur as a function of temperature (Kelsch and Neill 1990, Evans 1990). That is, for a species that partially compensates its metabolism across a temperature range (i.e., a fish acclimated at one temperature that is able to become more efficient with time spent at a higher temperature), maximum metabolic scope is defined by the greatest value for the difference AMR-SMR at a combination of acclimation and exposure temperatures. If the partially compensating fish is then acclimated at a higher temperature, the curves for AMR and SMR, plotted against temperature, shift to the right so that the new maximum metabolic scope is found at a higher temperature. The temperature producing maximum scope plus the preferred temperature shift with acclimation temperature.

The standard metabolic rate is calculated in terms of oxygen consumption extrapolated to zero activity. This would indicate 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). Active metabolic rate 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, as opposed to energy budgeting, which is relevant to entire life stages, 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 its SMR and SDA needs has little ability to deal with additional power demands caused by disease, the need to apply burst swimming to escape predators or swim against currents, etc. The seriousness of this situation is reflected in the danger of feeding fish in aquaculture in high temperature ranges, despite the fact that more energy is required at these temperatures. With the heightened power demand for SDA at high temperatures, any unnecessary stress can lead to metabolic power overload and mortality (Priede 1985).

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. This range of activity is totally aerobic, so no oxygen debt builds up. Some tests of sustained performance have documented swimming for periods of 2 weeks without fatigue for a variety of species. Prolonged swimming speeds define a performance of shorter duration (20 sec-200 min) that involves both aerobic and anaerobic metabolism. Exhaustion of glycogen stores can result in fatigue. Within the range of swimming speeds that define prolonged swimming at a particular temperature, anaerobic metabolism is responsible for an increasing fraction of the energy output with increasing swimming speed. Critical swimming speed is a special case of prolonged swimming. It is measured on fish swimming at a particular temperature (either a temperature to which they are fully acclimated or as an acute critical swimming performance for which a fish is acclimated and then exposed to a test temperature) by increasing swimming velocity in increments of 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 the period when the test speed is 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 of fish 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 mode of performance 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.

Data from Bainbridge (1960, 1962) for rainbow trout and Brett (1964) on sockeye, as summarized in a single figure by Beamish (1978), illustrate the sharp differentiation between 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 in the time period. The point where swimming can occur without fatigue 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 in metabolic processes (Beamish 1978). The transition from prolonged to burst swimming (i.e., at the critical swimming speed) occurs at approximately 3 and 5 body lengths/s in rainbow and sockeye, respectively. At these swimming 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 performance time period producing this metabolic transition.

A plot of prolonged swimming performances for a variety of species relative to temperature, as summarized from literature by Beamish (1978), indicates that sockeye swim at maximum speed at 15°C, while coho and lake trout reach maximum prolonged swimming speeds at approximately 17-18°C. This prolonged swimming speed can be reduced as oxygen concentration decreases below a critical threshold of approximately 9 mg/l (Dahlberg et al. 1968). This rapid decline in relative swimming speed was observed in coho reaching final swimming speeds in 10-min trials. Other factors can reduce swimming speeds (sustained, prolonged, or burst) at any temperature. For example, swimming performance of sockeye infected with the cestode, <u>Eubothrium</u> <u>salvelini</u>, is impaired (Smith and Margolis 1970, as cited by Beamish 1978). Infected sockeye reached the point of fatigue 34% faster than control fish. Beamish (1978) was unable to offer evidence of the effects of bacterial or viral infection on swimming performance, but recent evidence on these effects may now be available. Diel changes in swimming speed by a factor of approximately 2-3 have been observed in sockeye in coastal waters (Madison et al. 1972) and chinook in the Columbia River (Johnson 1960); swimming 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. It appears that light intensity or photoperiod provides a behavioral regulation of swimming speed. However, Hatch et al. (1993), using video time-lapse recording, detected significant sockeye movement past Zosel Dam on the Okanogan River between 2000 and 0600 h. In fact, the majority of all passage occurred during nighttime. Such was not the case at Tumwater Dam on the Wenatchee River, where daytime passage was predominant. It appears that sockeye on the Okanogan can take advantage of nighttime passage. Provided that nighttime water temperature is lower than daytime temperature, sockeye might significantly escape thermal stress. High net migration rates (up to 3.4 km/h) were observed in these sockeye populations (Quinn et al. 1997). This high rate of travel could either decrease exposure time to thermal stress or produce dangerous levels of fatigue under warm river conditions.

A swimming advantage was observed for small size sockeye relative to larger size sockeye over the length range 8 to 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 20°C. Swimming performance also depends upon prior acclimation temperature in relation to exposure temperature. The magnitude of this effect can be measured in acute temperature exposure tests of swimming performance. Griffiths and Alderdice (1972) found for juvenile coho that over a temperature range of approximately 2°C to 25°C, a low acclimation temperature of 2°C produced its maximum critical speed (5 lengths/s) at a test temperature of 14°C. As acclimation temperature was increased, the test temperature producing the maximum critical speed increased. At an acclimation temperature of 20°C, a test temperature of 20°C produced a critical speed of 6.0 length/s. Critical swimming speed declined dramatically as test temperature was increased above 20°C. An acclimation and test temperature of 20°C provided the highest critical swimming performance (Griffiths and Alderdice 1972). For juvenile coho salmon a temperature of 20°C appeared to provide maximum metabolic scope and swimming speed, given unlimited food.

Swimming performances have been suggested as a tool 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 to 24 h for complete recovery (Paulik et al. 1957). After 3 h of rest, recovery is only 67% complete. Whether exhaustion is produced by repeated attempts to negotiate falls or fish ladders, escape predators, or struggle against the line of a sport angler, reduction in total energy reserves, periodic temporary decreases in scope for activity, or simply unacceptably long delays in reaching holding or spawning areas due to need for metabolic recovery, the cumulative effect of swimming stress may result in pre-spawning mortality or reduced reproductive success.

The maximum potential aerobic power (i.e., $P_{scope}$) is the power that can be directed to functions such as growth, reproduction, and survival. $P_{scope}$ is computed as the difference between maximum active power output ($P_{max}$, measured as critical aerobic swimming speed power output) and SMR (or $P_s$), both measured at a given temperature (Kelsch and Neill 1990, Kelsch 1996). During maximum sustainable (aerobic) swimming performance (i.e., critical swimming speed (Priede 1985)), a fish directs its power output to $P_s$ (the standard metabolic demand to maintain life processes at zero activity) plus $P_a$, where $P_a$ is power directed to swimming activity. $P_s$ is a fixed quantity at a given temperature, but it increases with temperature. $P_a$ typically increases with temperature to an optimum and then decreases (Beamish 1978). At maximum swimming performance, $P_f$ (or the power required for food digestion, i.e., SDA) goes to zero. The capacity for a fish to swim at maximum rate is governed by maximum ventilatory capacity, which is related to gill area and oxygen transport capacity (Priede 1985).

$P_{scope} = P_{max} - P_s$. $P_{scope}$, in turn, is the sum of $P_a + P_f + P_g + P_p$, where $P_a$ is power directed to swimming activity; $P_f$ is power required for food digestion or specific dynamic action (SDA); $P_g$ is power used to maintain growth and reproduction; and $P_p$ is potential power available to deal with environmental extremes, diseases, predator avoidance (Kelsch 1996). If maximum swimming rate occurs, all power available in $P_{scope}$ can be directed to swimming (Priede 1985). If this occurs, no excess power is available for SDA, growth, reproduction, or coping with environmental stresses. Normally, fish operate at low to moderate swimming speeds and so, do not use the full capacity for swimming power output. Power budgeting for an organism takes place on a time basis of approximately one minute (Priede 1985). Power budgeting is the regulation of power expenditures at this time scale so that the organism can operate within its scope. When organisms operate under environmental conditions that demand energy expenditure in excess of $P_{max}$ due to burst swimming or operate in de-oxygenated water, causing brief lowering of $P_s$, energy deficits incurred during anaerobic metabolism must be made up during periods of rest. High mortality rates can be produced by these conditions (Priede 1977, as cited by Kelsch 1996; Priede 1985).

Type 2 selection, proposed by Priede (1985), is one that emphasizes power budgeting and favors a large $P_{scope}$. The larger the $P_{scope}$ the greater is the $P_p$; therefore, mortality rate would be smaller because the probability of the organism exceeding $P_{max}$ is lower. The alternative form of selection (type 1) for efficiency in expenditure of energy in swimming involves energy budgeting. By this means any phenotype able to be more efficient in its activity level (e.g., energy savings in swimming) in gaining food over its reproductive lifespan could direct more energy towards reproduction.

Energy consumed as food is partitioned into production (somatic and reproductive), metabolism (standard, routine, active, and specific dynamic action or feeding), and waste (egested feces and excretory products such as urea, ammonia, and mucus). Maximum growth efficiency, the percentage of energy that is consumed that is directed to growth, might be a useful index to fitness (Calow 1985). Fitness is a measure of the rate of increase per individual and is a function of survival (*s*), fecundity (*n*), and time to first breeding and intervals between breeding (Calow 1985). Temperature acts on the population as an indiscriminate stress, one that is not discrete in its action, and can kill a proportion of the population in relation to the degree of stress applied. Resistance to thermal stress is a normally distributed biological response. If 50% of the population is killed, the remainder will also be heavily stressed and could die with little extra applied stress (Brett 1958). One could also assume that temperature influences fitness in a similar indiscriminate manner. Thermal stress applied to salmon can influence fitness in all three forms of expression indicated above. For example, direct heat death influences *s*, but under optimal temperatures, energy invested in activity (e.g., swimming) leads to high *s*. Energy invested in somatic growth affects *t*. Growth is maximized at optimum growth temperatures, but if energy of production is then diverted away from reproduction in resident fish, there is a longer development time and increased risk of mortality (Calow 1985). In salmon, optimum growth rates (due to optimum temperatures and food supply) during the juvenile life phase can lead to emigration after one year in freshwater instead of two. Larger adult females have increased fecundity, leading to improved fitness. Energy of production invested in reproduction (gamete production rather than somatic production) increases *n*, the third component of fitness (Calow 1985).

The temperature that produces the maximum scope has ecological significance for any fish species. Precht (1958) (as cited by Kelsch and Neill 1990) described three types of metabolic compensation for whole-organism metabolism (partial compensation, no compensation, and inverse compensation). For a partially compensating fish acclimated at one temperature and then exposed at a higher temperature, the metabolic state of the fish will shift over time (via acclimation) to improve the metabolic efficiency at the higher temperature. There is a tendency for the maximum scope and the preferred temperature to shift upward in relationship to the new temperature. There is a correspondence between preferred temperature, maximum scope temperature, and maximum swimming speed temperature (Kelsch and Neill 1990, Kelsch 1996). The magnitude of change in scope on either side of the TMS (temperature of maximum scope) provides an indication of the probable sensitivity of a species' distribution relative to temperatures around its preferred temperature (see model of Kelsch and Neill

1990). For example chum salmon have a very narrow temperature preference that also appears to be independent of acclimation temperature (Brett 1952). That is, chum show a lack of temperature compensation during an acclimation period and do not become more efficient with exposure time after a transfer to a new temperature. In salmonids, cold water acclimation usually results in partial compensation of metabolic rates. At warm temperatures compensation is often inverse (Evans 1990).

In addition to the correlation between the maximum scope for activity and preferred temperatures, MS has other ecological importance. Survival of an individual fish is probably maximized by temperatures in the mid-range of the 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).

The time course for thermal compensation in rainbow trout required up to 96 h for upward or downward compensation to the exposure temperature (Evans 1990). By creating a power budget for a salmonid, Evans (1990) was able to demonstrate the advantage that acclimated individuals have over non-acclimated individuals (**Table 18**). Based upon standard metabolic rate data from rainbow trout in his experiments, and active metabolic rate data on coho and sockeye from the literature (note: all three species were considered to have very similar thermal limits, preferenda, and optima), Evans (1990) found that compared to fish acclimated at 20°C and exposed to 10°C temperature, there was a 21% increase in usable power for fish acclimated to 10°C and exposed to 10°C. That is, full acclimation to cold temperatures (≥ 2 wk) yielded 21% more usable power for fish tested at the cold temperature than to fish acclimated at warm temperature and tested acutely at cold temperature. With fish acclimated to the warm temperature (20°C) and exposed to the same temperature, there was a 51% increased power availability over that for fish acclimated at 10°C and exposed acutely to 20°C. That is, when fish were acclimated to 10°C and then exposed to 20°C the maximum power output (i.e., swimming performance) was less than for fish maintained continuously at 20°C. In addition, the resting power (SMR) output in the 10°C to 20°C transfer was greater than for fish maintained continuously at 20°C. The 51% increase in usable power in fish fully acclimated to 20°C relative to those fish forced to adjust to the transition in temperatures was caused by a simultaneous upward shift in the AMR and a downward shift in the SMR. This produced a larger scope.

One could surmise that as long as full acclimation occurs by prolonged exposure to temperatures near the preferred temperature, mortality effects would not be significant. But full acclimation to even higher temperatures would mean a reduced scope for salmonids. At these higher temperatures if food availability is low, more time would need to be spent in active searching to increase encounters with food items. In addition, resting metabolism would be greater. Available scope to cope with additional stresses then becomes reduced due to the overall greater power output.

**Table 18.** Power output (mg $O^2$/h), scope, and usable power under conditions of acclimation and test exposure temperatures for a salmonid. Data taken from Evans (1990).

| | Temperature (°C) | | Power output (mg $O^2$/h) | | | Max. sustained usable power (mW) | % gain in usable power |
|---|---|---|---|---|---|---|---|
| Type of compensation | Acclimation | Test | Max. power output (AMR) | Resting power output (SMR) | Scope (AMR-SMR) | | |
| Cold | 10 | 10 | 38.8 | 6.9 | 31.9 | 121 | |
| | 20 | 10 | 31.6 | 5.1 | 26.5 | 100 | |
| | adjustment | | +7.2 | +1.8 | +5.4 | 21 | 21 |
| Warm | 10 | 20 | 67.3 | 22.5 | 44.8 | 169 | |
| | 20 | 20 | 78.0 | 10.6 | 67.4 | 255 | |
| | adjustment | | +10.6 | -11.9 | +22.6 | 86 | 51 |

Kelsch (1996) tested the hypothesis that organisms, acclimated to a given temperature, select temperatures that maximize available power. Although this study was of bluegills, the principles involved are probably instructive for salmonids (see Fry 1957, Brett 1964, Beamish 1970; all as cited by Kelsch 1996). Critical swimming speed under the combination of prior acclimation temperature followed by exposure temperature is a measure of available power. This reflects the suitability of the environment (thermal regime) for the organism. Aside from power, the suitability of the environment can be indexed by growth, reproduction, and survival. Bluegills acclimated to 13, 25, or 30°C had a median temperature preference for 21.5, 28.1, and 30.4°C, respectively. Maximum swimming speeds were found at temperatures very close to preferred temperatures for each of the acclimation histories. Swimming speeds declined with greater frequency of time spent at temperatures different from preferred temperatures. From the information provided above it appears that for bluegills 30°C is approximately the final temperature preferendum. This may also be the optimal growth temperature if optimal growth occurs at the final preferendum (see Jobling 1981).

Griffiths and Alderdice (1972) found a similar reduction in maximum scope for activity between juvenile coho that were fully acclimated (2-3 wk) to a temperature and those that were transferred to the test temperature from a different acclimation temperature. These tests were conducted at temperatures within the range of thermal tolerance. When coho were acclimated to 5°C and then tested at 17°C, swimming speed was 5.0 lengths/s. Coho that were fully acclimated to 17°C achieved a critical speed of 5.2 lengths/s at a test temperature of 17°C. For coho acclimated to 5°C, they achieved a maximum critical speed of 5.0 lengths/s at 17°C (optimum for the test temperature range of 2°C-23°C), but the fish acclimated to 17°C were able to achieve maximum critical speeds (5.6 lengths/s) when exposed to a temperature of 20°C. The optimum swimming performance observed was 5.8 lengths/s in fish acclimated and tested at 20°C.

The study by Griffiths and Alderdice (1972) highlights the point that temperatures within the zone of thermal tolerance can limit performance in various ways. Within temperature boundaries defined by the tolerance zone, swimming, metabolism, growth, food conversion efficiency, reproductive capacity, embryonic development, and aggregation of fishes (Brett 1970, Alderdice 1972; both as cited by Griffiths and Alderdice 1972) may all have different response fields and may each have an influence on survival and fitness. Griffiths and Alderdice (1972) also showed that coho that were warm acclimated and tested at cold temperatures had a reduced swimming capacity relative to fish that were fully cold acclimated and then tested at the same cold temperature. These results indicate that performance can be limited (and available power reduced) during rapid shifts in temperature. That is, as field temperatures change from day to day, the perpetual difference between temperatures of acclimation and exposure cause variation in scope for activity. These studies do not, by themselves, fully clarify the reduction in scope for activity caused by various rates of temperature increase or decrease from a temperature to which fish are fully acclimated. For example, given field conditions where fish might be considered to be acclimated to an effective temperature (a single constant temperature that would represent the state of metabolic acclimation for an individual held in a fluctuating temperature environment) defined by a limited diel temperature cycle, it is then unknown precisely to what degree scope for activity is reduced when fish are then subjected to an increased amplitude of diel variation with the same mean. Rapidity of change in temperature affects the degree of partial acclimation achievable.

Dwyer and Kramer (1975) studied the active and standard metabolism of cutthroat trout that were allowed to fully acclimate (2 wk) to test temperatures after gradual transition (1°C/d) from the initial rearing temperature (**Table 19**). They found that active metabolism rose from 363 mg $O_2$/kg-h at 5°C to a maximum of 597 mg $O_2$/kg-h at 15°C. It then declined as temperatures increased up to the maximum test temperature of 24°C. Standard metabolism also increased from 47 mg $O_2$/kg-h at 5°C up to 120 mg $O_2$/kg-h at 20°C and then declined slightly. Scope for activity was greatest at 15°C and declined toward either side. At 24°C cutthroat were at a temperature approaching their ULT. The authors considered 15°C to be a temperature providing enhanced resistance to fatigue and higher survival for fish if confronted with reduced oxygen concentrations.

**Table 19.** Active and standard metabolism and scope for activity (mean mg $O_2$/kg-h ± 1SD) in cutthroat trout (90-g fish). Data are taken from Dwyer and Kramer (1975).

| Fish Weight (g) | Metabolic Measure | Test Water Temperature | | | | |
|---|---|---|---|---|---|---|
| | | 5°C | 10°C | 15°C | 20°C | 24°C |
| 71-113 | Active metabolism | 363 ± 16 | 495 ±16 | 597 ± 26 | 559 ± 16 | 401 ± 17 |
| 83-93 | Standard metabolism | 47 ± 5 | 74 ± 5 | 111 ± 11 | 120 ± 6 | 117 ± 5 |
| | Scope for Activity | 316 ±15 | 422 ± 17 | 486 ± 28 | 439 ± 17 | 374 ± 18 |

Similar results were reported by Dickson and Kramer (1971) for rainbow trout. Wild rainbow had standard metabolism that increased from 42 to 120 mg $O_2$/kg-h over a temperature range from 5 to 25°C. Active metabolism increased steadily to 592 mg $O_2$/kg-h at 20°C, but remained fairly constant to 25°C. Scope for activity, then, reached a maximum at 20°C, but declined very little at 25°C. This implies that wild rainbow trout had energy to cope with temperature stress at relatively high temperatures. However, it must be realized that at 25°C rainbow did not feed. Also, active metabolism (swimming) was measured with 1 to 6 days of prior starvation. Scope for activity increased with starvation, meaning that functions demanding energy expenditure (e.g., burst swimming) could be satisfied if needed because little energy was directed to SDA. It appears likely that under field conditions, when a fish must feed to achieve a size needed for overwintering or emigration, the energy directed to SDA must alter the temperature for maximum scope, probably shifting it to a lower level.

For sockeye, Brett (1971) found that swimming capacity, metabolic scope, growth on excess rations, and ingestion were maximized at 15°C. The temperature producing the growth optimum (15°C) also was the final thermal preferendum determined by acute tests (Brett 1952, 1971). A correlation between final temperature preferendum 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 20°C, but growth reached a maximum on excess rations at 17°C-20°C (Griffiths and Alderdice 1972). Maximum food conversion efficiency during early summer occurred at 11°C-14°C but in late summer at 14°C-17°C (Averett 1969). Efficiency of food conversion to growth was much less for temperatures of >17°C and >20°C, respectively, in early and late summer than at optimum temperatures for conversion (Averett 1969). Of course, as stated earlier, if food limitation exists in the field, growth rates would be less than the maximum for coho at 17-20°C. Growth rates in the field that are less than predicted in the laboratory under excess feeding have been observed 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 met with difficulty (Cada et al. 1987). This may result in limited scope for activity required to acquire food. Behavioral inhibition in swimming at higher temperatures and lack of competitive ability in foraging compared with warmwater tolerant fish can place salmonids at a disadvantage in deriving maintenance energy requirements.

Brett (1965) (as cited by Brett 1983) plotted the swimming efficiency of sockeye as the energy cost (kcal/kg/km) vs. swimming speed (km/hr) for 2.3 kg sockeye. Low speeds (<1 km/hr) required too great an overall energy expenditure because of the large maintenance metabolism cost in a prolonged migration period. Intermediate speeds (1.0-2.6 km/hr) were least costly in terms of total energy expenditure. Optimum efficiency was achieved at 1.8 km/hr. Interestingly, the mean current velocity of the Columbia River is 7 km/hr whereas maximum sustainable swimming speed is 5 km/hr. The rate of energy expenditure observed in sockeye was equated to a swimming speed of 4.3 km/hr 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 the Willamette River observed in the mid-run spring chinook (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 temperatures of 13-19°C (Schreck et al. 1994). Further investigation of the effective swimming speeds and energy cost is needed because of uncertainty about the total distances travelled. It is known that adult salmonid migration can involve considerable downstream and upstream exploration for a given net distance travelled upstream (Schreck et al. 1994). If frequent fall-back through dams occurs, the total travel distances and energy expenditure could become great, placing the individuals in considerable bioenergetic stress.

Growth rates of fish depend largely upon food available (quantity and quality of food) and feeding rates, although both of these can depend upon temperature. Quality of food suitable for salmonids can decline at higher temperatures (Li et al. 1994) as well as quantity (Bisson and Davis 1976). At certain temperatures feeding becomes inhibited energetically as fish have little scope available for swimming (Kelsch and Neill 1990) or physiologically as feeding thresholds are exceeded (Brett et al. 1982). As temperatures increase beyond the optimum, growth rate (except for anadromous salmonid adult stage) declines until reaching zero and then becomes negative as demands for standard metabolism draw upon energy reserves in tissues. If food is available in adequate quantity and quality and temperatures are within feeding limits, it is possible that food energy intake could meet requirements to allow maximum growth rate at a given temperature (i.e., feeding to satiation can occur and the food ingested would be of adequate quality to yield maximum assimilation at the temperature). A feeding frequency of 2-3 times/d under aquaculture is generally sufficient to permit maximum growth rate at a temperature (Grayton and Beamish 1977, as cited by Jobling 1993; Elliott 1975a). However, fish vary among species and also within species among seasons in time of feeding. Rainbow trout have peak feeding during daylight hours during summer and at dusk and dawn during spring and autumn (Landless 1976, Jorgensen and Jobling 1989; both as cited by Jobling 1993). This brings into question whether rainbow trout in the field can feed sufficiently during the summer, even if food supplies are adequate, if behaviorally, the combination of photoperiod and excessive daytime water temperatures limit consumption to less than the equivalent of 2-3 full meals/d. That is, the lack of food can definitely limit growth, but even if food quantity is adequate it may still not be useful if feeding cannot occur for behavioral reasons. Ingestion rates reach a maximum at intermediate temperatures within the range of thermal tolerance, but decline dramatically as temperatures approach the upper thermal tolerance limit (Jobling 1993).

## CONCLUSION FROM BIOENERGETIC EVALUATION

Temperature regulation is generally conceived of as maintaining water temperature within lethal limits, at least, and preferably aiming at optimum temperatures for life processes (reproduction, swimming, growth, metabolism, disease resistance, etc), life stages, and life history forms. Not all critical life processes or life stages have the same optimum temperature, so temperature regulation should aim to satisfy the most sensitive of these while ensuring that all others operate within acceptable limits. For example, first feeding by juveniles is a more temperature sensitive period than for subsequent summer rearing. And, juvenile chinook are more resistant to negative effects of high temperatures than are smolts or adults. Consequently, regulating a stream so that it is cold in the thalweg for large juveniles and adults will not preclude slightly warmer stream margins for the YOY, but a warm thalweg does not provide conditions suitable for all life stages. Optimum ranges for any process depend upon acclimation history as well as nutritional status, health, age, size, etc. Most key life processes have optima that are highly correlated, although it appears that temperature optima for swimming speed tend to be slightly higher than for growth. Growth optima and thermal preference tend to be similar. Bioenergetic considerations in protection of fish species involve both short- and long-term effects. In the long term, water temperature needs to be within thermal tolerance, within feeding limits given food availability and, within growth limits, at a minimum level of compliance. Exceeding feeding or growth limits for short periods each day or for a few days might not totally eliminate a species population from a stream reach but it reduces the ability of the individual experiencing these conditions to attain sizes required for smolting of effective reproductive activity. Chronic, long-term (throughout the life cycle) stress of this short reduces productivity. Short-term effects of bioenergetic stress include limitations to scope for activity that constrain sustained swimming performance, or which leave little power available for coping with disease or allowing burst swimming for migration or predator avoidance. Rapid changes in temperature that might alter the degree of acclimation to exposure temperatures can reduce the capability to meet these short-term power demands, as can even brief periods of temperature elevation beyond optimum. These effects from short-term impacts to the power budget can result in periodic increases in predation losses or increase frequency of infection by warmwater diseases. It can also result in periodic exhaustion during recuperation from anaerobic metabolism and inability to hold positions achieved during immigration. Proper management of water temperature in a watershed is typified as a holistic or systemic activity that optimizes population production, population health, and life history diversity by allowing full expression of the natural processes that maximize the extent of the downstream flow of cold water.

# MULTIPLE FACTOR EFFECTS: TEMPERATURE AND ASSOCIATED FACTORS

Mortality from temperature effects as observed in the field or laboratory can be complicated by the influence of other factors. These auxiliary factors can be variable in time. For example, the recent developmental history of a population can influence its response to temperature. If a population was recently exposed to a prolonged series of high temperature days, it may be infected with disease organisms that weaken its resistance to a new temperature exposure. This temperature history can leave the population weakened from energy depletion after a long period of inadequate food intake, high metabolic costs, and negative growth. The integrity of the mucus layer can be lost from migration injuries (impingement on traveling screens at dams, abrasion on rocks, fish nets, predator attacks), increasing vulnerability to disease. Concentration of bacteria released from diseased fish and contagion is increased in fish ladders. Acclimation history in the field may be unknown and lead to apparent variation in response to new exposure temperatures. Because most disease effects are amplified at higher temperatures, incipient lethal temperatures can cause greater percentage mortality on a population that is also subject to secondary effects of temperature, such as disease and bioenergetic stress from previous prolonged exposure. Synergistic effects of high temperature and toxic chemicals on fishes have been reviewed extensively by Cairns and Scheier (1957, 1959, 1962, 1963, 1964) and Cairns et al. 1975a,b (both as cited by Paladino et al. 1980).

Mortality in a population subjected to incipient lethal temperatures can be increased due to presence of other environmental factors not related to temperature. In field situations factors such as oxygen concentration can vary dramatically in space and time and aggravate rearing conditions. Many of these kinds of variables can be adequately controlled in laboratory situations, but in the field these factors can lead to excess mortality.

## CHINOOK

In the Willamette River a combination of average daily minimum dissolved oxygen (DO) of 3.3 mg/l and a water temperature of 22.4°C resulted in cessation of upstream migration of spring chinook past Willamette Falls (Alabaster 1988). In the San Joaquin Delta, data from Hallock et al. (1970) and Alabaster (1989) showed that the average minimum DO at which chinook migrate was about 4.2 and 3.5 mg/l, respectively. Alabaster showed that this threshold daily minimum DO was coupled with a temperature of 21°C. Hallock et al. (1970) concluded that chinook avoided temperatures >18.9°C during migration. The timing of first migration into the San Joaquin delta depends upon temperature and DO minimum requirements being met (Hallock et al. 1970). Although combinations of temperature and DO that result in no adult migration do not indicate that death of the adults ensured, these conditions at least cause stress, probable deterioration in condition, and also impairment of spawning success.

## ASSOCIATED SPECIES

Taking information from various sources, a case can be made for a combined effect of stressors (temperature, disease, and bioenergetic stress) on the mortality of Okanogan sockeye. Pacha (1961) reported that Anacker (1956) sequentially sampled the sockeye run into the Okanogan River, finding that columnaris frequency rose from 6.3% in August at Rock Island to 23.8% and then 38% in 9 and 15 d further along in the migration. At the termination of the run the disease incidence was 55% (Pacha and Ordal 1970). The Okanogan River has water temperatures so high as to seriously threaten the sockeye run and also columnaris strains of high virulence have been isolated in fish at Zosel Dam on the Okanogan River (Pacha 1961). Over 50% of adult sockeye sampled in the Okanogan in 1957 were infected with columnaris (Pacha and Ordal 1970). In this same year Paulik and DeLacy (1958) determined that the ability of adult sockeye to maintain fixed swimming speeds declined from McNary Dam to Rock Island Dam to Tumwater Dam on the Wenatchee River, a neighboring river to the Okanogan, and one that also has temperature problems. Further, in the 1956 the Wenatchee River sockeye exhibited erosion of swimming capability from Tumwater Dam to spawning grounds on the White River, a spawning stream entering Lake Wenatchee. Loss of ability to swim might indicate a natural deterioration in physiological capability of fish that accompanies utilization of fat reserves and change in body condition (Idler and Clemens 1959). However, under thermal stress the lack of energy that can be directed to swimming (reduced scope for activity) is probably coupled with increased rate of infection by columnaris, which would in turn negatively impact swimming performance.

Distribution of grayling in Odell Lake, Montana were able to extend to deep portions of the lake where DO concentrations were as low as 1.6 mg/l because water temperature there was 4-5°C. This combination of DO and temperature did not result in equilibrium loss (Feldmeth and Eriksen (1978), but presumably either lower DO or higher temperature could reduce distribution.

Erman and Leidy (1975) documented that trout fry can exist in isolated pools with temperatures as high as 22.4°C. One of these pools had oxygen concentrations of 3.5 mg/l. They attributed the capability to persist in these pools to presence of dissolved oxygen in groundwater seeping into the pool, mitigating negative thermal effects. Also, these fish swam near the surface to maximize oxygen uptake. Fish confronted with hypoxia are able to change activity level or location in a thermal gradient as a means of adjusting metabolic rate. The final temperature preference under lowered oxygen tensions was significantly lower in rainbow trout than under normal oxygen tension (Schurmann et al. 1991).

In addition to dissolved oxygen, alkalinity, hardness, and pH of water interact with temperature in determining mortality. Median resistance times of rainbow trout to thermal stress were lower in juveniles reared in hard water (229 ppm $CaCO_3$) than in soft water (30 ppm $CaCO_3$) (Craigie 1963). Resistance tests were determined in soft and in saline water. Hardness experienced during juvenile rearing, not egg incubation, was the significant factor in thermal resistance in softwater. Also, 12.5% seawater added to the hardwater medium to create a rearing medium conferred additional thermal resistance to the softwater- and hardwater-reared rainbow when it was also used as the resistance test medium. Resistance in the saline medium was greater in the softwater-reared group at all exposure temperatures.

Although a history of growth in a hardwater medium did not provide the level of resistance to thermal stress enjoyed by softwater-reared fish, resistance of rainbow trout to pH is greater in hard water (Lloyd and Jordan 1964, as cited by Kwain 1975). Incubation of rainbow trout embryos in water at pH <4.5 resulted in 0% survival at test temperatures of 5, 10, and 15°C. Temperature of 15°C produced survival of ≤10% at pH from 3.5 to 4.8, but was 44% even at pH 6.9. Effects of high temperature and low pH were additive in increasing mortality rate. For rainbow trout fingerlings acclimated to 20°C and then transferred to temperatures of 5, 10, 15, and 20°C, median lethal pH values progressively increased from 3.86 to 4.32 over this exposure temperature range. Reducing the acclimation temperature to 10°C lowered the tolerance to acidic conditions (Kwain 1975). Two strains of Lahontan cutthroat trout tested in waters with alkalinity of 1487, 357, and 69 mg/l had upper lethal temperature ranges of 18.6-20.2, 20.2-21.1, and 21.8-23.0°C, respectively (Vigg and Koch 1980). These trout had lowered resistance to temperature as alkalinity increased. Mercury toxicity to rainbow trout fingerlings increased as temperature increased (MacLeod and Pessah 1973, as cited by Paladino et al. 1980)

Presence of certain toxicants can alter the observed response to temperature. For example, equilibrium loss in fingerling rainbow trout in a CTM test (6°C/h rate of increase) occurred at 20°C with prior exposure to 3 mg/l Ni, whereas after exposure to 0.8 mg/l Ni this occurred at 26.6°C (Becker and Wolford 1980). A Ni concentration >1.4 mg/l was required to produce a significant reduction in LE-temperature compared to the control. Also, a nitrite concentration of 1.4 mg/l $NO_2$ was required to cause a decrease in CTM by a magnitude of 2°C in channel catfish (Watenpaugh and Beitinger 1985). Black et al. (1991) confirmed a linear relationship between uptake of a hydrophobic toxicant and oxygen consumption rate caused by a temperature induced change in the gill membrane of rainbow trout. By an acute reduction in temperature from 17°C to 8°C, both oxygen and toxicant uptake were reduced by 50%. Kovacs and Leduc (1982) found that rainbow trout (20 g) had increasingly poorer growth rates and swimming performance under sublethal concentrations of cyanide as temperatures declined within the range 18°C to 6°C. Also, at every temperature studied, mean specific growth rate declined as sublethal cyanide concentrations increased.

Although a great reduction in CTM of rainbow trout occurred after prior exposure to 3 mg/l Ni (Becker and Wolford 1980), even 5 mg/l Ni did not cause a reduction in migratory behavior or seawater survival in coho (Lorz et al. 1978a, as cited by Wedemeyer 1980). However, Ni is a relatively non-toxic heavy metal. Chronic exposure to 20-30 ug/l copper during coho smoltification can inhibit or inactivate the gill ATPase function. Even 5 ug/l copper can suppress gill ATPase and impair smoltification (Wedemeyer 1980). Mortality occurs only after the migrants enter saltwater, at which point the mortality is generally unnoticed (Wedemeyer 1980). If coho are simultaneously subjected to chronic copper exposure and thermal stress during emigration, it is very likely that ATPase activity and saltwater readiness would be even more impaired. Also, desmoltification might occur at even lower temperatures.

Servizi and Martens (1991) determined the 96-h $LC_{50}$ of underyearling coho exposed to suspended Fraser River fine sediment (75 µm median diameter). They found that fish at 7°C had the greatest resistance to suspended sediment concentrations. The 96-h $LC_{50}$ was produced by a suspended sediment concentration of 23 mg/l. When temperature was raised to 18°C, oxygen demand increased 100% whereas oxygen saturation decreased 22%. The temperature increase resulted in tolerance of suspended sediment at 18°C being 33% that at 7°C. Likewise, as temperature was reduced to 1°C, oxygen demand decreased and oxygen saturation increases. However, the authors surmised that the capacity of the fish to clear their gills via cough reflex and ventilation decreased. This may have led to the tolerance at 1°C being only 47% of that at 7°C.

## CONCLUSION FROM SURVEY OF MULTIPLE FACTOR EFFECTS

Maintenance of water quality as typically implemented under the Clean Water Act is most specifically attuned to ensuring that single water quality factors are within tolerance limits at a minimum and preferably are not injurious or provide optimum conditions for life processes. Full protection of the beneficial use can be considered a logical consequence of providing optimum water quality conditions. Many synthetic chemical contaminants (e.g., pesticides, heavy metals), could be considered to have optimal concentrations of zero, whereas other chemical constituents (pH, alkalinity, oxygen) or physical states (e.g., temperature) are needed in specific amounts. Streamwater of the Pacific Northwest with an atypical constituent composition (e.g., low or high pH, low oxygen, high summer suspended sediment, high alkalinity, or combinations of these) can cause upper thermal limits to fish distribution to be altered from the typical condition. Additionally, presence of chemical contaminants (e.g., pesticides, heavy metals) can further reduce thermal tolerance by synergistic action. Laboratory derived temperature criteria tend to be determined under optimal conditions for all other water quality factors. Combined effects of water quality constituents interacting synergistically with peak or prolonged high temperature can result in unpredictable increases in mortality. This calls for application of additional factors of safety in temperature criteria to accommodate likely combinations of factors.

# EFFECTS OF TEMPERATURE ON COMPETITION AND PREDATION WITHIN THE FISH COMMUNITY

Temperature regime is a key determinant of the outcome of competitive interactions in a fish community. Organisms operating within their optimum temperature range have an improved capability of performing relative to other species not within their optimum regime. Reeves et al. (1987) found steelhead to be dominant in steelhead/shiner interactions in laboratory streams when water temperatures ranged from 12.2-15°C but that shiners were dominant when water temperatures were 18.9-22.2°C. In addition to the direct lethal effects of temperature that become prominent above 22.2°C, the increased intensity of warmwater disease effects, and the general preference for temperatures <22°C even in the absence of competition, competitive interactions with warmwater tolerant species reduce the ability of salmonids to maintain feeding stations and grow in streams with temperatures approaching the upper growth threshold. Additionally, those salmonids attempting to inhabit the warmer stream zones have higher probabilities of dying from loading stresses produced by low or negative growth periods.

The competitive advantage of redside shiners at high temperatures in the range of tolerance for rainbow trout can be anticipated based upon UILT as a relative index to physiological adaptation. <u>Oncorhynchus</u> <u>mykiss</u> (<u>kamloops</u> subspecies) fingerlings (formerly <u>Salmo gairdneri</u>) acclimated at 11°C have a UILT of 24.0°C. UUILT for <u>O</u>. <u>mykiss</u> is 26.5°C (Alabaster and Welcomme 1962, as cited by Coutant 1972). UILT for redside shiners acclimated to 14°C is 28°C (Black 1953); the UUILT would be somewhat higher than this. Ability of the trout to successfully compete in the short or long term at the upper end of their tolerance range involves consideration of factors such as swimming performance, ability to defend feeding stations, fecundity (especially of resident fish of low mobility) under a warm thermal regime, ability to consume food even in the absence of competition, sustain maintenance requirements and grow, ability to find coolwater refugia and escape cover, ability to avoid cumulative mortification (Kilgour and McCauley 1986), direct short-term thermal death, and resist disease. Non-thermal factors shaping community structure include flow fluctuations (extreme highs and lows) and channel gradient.

Temperatures are also influential in regulating the outcome of competition among native and exotic trout. Under water temperatures optimal for brook trout (13°C), brook trout were dominant in laboratory interactions with rainbow trout (Cunjak and Green 1986). However, at 19°C, a temperature close to the optimum for rainbow, neither species had an advantage in competitive interactions. It is possible that the lack of dominance by rainbow at 19°C was attributable to the pool-like environment for the test.

Competition among native species is partially regulated by temperature. Upstream shifts in longitudinal temperature zonation presumably cause the displacement of native cutthroat and bull trout by rainbow trout in Methow River tributaries (Mullan et al. 1992). Distribution of fish species can be evaluated in terms of relative physiological adaptation to the thermal regimes occurring longitudinally in a river system. For example, CTM is a useful relative index to thermal adaptation that helps explain why the native cutthroat trout are able to outcompete introduced fish species in headwaters of the Big Hole River, Montana (Feldmeth and Eriksen 1978). However, similar CTMs and critical oxygen minima for grayling and cutthroat would indicate that these two native species should be competing in the outlet stream to Odell Lake, Montana. Differences in requirement for spawning gravel conditions cause niche separation.

The ability of mesothermic species to function well at the upper end of the temperature tolerance range of salmon and trout makes competition and predation in the zone of overlap a significant problem. Upstream extension of the range of mesothermic fishes in mainstem areas is apt to increase predation loss of emigrating smolts. For example, smallmouth bass inhabiting mainstems of many river systems begin feeding in the spring at 8.5°C (Keast 1968, cited in Scott and Crossman 1985). Exotic fishes such as this and channel catfish have been planted in the John Day River by the state fish agency (Claire and Smith 1990), despite its beneficial use designation as a cold water fishery. Smallmouth bass were stocked from 1971 to 1982. Despite efforts to reduce populations of native predators of juvenile salmon in the mainstem Columbia River such as the northern pikeminnow, deliberate stocking of exotic predaceous warmwater fishes still occurs in many locations in the Columbia River confluent with salmon rearing and migration areas. An 8.5°C feeding threshold for smallmouth bass is well below that encountered during spring smolt emigration, even though the fish agency claims that significant predation does not occur. Data from STORET (provided by Oregon DEQ per request) indicate that water temperatures measured between April 10-22 for years 1993-98 at noon (±1 h) ranged from 8-14°C in the mainstem John Day River at Service Creek (Wheeler County) just downstream from Spray, Oregon. Temperatures in this range are well within the range of feeding by smallmouth bass. Smallmouth bass has a sharply increasing population size from 1986 to 1989 and their distribution extends to RK 345 (Dayville, OR) on the mainstem and to RK 48 on the North Fork (Claire and Smith 1990). Data taken by hook and line sampling in 1988 showed a size distribution of bass from 15 to 46 cm length, with a predominance of fish from 15 to 30 cm length (Claire and Smith 1990). The bass population is fully capable of consuming smolts by virtue of size and temperature.

With the presence of predaceous fishes in the mainstem reservoirs and tributaries, some of which (e.g., smallmouth bass) are operating in waters that represent a transition from salmon and trout waters to optimal conditions for warmwater fish, migrating salmonids must have scope for activity available to allow burst swimming to avoid predators. However, when challenged by either a low-to-moderate or a high infection level with Renibacterium salmoninarum, the infective bacterium for BKD, infected chinook subyearlings were twice as likely to be consumed as non-infected ones by either northern pikeminnow or smallmouth bass (Mesa et al. 1998). The authors suggested that infection with the disease reduced the scope for activity, making the chinook more vulnerable to predation. Infection accompanied by even higher temperatures would probably result in higher mortality rates.

Native fish of Deer Creek, California have longitudinal distributions governed by a combination of factors, including thermal regime, gradient, substrate, and riffle/run/pool habitat composition, competition, and predation (Moyle and Baltz 1985). The eight fish species present had broad patterns of overlap in distribution but also centers of dominance in the three major elevational stream zones. With this overlap in habitat use, there was differential use of microhabitats, but the potential competitive interactions were lessened by variation in feeding habits. Apparent habitat segregation observed may be the result of competition that has occurred. For example, riffle sculpins, one of the species in Deer Creek, can exclude dace from riffle habitats at low, but not at high, temperatures (Baltz et al. 1982, as cited by Moyle and Baltz 1985). In Rocky Mountain streams competition and thermal regimes were largely responsible for the fish zonation observed, with brook trout at high elevation, brown trout at middle elevations, and creek chub at low elevations. In laboratory tests, creek chub were competitively dominant over brook trout at 24°C and brown trout at 26°C, but in the field, trout were typically replaced by chub in the range 22-25°C (Taniguchi et al. 1998).

The ability of steelhead in the John Day River tributaries, and other similar streams with heavily reduced riparian cover in warm climates, to tolerate maximum ambient stream water temperatures exceeding 22°C is often due to the availability of cool water temperature refuges. In the John Day River, juvenile steelhead have been observed rigidly confined to portions of pools having inflows of cool groundwater during periods of ambient water temperature extremes (Li et al. 1994). Under less extreme temperature conditions, increases in water temperature above optimum levels for rainbow trout can result in rainbow seeking faster water zones, presumably to increase ability to capture more food (Smith and Li 1983, as cited by Moyle and Baltz 1985). In the same river, adult spring chinook holding in tributaries such as the Middle Fork John Day are similarly confined to isolated cool portions of pools (McIntosh et al. 1995a, Torgerson et al. 1995, Torgerson 1997). Such behavior has been known for many species (King 1937, Mantelman 1960, Gibson 1966, Nielsen et al. 1994). The surface area or volume of these refuge habitats would likely contract with continued reductions in streamflow and increasing water temperatures during the summer season. Contraction of available rearing habitat for species able to feed to satisfy metabolic demands increases competition for food and space. Reduced streamflows, in addition to aggravating the thermal environment (increased ambient temperature and reduced refuge volume) decrease transport and delivery of food organisms in the water column. Increased competition results in increased density-dependent control on fish survival.

A minimal amount of thermal compensation can be achieved by juveniles entering the substrate. During summer months water temperatures flowing though the streambed substrate can be approximately 0.5-1.5°C, and in places as much as 6°C, cooler than water column temperatures (Shepherd et al. 1986). Typically, in freshwater environments the influence of groundwater inflow to a stream reach will cause intragravel temperatures to be cooler in summer and warmer in winter (Shepherd et al. 1986, Iron et al. 1989, White et al. 1987). The daily variation in intragravel temperatures is also attributable to variation in discharge rates, precipitation, and factors controlling groundwater flow (Iron et al. 1989). Intragravel temperature regime can have significant effects on egg development rates to hatching and emergence (Crisp 1990, Shepherd et al. 1986). Fish detecting groundwater upwelling from the substrate are able to benefit by spawning in such locations in cold climates because anchor ice does not form in these zones (Needham and Jones 1959, as cited by Iron et al. 1989). Despite the potential value of more moderate temperature in intragravel environments for eggs or juveniles, the presence of subsurface flows of moderate temperature is spatially variable and cannot be relied upon to uniformly lessen thermal effects. For juveniles constrained to feed in the water column, subsurface retreat is only of temporary benefit. In addition, penetration into the substrate generally needs to be ≥10 cm and this is frequently not feasible given either degree of cobble embeddedness or fish size relative to interstitial space.

Burrowing into the substrate can reduce thermal stress, inter- and intra-specific competition, and predation by warmwater species somewhat from that experienced in ambient water column conditions. However, during the period of escape, active feeding would be minimal. In addition, streams having elevated water temperatures often have elevated fine sediment levels in the substrate that would be apt to restrict availability of subsurface retreat from thermal conditions.

## CONCLUSION FROM SURVEY OF COMPETITION AND PREDATOR/PREY INTERACTIONS UNDER THERMAL STRESS

Fish community composition is a product of many habitat factors, such as temperature regime, substrate composition, riffle/run/pool habitat composition, and gradient. Temperature regime operates directly on community composition through a species' thermal tolerance and preference. General outcomes of competitive or predator/prey interactions in the field in various temperature ranges can be inferred from laboratory tests of tolerance (UILT or CTM) or preference relative to other species. Temperature regime influences the seasonality and intensity of competition and predation--indirect effects that structure the community. Community structure can also be a reflection of antecedent physical events (eg., floods, droughts) and the frequency of such events. It can also reflect competition and predation that occurred during periodic thermal events in the past or ongoing biotic interactions. With so many warmwater tolerant species available to fill niches in stream zones with thermal regimes exceeding those that are optimum for salmonids, habitat area suitable for salmonids readily shrinks.

# ANALYSIS AND DESCRIPTION OF THE TEMPERATURE REGIME

## PROBLEMS

Temperature influences the survival of salmon at all stages of the life cycle. Alterations in the temperature regime from natural background conditions can be assumed to present threats to native fish production or population viability when considered at a systemic watershed scale, or on an individual stream reach basis. Evaluation of the temperature regime may take place for purposes of research or regulation. Objectives in research on temperature in the freshwater environment include (1) improving our understanding of the influence of temperature on performances of life stages for various species, including the ability to model and predict these relationships (2) improving our ability to understand, model, and predict the influence of temperature on a species population as the effects cascade through the entire life cycle, (3) understanding the dynamics of temperature control on the aquatic community, its species composition and diversity on an annual and multi-annual basis, (4) and determining for various stream systems or reaches how landscape features, current conditions, and anthropogenic alterations create spatial and temporal patterns of thermal conditions and thereby the template for understanding species distribution, density, biomass, and production on a watershed basis. Objectives in regulation of temperature include: (1) application of what is known about the biology of the most temperature sensitive species governed by a beneficial use designation to set criteria that fully protect the species, (2) application of what is known about the physics of stream heating to regulate or modify the most likely sources.

The life stages of concern in fish species research or protection include egg (at fertilization and later embryo stages), alevin, juvenile (fry, fingerling, parr), smolt, adult (migrating, pre-spawning, spawning). Coldwater species of greatest concern in the Columbia River basin include the native species chinook (spring, summer, fall), coho, chum, sockeye, steelhead (summer, winter), rainbow trout, redband trout, bull trout, and cutthroat trout. These species inhabit lakes and/or streams. Stream habitats for these species as a whole range from fairly steep headwater streams to large rivers. Each individual species can occupy habitats spanning streams of many sizes. The tendency of these species, whether anadromous or resident, to utilize many different stream reaches (classifiable by stream order, width, gradient, or geomorphic association, such as meadow, wetland, stream mouth), channel units (e.g., riffles, pools, side channels, off-channel pools), or microhabitats (e.g., margins, overhanging banks, interstitial spaces in the substrate) makes it complicated to precisely know the thermal history throughout their life cycle. Water temperature in a stream system generally increases from headwater areas to a river mouth, describing a longitudinal profile that reaches an asymptote at equilibrium with air temperature. Deviations from this idealized trend take place on individual stream reaches given various anthropogenic impacts; also the rapidity of reaching equilibration with air temperature above the canopy is a function of canopy cover, stream width and cumulative anthropogenic impacts along the course of the river. The idealized smoothly increasing temperature trend along a stream course is, however, frequently interrupted by exceptions according to the natural geographic pattern or temporal variation in groundwater or tributary surface water entry or alternations in channel width and depth.

The temperature regimes at any point on a river continuum and along the continuum over time are broadly generalizable (see Vannote et al. 1980), but incorporate spatial and temporal complexity. In a regulatory sense and in a spatial context, it can be assessed whether temperatures increased (or decreased) (1) on any particular stream reach that is part of or contributing to fish habitat, (2) on any individual or group of habitat types important to survival and production of the species (i.e., habitats specially utilized by a life stage), (3) or longitudinally over the course of a stream system so that net essential habitat area is lost. In a temporal context, it can be assessed whether the extremes, frequency, duration, or seasonality of temperature is injurious and altered from previous conditions. The literature on scientific study of physical aspects of water temperature and biological response contains numerous methods for statistically summarizing the thermal environment. A review of these studies should not be made with the purpose of recommending complex spatial or temporal statistics for regulatory needs, but to find assurance that by applying simple indices, biological protection is the result, given all the complexities of the life cycle.

In a practical sense, monitoring of temperature in a stream system for regulatory purposes has simple spatial and temporal aspects, despite the apparent environmental complexity. It should be determined whether conditions that are optimal, or naturally colder, are found in all coldwater species' habitats. If existing summer rearing temperatures are naturally colder, these temperatures should not be increased. If optimal conditions are exceeded, all feasible actions based on natural recovery processes (i.e., removing anthropogenic perturbations) should be employed. In monitoring, maximum water temperature should represent the average for the entire cross-sectional discharge as a basic method. Temperatures in coldwater refugia should not be a focus for regulation because these habitats represent safety valves for species conservation in extreme conditions that are present in the system only given the current state of many other factors, such as LWD loading, sedimentation, and water discharge. A management system based on reliance on refugia would create a highly fragmented habitat system which ensures low productivity. Protection of any individual refuge is a worthy pursuit. Actions that could directly destroy the refuge, such as LWD removal, irrigation withdrawal, or clearcutting adjacent to an off-channel habitat should be rejected but controlling temperature at these point locations does not necessarily translate to control of other cumulative management effects upstream that set the environmental context for the refuge.

An exception to the spatial monitoring approach focused on general alterations to the longitudinal temperature profile resulting in temperature exceedance would be determining whether temperature criteria are exceeded in critical and unique habitat or microhabitat types forming a bottleneck for a substantial portion of the population. For example, in the mainstem Columbia or Snake, if shallow stream margin rearing areas provide critical rearing habitat not found elsewhere in the reservoir and are heated beyond optimum temperatures, solutions need to be found for this distribution of temperature. In tributaries, off-channel rearing areas can have little mixing with the main channel and become excessively warm. Special protection of these areas could be suggested through monitoring of unique areas. However, care must be exercised not to monitor stream temperature at the site of major groundwater entry to a channel and mistake this for average stream conditions. In a temporal context, ensuring that temperatures are adequate during spawning season may be difficult because of the conflict in when spawning should be taking place and when it is actually taking place currently due to existing levels of warming. During the summer rearing period it must be recognized that mortality can occur during brief daily exposures to high temperatures and in multiple exposures to high temperatures over consecutive days. Even though extreme high temperatures are generally relatively brief, mortality can occur given the needed combination of temperature and duration. Air temperatures on the upper extremes of their distribution would tend to produce the highest water temperatures, but anthropogenic perturbations to the stream would tend to exacerbate stream heating at these times. For this reason, regulators should not be blinded to obvious locations on the landscape where excess stream heating occurs by preoccupation with extreme climatic events. With this introduction to spatial and temporal aspects of monitoring and regulating temperature regime, the influence of thermal regimes in salmon habitats by life stage will be examined, followed by a review of some temperature indices that have been used in the literature to describe the thermal environment.

## INFLUENCE OF TEMPERATURE REGIMES DURING THE SALMONID LIFE CYCLE

Consideration of temperature effects on a species has at least two important elements: (1) determination of effects on individual life stages in individual reaches according to changes in temperature regime at those locations, and (2) determination of effects on the entire population for a particular geographic production area, taking into consideration the longitudinal shifts in temperature regime from natural or anthropogenic causes. Analysis of temperature regimes and alterations in temperature regimes should involve assessment of reach-specific effects on life stages as well as an aggregated analysis of all reach effects. Such an analysis might be fairly straightforward at the egg-alevin stage, because the organisms are stationary at this stage. Even at this stage, though, temperature effects can be aggravated by fine sediment and organic material concentrations in egg pockets, oxygen concentrations, and other factors. The ability of the organism to migrate among reaches in a production area during other life stages makes it more difficult to predict exact impacts to a population (e.g., effectiveness of barriers to intrabasin migration may not be known; the ability to locate and pack particular refuge habitats as suitability of reaches or individual habitats declines is also unknown). Spatial distribution of thermal impacts to juveniles in summer rearing habitats may form a key to population production.

Temperature generally increases in a downstream direction and temperature monitoring done in any particular reach can indicate that unacceptable increases in temperature are occurring there (e.g., a TMDL for a basin is being used up rapidly) or a maximum allowable temperature was exceeded. In Oregon the Department of Environmental Quality adopted a standard based upon a 7-d moving average of the daily maxima (ODEQ 1995). The critical adopted was 17.8°C as the 7-d mean of the daily maxima for summer rearing. Idaho has a standard of not exceeding 19°C as a maximum daily mean temperature or a single maximum daily value of 22°C. A maximum water temperature of 22°C is typically that which results in total elimination of salmonids from a stream reach based on this literature review, so this standard merely establishes the upper limit of salmonid distribution as the allowable limit. Oregon's standard of 17.8°C approaches the level at which chinook or sockeye growth rates are substantially reduced. Standards that involve averages can easily be criticized biologically for the peak temperatures that they average away. But on the other side of the coin it is also argued that a particular threshold is unachievable as a restoration target for certain streams. The thesis held in this discussion of measurement and criteria setting is that standards for coldwater biota should reflect biologically optimum conditions, not the upper limits of distribution, and also not incorporate some percentage reduction in productivity. As long as historic temperature profiles for stream systems are not known and are largely incalculable, it is best to follow the prescription of making all feasible efforts to allow riparian cover and channel morphology to recover.

An assumption underlying the Oregon temperature standard is that by controlling summertime water temperatures, temperatures during other critical seasons will, likewise, be controlled. A rationale behind this is that land management practices that lead to increases in water temperature in a reach, such as riparian timber harvest or thinning, also lead to wintertime cooling. Controlling one effect also controls the other. Importantly, the sensitivity in survival rate to a 1°C decrease in wintertime temperature is much greater than to a 1°C increase in summertime temperature when temperatures are at the edges of the optimum winter or summer temperature range. That is, survival can decrease from 100% to 0% with as little as a 2-3°C temperature decrease for incubating eggs during the winter. Temperature increases beyond the optimum during summer rearing result in more gradual declines in survival, growth rate, and density. The greater range in high temperatures in the zone of resistance allows shifts in temperature regime to be more easily detected and halted. A prolonged decrease of as little as 1°C during winter can result in weeks of additional incubation.

Changes in temperature regime can be indexed as changes in maximum, minimum, or mean temperatures calculated on a daily, weekly, or monthly basis. Biological responses to temperature described in the literature often use more complex indices of temperature. For example, diel temperature fluctuation (range), instantaneous shock temperatures (rapid plunges or increases of 10-20°C), cumulative degree days above a low baseline temperature, time of exposure to a particular high temperature after acclimation to a lower temperature, cumulative exposure to lethal temperatures, seasonal temperature pattern, frequency of temperature events exceeding certain bounds, etc., could all be useful in explaining biological responses. Even more complex shifts in thermal regime could occur as a result of management actions, having implications for survival. For example, temperature regimes during spawning season relative to temperature and flow conditions in the following spring emergence period could be biologically significant. Timing of smolt emigration to seasonal windows might lead to genetic differentiation of juvenile life history (Taylor 1990). However, ability to effectively emigrate is also dependent on spawn timing. Both life history functions are under control by seasonal temperature regimes. Timing and/or predictability of these seasonal thermal regimes as influenced by land management actions have the potential to influence selective forces in unforeseen ways. Biological response to temperature or change in temperature from a base temperature can be assessed from scientific studies such as those showing preference in the laboratory, distribution in the field, survival upon transfer from an acclimation to a final temperature, or gradual heating from a base acclimation temperature. However, the tendency of many stream reaches to experience fluctuating temperatures in which the cycle peaks within the resistance zone presents more difficulties in estimating biological effects. For example, when the exposure time during a single day is sufficient to kill only a portion of the population or is estimated to be insufficient to cause mortality, there is a question about cumulative effects from repeated cycles.

An increase in water temperature in cold headwater tributaries may result in site-specific adjustment in the temperature regime for chinook toward optimum temperatures for that species. However, exposure of stream surface area to solar heat loading results in elevation of headwater temperatures and full equilibration with ambient air temperature. Continued downstream increases in water temperature then occur as air temperature increases with descent in elevation and additional solar loading occurs. The net result of systemic shifts in temperature regimes longitudinally in a stream network is that cold water habitat area decreases; the optimum temperature zone is displaced further headward (i.e., shifted to streams that are smaller, have higher channel gradients, and larger bed material, features not conducive to chinook production); and the historic spawning and rearing areas that were most productive have increased water temperature. Longitudinal increases in thermal regime in tributaries of the Columbia River basin can result in diminishment of bull trout and cutthroat trout habitat (i.e., increasing confinement to higher elevation and more disjunct headwater reaches), net elimination of usable rearing area for spring and summer chinook, and increased competition between chinook and warmwater exotic species in lower mainstem areas of tributaries. There is not merely a displacement in a short zone where competition is focused; rather the habitat area conducive to warmwater fish expands and it is this entire area in which salmonids are disfavored by a combination of direct and indirect thermal effects.

As indicated from a review of the literature on distribution of salmonids, salmonid species populations decrease in density toward zero as various measures of temperature increase. Continued headward shifts in occurrence of critical upper threshold temperature conditions result in a coincident headward shift in the zone where population density declines to zero. Coupled with the thermal effects on species distribution are stream gradient effects. Distribution of brook trout is restricted beyond gradients of 15% while cutthroat are limited to gradients of <14 to 27% (Fausch 1989). Maximum density of brook trout is found at gradients of <3%, whereas cutthroat are in highest density at gradients of 6-14%. Brook trout densities decline as gradients increase from 3%. Cutthroat densities decrease as gradients decline from 6% to 3% (downstream limit) and also as gradients increase from 14%. Similar observations were made regarding zonations in juvenile chinook and steelhead according to gradient in the Salmon River, Idaho (Platts 1974).

The stream zone between the historic point where optimum temperatures were available during summer rearing and the downstream zone where spring chinook density, for example, declines to zero (presence/absence transition zone for this species) is a zone in which there is a general decline in growth rate, decreasing competitive ability beyond a threshold that is higher than the optimum growth temperature, and a decreased survival probability related to direct thermal death, disease effects, and predation. Temperature and gradient interact to determine a species' distribution. Distribution is also shaped by interspecific competition, the strength of which varies by stream reach according to the temperature/gradient combination, species pool, and factors such as peak and low flow histories. The tendency for coldwater species to decline in population density headward as stream gradient increases beyond the level producing maximum density is significant. That is, even though water temperature may be highly favorable at higher gradients, salmonids reach a limit beyond which they cannot perform (e.g., swimming and feeding capabilities are limited). For population production to be maximized it is critically important for temperatures to be optimal in stream reaches having gradients that provide bioenergetic efficiency. Reaches providing bioenergetic efficiency would have a combination of temperature and gradients that result in food supplies in excess of metabolic demands so net population growth is optimized. In addition, these same reaches must not have exotic and/or warmwater tolerant competitors that also find these temperature/gradient conditions to be near optimal and limit the downstream penetration of coldwater fish into their zone of resistance. For best population production on a subbasin level, the downstream extent of cold water flow would be the maximum possible given the inherent vegetative, stream channel morphology, and discharge conditions of the stream at all reaches.

Shifts in thermal regimes longitudinally on a stream network scale have the potential to affect segments of the population with certain life history expressions more than others. For example, the early immigrating portion of the run may spawn earlier and the later portion of the run may spawn later. This appears to be frequently the case for chinook (Healey 1991) and coho (Sandercock 1991). However, some early entering coho hold for months before spawning in certain streams (Sandercock 1991). If the early adults proceeded first to the headwaters and the later fish occupied the downstream reaches of historic habitat, thermal alterations could possibly place downstream spawners at greater relative risk. In the Blue Mountains of Oregon, spring chinook spawn earlier in cooler streams than in warmer streams (McIntosh et al. 1995). This may reflect both the effect of water temperature on the timing of suitable spawning temperatures and also the significance of commencing incubation earlier under colder water conditions to accumulate sufficient degree-days. The relationship between time of entry, spawning location in the tributary, and time of spawning need further clarification. Spring chinook must hold in deep pools that are cool enough so that maturing eggs maintain their viability. Adults must have enough energy reserves to bioenergetically survive the holding period and travel to nearby spawning areas. Adults must also wait a sufficient time before spawning until daily maximum temperatures begin declining and are below 16°C. A declining temperature trend from a high of 16°C may permit the spawning act and lead to increased egg survival at deposition with temperature decline to approximately 12°C. The historic spawning areas in downstream reaches would typically be of lower gradient and more susceptible to accumulation of fine sediment loads from cumulative activities in the upstream watershed. Fine sediment in spawning gravel has the capability of aggravating the biologic effects of water temperature extremes. That is, if eggs are deposited in gravels by adults responding to the 16°C threshold, the eggs would be subject to greater respiratory stress in gravels with high levels of fine sediment than in clean gravels because of the poorer oxygen concentrations and poor intragravel flow. Reduced water flow through an egg pocket leads to oxygen deprivation, a condition aggravated by warm incubation temperatures that may barely meet the threshold condition permitting the spawning act. Temperature regimes in downstream reaches during the summer juvenile rearing period that are increased over historic conditions are also accompanied by increased temperatures during the spawning period. Historic spawning areas of downstream reaches may not currently be suitable for a segment of the stock (i.e., for certain life history expression in the gene pool) if the timing of immigration and spawning is no longer matched to the temperature regime. For example, the genetically determined time window for spawning may not coincide with suitable water temperatures or a later date of egg deposition might not allow sufficient accumulation of degree days for timely emergence. Whatever spawning that does take place under unseasonably warm conditions may tend to produce low egg viability in females prior to spawning, low survival of eggs deposited, and delayed developmental effects and mortality in alevins. Increased fine sediment levels typical of the more downstream historic spawning areas act synergistically with temperature to further reduce egg and alevin survival.

At the point of egg fertilization, water temperatures must not also be extremely cold. The early stages of embryo development are very sensitive to cold temperature extremes. Such temperature conditions, though, are uncommon for chinook spawning and egg incubation except under some hatchery conditions or influence of hypolimnetic releases from impoundments. More typically, initial incubation temperatures must not exceed approximately 14°C for survival to be above 0% and preferably temperature maxima should be ≤12°C.

In addition to concerns about exceeding maximum temperatures during the incubation period, and especially during the initial stages of embryo development, the temperature regime during incubation from egg deposition to emergence must provide a degree-day accumulation that will result in emergence at an appropriate time. That is, a constant temperature of 10°C during the entire incubation period might provide a high survival rate to emergence but would result in more rapid development and earlier emergence than under historic conditions for salmon-bearing tributaries. Early emergence would most likely result in subsequent high fry mortality due to high flows in late winter. Research has demonstrated that rate of development, time to hatching and emergence, and alevin and fry size and survival rate are related to temperature experienced during incubation. Degree-days accumulated during incubation are a reasonable index to these parameters but there are somewhat different responses to temperature during various stages of development (e.g., fertilization to eye pigmentation, eye pigmentation to hatching, hatching to emergence). Magnitude and direction of shift in temperature from one period to the next has a bearing on survival, development, and size attained. Development rate and size attained may not have a direct bearing on survival at emergence, but they can influence subsequent survival due to the conferred ability to cope with the environment (e.g., temperatures, flows, food availability), including competing species.

Temperatures during the major phases of incubation are not constant within phases. A desirable general trend in the field for spring chinook (an autumn-spawning species) is for temperature to be approximately 12°C maximum in early incubation, declining to fairly stable low winter temperatures and then gradually increasing to a maximum temperature of approximately 12°C at emergence. Decreases in winter minimum temperatures due to riparian canopy removal could delay development during this season or could result in alevin mortality if temperature declines to <1.7°C. It could be argued that a delayed winter-season development caused by canopy removal would be offset by an increased spring-time development rate leading to emergence because water temperature warming would also be more rapid with reduced canopy conditions. However, the effect of stepped variation in temperature from phase to phase has been demonstrated (see Egg section, p. 19). Higher egg/alevin survival is possible by avoidance of extreme shifts in temperature between phases and also if moderate, natural regimes are allowed. Within incubation phases, diel temperature fluctuations are expected. Some authors have shown that developmental rates predicted based on constant temperature experiments, from mean temperatures of a fluctuating temperature environment are similar to developmental rates exhibited in the field (Elliott 1994). Other authors have demonstrated a more rapid development rate from incubation in fluctuating temperature environments than would be predicted under constant temperature regimes equal to the mean for the fluctuating regime. It has been recommended by these authors that natural incubation temperature regimes be maintained to ensure proper development rate and survival. Although considerable temperature shocks (rapid change in temperature) having extreme temperatures within the bounds of approximately 4°C-16°C have been shown to produce minimal effects on eggs in the short term, long-term effects or effects of repeated shocks may not be minor. A rapid temperature increase to winter-incubating embryos, such as provided by a periodic discharge plume of warm water, is typically followed by a reverse cold shock when the discharge ends. Despite the evidence available on the benign nature of certain magnitudes of shock and final exposure temperatures reached, the precision of the control on egg development and survival shown in all studies of egg development under constant and fluctuating temperature would dictate caution in allowing exaggeration to diel cycles, increases in mean seasonal temperatures, or temperature shocks.

## TEMPERATURE INDICES SUGGESTED FROM THEIR APPLICATION IN THE LITERATURE

In order to predict the effects of water temperature on salmonids in various life stages, it is necessary to know the temperature regime experienced by the organism. Temperatures can be highly variable within a stream reach (Torgerson 1997).

During the summer, coldwater refugia can provide a seasonal survival mechanism for at least a portion of a salmon population and can also offer a respite from high temperature stress for individuals able to migrate through warmwater zones between coldwater refuges (see Berman and Quinn 1991). Bilby (1984) identified four sources of cold water for warmed stream reaches during summertime: lateral and pool bottom inflow from seeps, mouths of cold tributaries, and intragravel flow in the streambed. Tributary mouths providing cold water to a mainstem river create a mixing zone with temperatures intermediate between the mainstem and tributary. Inflow from seeps can provide an effective refuge provided there are channel morphological or structural elements (e.g., pool bed morphology, large woody debris) that can prevent immediate mixing of the cool water with ambient mainstem water. Intragravel flow during summer can provide a small amount of temperature reduction from ambient conditions for organisms able to seek refuge below the streambed surface. If the streambed is unembedded by fine sediment, this is possible for the smaller size classes of fish. Intragravel flow and seeps can also provide localized thermal zones slightly warmer than ambient in winter. Bilby (1984) found that coldwater areas in a fifth order Washington stream constituted only 1.6% of total stream area and 2.9% of the water volume on the study reach. The mean temperature depression provided by pool bottom and lateral seeps was 4.9°C and 4.7°C, respectively. Availability of refuges undoubtedly varies according to land use; that is, streams lacking large woody debris and meanders or whose pools are filled by sediment would provide less thermal diversity and less refuge space. A useful single index of temperature for a reach would be one that reflects the majority of the potential spawning or rearing area for the reach. Focusing temperature monitoring on coldwater refuges is not an adequate means to ensure high productivity of summer rearing habitats or spatial connectivity among those habitats. As pointed out by McIntosh et al. (1995a) and Torgerson et al. (1995), if cool water is found in riffles as well as coldwater refuge pools during the summer rearing season, salmonids utilize a far greater proportion of the reach.

Thermal regimes can be locally higher than ambient (i.e., the well-mixed thalweg of a stream in a fast flowing zone) in stream margins. This zone is frequently occupied by the 0+ age class, partially because of preference for warmer temperatures than older age classes and also as an outcome of competition and predator avoidance. Channel bar development in unstable channels can create lateral areas pool that can become isolated from the main flow. Pool isolation and fish stranding can be accentuated by dam operations, irrigation water withdrawal, or rapid rate of recession that can be produced in watersheds having diminished wetland area or increased drainage density (e.g., from road and culvert development). These effects may cause increased frequency of stranding in which fish are confined to excessively warm conditions or they reduce the capacity of the watershed to sustain summer flows, thereby elevating overall stream temperatures. Although thermal regimes of lateral rearing areas as well as coldwater refuges are important biologically, the control on ambient stream temperature conditions exerted by land management is the clearly defined matrix within which the exceptions (e.g., lateral warm microhabitats, or cooler pool, seep, or intragravel microhabitats) exist. This makes measurement of ambient temperatures the more tractable index to overall thermal health of a reach. The temperature regimes within pool refugia, intragravel zones at depths approximating that of egg pockets, and many lateral pool areas be influenced by either coldwater seeps or by warming are all highly dependent upon ambient stream water temperatures. A useful index to ambient conditions that more effectively integrates areal variation than does a single point estimate in a thalweg is the use of thermal scanning imagery (McIntosh et al. 1995a, Torgerson et al. 1995, Torgerson 1997)

While continuous measurement of ambient stream temperature in one or more thalwegs in one or more reaches (or thermal imagery of a reach) may be the best means to monitor temperature, there are many different approaches used to index the potential biological effects in any single reach. Magnitude of biological effect is known to be related to duration of exposure and exposure temperature. When the exposure temperature varies, one can attempt to predict effects from duration of exposure above a critical threshold or duration within various temperature classes in which mortality for a given duration increases with higher temperature class. Anderson and Miyajima (1975) (as cited by Bartholow 1989) noted that temperature in certain pools were 0.6°C-2.2°C lower than the mainstream. The duration of water temperature >20°C was only 1-2 h in these pools, whereas that in riffles was 12 h in response to air temperature >22°C. McRae and Edwards (1994) evaluated the thermal characteristics of Wisconsin streams in terms of suitable brook trout habitat by categorizing temperature ranges as <11°C (lower range), 11°C-16°C (optimal range), 17°C-23°C (upper range), and ≥24°C (lethal range). The number of hours duration in each of these temperature ranges was used to predict suitability within a reach. Thermal suitability among reaches within a stream system is also a function of the seasonal temperature range. In Deer Creek, California the lower, middle, and upper sections of the river have summer temperature ranges of 19-32, 14-20, and 13-18°C, respectively (Moyle and Baltz 1985). Temperature ranges were undoubtedly highly responsible for determining the distribution patterns and abundance of rainbow trout and brown trout. Rainbow trout had a percentage composition in the fish community of 2, 39, and 86% in the three zones, respectively; brown trout had a percentage composition of 0, 0, and 13% in the three stream zones, respectively. The presence of rainbow trout in the lower zone where temperatures as high as 32°C were found probably indicates that coldwater refuges were present and that exposure time duration must have been favorable enough for limited survival rates. Obviously an index of duration must be considered as well as temperature range for distribution and abundance to be fully explained.

Bartholow (1991) used a similar method to evaluate thermal regimes in brown and rainbow trout habitat. He used 23.3°C as the maximum temperature goal for achieving self-sustaining populations. This temperature was approximately 2°C less than short-term (3-h) exposure temperatures calculated for these species using the method of Brungs and Jones (1977).

Bartholow (1989) suggested use of a temperature recurrence interval as proposed by Moore (1967) to estimate probability of exceeding a fixed temperature threshold. For example, if a correlation can be established between the 7% exceedence air temperature and a critical water temperature maximum (e.g., 20°C), then the probability of water temperature being ≥20°C can be estimated. Alternatively, an analysis of a water temperature data set can also establish the probability distribution of equilibrium water temperatures. A 2-year data set is sufficient to establish this distribution as well as a 10-year data set (Hogan et al. 1973) (as cited by Bartholow 1989). However, as pointed out by Bartholow (1989) air temperature in combination with humidity, wind speed, riparian canopy, and other factors establishes the equilibrium water temperature. This implies that water temperature may be quite variable for any given air temperature. A given day's maximum may also depend upon the maximum for the previous day. In summary, air temperature recurrence intervals might indicate recurrence of water temperature maxima but many factors affect this correlation. Recurrence interval calculations from water temperature data alone indicate something about the degree of exceedence of critical temperatures. Although not the incidence of a number of consecutive days of adverse temperature. Also, even though air and water temperature performances are correlated this is not indicative of the ability of riparian or channel restoration to cause a systemic decrease in water temperature that is still correlated with behavior of air temperature.

Determining the correlation between air temperature and water temperature exceedance conditions may well describe current conditions (i.e., the ability of a stream to be heated, given its present width, riparian canopy, groundwater input rate, etc.) but does not indicate what the temperature should be under restored conditions. Although air and water temperature are correlated, the mean of the water temperature probability distribution is relative to overall upstream riparian condition (as well as natural and land management factors influencing water inflow to the channel) and very strongly controlled by riparian condition immediately upstream (e.g., within 2.5 km, see Barton et al. 1985).

In addition to the correlation of daily surface water temperature to air temperature, there is a strong correspondence between groundwater temperature and mean annual air temperature + 1°C (Collins 1925, as cited by Meisner 1990). The volume and distribution of groundwater input to stream channels strongly influences surface water temperature as well as abundance and reproductive success of fish (Meisner 1990). There is a latitudinal gradient in groundwater temperature in the U.S. from Florida to Maine of 25° to 3°C. The 4.1°C increase in air temperature predicted from climatic warming in the near term is expected to result in a 4.8°C increase in groundwater temperature. This would result in a 30%-42% decrease in summer rearing habitat for coldwater species by upstream migration of thermal barriers. Removal of riparian canopy can result in an increase in weekly maximum water temperature by 1°C-7.7°C (Levno and Rothacher 1969) (as cited by Mattax and Quigley 1989). Canopy removal would increase daily maximum and mean temperatures. A greater rate of cooling at night plus an increased maximum temperature would result in greater diel fluctuation. Increase in groundwater temperature from climatic warming would also result in a long-term increase in minimum temperatures. These combined effects would seriously increase duration of adverse temperatures. Control of groundwater temperatures by air temperature makes it clear that stream temperature management cannot be accomplished by a focus on coldwater refuge management.

Eaton et al. (1995) used the 95th percentile of the weekly mean temperature to estimate the maximum temperature tolerated by a fish species. This method is based upon 1000 observations of a species' distribution in relation to temperature. The upper 5 percentile of the distribution was discarded to eliminate the marginal associations of a species with high water temperature and to provide more biologically conservative results. The 95th percentile temperature was always less than the UILT for a species. This could imply that factors other than temperature, such as competition, also are at work to restrict a species' distribution (see Hokanson (1977). It may also indicate that if mean weekly temperatures less than the UILT limit distribution, distribution may more generally be limited by factors other than instantaneous lethal effects, such as preference, disease, cumulative stress, and medium-term growth response.

The method of Eaton et al. (1995), though based upon a minimum of 1000 observations per species, does not necessarily reflect a geographically unbiased subsample of temperatures tolerated in the field. That is, it is possible that because data points were not derived from a methodical research design, observations could have been made preferentially in the geographic center of species distribution. Nonetheless, the method appears to provide thermal limits to distribution that match UILT data from laboratory experiments and also more intensive field observations on various salmonid species available in the literature.

Hokanson (1977) used the statistical distribution of weekly mean temperatures for a set of streams inhabited by yellow perch to explain the geographic distribution of this species' spawning period. They found that streams at the 95th percentile weekly mean temperature for a 21-wk period had early spawning (mid-March to mid-May). Those streams at the 5th percentile for weekly mean temperature had late spawning (early May to the end of June). The 95th percentile streams represented the upper thermal limits of distribution because the mean weekly temperature for a 21-wk period must be <10°C in order for maturation of oocytes prior to spawning. Yellow perch populations in Canadian lakes that are stunted from lack of food during warm summer conditions do not develop necessary fat reserves that would allow normal maturation during winter (Newsome and LeDuc 1975). Reduction in optimum growth temperature with food limitation, or excessive summer temperatures alone (see Elliott 1975b), may not result in immediate mortality but can reduce population production and reproductive performance.

Implications of temperature regime for population dynamics are well explained for lake populations of yellow perch by Hokanson (1977). Similar kinds of relationships could be expected for other species that are resident and not highly migratory. Also, some of these effects might be applicable to sockeye, a lake-dwelling species during its freshwater rearing stage. Hokanson (1977) noted that the coldwater regime, represented by populations at the 5th percentile of the mean weekly temperature would have a low survival of larvae in summer and poor overwinter survival. Growth rate is low and mostly confined to summer.

Population biomass is high, but resiliency is low (i.e., the stock cannot support fishing). The age of maturity is high and natural mortality is low. For populations at the 95th percentile, recruitment is low because females do not mature and gamete viability of males is low at high temperatures. Juvenile survival is low because of food limitation and effects of predation. The growth season is long, but growth is impaired in summer during peak temperatures. During summer peak temperatures, distribution is limited to coldwater refugia below the thermocline, a lake zone that is least productive. Age of maturity is low, but natural mortality rate for all age groups is high. Population biomass is lowest under extreme high temperatures. Vulnerability to population exploitation would be high because there are few mature age classes. Population biomass and resiliency are high for populations occupying the median thermal envelope.

Hokanson (1977) also reported data from McCormick (1976) that the temperature limits for zero net biomass gain for yellow perch have lower and upper bounds of 6°C and 31°C, respectively. Interestingly, the growth optimum was 28°C. This indicates that there is very little tolerance for temperatures exceeding 28°C for this warmwater species because of the dramatic impacts to the population's net biomass gain. The minimum temperature producing zero net biomass gain would be increased and the maximum temperature decreased if food were limiting. Likewise, for largemouth bass McCormick and Wegner (1981) found that the maximum growth (Op) rate occurred at 32°C but the temperature producing zero net growth (ZNG) was approximately 35°C.

Maximum weekly average temperature has often been assumed to be a temperature level that would be protective. MWAT can be calculated as either [T(Op) + T(ZNG)]/2 or as MWAT = T(Op) + [UILT - T(Op)]/3. For both northern and southern stocks of largemouth bass MWAT averaged 33.5°C when calculated by each method. This method holds that the MWAT should be a temperature some amount higher than the growth optimum. In the first case it is halfway between the optimum growth temperature and the temperature producing zero net growth. This is the preferred method of calculation if the data are available (McCormick and Wegner 1981). By the second method one would increase optimum growth temperature by a value equal to a third of the difference between the UILT and the optimum. MWAT is intended to define an upper boundary to the normal temperature range (Taylor and Barton 1992). As Hokanson et al. (1977) point out, these calculations of MWAT sacrifice some level of production and are not necessarily protective. Also, because they are based upon weekly averages, the weekly maximum or mean weekly maximum could have biologically significant effects even if MWAT does not. Most importantly, recommending a temperature criterion that is between optimum and a level resulting in ZNG or incipient lethality, often small difference in these values, appears to unnecessarily flirt with placing a species at an impairment threshold in the field. The mean ZNG temperature for both stocks combined was 35.1°C, a temperature only 3.1°C higher than the optimum growth temperature. This small difference makes land management aimed at providing MWAT a very sensitive, thereby precarious, control on population viability.

Bartholow (1989) recommended, in addition to determining probability of a single exceedence of a specified threshold temperature, that the cumulative probability of a sequence of events with a specified duration be calculated. It appears obvious that a single exceedence of a maximum temperature threshold of an extreme magnitude would be sufficient to instantaneously eliminate a species in a particular reach, assuming no coldwater refuges were available and upstream migration was not efficient (barriers, distances, and rate of stream water heating are too great to allow escape). However, for less extreme maxima, the cumulative effects of consecutive days of maxima exceeding critical limits may produce negative biological responses, such as cumulative stress leading to death (Elliott 1981), disease, poor reproductive success, or poor growth. All these responses, even those not resulting in immediate death can lead to mortality prior to reproduction or reduced fecundity. These factors result in reduced productivity of a stock and reduced population size. In addition to the seasonal probability of consecutive days of critical maxima, consecutive years with serious cumulative thermal effects over significant portions of a species' range for one or more life stages can lead to dramatic reduction in stock viability.

Lohr et al. (1996) examined the summer distribution of Arctic grayling in a reach of concern in the Big Hole River of Montana in relation to daily temperature indices. This population is a remnant of the riverine populations that historically inhabited the upper Missouri River and tributaries. Lohr et al. measured a UILT of 25.0°C at 20°C acclimation temperature. The mean CTM at the same acclimation temperature was 29.3°C. LaPerriere and Carlson (1973) (as cited by Lohr et al. 1996) measured a UILT of 24.5°C in an Alaskan population of this species. In the Big Hole River study reach, maximum daily temperatures reached or just slightly exceeded the UILT (i.e., 25°C) for no more than 2 d per year and ≤4 h/d in three consecutive years at stations 1-3. However, at station 4 a threat to persistence of the grayling population existed. Here the maximum daily temperature reached a maximum of 27.5°C in one year and 26.5°C in another. In addition, daily maximum temperatures ≥25°C occurred on as many as 11 d and persisted for daily periods of up to 6 h. For the year having a maximum daily temperature of 27.5°C (annual maximum for the year), the highest mean daily temperature was only 20.3°C. It is interesting that critically high temperatures can be sustained for up to 6 h when a daily mean and maximum can be 20.3°C and 27.5°C, respectively. This maximum temperature, between the CTM (of 29.3°C) and the UILT (of 24.5°C), provides very little margin of safety according to Lohr et al. (1996). Unfortunately, these authors did not measure the reduction in biomass that typically accompanies increases in temperature toward the extinction point.

One means of assessing the biological adequacy of employing one temperature statistic vs. another is to model the growth response using each statistic. For example, based upon regression equations for growth rate vs. temperature developed in constant temperature growth experiments, Elliott (1975a) calculated the overall growth rate a 42-d period. Overall brown trout growth rates for 42-d periods were well predicted from mean temperatures for individual three 14-d growth periods. The maximum temperature variation in the 42-d periods as well as within any 14-d period was 4.7°C. Maximum diel variation was probably somewhat less. Edwards et al. (1979) likewise found that for four rivers in England that brown trout annual growth computed on the basis of monthly mean temperature was a maximum of 9% higher than growth estimates based on daily mean temperature applied to the regression model. As Edwards et al. (1979) pointed out the English chalk streams have a relatively low annual variation in monthly mean temperatures. Also, in Elliott's study the temperature range during the 42-d period was not great. It is possible that homothermic conditions may contribute to good correspondence between growth rate estimates based on daily vs. monthly average temperature. When fish inhabit rivers with spatially heterogenous thermal regimes and the degree of migration or movements is unknown, placement of temperature recorders might not provide mean temperatures that correspond to the mean experienced by the fish. In addition, if growth occurs in a temperature range for which growth is not a linear function of temperature, mean temperatures may not yield the same growth increment from a regression equation as would an integration of growth increments from hourly means.

Under unmanaged conditions the amplitude of diel temperature fluctuations varies with stream size or position on a river continuum (Vannote et al. 1980). Diel variation increases from order 1 to approximately 4 or 5 and then decreases with increasing stream order. The degree of riparian canopy control on diel variation is great in low order streams and becomes less as stream width increases. Increases in average maximum temperature in Pacific Northwest streams from canopy removal range from 3 to 10°C generally (Beschta et al. 1987). These anthropogenic effects also alter diel variation. The species compositions of insect and fish communities are attuned to seasonal and longitudinal temperature patterns and are influenced by management related perturbations. Vannote and Sweeney (1980) suggested use of Colwell's (1974) algorithm for analyzing a temperature record for annual and seasonal predictability. Predictability (P) consists of two components, constancy (C, temporal uniformity) and contingency (M, temporal variability in an order sequence).

The use of weekly mean temperatures (as applied in growth rate studies) or maximum 7-d moving mean temperatures calls into question the correlation between a 7-d mean and other related temperature statistics. That is, what is the correlation between the 7-d mean temperature (mean of 7 consecutive daily mean temperatures) and: the 7-d maximum (maximum temperature for a 7-d period); the mean of 7 consecutive daily maximum temperatures (i.e., the Oregon statistic); the cumulative duration of temperatures exceeding thresholds over 2- to 7-d periods. Macan (1958) (as cited by Preall and Ringler 1989) indicated that a mean weekly temperature calculated from a weekly maximum and minimum temperature is typically within about 1°C of that calculated from hourly temperatures for the week. If this relationship holds true under various degrees of riparian treatment, it would mean that max/min thermometers are about as suitable as continuous recording thermometers for assessing mean weekly temperature. However, the correlation between mean weekly and mean maximum or maximum weekly temperature needs to be determined for various stream sizes in good and bad condition before weekly averages can be assumed not to hide serious biological effects. In addition, it would be advised to study temperature-exposure duration relationships at various mean temperatures and max/min combinations for reach types under various degrees of perturbation. It may also not be totally apparent to a land manager whether a weekly mean temperature of 22°C ±2°C is equivalent in biological effects to 22°C

±5°C.

Stoneman and Jones (1996) provided a useful method for assessing the thermal stability of streams that is well correlated with salmonid distribution. They plotted maximum daily water temperature against maximum daily air temperature. Streams classified as coldwater, coolwater, and warmwater according to their fish community composition had very different relationships between water and air temperatures. The coldwater streams studied in southern Ontario increased in water temperature from approximately 13 to 16°C as air temperatures increased from 25 to 34°C. The coolwater streams had water temperatures of 18 and 23°C as air temperature increased from 25 to 34°C, while warmwater streams ranged from 23 to 28°C under this range of air temperatures. Water temperature measured at 1600 h was found to represent the maximum daily temperature within 0.5°C. The temperature of a stream taken at 1600 h in relation to the maximum daily air temperature permits assessment of thermal stability of the stream. Scatter around regressions of water temperature on air temperature for the cold-, cool-, and warmwater streams, respectively, had very little overlap. Variation about the regressions was influenced by factors such maximum air temperature on the preceding day. That is, for a day in which the maximum daily air temperature is less than for its antecedent day, the maximum water temperature tends to be greater than predicted by the regression in all three classes of streams. In addition to the effect of air temperature on water temperature, the diel change in air temperature produced almost no change in diel water temperature fluctuation in coldwater streams but did influence the diel variation in coolwater and warmwater streams. Over a range of diel air temperature fluctuation of 5-20°C, water temperatures fluctuated between about 1 and 2°C on a diel basis in coldwater streams. Over this same range in diel air temperature fluctuation, diel water temperatures fluctuated from approximately 2 to 8°C in coolwater and warmwater streams.

## CASE HISTORY: EVALUATING THE EFFECT THERMAL REGIMES ON CHINOOK PRODUCTION IN THE TUCANNON RIVER

### Background

Perhaps examination of a case history would be useful in considering the various ways in which temperature indices could be used to explain observed biological response.

The Tucannon River originates in the Blue Mountains region on the Umatilla National Forest at 1650 m elevation and enters the Snake River at river kilometer (RK) 101 (150 m elevation) (TSP 1990). The river was divided into five major sections by Washington Department of Fisheries staff (Bugert et al. 1992). These are the Lower (RK 0-17.9), Marengo (RK 18.0-42.1), Hartsock (RK 42.2-54.8), HMA (RK 54.9-75.1), and Wilderness (RK 75.2-85.3). These river sections are, then, 17.9, 24.1, 12.6, 20.2, and 10.1 km long. In recent years these reach boundaries were modified slightly (Bumgarner et al. 1997). The river flows from wilderness headwaters on the Umatilla National Forest, through a Washington Department of Wildlife habitat management area, private rangelands, and agricultural lands in the lower section (TSP 1990). Land use in the Tucannon watershed is 37% cropland, 35% rangeland,

and 27% forest.

The Lower section has high summertime stream temperatures, heavy streambed sedimentation, irrigation diversions, very little riparian vegetation, and unstable banks. The Marengo section has temperature and sediment problems, diminished riparian vegetation, and channelization. Overgrazing is a dominant impact in the Lower and Marengo sections. Channelization, widening, and straightening of the stream channel occurred during the period 1937-1978, but took place predominantly after the major floods of 1964-65. This activity decreased sinuosity by approximately 50% (TSP 1990, p. 7) and reduced pool/riffle ratio. Pataha Creek enters the Tucannon at the head of the Lower section and provides input of high sediment and thermal loads owing to agricultural development right to the channel margin and high road density (3.4% of watershed area) (TSP, p. 11). Small shallow lakes and ponds draining into the Tucannon River contribute to temperature increases (TSP, p. 15).

The Tucannon currently has depressed populations of spring chinook and summer steelhead. Redside shiners are a common species from RK 9.2 to 61.1. This species was shown by Reeves et al. (1987) to present a formidable competition challenge for steelhead when water temperature ranges from 18.9°C-22.2°C Smallmouth bass are present but are not reported beyond the lower stream section (TSP, p. 31).

Historically, the Tucannon River is considered to have produced at least 2400 adults (TSP 1990) but produced only from 54-247 adults per year in years 1994-1996 (Bumgarner et al. 1997). Juvenile chinook production below RK 51.5 has been reduced by a combination of high temperature and sediment levels. The remaining habitat of higher quality exists between RK 51.5 and 111.0 although the gradient in the upper 16 km is too steep for spring chinook juvenile rearing (TSP 1990). Gradients within the lower 10 km of the wilderness zone varied from 1.2-1.6% with a mean wetted width of 7.9 m (Bugert et al. 1991).

Spring chinook adults arrive at the Tucannon weir between late April and late September with the peak in arrival around May 25 (Bumgarner, WDFW, pers. comm.). Spawning occurs between late August and late September, with a peak in the first 2 weeks of September. Typically this peak has been between September 11-15 (Bugert et al. 1991, J. Bumgarner, WDFW, Dayton, WA, pers. comm). Temperature data (daily minimum and maximum) are available for the summer months at 8 sites along the mainstem Tucannon River between RK 21 and 76 for 1991 (Bugert et al. 1991).

### Evaluation of the Thermal Regime and Potential Juvenile Mortality in Two River Sections

Work by DeHart (1975) indicated that predicted time to 100% mortality from accumulated fractions of lethal doses over natural cycles of temperature fluctuation was very similar to observed mortality rates. In order to evaluate the effect of a fluctuating regime on cumulative mortality one would need to estimate the effective acclimation temperature provided by the regime. In laboratory experiments, full acclimation is generally considered to be in effect after approximately one week at the acclimation temperature. Fluctuating regimes in the field would not have the same maximum and minimum on a daily basis so it could be questioned to what extent the current effective acclimation temperature is a product of the current day's temperature extremes vs. that of preceding day's regimes. Assuming that the daily cycles are relatively stable, there is reason to believe that chinook juveniles rearing in fluctuating temperature environments can achieve acclimation equivalent to that at 0.75 x (max.-min.)°C above the daily minimum temperature (demonstrated by Golden and Schreck (1978) for cutthroat trout) although Heath (1963) reported that cutthroat trout (Salmo clarki) appeared to acclimate to the maximum temperature rather than mean for temperatures cycled between 10 and 20°C. Using these concepts of effective acclimation temperature and accumulated lethal doses, one can evaluate fluctuating temperature regimes in the field. The hypothesis to be tested then is that presence/absence or densities of salmonid juveniles reflect accumulated lethal doses over periods of 2, 3, or more days during summer months.

Time to death under combinations of constant acclimation and exposure temperatures can be calculated using coefficients from laboratory studies on chinook. Armour (1990) provided an equation from Coutant (1972) describing the expected survival time for 50% of a population at various exposure levels given acclimation temperature. This equation is of the form log (minutes survival) = $a + b$(exposure temperature, °C). Coefficients for $a$ and $b$ at 20 and 24°C acclimation temperature listed for spring chinook by Armour (1990) are (22.9065, -0.7611) and (18.9940, -0.5992), respectively. Using this equation one can calculate 50% survival of a population acclimated to 20°C when exposed to 24, 25, and 26°C for 727.7, 126.1, and 21.9 h, respectively. When acclimation temperature is 24°C, 50% survival occurs at 684, 172, and 43 h, respectively, at this series of exposure temperatures.

Blahm and McConnell (1970) (as cited by Armour 1990) provided coefficients for $a$ and $b$ from their tests on Columbia River spring chinook acclimated at 20°C for computing time to 10, 50, and 90% mortality. Their $a$ and $b$ coefficients for 50% survival are 21.3981 and -0.7253, very similar to those summarized by Armour (1990). Using coefficients from Blahm and McConnell one can calculate times to 10, 50, and 90% mortality of 24.9, 30.7, and 39.0 h at 25°C. Using these data one might assume that 39.0 h represents very nearly the time required for 100% mortality. Times to 90% mortality at 24, 25, 26, and 27°C are 196.6, 39.0, 7.74, and 1.5 h, respectively **(Fig. 10)**. A similar figure taken from Brett's (1952) data shows the temperatures that will produce 50% mortality (UILT method) for 20 and 24°C acclimation temperatures **(Fig. 11)**. An increase in acclimation temperature from 20 to 24°C results in only about 1.5°C increase in the UILT. Given the variation in these coefficients, it is more biologically conservative to apply those of Blahm and McConnell.

Before application can be made of the formulas for time to death to the temperature regime for a period of warm days, the statistics describing the temperature regime need to be identified. An evaluation of the August 1991 temperature data for the Marengo Bridge site at RK 41 reveals that for the first 9 days of the month daily maximum temperatures ranged from 24.4 to 27.2°C; daily minimum temperatures were 19.4 to 21.7°C; daily means ranged from 22.8 to 24.4°C. The mean daily temperature for all 31 days in August at this site (mean of all daily means) was 22.4°C.

For the period August 1-9 period at Marengo Bridge, one can calculate approximate hours of each day spent at 24-25, 25-26, 26-27, and 27-28°C (**Fig. 12**). By application of the Blahm and McConnell coefficients to the mean temperature for each 1°C increment of temperature, the daily percentages of a lethal dose can be calculated and summed. For days 1-9 the daily percentages of a lethal dose were 10.4, 16.2, 42.1, 45.9, 2.0, 56.1, 24.3, 81.5, and 56.1%, respectively. Temperatures fluctuated between approximately 20 and 28°C on these days. One might assume that effective acclimation temperatures of 24°C (or less) would be reasonable to use in calculations. Higher temperatures would not be possible because they are beyond the UUILT. Using the cumulative lethal thermal dose effect studied by DeHart in juvenile coho, blackside dace, and sculpin, one would expect 100% mortality of the Marengo chinook populations in combinations of 2 or 3 days of temperature cycles.

Using the less stringent coefficients provided in Armour one calculates for August 1-9 with a 20°C acclimation time daily percentages of lethal dose of 3.1, 5.2, 14.3, 15.6, 0.5, 19.1, 7.8, 28.1, and 19.1%. For the 9-day period total % lethal dose is 112.8%. It is uncertain whether the Armour equations are too liberal, what the effective acclimation temperature would be in an irregularly fluctuating temperature regime, and whether the response shown by DeHart, when applied to cumulative portions of a lethal dose extends beyond 2- to 3-d periods to as much as 9 d. During the August 1-9 period daily minima varied little. Effective acclimation temperatures were then about 24°C using the Golden and Schreck equivalent acclimation temperature for fluctuating temperature regimes. Again, using Armour's liberal coefficients for 24° acclimation, one calculates a 66.4% lethal dose would be accumulated over the 9-d period.

### Distribution of Spawning and Rearing Along the Mainstem in Relation to Temperature

Because chinook spawning and surveys of parr densities (0+) occurred during the late summer-early fall period in 1991, these data might be useful in inferring suitability of temperatures for rearing chinook. Parr surveys were made from July 31-August 29, July 31-September 24, August 7- September 26, and October 9- October 17 in the Wilderness, HMA, Hartsock, and Marengo stream sections, respectively. Because the observations in Marengo were made so much later than in other sections, Bugert et al. (1992) did not use these data to calculate parr production for this section in 1991. In 1990, however, Marengo was sampled from July 12 to August 23, a period during which summer rearing densities would be reflected, and no chinook parr at all were found by snorkeling. Snorkel surveys were typically done with at least 2 replicates for each major habitat type: riffle, run, and pool. The total number of index sites surveyed in the Wilderness, HMA, Hartsock, and Marengo sections were 9, 25, 9, and 6, respectively (Bugert et al. 1991) . Even though there were fewer index sites (6) surveyed at Marengo than in the other sections, they did represent replicates of all three major habitat types. Also, the number of snorkel sites per section might not be at all adequate for expansion to a total count for each section, but the number of sites surveyed in Marengo was not substantially less than at Wilderness and Hartsock. Water clarity declines greatly in the Marengo section, making it more difficult to see fish that might be present (Bumgarner, pers. comm.). However, under probably similar circumstances in

October 1991 chinook rearing densities of 10/100 $m^2$ were observed in a pool based on survey of only three index sites. It seems, then, that in terms of presence/absence the data on juveniles from Marengo could be indicative.

Total redd counts were determined for each section in 1991. There were 3, 67, 18, and 2 in the Wilderness, HMA, Hartsock, and Marengo sections, respectively. In 1991 the numbers of 0+ chinook were 1861, 40467, 21024, and 0 for these four sections, respectively (Marengo value assumed based on 1990 data). The mean density of juvenile chinook was 44 per 100 $m^2$ in pool habitats in the HMA section, which was approximately twice as great as for pool habitat in both the Wilderness and Hartsock sections. Population densities in run habitats in the Wilderness section were extremely low relative to those in the other two sections, presumably because of generally higher stream gradients. Total numbers of redds counted in 1990 were 20, 93, 60, and 2 in these same sections. In both years the redd count in the 8 km long Marengo section was very small. Redd counts in the Wilderness section, on the contrary, were approximately 7 times greater than in 1991. In 1985 and 1986, 83 and 53 redds, respectively, were counted in the Wilderness, while 0 redds were found in the Marengo section in 1986. Peak days of spawning tend to occur sequentially from Wilderness (first week of September), to HMA (mid-September), to Hartsock (third week of September), to Marengo (late September to early October) (Bumgarner, WDFW, pers. comm., Bugert et al. 1991). The value of these data is to indicate several important conclusions. Adult spawning appears to be timed to coincide with a decline in water temperatures below a critical threshold. Over a period of several years, representing various annual climatic patterns, there has been extremely low use of the Marengo section for spawning despite the historic tendency to delay spawning until temperatures declined. This might be attributable to poor substrate conditions for spawning, distance from suitable holding areas upstream, inability to delay spawning sufficiently long to make use of the Marengo section, or past high mortality of eggs and fry from this section due to high levels of fine sediment or high summer rearing temperatures. The parr counted in the 1991 snorkel surveys originated from the 1990 brood year. The HMA section had both the highest summer parr densities in 1991 and also the greatest number of redds in 1990. Although juveniles rear in the Marengo section in October, based on 1991 snorkel surveys (Bugert et al. 1992), it appears that they probably do not originate to any degree from redd deposition in that section, but from downstream migration.

During the August 1-10, 1991 period at the Deer Lake site (RK 62) on the mainstem Tucannon River, maximum daily temperatures ranged from 23.9°C to 24.4°C and mean daily temperatures ranged from 19.7°C to 21.4°C. Maximum daily temperatures exceeding 24°C were experienced for 6 consecutive days **(Fig. 13)**. RK 62 occurs in the lower 9 km segment of the HMA section. This 9 km segment had 39 chinook redds in August-September 1991, 34 in 1990, and age 0+ juveniles were readily located by snorkeling between July 31 and September 24, 1991.

Although the absence of rearing juveniles in the Marengo section can be attributed to a combination of factors such as high stream temperatures, streambed sediment levels, and low pool availability, it is probably safe to assume as a starting point that maximum daily temperatures of 25°C-27°C in a fluctuating thermal regime are lethal over a period of days. There were few redds deposited in 1990 in the vicinity of the 1991 juvenile surveys, but this is unlikely as a reason for the lack of juveniles observed. Juveniles from upper sections should be capable of migrating downstream to rear at Marengo in spring and then migrating back upstream (at least as far as the weir) as temperatures increase in summer (see Lindsay et al. 1985). Their absence, then, appears to be either attributable to insufficient stream bottom snorkeled or poor visibility at Marengo (as suggested by Bumgarner, pers. comm.) or high water temperature causing death or migration to a zone having preferred temperatures.

It is obvious though that stream system temperatures cannot be elevated from the headwaters downstream without loss in usable rearing area. If stream channel conditions and adult escapement remain constant and the zone of adverse warm waters moves continually upstream, juveniles cannot continue to pack the shrinking rearing space having suitable temperatures. As temperatures in the downstream zones increase, stream reaches with suitable temperatures are found predominantly in higher gradient reaches that are not inherently as suitable as chinook rearing areas as lower gradient reaches. In addition, the total carrying capacity of the stream system declines with increasing temperatures and other degradation of habitat quality that may accompany stream temperature increase would result in further carrying capacity reduction.

### Evaluation of Distribution in Relation to Growth Optima

Hokanson and Beininger (see Armour 1990) indicated that 19.1°C is the temperature at which growth becomes zero for spring chinook. The growth curve developed by Brett et al. (1982) for spring chinook specifies a growth rate at 19°C that is about 60% of the optimum rate occurring at 14.8°C, while zero growth occurs at about 21°C. Adopting 19°C as the zero growth threshold, one can calculate that during August at the Marengo site, 97% of the time temperatures exceeded 19°C. At the Deer Lake (RK 62) and Cummings Creek (RK 58) sites, both in the HMA section, temperatures exceeding 19°C occurred 63 and 58% of the time, respectively. The Deer Lake site had a 6-consecutive-day period with daily temperatures above 19°C for >80% of each day **(Fig. 13)**; the Cummings Creek site had a 5-day period with temperatures above the threshold for >90% of each day.

Snorkel sampling in the HMA section took place from July 31 to September 24, 1991. The estimates of 40,467 parr and average densities by habitat type (Bugert et al. 1992, p. 29) from this entire section were calculated from all sites snorkeled during this period. A run and a riffle site near Deer Lake (HMA 6 and 9, respectively) were sampled between August 1 and 29 (Bumgarner, pers. comm.). Parr densities in these habitats in 1991 were the lowest levels observed over the period from 1986 to 1991 and were each approximately 10% of the maximum densities observed. It is interesting that between 1985 and 1992 there were from 302 to 605 fish spawning in the river (Bumgarner et al. 1997). The highest number of spawners for this period (605) occurred in 1990. Despite having a relatively large number of spawners, it led to the lowest observed densities of parr the following year for this period at HMA 6 and 9. It should be recalled that the HMA section spans RK 54.9-75.1 on the mainstem. The Deer Lake and Cummings Creek sites are at the downstream end and the Tucannon Hatchery intake occurs at RK 59. This is a migration barrier to adults and juveniles. It appears then that juvenile density at the lower two sites could not be replenished by migration downstream at this time. However, it needs to be further investigated what the specific sampling dates were for sites above the weir. It is possible that in the latter portion of the sampling period (e.g., September), juveniles moved downstream to make use of the cooler temperatures. For the investigation of suitable temperature indices to be most conclusive, narrower sampling windows will be needed. Also, sample periods would need to be comparable from year to year.

**Evaluation of Distribution of Juveniles by Age Class and Stream Section**

Snorkel sampling in 1995 of riffle, run, pool, and side channel habitat types yielded population estimates of subyearling chinook/100 $m^2$ for the Wilderness, HMA, Hartsock, and Marengo sections. Subyearling densities, converted to total population estimates (in thousands of fish) for these sections of the mainstem, were approximately 2.2, 1.5, 8.4, and 0.6 (x1000), respectively. Yearlings had populations (in thousands) of 2.2, 2.0, 0.1, and 0.07 (x1000), respectively (Bumgarner et al. 1996). The subyearlings were the product of the 1994 brood, whereas the yearlings were of the 1993 brood. It is known that subyearlings of many fish species tend to be more tolerant of high temperatures than older juveniles. For this reason it is not surprising that the two upper river sections (i.e., upstream of RK 54.9) accounted for most of the summer production of yearlings. The significance of the Wilderness reach for rearing, if not for spawning, is even more apparent when one considers the frequently low spawning densities there compared to the HMA section in years when adults are allowed to spawn above the weir site (see Bugert et al. 1992). The ability of yearlings to seek cooler temperatures in the Wilderness section makes this a vital production reach.

This distribution of 0+ and 1+ age class chinook by stream section was also apparent in the Tucannon River in snorkel sampling in 1994 (Bumgarner et al. 1995). Population size of 0+ age chinook for the Wilderness, HMA, Hartsock, and Marengo sections (in thousands) was approximately 16.6, 41.8, 22.8, and 5.6 (x1000), respectively. Yearlings had population sizes for these sections of 1.5, 1.3, 1.9, and 0.0 (x1000). Sampling dates during the summer were not clear from this report. However, it is clear that the production from the upper three stream sections is very significant compared with the river downstream. Based upon snorkel surveys made between July 16 and August 18, 1990 the population estimates of subyearlings for these four river sections were (in thousands) approximately 6.6, 45.4, 8.6, and 0.0 (x1000) (Bugert et al. 1991). Total redd counting by section in 1989, the parental generation for the 1990 subyearlings, revealed 29, 54, and 23 redds, respectively, for the first three sections. Redds were not counted in the Marengo section in 1989, but in 1986 and 1990 only 0 and 2 redds, respectively, were found. The distribution of redds in 1989 appears to be similar to the late summer subyearling distribution. In addition there was similarity between 1994 and 1990 in subyearling distribution among the river sections, with highest numbers in the HMA and lowest in the Marengo section. Also, yearlings consistently seem to only be able to survive in the upper three sections. For yearlings not to occur in the Marengo section, they probably either die there during summer or migrate upstream, at least as far as the weir at RK 59.

### Evaluation of the Use of MWAT

Armour (1990) provided a formula for estimating the maximum weekly average temperature (MWAT) for juvenile rearing. MWAT = OT + (UUILT - OT)/3, where OT is optimal temperature and UUILT is ultimate upper incipient lethal temperature. Using the OT of Brett et al. (1982) of 14.8°C and the UUILT of Brett (1952), the calculated MWAT =18.2°C. The Deer Lake and Cummings Creek sites (both in the lower HMA section) averaged 19.9°C and 19.4°C for the entire month of August 1991 **(Figs. 13 and 14)**. Mean July temperatures at these sites were not much better (19.2°C and 18.6°C, respectively). Maximum temperatures at the Deer Lake station were >24 °C for a 6-d period in early August and a 4-d period later in August **(Fig. 13)**. The lower OT provided by Wilson et al. (1987) (see Armour 1990) resulted in an even lower MWAT of 15.6°C. By this estimation procedure for MWAT, one would conclude that the July and August temperatures in the Tucannon River in the lower portion (RK 58-62) of the HMA section were not desirable for juvenile chinook production. Temperatures in the Marengo section in 1991 appeared to exclude juvenile production during July-August at a daily mean temperature of 22°C and periodic daily maxima of 27°C based on the 1990 juvenile survey conducted between July 16 and August 18, 1990 (a year of lower water temperatures, see **Figs. 12 and 15)**. The fact that no juveniles were found rearing in the Marengo section in 1990 (a cooler summer) provide additional support for this river section being adverse to production in average years. Temperatures in the North and Middle Forks of the John Day River excluded juvenile rearing when the mean weekly maxima exceeded 22.7°C and 19.5°C, respectively (Lindsay et al. 1986). Chinook juveniles did rear in the HMA section in August as well as in the 13-km Hartsock section below it. Their presence, however, does not indicate that the temperatures found there are conducive to good growth or health or optimum survival. The transition from summertime salmon habitat to non-salmon habitat downstream occurs in the stream section (Marengo) where maximum temperatures in summer are in the general range 22-24°C that has typically been found to be the threshold between presence and absence in most salmonids.

Hokanson et al. (1977) advised caution in application of short-term exposure experiments to calculations of acceptable long-term exposures such as with MWAT. They reported for Oncorhynchus mykiss that, given a physiological optimum of 16°C-18°C and an upper incipient lethal temperature of 25.6°C (at 16°C acclimation), one would calculate an MWAT of 19°C and a maximum temperature (applying the 2°C safety factor of Coutant 1972) of 24°C for short-term exposure. Measurement of rainbow trout growth showed that at a fluctuating temperature of 22 ±3.8°C specific growth rate was zero (Hokanson et al. 1977). Under this temperature regime mortality rate was 42.8%/day during the first 7 days. For experiments within the optimum range (15.5°C-17.3°C for a fluctuating regime), average specific mortality was 0.36%/day. Combining data on specific growth and mortality rates, the authors were able to predict population 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 23°C and a fluctuating temperature with a mean of 21°C ±3.8°C because growth balances mortality. Several sources report temperatures of 21°C to 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 22-24°C (see Distribution section, p. 87).

With this lab information on constant and fluctuating temperatures and corroborating field information, Hokanson et al. (1977) recommended a mean weekly temperature of 17±2°C for rainbow trout to allow no more than a 27% reduction from maximum yield in fluctuating temperature regimes. Given the general similarity in temperature responses among Oncorhynchus spp., these observations on rainbow trout are relevant to chinook. To summarize this discussion of the use of MWAT, various calculations of MWAT for chinook from literature range from 18.2°C to 15.6°C. Hokanson et al. (1977) calculated an MWAT for rainbow trout of 19°C. Despite this they showed that even a mean weekly temperature of 17 ± 2°C was not conservative enough to provide optimum production. Even though the HMA section of the Tucannon River had the greatest total numbers of juveniles, it also had extended periods where the temperature exceeded 19°C for large portions of each day. This implies that major increases in production (and possibly survival) are achievable by reducing temperature in the HMA and other sections. Increases in total production capacity from the entire Tucannon River system are predicted from general cooling downstream to the mouth that would accompany habitat restoration (Theurer et al. 1985).

An evaluation of the temperature statistics for the July through August period for the Marengo Bridge site (RK 41, the upstream end of the Marengo section) and the Cummings Creek site (RK 58, the lower portion of the HMA section) can help reveal the utility of various indices of temperature in explaining the biological responses observed. During this 62-d period (July 1-August 31, 1991) on the Marengo Bridge site the distribution of maximum daily water temperature indicates that approximately 32% of the days experienced water temperature ≥25°C (i.e., the UUILT). The majority of days had temperature maxima of 23-25°C **(Fig. 16)**. The maximum temperature reached was 27.2°C (July 23 and also August 8) **(Figs. 12 and 17 )**. The maximum 7-d moving average of the maximum daily temperatures was 26.3°C (August 9, with the 7-d moving average calculated as the mean of the August 9 maximum temperature plus the means of the preceding 6 days) **(Fig. 17)**. The maximum daily mean temperature was 24.4°C (August 8) and the maximum 7-d moving average of the daily mean temperatures for the period was 23.8°C (August 11). The maximum daily temperature experienced during this period occurred on a day that culminated a transition from daily maximum temperatures of 21.1°C to 27.2°C over a 7-d period. The highest daily maximum temperature (27.2°C) occurred during a week with a weekly mean temperature of 20.9°C and a weekly mean of maximum temperatures of 24.7°C. It is clear that a single day of peak temperatures could be overlooked in a monitoring scheme directed at weekly averages of daily maxima or daily means. In this data set, however, a 15-d period of daily maximum temperatures from 24.4°C to 26.7°C also produced moving 7-d means that reached a high of 26.3°C. It cannot be assured that for every summer period high daily maximum temperatures would consistently be clustered in 7-d windows, resulting in 7-d moving averages that were nearly as high as a single daily maximum temperature. In this Tucannon example a monitoring scheme based upon 7-d moving averages of daily maxima would have fortuitously revealed biologically adverse conditions. In this case the consecutive days with high maximum as well as high mean temperatures may have presented a more serious biological challenge than the single peak temperature. This may not always be the case as single peaks can be hidden by moving averages.

### Evaluation of Thermal Regimes for the Spawning Period

Periods of high water temperature during the summer are not the sole concern during the life cycle of spring chinook in the Tucannon River, although summertime thermal regime problems are probably linked to problems in other seasons. At the Marengo Bridge site starting on August 19, 1991 maximum daily temperatures fell from 26.7°C to 20.6°C over an 8-d period. Moving 7-d maximum daily temperatures declined steadily during September and reached approximately 21°C by September 15, the center of the spawning period in the Tucannon. Even the moving 7-d mean of mean daily temperatures was still 19.5°C by this date **(Fig. 18)**. This temperature is clearly too high for successful spawning or egg survival, which no doubt accounts for typical Marengo spawning dates of late September to the first week in October.

Moving upstream only 17 km to the Cummings Creek (RK 58) site, one of the key spawning reaches on the mainstem Tucannon River in the HMA section, the 7-d moving average of daily maximum temperatures was 17.8°C and the 7-d moving average of the daily mean temperatures was 16.2°C on September 15, the typical center of the spawning period for the entire Tucannon River **(Fig. 19)**. In the HMA section, the center of spawning distribution is also in mid-September as an average for the years observed (Bumgarner, pers. comm). Because a 7-d moving average incorporates a lag effect, reflecting the 7 days prior to any individual date, it may not be the best index to appropriate spawning conditions. This index does, however, smooth out the overall trend. The 7-d moving average of maximum temperatures as viewed on September 22, 1991 (i.e., 7 days beyond the peak of the spawning period) was 17.1°C, not much less than the value calculated for the 15th. When looking at actual daily maximum temperatures for September 15 ±5 d, maximum daily temperatures varied only from 16.7 to 18.9°C. Mean daily temperatures during this 11-d window of the typical spawning period varied from 15.3 to 16.9°C. There is reason to believe that these temperatures potentially inhibit spawning, reduce fecundity, impair egg viability and subsequent survival after deposition, and cause alevin developmental anomalies from other studies reviewed in this report. This spawning reach is located in the lower part of the HMA reach. By any of the thermal statistics used above one would conclude that spawning temperatures in this spawning reach (assuming that spawning in 1991 occurred during the average spawning window for this site) were too high for good survival, even by assuming that if eggs were deposited in redds, temperatures in the egg pocket could be 1-2°C cooler than ambient surface water. Maximum daily water temperatures at the Deer Lake site (RK 62) average approximately 1-2°C warmer than at the Cummings Creek site (Bugert et al. 1992), making it even worse as a spawning area .

The age distribution of adults based on surveys from 1985-1997 was 2% age 3, 70% age 4, and 28% age 5 (Bumgarner, pers. comm.). In 1995, however, there was a much larger percentage of age 5 adults than on average (67%). Smolts typically leave the Tucannon as 1+ but 2+ smolts are also occasionally observed (Bumgarner, pers. comm.). From 1990 to 1996, there were 605, 383, 575, 433, 70, 11, and 35 adults estimated to be in the river (Bumgarner et al. 1997). From 1990 to 1994 the estimated number of smolts leaving the basin (x1000) was 50, 26, 51, 50, and 7. Progeny from the 1991 brood year would have left the Tucannon as smolts primarily in spring of 1993. The eggs deposited in late August and September 1991 were exposed to higher than normal spawning temperatures but they were not in the gravel during the extremes in temperature in early August. Adults from the 1991 brood would return in 1995 and 1996 at age 4 and age 5. The sharp decline in adult numbers that occurred in 1995 and 1996 could by itself be thought to be an indication of failure of the 1991 brood. However, the egg-to-fry survival for natural fish in the Tucannon River was 10.2% in the 1991 brood year. Values for 1985-1994 ranged from 6-11.1% (Bumgarner et al. 1997).

The 1990 brood was in the fingerling stage during the summer temperature extreme of 1991. This brood year had a fry-to-smolt survival of 77%, a value which was the maximum observed during the period 1985 to 1994. Fish from the 1990 brood year left the Tucannon primarily in 1992, a year that produced a large number of smolts relative to observed smolt production for 1990-1994. From data reported above on spawner numbers and smolts emigrating, it does not appear that the number of smolts leaving the basin in either 1992 or 1993 was affected by high temperatures of 1991. However, with the low number of adults utilizing the basin, it is possible that habitats that are occupied have sufficient food to sustain juvenile growth and that juveniles simply avoid river sections such as the Marengo. Bumgarner (pers. comm.) attributes the low adult returns of 1994 and 1995 to El Niño events of 1991 and 1992. It is also possible that in a watershed like the Tucannon that has been so heavily subjected to anthropogenic warming that the primary effects of elevated temperatures today are expressed in prevention of use of the lower 40 km (± several km) of the mainstem. Reduction in survival rates that probably occur longitudinally as the Marengo section is approached on any extreme summer period might be obscured by other temperature or habitat quality effects that occur in other seasons or years during the juvenile development period. But the summer of 1992 was even warmer than the summer of 1991 for which the estimates of cumulative mortality were estimated. It is also possible that poor adult returns in 1995 could have been linked to the summer extreme temperatures in 1992 experienced by the juveniles from the 1991 brood year.

The spawning reach at Cummings Creek is located in the lower part of the HMA reach. In 1995 the entire HMA reach contained only 2 redds, as determined from spawning counts made between August 30 and September 27 (Bumgarner et al. 1996). Only 3 other redds were observed in the river aside from this, located in the Hartsock reach downstream. The Tucannon Hatchery weir is located at river km 58, above the spawning grounds near Cummings Creek. Because all adults were trapped here and none were passed upstream of the weir, it was not possible for these adults to either hold or spawn in cooler waters that are found in upstream reaches. The peak of the run into the Tucannon River occurs on approximately May 28 (Bumgarner et al. 1995). This means that adults must find suitable holding pools through the months June-August. In a nearby stream in the Blue Mountains, the Middle Fork John Day River, spring chinook adults held in waters during July and August that exposed them to temperatures near the UILT (McIntosh et al. 1995b).

Although incomplete August temperature data were recorded in the Tucannon River near Panjab Creek (RK 78) in 1991, it appears that maximum daily temperatures there were approximately 4.4-5.0°C cooler than those at the Cummings Creek site. Allowing naturally spawning spring chinook to pass upstream to hold and spawn in more suitable temperatures would probably lead to far greater survival and greater smolt production. Chinook forced to spawn in elevated water column temperatures near Cummings Creek could possibly seek out thermal refuges in pools (if deep pools retaining cool groundwater are actually available) or deposited eggs might be able to benefit from up to a 2°C temperature reduction in the substrate (see Shepherd et al. 1986) , also assuming favorable interchange with groundwater (Vaux 1962). However, the probable impairment to population viability caused by an overall increase in ambient temperatures cannot be compensated by chance occurrence of thermal refuges.

To investigate the feasibility of improving temperature in the mainstem Tucannon we can look to the data of Theurer et al. (1985). Theurer et al. (1985) used a stream segment temperature model developed by the Soil Conservation Service and the U.S. Fish and Wildlife Service to predict stream temperature profiles along the Tucannon's entire mainstem length under historic climax vegetation and channel morphology condition, the current temperature profile, and temperatures under two management alternatives. Alternative 1 called for restoration of riparian vegetation from the headwaters to Pataha Creek at RK 19; below Pataha Creek the management scenario was current riparian vegetation and channel morphology. Alternative 2 provided management only below Pataha Creek by returning climax vegetation cover and maintaining existing channel morphology. **Figure 20** indicates the average mean daily temperatures for a normal July water year. The current temperature profile for July (based on existing riparian vegetation and channel morphology) exceeded an average <u>mean daily</u> temperature of 20°C from RK 40 all the way downstream to the river mouth. When historic climax vegetation and channel morphology were provided, the mean July temperature was restored to 16.3°C. Under these same vegetation and channel criteria expressed all the way to the mouth, mean daily water temperatures did not exceed 19.5°C for July. Applying an MWAT of 18.2°C or a zero growth threshold of 19.1°C, one could safely assume that the current mean daily July temperatures occurring from RK 40 (20°C) to the mouth (22.4°C) are unsuitable or at least extremely poor for juvenile growth. Current <u>mean maximum</u> temperature for July is 26°C at the river mouth in Theurer et al.'s model and was estimated to be at 22°C historically. The temperature model infers that the lower 40 km in this fairly short stream (100 km) is no longer useful for chinook production but was suitable before development. Juveniles do not appear to use the Lower section for summer rearing based upon observation (see data of Bugert et al. 1991). Critical temperatures that negate summer rearing in this Lower section appear to be average mean daily temperature in July of

≥20°C and an average maximum daily temperature of ≥24°C (Theurer et al. 1985).

Theurer et al. (1985) estimated the temperature reduction that could be produced by improving the riparian cover and channel morphology for the Tucannon River mainstem, and with this information, the potential increase in total chinook production. This estimate did not account for improved production that might accrue from improving the current poor sediment conditions. The estimate was also based solely on mainstem riparian vegetation and channel restoration, not restoration in Tucannon tributaries. Estimated improvement in mainstem temperature regime would result in an increase in adult returns from 884 existing to 2240 **(Fig. 1)**. Chinook rearing capacity would increase from 170,000 to 430,000. The conclusion from the reconstruction of the longitudinal temperature regime in the Tucannon River is that an increase in production would result from improved condition in all river sections below the Wilderness, which was unchanged.

### Evaluation of Thermal Regimes for the Egg Incubation Period

Thermal effects on Tucannon River spring chinook are apt to occur during the months for egg/alevin incubation as well as in the summer rearing months. For example, the normal spawning peak occurs near September 15. Fry emergence occurs in February (Olsen et al. 1993). Daily minimum and maximum temperatures for September 1990-February 1991 are available in Bugert (1991) as well as mean monthly temperature ranges. Using the monthly ranges as a convenient means of calculating monthly mean temperature for the Wilderness section near Panjab Creek (RK 76), Cummings Creek (RK 58), and Marengo Bridge (RK 41), it is possible to compute degree days during the incubation period. If incubation took place for the entire month of February, the total number of accumulated degree-days for the period September 15-March 1 was 767, 769, and 1426 for these three sample points on the mainstem Tucannon River, respectively. During January, for example, the mean monthly temperature for these river sections, respectively, was 2.6, 1.4, and 5.4°C. Given the high mean temperature during September at the Marengo site, it is clear that were spring chinook to spawn there, it would be advantageous to delay spawning into late September or early October. In the Middle Fork and Mainstem John Day Rivers, it was observed that spring chinook spawning occurred late (mid-September through early October) whereas in cooler streams in the region such as the North Fork John Day and the Imnaha River, spawning occurred from mid-August to early September (McIntosh et al. 1995b). In the Tucannon River, adults that spawn near Marengo would be at a disadvantage by holding in the vicinity until spawning time and would most likely have to hold upriver and redescend to spawn. Further, given the high incubation temperatures at Marengo relative to the other sections, emergence would be early. If adults were able to delay spawning until October, a similar number of degree-days to the other sites could be accumulated as early as January 1 for emergence to occur, assuming no compensation. It appears that the typically low number of spawners in the Marengo section and the low number of summer rearing juveniles may be a result of high spawning temperatures, high incubation temperatures that would result in extremely early emergence, and high rearing temperatures resulting in either avoidance or high mortality.

## Evaluation of the Relationship between Water Temperature, Air Temperature, and Stream Discharge

Water temperature is known to be correlated with air temperature. Stream discharge patterns also affect the trends in water temperature. Periods of summer rainfall are associated with cloud cover and changes in air temperature and/or discharge. Changes in discharge commonly produce opportunities for fish migration in various seasons. Data available from the Oregon Climate Service on air temperatures for LaGrande, Oregon were plotted with maximum daily water temperatures for the Tucannon River at Cummings Creek for 1988 and 1992. LaGrande is 125 km air distance from the Cummings Creek site. Periods of increasing air temperatures were typically linked with increasing water temperatures **(Fig. 21)**. However, the rate of response to air temperature increases or decreases seems not to be the same during all periods in the month examined.

For the year 1989, July-September maximum daily water temperatures were plotted in **Figure 22** along with the ratio of (maximum daily water temperature)÷(mean daily discharge). Again, air temperatures were those recorded for the LaGrande, Oregon station and water temperatures were taken on the mainstem Tucannon River at the Cummings Creek site. These plots reveal a very close association between water temperature and the ratio. This relationship appears to explain more of the variation in water temperature than is accounted for by air temperature alone. It is interesting that a very substantial change in the T(air)/Q ratio at day 54 in this 3-month period produced a corresponding change in water temperature but not as great as that produced by other smaller changes in the ratio. Despite the correlation between water temperature and air temperature and discharge, the key to maintaining healthy salmon habitat is to delay the warming effect as far downstream as possible. That is, one would expect a correlation between local water and regional air temperature at all points down the river continuum. The correlation in the Wilderness reach, however, would be with a lower maximum daily temperature. In addition, one would expect that local climatic (air temperature) conditions under the riparian canopy in this reach would be responsible for the lower maximum daily temperature and would, itself, be correlated with the regional air temperature.

# RECOMMENDED STANDARDS

## OVERVIEW OF THE PROBLEM

The process of developing temperature standards for salmonids in freshwater habitats is one requiring great care and consideration. There are a variety of approaches that can be taken. For example, it is possible to base a standard or its application to a whole stream system on (1) the distribution of the species in its current range of habitats and the temperature limits to distribution, (2) suitable temperatures for what is considered to be the most sensitive life stage, (3) suitable temperatures for single or multiple life stages, (4) effects on survival only, or (5) effects on a variety of life processes and activities such as avoidance, preference, growth, reproduction, migration, disease, feeding, territoriality, and aggressiveness, in addition to survival. These are all valid biological considerations. As matters of policy, there are separate issues of whether (1) a species would be protected fully or partially throughout its range, (2) all native coldwater species would be protected on an ecosystem basis within subbasins designated as coldwater beneficial uses, and as a subset, or (3) whether native fish habitats would be spatially linked or disconnected fragments. In response to both biological requirements and policy decisionmaking, it is necessary to formulate a means of identifying level of suitability or protection. Does full protection mean being able to fully occupy all historic habitats within the historic range of the species? Under these conditions, would survival be the optimum for a life stage under the dynamic geomorphic, vegetative, and climatic processes that historically occurred? Would certain habitats be bottlenecks to production and population viability on account of quantity, quality, and spatial connectedness? As a matter of land management, will land management standards be developed so that water temperature standards can be met? (See Rhodes et al. 1994 for an explanation of the linkages between land management and stream processes and McCullough and Espinosa 1996 for monitoring protocols). In this process there are decisions to be made concerning whether land management is to be conducted on an ecosystem basis or on a more reductionistic basis, such as focusing protection on key sites and dominant portions of the watershed (e.g., riparian zones). It must also be decided whether the standards that apply to biologic criteria and land management practices would incorporate margins for error in estimation of biologic effects and management outcomes and the natural stochasticity of environmental processes. The alternative is that species' habitats would be managed as close to the brink of serious decline or extinction as possible to maximize all other resources having conflicting impacts to fish habitat.

It could be instructive, in discussing all possible approaches to standards, to review the many ways in which freshwater temperature regimes have been perturbed in recent development of Columbia River subbasins. The management activities (e.g., riparian harvest, wetland draining or filling, diversion of groundwater flows by road cuts) that have been responsible for the existing spatial patterns of alteration to thermal regimes suggest both the possible mechanisms for impact to salmon populations and life histories (see Rhodes et al. 1994) but also the logical means to monitor and summarize data on environmental quality (see McCullough and Espinosa 1996). It would also be worth reviewing our past processes for managing land and monitoring and regulating water temperature to understand why these actions have led to an ever shrinking quantity of available coldwater habitat for salmonids. The reasons for continued erosion in habitat quality undoubtedly are a combination of factors: complexity and difficulty in understanding all the biological effects involved, the tendency to allow degradation of water quality as a ready compromise in deriving non-aquatic benefits from a watershed, and political difficulty in coming to grips with the geographic scope of the problem, and resistance to fully believing or using what the scientific community has provided. <u>Among the positions taken by various managers, regulators, the public, or sometimes by scientists themselves that have contributed to failure to halt the continuing thermal pollution problem are:</u>

> It is good to open up the canopy because the water temperature in streams of the Pacific Northwest is too cold. Salmonid abundance and growth rate improve when water temperature increases.
>
> Salmon endemic to streams of eastern Washington and Oregon are adapted to warmer water temperatures than those endemic to streams west of the Cascade Mountains because the climate is warmer on the eastside. These inherent differences in tolerance make it ridiculous to apply a uniform standard state-wide.
>
> Increasing the water temperature might be disadvantageous to one salmonid species but it would merely improve conditions for other salmonids.
>
> If water temperature in a stream reach attains upper lethal levels for a salmonid, this is not a problem as long as the temperature cools off at night.
>
> Salmonids have been observed in streams having very warm temperatures, proving that in some locales these species have very different water temperature requirements.
>
> As long as the mean daily temperature is within the range of temperatures that a salmonid species has been shown to tolerate in short-term laboratory tests, there will be no effects on the individual or the population.
>
> Laboratory tests on temperature preference or lethal limits do not apply under field conditions, so cannot be used to set temperature standards.
>
> There are numerous thermal refugia in streams so there is seldom a problem for a population maintaining itself during warming periods.
>
> Just because salmonids prefer cold water in thermal gradient experiments, that does not mean that they will not do well under warm water conditions. Densities of

> salmonids appear to be high in warm water.
>
> Much of the literature used to develop temperature standards is for salmon stocks not in the Columbia Basin, so is irrelevant. We need to do much more research before considering stringent standards.
>
> You seldom see the dead carcasses of fish in the river so the importance of diseases and other indirect sources of mortality must be overblown.
>
> For a stream reach supporting steelhead, spring chinook, and bull trout, it is possible to monitor only one species as a management indicator species. Steelhead are present in sufficient numbers so will make a good choice for indicator species.
>
> No matter what the condition of the stream, coldwater refuges exist where there is groundwater entering a stream, and this will support fish throughout any summer period. The fish merely need to seek out these refugia.
>
> Devise a temperature standard for maximum allowable temperature but also allow impacts in the headwater riparian zones that progressively move the point where the standard is exceeded in an upstream direction.
>
> Select a standard that is in the resistance zone (i.e., where mortality is a function of exposure time) because any lower standard might not appear to be linked to heat death or might be judged *a priori* to be physically infeasible to attain.
>
> Stream environments are naturally heterogeneous and salmon stocks have evolved in such physical uncertainty and can cope with it. Salmon do not always have optimum conditions under natural conditions, so optimum should not be a management standard.

None of these approaches above can be considered to meet the biological needs of a species or to maintain health of the freshwater ecosystem. They are only mentioned because sometimes it is easier to see how to do things right when contrasted with the voluminous tendencies to do the opposite, whether that be through sheer management convenience or lack of sufficient information to make a good decision.

As revealed in this review of thermal effects on salmonids, there are significant impacts to survival due to temperature regime worth considering in all life stages. In addition, there are other impacts considered to be sublethal on life processes such as growth, survival, reproductive success, migration success, disease, feeding, territoriality, aggressiveness, swimming, bioenergetics that cumulatively can result in diminished survival and production of the population. It is essential for anyone setting a temperature standard for any season or portion of a life history phase to thoroughly understand the breadth of control that temperature exerts on population viability. When this is accomplished it is up to land managers to also fully consider the impact of their actions in an ecosystem context on the temperature regimes found throughout a stream system from headwaters downstream. That is, freshwater habitat protection involves full protection and restoration of all riparian areas (fish-bearing, non-fish-bearing, intermittent) as well as the entire watershed so as to support all processes contributing to habitat quality and quantity (including water quality) (Rhodes et al. 1994, Henjum et al. 1994, Reeves et al. 1997).

## SELECTION OF A STANDARD FOR A RIVER CONTINUUM

All species encounter adverse environmental conditions at the limits of their range (e.g., latitudinal or within a stream system) and periodically within their normal home range with annual or seasonal variation in climatic events. For example, yellow perch distribution in North America corresponds to the 15.6°C isotherm for mean July air temperature to the north (Ryder et al. 1964) and the 30°C isotherm for mean maximum midsummer air temperature (Weatherley 1963) to the south. The 20°C isotherm for annual air temperature establishes the southern limit to lamprey distribution (see references cited by Potter and Beamish 1975). Smallmouth bass are restricted in northward distribution by the 18°C isotherm for mean July air temperature (Inskip and Magnuson 1983). These air temperature indices correlate well with general fish distribution because of the linkage between air temperature and water temperature (Hokanson (1977). However, within a river system, temperature regime varies longitudinally with stream order (also correlated with width and elevation) and is modified by management perturbations to channel width, riparian canopy cover, pool volume, watershed runoff timing, and instream flow (Rhodes et al. 1994). Downstream limits to fish distribution have often been linked to maximum temperature attained in the reach. For example, brook trout are limited in downstream range to water temperatures <19°C (McCormick et al. 1972). The point in a stream system where this threshold is reached is, then, an outcome of management influence on the inherent temperature regime.

Maximum monthly or annual water temperature typically increases gradually in a downstream direction on a river continuum. Other key indices of the temperature regime likewise vary longitudinally. For example, the rate of degree day accumulation during the winter egg incubation period also changes in a downstream direction, leading to variation in emergence date and duration of the emergence period. Timing of spawning must also coincide with the incubation temperature regime so that proper development time is allowed for emergence to occur before adverse high springtime temperature. Salmonid species exhibit considerable variation in life history patterns to accommodate the patterns of temperature regimes found along the river continuum. Management of the spatial array of thermal regimes found in the system of linked stream reaches can be simplified by ensuring that management impacts distributed throughout a watershed do not interfere with the ability of coldwater from headwaters or from groundwater sources to flow downstream to the greatest extent before reaching equilibrium with air temperature. A successful river management program would seek to provide optimum conditions to the extent that they are characteristic of the unmanaged, native state of the particular river segment. Obviously, not all reaches in a river system can be at optimum temperatures for every month for each fish species inhabiting the stream system. Summer months are vital to juvenile rearing and temperatures above the optimum, which are increasingly found in downstream reaches, result in reduced individual growth rates, reduction in population net biomass gain, increased mortality rate, reduction in population density, and eventual elimination of the species. Documenting the occurrence of a few individuals in a downstream reach does not allow concluding that the temperature regime for the reach is adequate. Rather, if a threshold maximum temperature is exceeded, there is reason to determine whether all management actions upstream have been taken that would result in restoration of natural cooling or thermal buffering processes.

In the management of coldwater fish species, the greatest degree of expression of life history variation by species is achieved by restoration of the thermal regime on a stream system-wide basis, along with other pre-management conditions of channel morphology and the watershed. Moving the summer maximum temperature threshold upstream constricts the available spawning or rearing area of all coldwater fish species. Fish zonation from headwaters to downstream reaches in the Pacific Northwest can be characterized roughly as proceeding from bull trout/cutthroat trout to steelhead, to spring chinook/coho, to summer chinook, to fall chinook, to chum (Li et al. 1987). With the exception of bull trout, the other species do not vary substantially in their response to summer maximum temperature. However, they do vary in their preference for size of spawning and rearing stream, size of spawning gravel, and stream gradient tolerated. Increase in summer maximum temperature in headwater stream zones cannot occur without causing increase to downstream reaches. Constraining species more and more to compete in high gradient streams that may provide suitable water temperatures would severely limit production and impair survival in the majority of the historic habitat of each species, but further, it is not feasible energetically for large-stream species to occupy smaller, high gradient streams.

Ideally management of watersheds could be done in such a way that historic temperature regimes would be restored in all stream reaches throughout each stream system. Theurer et al. (1985) demonstrated that, given a large modeling effort, the restored longitudinal temperature profile for summer months could be estimated under restored riparian vegetation and channel width for the Tucannon River mainstem. This model demonstrated that through restoration efforts focused on the mainstem that the lower 40 km of river could be made inhabitable by juveniles during summer. It is likely that full watershed restoration (restoration of tributaries and their watersheds) would result in even greater production potential. Taylor and Barton (1992) recommended that the ultimate management goal is to restore natural frequencies of temperature exceedences with no perturbation by management influence. They state that management of frequency of temperature exceedence is needed to ensure that populations living in marginal habitat are not further stressed. Populations living in marginal habitat suffer high frequencies of temperature exceedence; increases in their probability of experiencing stress from temperature exceedence results in greater acute mortality.

Although the ideal may be to determine an historic longitudinal temperature profile and manage the watershed to recreate this condition on average, this approach is not practicable. The data requirements for reconstructing historical profiles for all streams in the Columbia River basin would be severe. Gathering information on historic riparian condition would be challenging in itself, but many other factors such as historic channel morphology, channel volume, drainage density, and hydrologic conditions (e.g., linkages to wetlands or groundwater) contribute effects to the thermal regime. Even with adequate knowledge of historic conditions, precise modeling of these effects is unlikely. If an ideal longitudinal temperature profile were created, it would represent a long-term average condition that would have to be bounded by a probability density function. The most reliable means of determining this profile with its frequency distribution at each point along the curve is not by modeling but by restoring the watershed and then monitoring the profile for several years.

If this ideal profile and its frequency distribution were available as a standard, how would future monitoring take place to identify violations of the standard. There are a number of alternatives that could be proposed. In one scenario, several years of data at points along the profile would have to be averaged before it could be determined whether a significant deviation from the historic mean occurred for each selected point along the profile. And this comparison of recent condition with baseline years of record implies a stationary climatic regime.

Another alternative is to monitor the maximum temperature at a point on the profile and determine where that value falls in the frequency distribution. Values in the upper 5th percentile could be considered to be a violation because they are so rare one would not expect them. The "range of natural variability" is sometimes used to determine acceptability of a resource condition. That is, values that occur within the 5th and 95th percentile of historic natural conditions could be considered normal. Unfortunately, this method is fraught with conceptual problems that render it unusable (Rhodes et al. 1994). If maximum water temperature were at the 6th percentile level for annual maximum temperatures, one could not know whether this occurrence reflects part of the natural historic distribution or a new distribution shifted toward higher mean temperatures unless more years of data were collected. At this point, unacceptable damage could be done. Ironically, another variation to this theme proposed in the recent revision to the Oregon temperature standards was to excuse the extreme temperature values as basically acts of God. With these two concepts in tandem, one would accept the center of the distribution as within the range of natural variation and the extremes as acts of God.

One other alternative for determining temperature violations from a single year of data would be to first assess where the maximum temperature occurs in the ideal distribution for a particular point on the profile and then to determine whether this extreme was predictable. That is, if under the desired future watershed/riparian conditions it would take a high air temperature, full sun, high humidity, low wind speed, and high maximum water temperature for the previous day to produce a 1°C temperature exceedance at a particular point on the ideal profile, but under current conditions such an exceedance occurs under more benign conditions, one would conclude that management changes need to occur. Although this method would be effective, we do not typically have a complete knowledge of historic conditions, historic temperature profiles and their frequency distributions, or adequate current environmental data with which to predict temperatures. Even with abundant data of this type, predictions on a stream network basis are not highly accurate.

Use of a single maximum temperature standard for an entire watershed is often ridiculed as a "one size fits all" standard.  Recommendation of such an approach though does not imply that all watersheds are created equal but that each species that we manage has relatively uniform water quality requirements.  In practice, the management response to detecting a variation from the historic longitudinal profile would be the same as in managing according to a single basin maximum temperature standard.  That is, if the recent multi-year mean of annual maximum temperatures were greater than the historic mean of annual maximum temperatures within a particular reach, management actions within the reach and in the upstream watershed would have to be modified.  The minimum requirement for restoring the historic profile would be to allow for passive restoration of all riparian zones and channel morphology in the stream network.  To hold that less than full riparian restoration can be done means, as a minimum, that one is content with marginal improvement or a fraction of full fish production and that the responsibility can be borne by some landowners but not all.  Of course, simply focusing efforts on the riparian zone (and maybe even a small riparian buffer not functionally capable of reducing solar input or shaping channel morphology) is not sufficient.  Maintaining and restoring wetlands and other sources of cold water and rearing area are significant as are reduction in road density and other watershed measures.  One thing that a well described historic longitudinal temperature profile could do very well if it were ever feasible would be to alert regulators to local deviations from the desired profile, especially in the upper watershed areas.  This is the location where cold waters might be warmed significantly, but to levels below optimal.  It is important not to incur widespread warming of headwater streams. This effect would be detected at some point downstream, but then the task would be to take corrective action later to address all cumulative upstream landscape alterations that led to this problem.  Because the ideal profile tends to reach an asymptote far downstream where equilibrium with air temperature is attained, this is not the most sensitive site for monitoring temperature.  The greatest deviations from the ideal profile occur upstream, and this is where preventive actions need to be taken.

Averaging annual maximum temperatures in a reach over a 20-year period to compare it with an ideal profile describing the historic mean would require too long a data collection period before corrective actions could be taken.  Any individual year could have an annual maximum temperature that exceeds the long-term natural profile.  It would not be feasible to determine whether an annual exceedance is natural or has a management-related cause without attempting to correlate the annual maximum with annual air temperatures and account for all antecedent air and water temperatures, variations in groundwater input, etc. (see Stoneman and Jones 1996).  Obtaining a long (e.g., 20-year) record of temperatures in order to estimate the statistical likelihood that temperatures are attributable to natural rather than management causes does not allow timely adaptive management.  It is far more direct to address management actions known to lead to temperature increases than to attempt temperature reconstruction and estimations of probabilities.

In conclusion, use of a single maximum summertime water temperature as a management tool is as useful as knowing the historic longitudinal profile because the response to exceedence is the same. That is, exceedence of the threshold maximum temperature would cause upstream management actions to be modified if they were found to be impairing the ability of the riparian zone to achieve its natural vegetative cover and to control channel morphology. As previously stated, other watershed functions must also operate so that natural water and sediment delivery regimes are maintained. Exceedance of the temperature standard is the trigger to initiate adaptive watershed management. However, no temperature standard, even one fully linked in technical documentation to its biological consequences, can force land managers to recognize or address the effects of management actions on water temperature when there is an unwillingness to do so. Basically, the physical principles of stream heating are well known. Actions that cause temperature increases are well documented (Rhodes et al. 1994). Predicting the exact magnitude of increase is more difficult but it is seldom contested that cumulative reduction in riparian canopy cover for a stream system cumulatively warms streams.

If it is concluded that a single maximum summertime temperature should be the statistic used to identify a potential stream temperature violation, one must decide what the exact temperature should be. One alternative is to choose the temperature that finally results in elimination of the species from the stream. For a wide variety of salmonids, maximum temperatures of approximately 22°C-24°C have been shown in the literature to result in a limit to distribution. Fish species are typically eliminated by temperatures less than their UILT (Hokanson 1977). McCormick et al. (1972) found brook trout distribution to be limited to temperatures <19°C. This threshold for species presence was also close to the zero net growth temperature of 17.9°C. It appears that the field limit to distribution is a temperature between the ZNG temperature and the UILT. Setting this temperature (approximately 22°C-24°C for spring chinook) as a maximum instantaneous temperature standard would serve little purpose as a management tool. If all stream reaches were increased to the standard, the species would be eliminated throughout the stream system. It makes far more sense to set the growth optimum as the standard. For spring chinook this is approximately 15.6°C. During the summer, temperatures less than this cause no reduction in survival, whereas temperatures greater than this begin to reduce growth and lead to increasing mortality rates. Monitoring stream temperature in stream orders 4-6 would allow comparison to the maximum allowable temperature. Exceedance in any of these monitoring locations would require evaluation of management practices upstream. If maximum temperatures were limited using proper watershed management, amplitude of diel fluctuation would also be limited, as would frequency of exceedence of the maximum. Restoration of stream temperatures in the spring chinook zone would require restoration of conditions producing cold water throughout the drainage; this should ensure that the even lower maximum temperature requirements for bull trout are met in lower order streams. However, even though temperatures in the mainstem are influenced by cumulative impacts in headwater streams, significant biological damage can occur in the headwaters before an increasing temperature trend is detectable in the mainstem. Consequently, for protection of the local bull trout/cutthroat trout populations to be full and for cumulative effects to the mainstem fish populations to be minimized, full protection of all processes delivering coldwater must be maintained. Assuming a longitudinal zonation from bull trout and cutthroat trout in headwater streams to spring chinook and steelhead in stream orders 4-6, it would be probable that in terms of temperature alone, if bull trout habitat is in optimal condition throughout its range, the opportunity for spring chinook and steelhead habitat to have optimal conditions is great. Such a management scenario would represent ecosystem management at its best.

# SUMMARY

## HISTORICAL BACKGROUND

The Federal Water Pollution Control Act, amended in 1965 as the Federal Water Quality Act, called for standards to be established for protection and enhancement of water quality in waters of the US. In 1968 the Columbia River Thermal Effects Study was begun in response to adoption of temperature standards by Oregon and Washington that were inconsistent with one another. This study was authorized by the US Secretary of the Interior. In 1970 the National Marine Fisheries Service (NMFS) was created within NOAA to replace the Bureau of Commercial Fisheries in the Department of Interior (DOI). Also in 1970, EPA was created, replacing the former Federal Water Quality Administration and was given authority for overseeing environmental protection, including water quality. In January 1971 EPA in cooperation with the Atomic Energy Commission (AEC, represented by Battelle Northwest) and NMFS released the publication entitled Columbia River Thermal Effects Study. Results of 51 new studies on biological effects were reviewed in this publication in addition to much significant past research. The studies completed for this review included research conducted by the Federal Water Quality Administration, NMFS, and the AEC.

Impetus for this review came also from perceived changes in the Columbia River system.

> *The upriver runs of Columbia River fish resources have been reduced and endangered by the physical alteration and blockage of migration routes by the Nation's largest system of dams and reservoirs. The quality of the aquatic environment has also been modified by the discharge of pollutants and impoundment of the river's flow in a series of reservoir lakes reaching into Canada. Particularly regarding temperature quality, the Columbia River temperatures have been both spatially and temporally altered by man's activities and use of the water resources of the Region.*

There was at this time increasing concern for numerous point source discharges of heated power plant effluents.

Today, 27 years later it is clear that temperature control on the mainstem and tributaries of the Columbia River is of even greater concern. The historic thermal regimes have been altered on a geographically extensive basis by a history of land management decisions and land uses. Many ongoing activities continue to inhibit thermal restoration and new activities threaten to worsen the thermal regime, moving the stream zone at which salmonids are finally displaced by high summertime water temperatures further and further in an upstream direction. In addition to point source discharges, it has become obvious that extensive nonpoint source thermal pollution is also a significant problem. Recent progress has been made in understanding the spatial distribution of temperature within the Columbia River reservoirs (Fryer et al. 1998) and the ability to modify reservoir temperatures through releases of cold storage water (Karr et al. 1992). In 1971 the field of restoration biology was not recognized, but today practical experience has been gained in bringing about basinwide reductions in stream temperature through riparian recovery (e.g., Hostetler 1991); predictions of thermal recovery potential have also been made by use of stream temperature models on tributaries (Theurer et al. 1985, Chen and Chen 1993).

Monitoring of tributary water temperature today has become much easier with the advent of cheap, digital thermographs whose data can be readily downloaded to computers. This has increased the spatial extent of monitoring and a greater appreciation of the magnitude of thermal alterations to the region's waters. Increased monitoring of temperature of waters of the Pacific Northwest has led to listings of hundreds of streams as water quality limited, that is, no longer fully providing beneficial uses. At the same numerous species have been listed as threatened or endangered under the ESA. Fish runs that are cause for concern, leading to the EPA and NMFS report, are generally in far worse condition today. Although water quality is not responsible for all listings, it is certainly influential as a factor limiting production potential, distribution, and survival in streams of the Columbia River Basin. Elevated water temperature is probably the single most significant water quality factor limiting salmon survival.

In all temperature criteria adopted in the PNW, maximum upper limits were set for streams. Theoretical concepts of maximum thermal limits arose from pioneering work of Fry et al. (1946), Fry (1947), Hart (1947, 1952) and Brett (1952). This and other work was later synthesized by Coutant (1972) in an EPA handbook that differentiated ideas about allowable short-term exposure and long-term exposure. The methodology for estimating upper incipient lethal temperature (UILT) incorporated concerns about short-term exposure. Today, there is considerably more understanding of effects of long-term exposure, sublethal, indirect, cumulative, and synergistic effects, and the impacts of these effects throughout the salmon life cycle.

The process of setting temperature criteria requires evaluation of the biological needs of all species utilizing a watershed. In the Columbia River Basin, streams in the current or historic range of anadromous fish are designated as having a coldwater beneficial use (unless the use was specifically downgraded), although there are also trout streams in non-anadromous watersheds. Satisfying these uses involves satisfying the needs of the most sensitive species. Among the Salmonidae, the most valuable coldwater-dependent fish resource, there is a small amount of variation in thermal sensitivity among species, with bull trout being highly coldwater-dependent and the salmon being somewhat more tolerant of higher temperatures. Redband trout are considered to be the least dependent on cold water. Nonetheless, all these salmonids are coldwater species and their distributions generally follow longitudinal patterns of water temperature increase from headwaters downstream. This distribution pattern of salmonids is linked to the natural pattern of downstream warming of streams. In addition, distribution is related to the species' requirements for channel gradient, spawning substrate size and condition, pool frequency and quality. Abundance of a species tends to be related to all these factors, but is also influenced by numerous other habitat factors, such as water chemistry, large woody debris frequency and abundance, bank condition, etc. Proper water temperature, however, is a vital need for both distribution and abundance. If the water is too warm in any stream reach, it does not matter how good any of the other habitat factors might be. In an ecological management sense, salmonids of all species would find the best match between needs for cold water temperature and all other habitat factors mentioned provided that the watershed is managed in such a manner to allow cold water to flow downstream to the greatest extent before becoming too warm to be useful to salmonids.

The process of setting water temperature standards requires first identifying the most sensitive beneficial use. Salmonid spawning and rearing tend to be uses that require water that is as cold as physically feasible from the watershed involved. Temperature criteria have been set utilizing various basic information, such as the UUILT, the optimum temperature, final preferred temperature. Criteria set by regulatory agencies have used formulas such as MWAT that incorporate policy decisions to allow a certain amount of warming beyond the optimal temperature. They can also rely on assumptions that safety factors of a certain magnitude are adequate to keep a fish population from getting too close to a threshold temperature, beyond which negative effects become increasingly severe. Temperature criteria can also be based upon optimal conditions, because it is known from experimentation that survival, growth, reproductive capacity, scope for activity, disease resistance, etc. are best under these conditions. Because the effects of warm water are much more completely known today than in 1971, especially of sublethal effects, there is today a more compelling basis for managing for optimal conditions. In terms of providing a summary of this report, critical quantitative information can be found in figures and tables, such as the figure illustrating the temperature criteria for spring chinook. Tables are also presented on UUILT and CTM values for various species. The greatest value in this report, however, is not in statistical information but in the concepts and their biological basis that can be used in conjunction with thermal response statistics to support maintenance and restoration of optimum conditions. A temperature threshold provides the target (e.g., an optimum temperature for an activity), but the concepts stemming from all research available on biological effects provide the impetus for managing streams and their watersheds to achieve the target, and to manage with clear conviction and intent.

## THE CURRENT DOCUMENT

This document provided a review and analysis of thermal effects reported in recent literature, as well as some of the most significant older literature upon which most of our present concepts are still based. The 1971 Columbia River Thermal Effects Study provided a major synthesis of research available on effects to salmon in the Columbia River. The ideas presented in this report were very comprehensive and could easily have been sufficient documentation to support stringent actions to control water temperature increases. For whatever reason the numerous concepts presented in this report did not appear to be taken seriously in the field of temperature regulation. Possibly the reason for this was a preoccupation with investigation of damaging effects of power plant effluents (point sources) or maybe because the emphasis was on the mainstem effects rather than tributaries it was believed at the outset that little could be done to improve the thermal environment with the system of dams in place. In any case, the current review substantiates the positions held in the previous document, amplifies many of its points, and adds considerable new information and conceptual material from the recent literature that makes the need for action even more compelling.

The main messages in this document can be summarized in contrast to what was available or not available in the Thermal Effects Study (TES). The TES had physical and biological effects components. Physical measurement and analysis of river temperatures provide the monitoring data for expressing the state of the environment and indices to potential biological impacts. In the TES water temperatures were measured with chart recorders. Currently, the capability of monitoring water temperature has increased dramatically with inexpensive digital recorders that allow data downloading to computers for analysis at programmable time intervals. A new device, forward looking infra-red (FLIR), allows thermal scanning of entire stream surfaces where not blocked by riparian canopy. These instruments working in tandem provide a powerful means of performing rapid, extensive surveys. In 1971 the influence of mainstem dams in altering the distribution of heated waters both spatially and temporally was known. Research indicated a shifting of high water temperature into the autumn period and a loss of the normal daily fluctuation with the reservoirs in place.

Prior to 1971 experiments were undertaken to release water from Grande Coulee to lower Hanford Reach water temperatures. In recent years releases from Dworshak Reservoir were conducted to demonstrate a lowering of Snake River water temperature. The TES conducted modeling of river temperature for water management. The recent development of numerous mainstem and tributary temperature models allows prediction of temperature under river operation conditions with expected tributary inputs and also tributary temperatures based on channel morphology and riparian condition and other physical factors.

Biological effects were the main focus of this document and Volume 1 of the 1971 report. Numerous thermal effects on adults were recognized in the 1971 report. It was recognized that adults of any species have been observed to spawn within a fairly extensive temperature range but that for any species there is an upper and lower limit beyond which spawning is increasingly inhibited. It was known that high water temperature subjects adults to increased rate of disease and a higher metabolism that can easily deplete energy reserves. Adults enter the Columbia River with an initial energy supply that is largely exhausted by the time spawning is complete. Adults were known to use thermal refuges to escape high water temperature. Elevated water temperature can cause migration blockages. Sonic tagging of fish indicated a complex migration pattern of individual fish, with actual distance travelled being much greater than the net distance to spawning grounds. The effects of disease on adults were studied intensively, especially the incidence and survival rates of columnaris infections. It was known that warmwater diseases in general increased in terms of percentage mortality and virulence with temperatures beyond a threshold of approximately 15.6°C. It was also learned that adult salmon have a substantially lower thermal resistance (UILT of 21-22°C) to elevated temperatures than do the juveniles, making it dangerous to set temperature standards on the basis solely of juvenile exposure research.

Today bioenergetic studies are available that reveal energy allocation to growth, respiration, swimming, and other activities. Managing water temperature to provide optimal scope for activity helps ensure that adults will not have stress levels so high that there is little energy available for disease resistance. It has been well documented that temperatures of approximately 21-22°C establish migration barriers to most adult salmonids. Delays in migration that have been observed are significant enough so that the probability of surviving to spawn or to reach spawning grounds in time to spawn becomes low. The importance of coldwater refuges has been well documented using radiotracking devices. In addition, it has been found that coldwater refuges themselves are typically small in surface area and their availability (frequency and size) can be compromised by management actions. For example, loss of LWD, sedimentation of primary pools, channel widening, increases in road density, and loss of wetland habitats can lead to reduced inflow and retention of cool groundwater bottom areas of the channel. Migration patterns are increasingly well understood, using radiotracking equipment. Complex migration routes are observed in different portions of a run. Adding thermal blockages imposes delays in migration and also tends to lengthen the migration paths by increasing exploration and retreat behavior in which fish seek cold refuges and avoid warm water zones, followed by attempts to seek natal spawning grounds later under cooler conditions. There is currently much greater understanding of the effects of elevated temperatures in controlling the infection rate and course of warmwater diseases. The percentage survival and the time to death from the point of infection both decrease with increased temperature beyond the disease threshold. A great increase in understanding of the importance of prespawning temperatures occurred after the TES study. Effects on adults occurred as thermal death, increased disease, inability to migrate, and inhibition of spawning. In addition, elevated temperatures cause reduction in gamete production and viability. Even when fertilization occurs in warm waters (especially waters >16°C) delayed mortality is observed as well as growth abnormalities.

The egg stage was known in 1971 to be a sensitive stage in development. As a general rule, salmonid eggs are sensitive to water temperatures <4°C and >14.4°C. It was found that eggs could withstand temperatures approaching 0°C if they were presented after the 128-cell stage of development. The ideal egg incubation temperature was considered to be approximately 5.5-12.8°C for all salmon species, although tolerance to temperatures as high as 18°C was thought to occur in some species in fluctuating temperature regimes. Diel temperature fluctuations were thought to be beneficial during incubation as opposed to constant temperature incubation.

Today a vast increase in information on the thermal effects on eggs is available. The rate of egg development of all salmon species with temperature is highly predictable. In addition, data on survival rates for eggs incubated at temperatures <4°C and >14.4°C are available. For almost all salmonids these temperature thresholds remain as meaningful guidelines for observing impacts of higher and lower incubation temperatures on survival. There are some statistically significant differences among stocks and families within stocks in survival at low and high temperature ranges. However, in terms of absolute degrees temperature the differences tend to be small. Salmon stocks from inland populations tend to be adapted to colder winter conditions and those from coastal populations are better able to withstand warmer winter incubation temperatures. This can be attributed to the more moderate thermal conditions in coastal streams than interior streams. Stocks that are more thermally tolerant than others tend to have less capability for any further selection of tolerance characteristics.

In terms of egg incubation temperature it is reasonable to establish maximum allowable temperatures at egg deposition stage. Excessive temperatures reduce egg viability and fertilizability. However, just as important as meeting critical threshold temperatures at deposition is accumulating the required number of thermal units during development. The entire thermal regime during the incubation phase is important to the proper timing of fry emergence. That is, even though temperatures of 10°C would provide high survival to emergence, the greater rate of development would lead to very early emergence. Development times under fluctuating thermal regimes during incubation can be estimated from mean temperatures. However, compensation has been documented as a mechanism that tends to help maintain emergence at a prescribed number of days incubation, despite variation in temperature, within tolerance limits. Emergence times can be predicted by using mean temperatures for a sine wave thermocycle or also by using an egg development rate equation at each time increment during the cycle and calculating the percentage of a full development to emergence period that is completed at each increment.

In 1971 it was known that thermal effects to fish (and especially to juveniles, because most test fish were juveniles) were a function of thermal dose, which was related to time and temperature of exposure. Also, the resistance time to constant temperature exposure is a function of the prior acclimation temperature. In the field, fish are acclimatized to a certain temperature regime and the thermal response to elevated temperatures depends on this history of exposures and also on other factors, such as health, condition, size, age, etc. Upper and lower exposure limits were described for all salmon as well as preference temperatures in the work of Brett (1952). Studies of the effect of temperature on growth resulted in establishing optimum growth ranges, beyond which growth rates decline significantly. Knowledge of the optimum temperatures and the lethal limits led to establishing criteria to protect fish. Temperatures of >17°C were cited as leading to increased risk of disease. In addition, high temperatures were discovered to be linked to increased predation risk. Thermal shocks also were found to produce greater predation risk. Repeated exposure to lethal temperatures for sublethal times were not considered to have an effect. However, exposure to multiple stress, such as temperature and heavy metal toxicants was found to reduce resistance times.

Since 1971 a great amount of new information has become available on juvenile effects. The UUILT of most salmonids falls within the range 21-26°C. However, it seems clear that direct mortality can be produced from single exposures or in cumulative exposures over a series of 2-3 days, resulting cumulatively in 100% of a lethal dose. Temperatures above 24°C become increasingly significant in adding to a lethal dose. Using constant temperature experimental results, the time to death can be predicted from increments of temperature above 24°C on single or multiple days exposure. Because fish in the field are acclimatized to temperatures experienced over days preceding a critical exposure, it is problematic to estimate what the effective acclimation temperature is. Experimental work has revealed that effective acclimation temperature in a thermocycle tends to be equivalent to a temperature between the mean and the maximum of the cycle. Most work indicates acclimation either to a temperature midway between the mean and the maximum or to the maximum.

Although salmonids can be excluded from a stream reach by lethal temperatures they can also leave voluntary due to thermal preference. Intrabasin migration has been well documented in salmonids and allows juveniles to move to temperatures more nearly meeting preferences. However, migration barriers, thermal barriers, limited area of coldwater refuges, or inability to swim the distances needed to retreat to cold water all can lead to exposing a portion of the population to thermal death under warming stream conditions during the season. On a multi-annual basis continued riparian cover loss leads to overall restriction in productive capacity of the stream. Despite the upper lethal limits, fish tend to be limited in distribution to upper temperatures in the range 22-24°C. That is, the downstream limit to distribution tends to be 2-3°C less than the UILT. This temperature range establishes the point on the mainstem of a tributary at which salmonids make the transition from present to absent. Population density declines to zero in this zone. Upstream of this zone temperatures are typically colder, and as temperatures enter the optimal range under other optimum habitat conditions (e.g., gradient, pool frequency and quality, etc.), population density can reach an optimum (this is a highly simplified concept because carrying capacity involves many more factors, see McCullough 1996). Fish survival is not impaired by summer cold temperatures, but growth rates could be low in certain streams, requiring an extra year of development to emigrate (anadromous) or to mature (resident).

Growth rates in the field are a useful index to optimal temperatures. Survival rates are high under these temperatures, but at the growth limit, increasing stress occurs. Very significant information was provided in studies on sockeye by Brett (1971, 1983) and brown trout by Elliott (1971, 1994), showing that as food becomes limiting, optimum growth temperatures decline. Typically under field conditions fish are not able to feed to satiation so growth rates are seldom as high as might be predicted from constant temperature experiments under satiation feeding. At the same time as food supply diminishes, loading stresses influence survival at lower temperatures. Many studies have related growth rates in the field under fluctuating temperatures with growth rates in the laboratory under constant temperatures equal to the mean temperature in the fluctuating regime. Some studies have concluded that there is no difference in growth rates among populations in different environments under similar mean temperatures in a fluctuating regime and consequently no genetic differences. Other research implies that growth rates in fluctuating temperature regimes are greater than under constant temperature regimes.

Genetic differences in growth rates are sometimes demonstrated among stocks reared at constant temperatures, but they are frequently only evident at the extremes in temperature within the tolerance range of the species. Certain stocks are found to have somewhat greater resistance times to extreme temperatures than other stocks, but most typically, when differences occur they are associated with morphological differences and with differentiation as subspecies.  The absolute differences in resistance times are small and do not ever result in a conclusion that higher critical levels should be established for certain stocks.

Bioenergetics and power budgeting are important new ways to view the energy allocations made by fish to accommodate their growth, metabolism, and activity needs.  The scope for activity is a function of acclimation and exposure temperatures in the same way as lethal responses.  The greater the scope for activity under a combination of acclimation and exposure temperatures, the greater is the ability of the fish to perform burst swimming activity to negotiate falls or escape predators.  Also, if the fish is able to maintain a large scope given its exposure temperature regime, it is more able to resist disease.  Power budgeting is energy allocation made under very short time periods (seconds to minutes).  High levels of exertion requiring long periods of rest result in short-term inability to perform other functions necessary to survival.  Bioenergetics can be considered as the long-term allocation of energy resources to perform life functions, such as migration and spawning.  Storage of fat and protein prior to migration is essential so that the migration distance can be traversed, holding occurs, and spawning activity and nest guarding take place.

Much has been learned in recent years about role of temperature in mediating the outcome of competitive interactions between fish species.  Overlap in habitat use is established by preference for factors such as channel gradient, depth, substrate composition.  Given a resource used in common, the outcome of competition is typically related to size and aggressiveness.  This is frequently reported in studies of competition among salmonids.  However, temperature is very important in shifting competitive dominance between two species having different thermal preferences.  In competition between salmonids and coolwater tolerant species, this transition in dominance occurs 2-4°C lower than the range of maximum temperatures that is usually associated with total elimination of salmonids in a river continuum (i.e., 22-24°C).

Synergistic effects on salmonid survival are much more adequately understood today than in 1971.  Temperature combined with numerous other water quality factors, such as dissolved oxygen, suspended sediment, heavy metals, and cyanide, effectively reduces the resistance time to death at a certain temperature, or conversely results in 50% mortality within 24 h at a lower temperature.  Synergistic effects have been well studied on juvenile survival, but their impacts are also documented as causing migration delays in adults and egg mortality in spawning gravels.

The TES report provided some information on smolt migration under the influence of thermal exposure.  It was known that due to the effect of dams the rate of migration to the ocean was reduced.  Premature or delayed entry to saltwater reduced survival.  Warm water in reservoirs was known to inhibit migration, increase residualism, predation risk, and disease occurrence.  Thermal shocks that occur within and do not exceed the range 5-23°C were thought not to impair swimming performance.  A temperature range of 5-17°C was considered acceptable for smolt migration.

Since the TES report many new studies became available concerning the influence of temperature on smoltification. Dynamics of smolting involve the interaction of temperature, photoperiod, and the trend in both temperature and photoperiod. However, under field conditions photoperiod and the direction of change in photoperiod are not subject to modification and altered temperature conditions become the primary means of impact to the smoltification process. It has been learned that temperatures that become inhibitory to smoltification for certain species can be as low as 13°C. Incomplete smoltification or desmoltification caused by elevated emigration temperatures reduces the saltwater readiness and impairs their marine growth and survival.

# FIGURES

**Figure 1.** Effect of temperature profile in the Tucannon River on spring chinook rearing capacity and adult returns based on three restoration scenarios. Taken from Theurer et al. (1985) and a calculation of Jon Rhodes, CRITFC hydrologist.

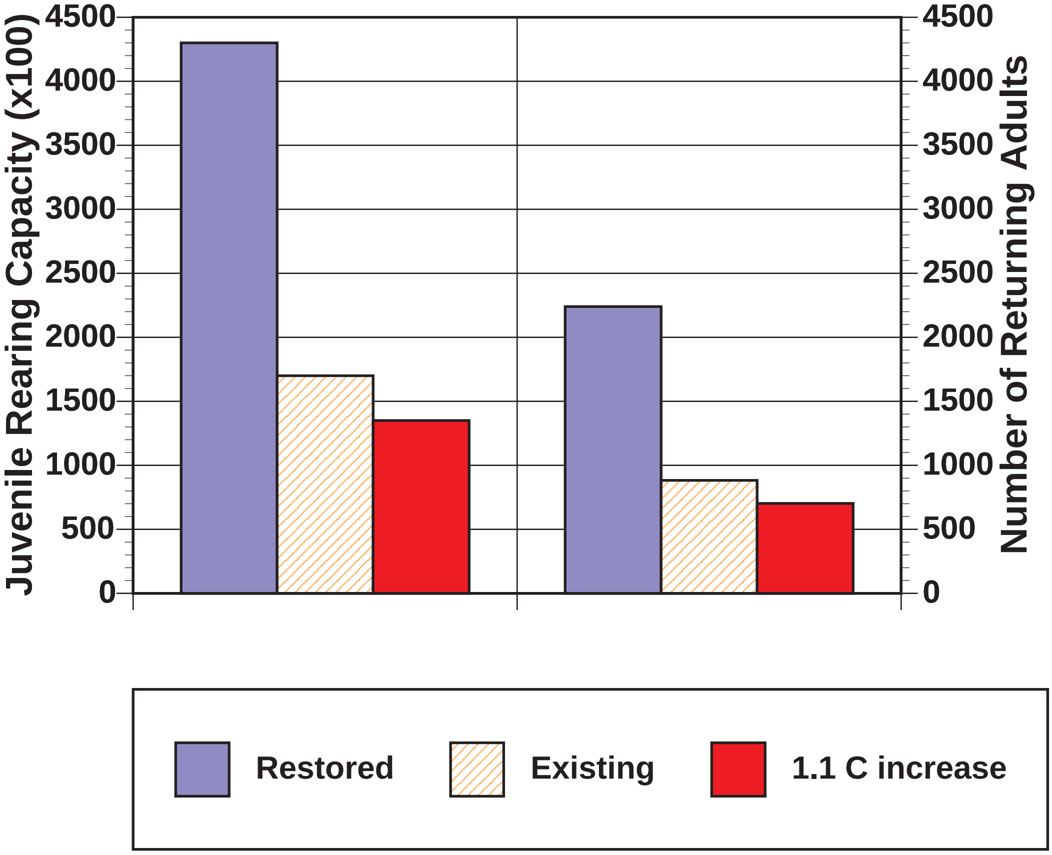

Juvenile Rearing Capacity (x100)
Number of Returning Adults
0
500
1000
1500
2000
2500
3000
3500
4000
4500
Restored
Existing
1.1 C increase

Figure 1.

**Figure 2.** Spring chinook temperature requirements.

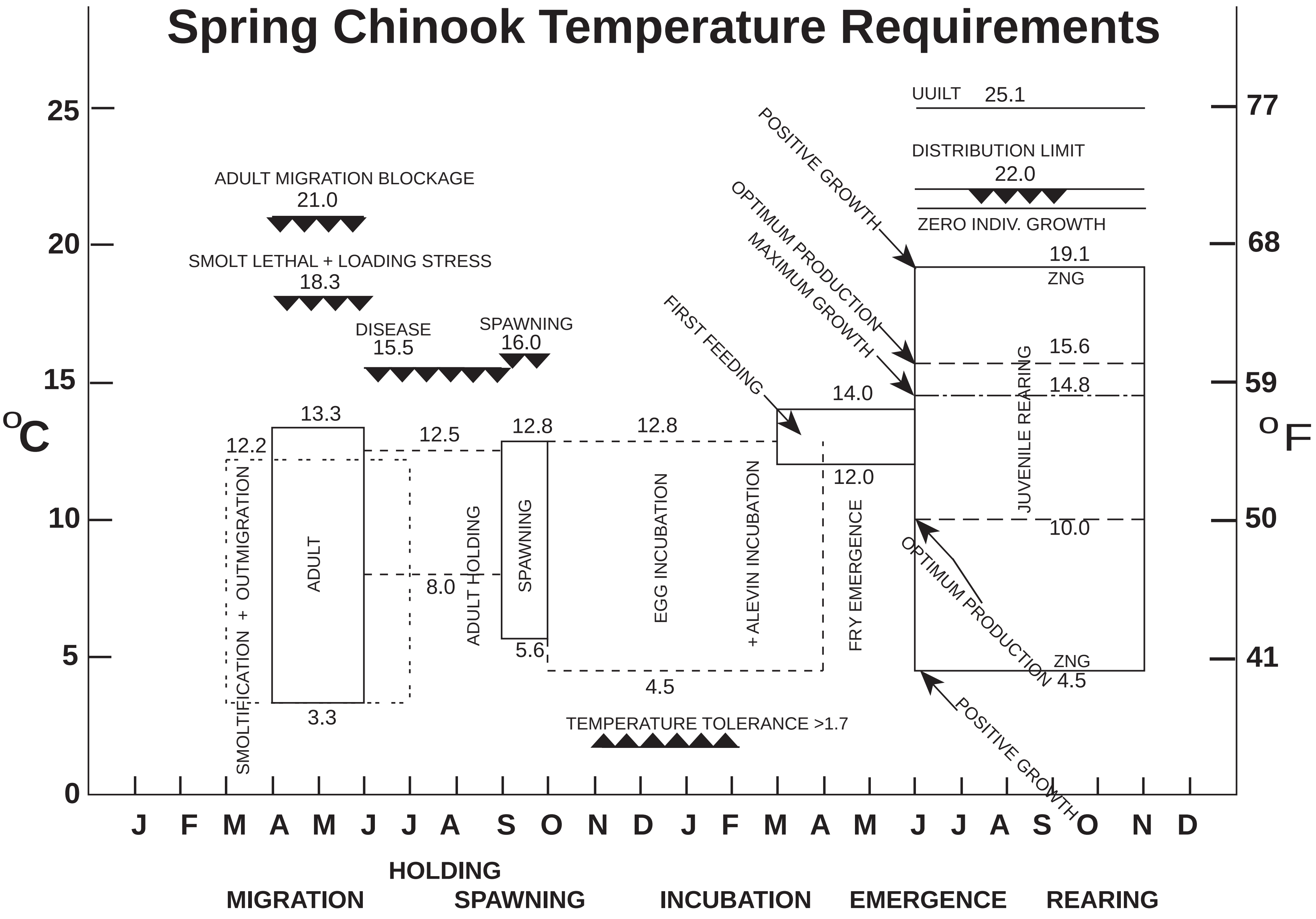

Spring Chinook Temperature Requirements
°C
°F
25
20
15
10
5
0
77
68
59
50
41
ADULT MIGRATION BLOCKAGE
21.0
SMOLT LETHAL + LOADING STRESS
18.3
DISEASE
15.5
SPAWNING
16.0
13.3
12.2
12.5
12.8
12.8
8.0
5.6
4.5
3.3
SMOLTIFICATION + OUTMIGRATION
ADULT
ADULT HOLDING
SPAWNING
EGG INCUBATION
+ ALEVIN INCUBATION
FRY EMERGENCE
FIRST FEEDING
14.0
12.0
TEMPERATURE TOLERANCE >1.7
UUILT
25.1
DISTRIBUTION LIMIT
22.0
ZERO INDIV. GROWTH
POSITIVE GROWTH
OPTIMUM PRODUCTION
MAXIMUM GROWTH
19.1
ZNG
15.6
14.8
JUVENILE REARING
10.0
OPTIMUM PRODUCTION
ZNG
4.5
POSITIVE GROWTH
J F M A M J J A S O N D J F M A M J J A S O N D
HOLDING
MIGRATION
SPAWNING
INCUBATION
EMERGENCE
REARING

Figure 2.

**Figure 3.** Days from fertilization to emergence for chinook, coho, and sockeye salmon calculated from formulas of Beacham and Murray (1990).

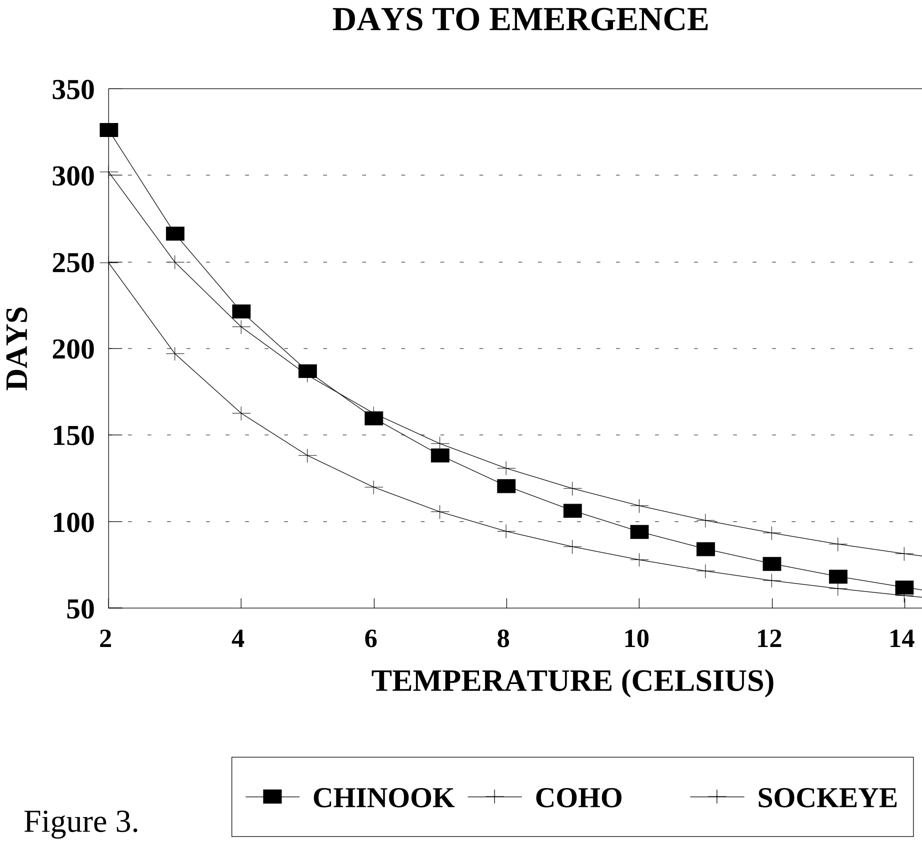

DAYS TO EMERGENCE
350
300
250
200
150
100
50
DAYS
2
4
6
8
10
12
14
16
TEMPERATURE (CELSIUS)
CHINOOK
COHO
SOCKEYE

Figure 3.

**Figure 4.** Reduction in number of days to emergence for each 1°C increase from a base temperature of 2°C, calculated for chinook, coho, and sockeye. Calculated from data plotted in Figure 3.

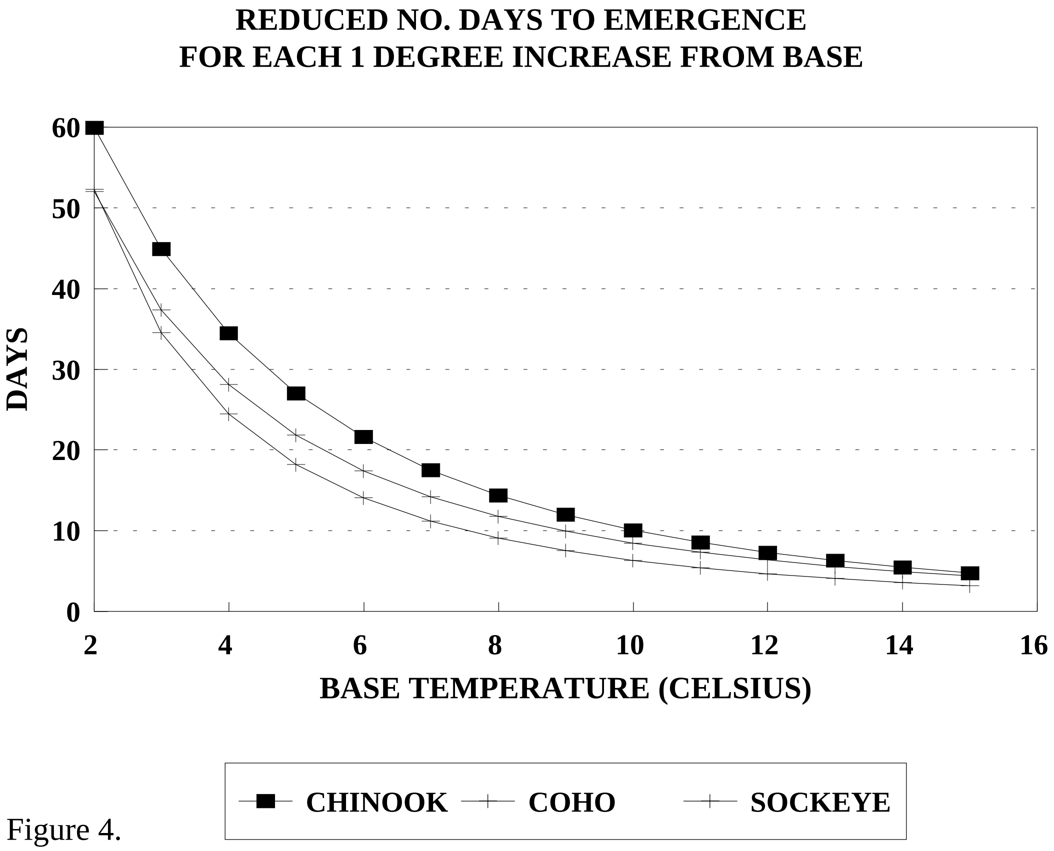

REDUCED NO. DAYS TO EMERGENCE
FOR EACH 1 DEGREE INCREASE FROM BASE
DAYS
0
10
20
30
40
50
60
2
4
6
8
10
12
14
16
BASE TEMPERATURE (CELSIUS)
CHINOOK
COHO
SOCKEYE

Figure 4.

**Figure 5.** Cumulative thermal units (degree days for temperatures >0°C) for spring chinook incubation periods in the mainstem John Day (RK 422) and the North Fork John Day (RK 97) for years 1980-81 and 1982-83. Thermal units are plotted against days from peak spawning on the mainstem John Day. Data taken from Lindsay et al. (1986).

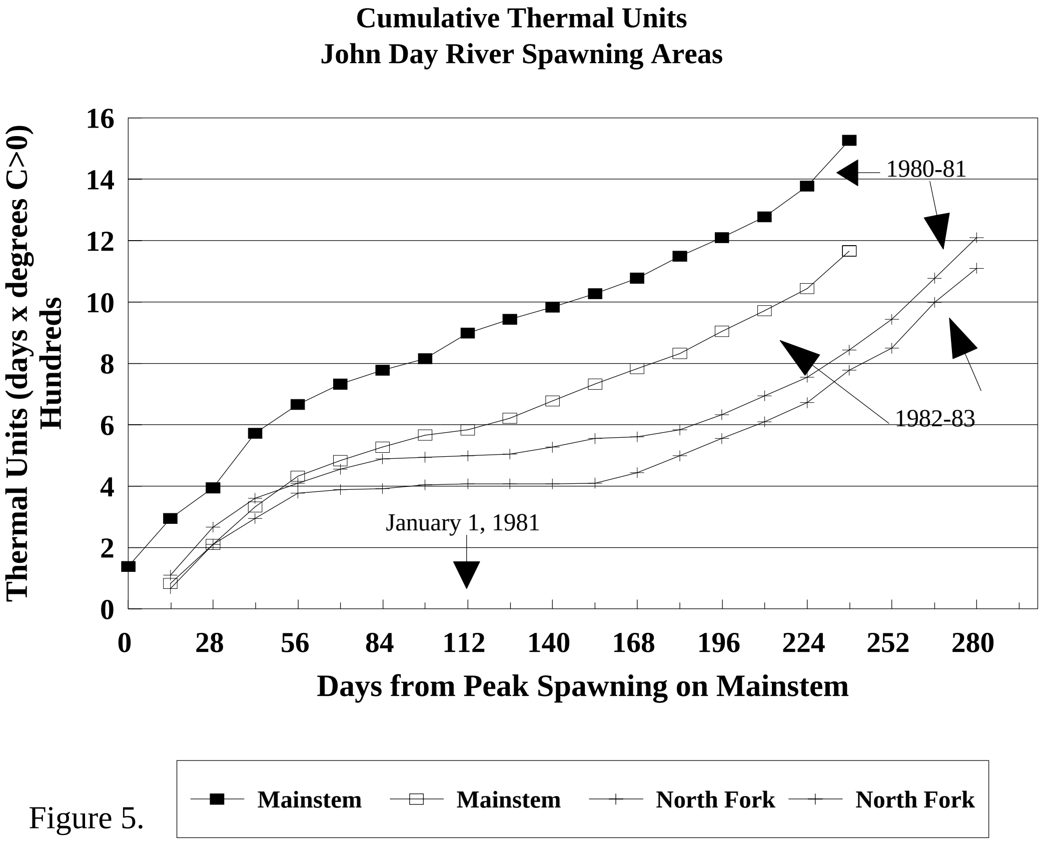

Cumulative Thermal Units
John Day River Spawning Areas
Thermal Units (days x degrees C>0)
Hundreds
16
14
12
10
8
6
4
2
0
0
28
56
84
112
140
168
196
224
252
280
Days from Peak Spawning on Mainstem
1980-81
1982-83
January 1, 1981
Mainstem
Mainstem
North Fork
North Fork

Figure 5.

**Figure 6.** Cumulative percentage of time from fertilization to emergence on the North Fork John Day for the 1980-81 incubation period estimated using the formula $\ln D = 10.404 - 2.043 \ln(T + 7.575)$ from Beacham and Murray (1990), where days (D) are a function of incubation temperature (T) and from the mean temperatures taken from Lindsay et al. (1986).

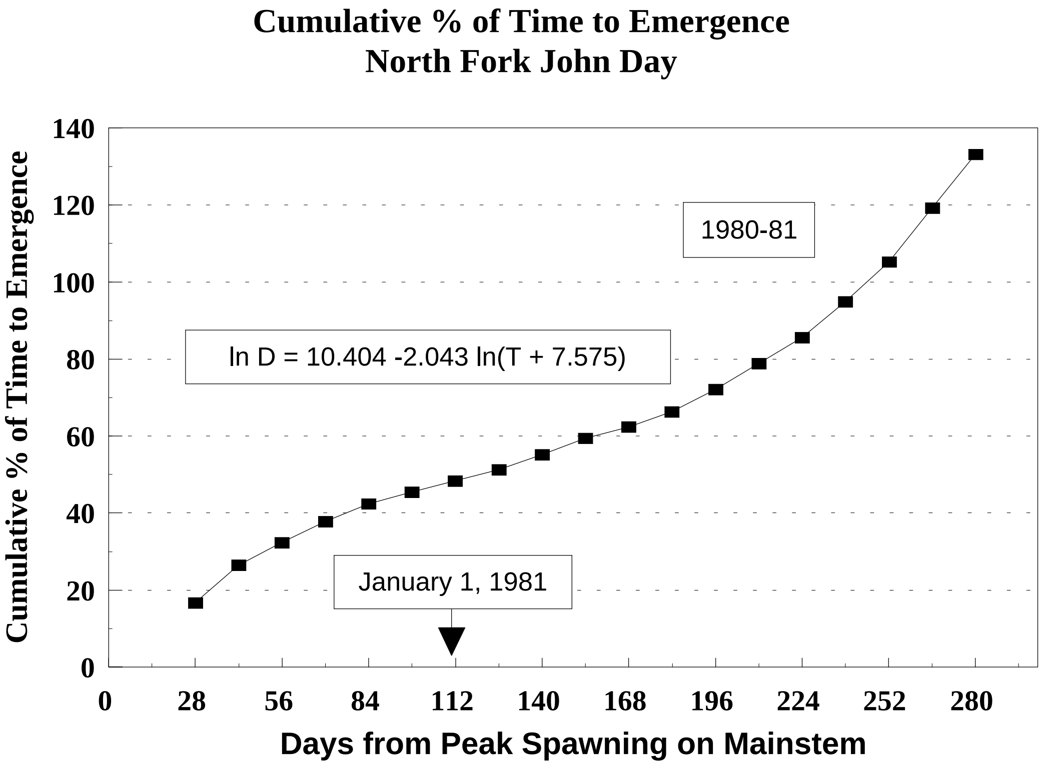

Cumulative % of Time to Emergence
North Fork John Day
Cumulative % of Time to Emergence
140
120
100
80
60
40
20
0
1980-81
ln D = 10.404 -2.043 ln(T + 7.575)
January 1, 1981
0
28
56
84
112
140
168
196
224
252
280
Days from Peak Spawning on Mainstem

Figure 6.

**Figure 7.** A thermal tolerance diagram for spring chinook, Oncorhynchus tshawytscha. This diagram has UILT, UUILT, LILT, LULT lines taken from the work of Brett (1952). The growth zone and spawning zone were modeled on Brett (1958) and Elliott (1981), but using upper growth temperatures and upper optimal growth temperature taken from Armour (1990). Final preferendum and acute preference line were taken from Brett (1952). Resistance zones are modeled on Elliott (1981). Critical thermal maximum (CTM) and chronic thermal maximum (ChTM) were taken from results for brown trout at 15 and 20°C acclimation from Elliott and Elliott (1995). CTM and ChTM were estimated from heating rates of 18°C/h and 0.01°C/h, respectively, in their study. The CTM line has also been considered to parallel the UILT line (Jobling 1981, Bennett et al. 1998), but Elliott and Elliott (1995) found the CTM values to be similar at the two acclimation temperatures used.

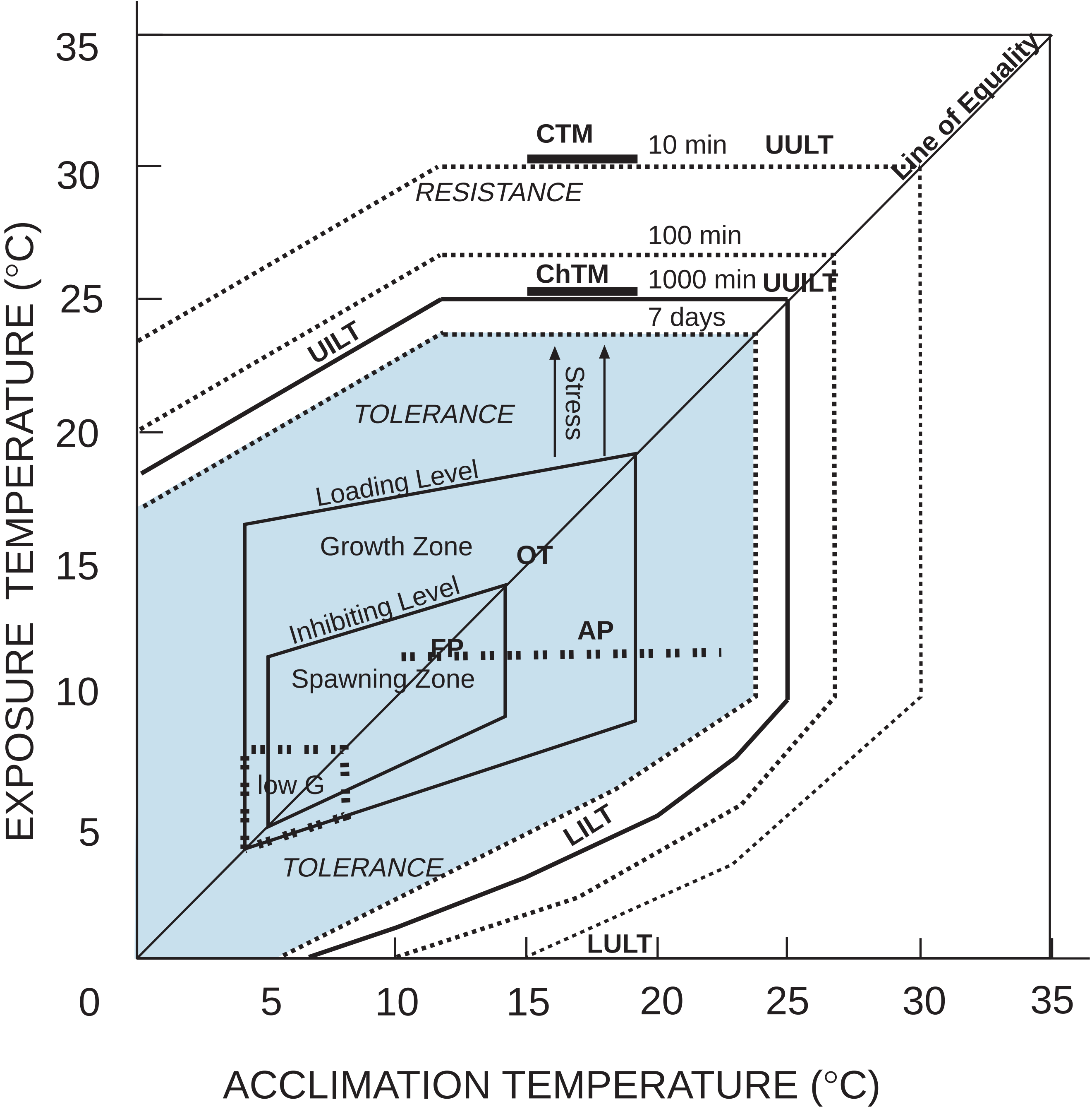
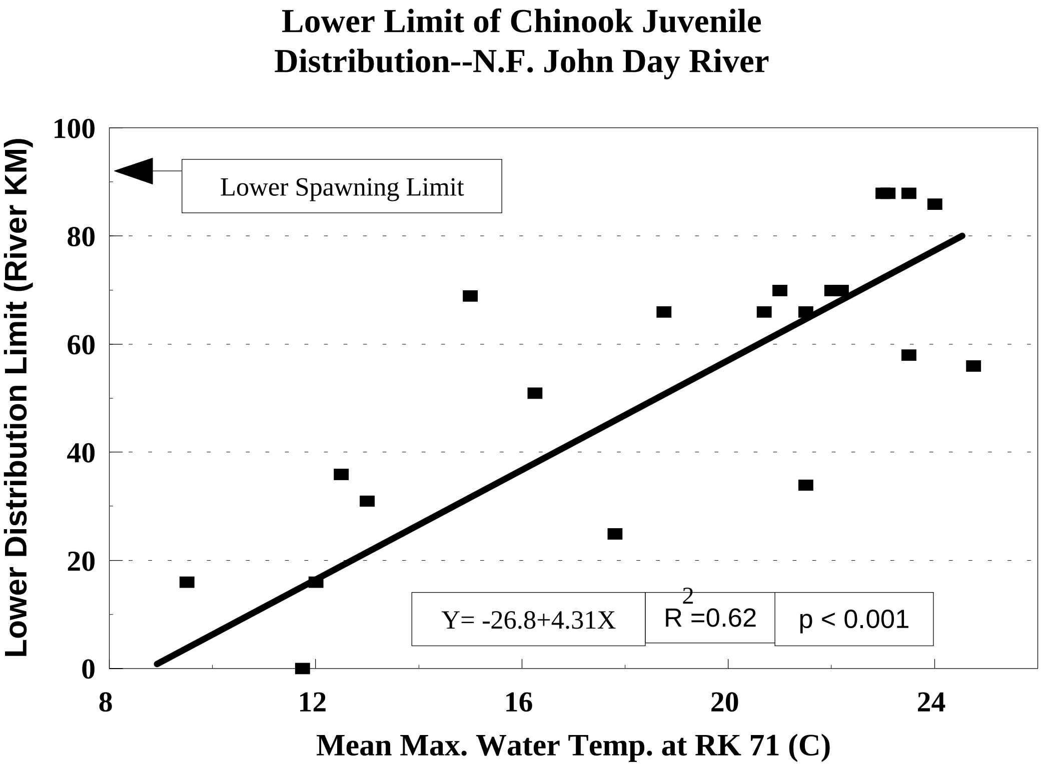

35
30
25
20
15
10
5
0
5
10
15
20
25
30
35
EXPOSURE TEMPERATURE (°C)
ACCLIMATION TEMPERATURE (°C)
CTM
10 min
UULT
Line of Equality
RESISTANCE
100 min
ChTM
1000 min
UUILT
7 days
UILT
Stress
TOLERANCE
Loading Level
Growth Zone
OT
Inhibiting Level
AP
FP
Spawning Zone
low G
LILT
TOLERANCE
LULT

Figure 7.

**Figure 8.** The lower limit to distribution of spring chinook juveniles observed in the North Fork John Day by Lindsay et al. (1986) in terms of mean maximum water temperature (°C).



Lower Limit of Chinook Juvenile Distribution--N.F. John Day River

Figure 8.

**Figure 9.** The maximum extent of distribution of spawning and rearing of spring chinook in the John Day River, showing the mainstem John Day, North Fork John Day, Middle Fork John Day, and Upper Mainstem John Day as separate production units. Rearing area is marked in dotted red; spawning are is marked in solid blue. Rearing can occur in spring to the downstream extent indicated; below this point rearing is not feasible because of excessive temperatures. Rearing, but not spawning, can also occur in certain headwater areas indicated. Based on information taken from Lindsay et al. (1986).

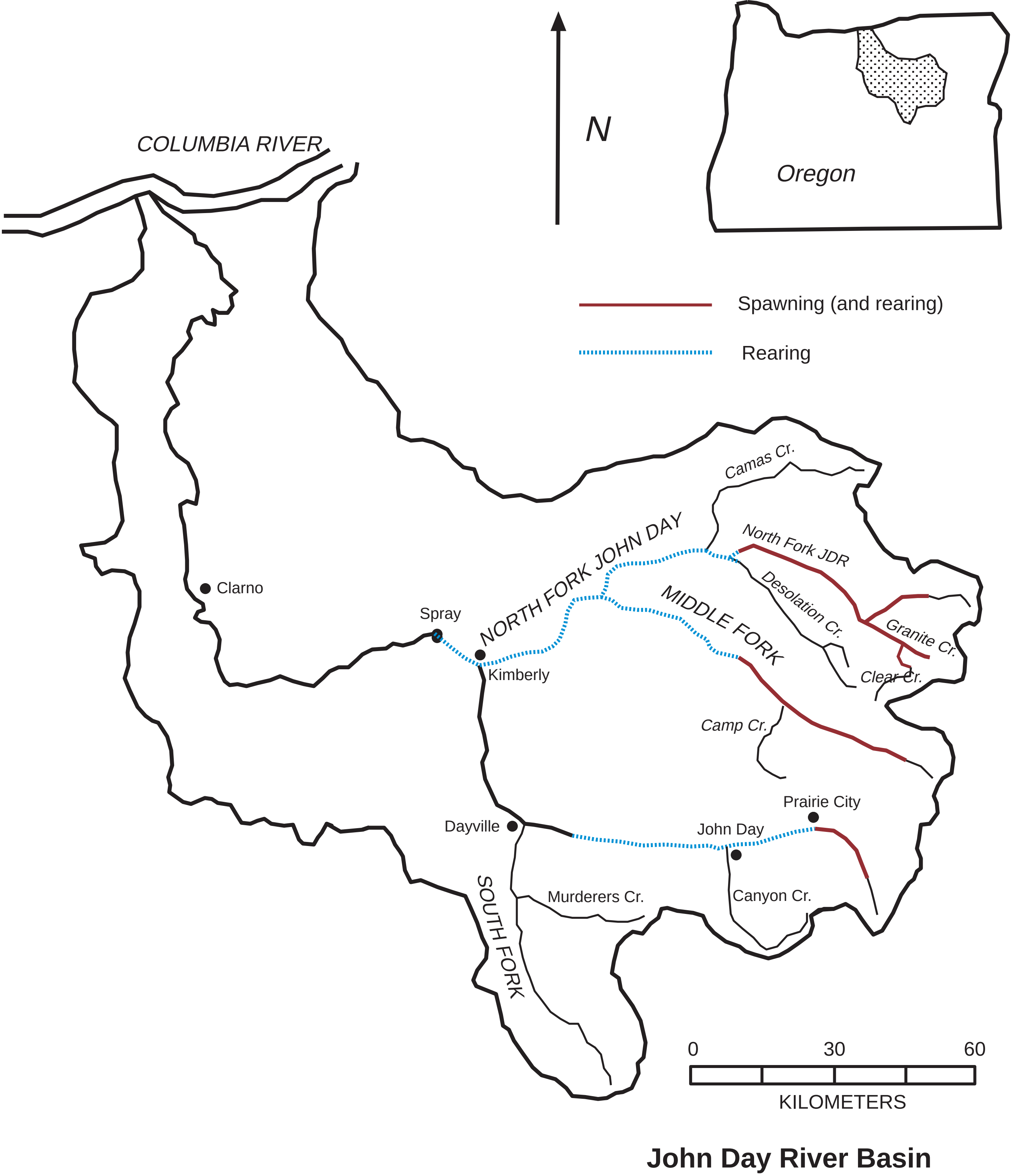
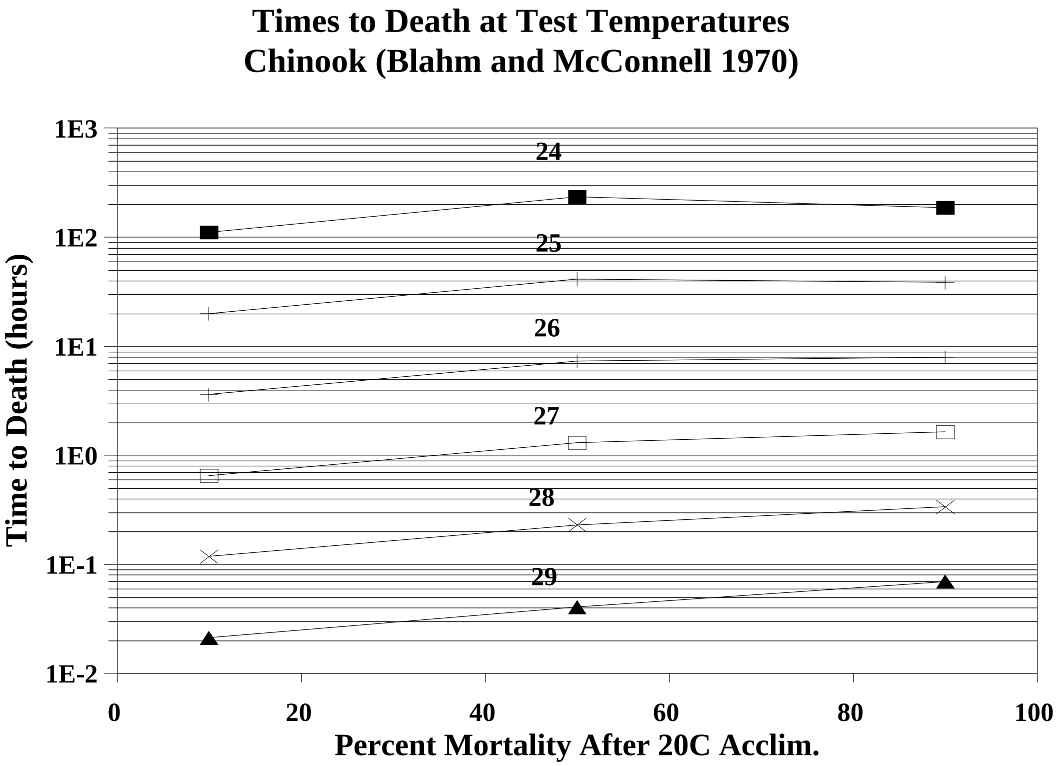

COLUMBIA RIVER
N
Oregon
Spawning (and rearing)
Rearing
Camas Cr.
North Fork JDR
NORTH FORK JOHN DAY
Desolation Cr.
MIDDLE FORK
Granite Cr.
Clear Cr.
Camp Cr.
Clarno
Spray
Kimberly
Prairie City
John Day
Dayville
Murderers Cr.
Canyon Cr.
SOUTH FORK
0
30
60
KILOMETERS
John Day River Basin

Figure 9.

**Figure 10.** Times to 10, 50, and 90% mortality of chinook at test temperatures ranging from 24°C to 29°C in 1°C increments based on a formula by Blahm and McConnell (1970) as reported in Coutant (1972).



Times to Death at Test Temperatures
Chinook (Blahm and McConnell 1970)
1E3
1E2
1E1
1E0
1E-1
1E-2
Time to Death (hours)
24
25
26
27
28
29
0
20
40
60
80
100
Percent Mortality After 20C Acclim.

Figure 10.

**Figure 11.** Times to 50% mortality for juvenile spring chinook acclimated to either 20 or 24°C. Data taken from Brett (1952).

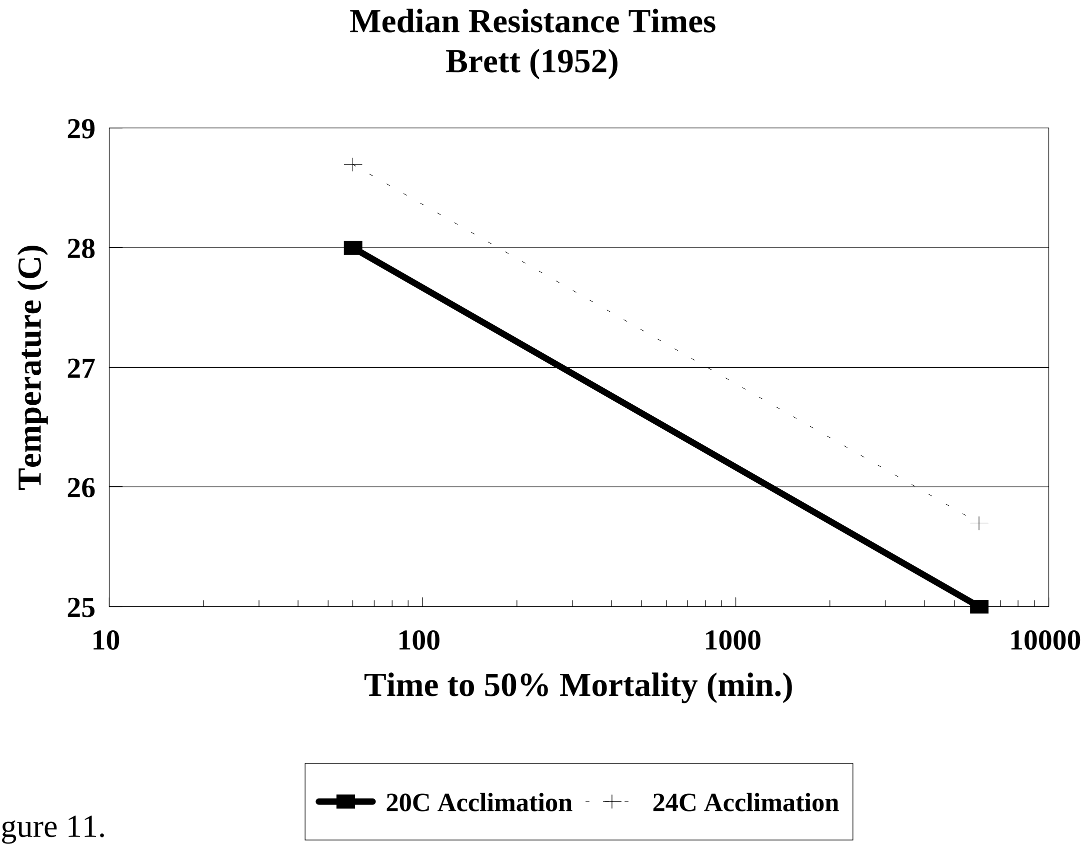

Median Resistance Times
Brett (1952)
Temperature (C)
29
28
27
26
25
10
100
1000
10000
Time to 50% Mortality (min.)
20C Acclimation
24C Acclimation

Figure 11.

**Figure 12.** Tucannon River water temperatures (daily maximum, mean, and minimum) for August 1991 at the Marengo Bridge site (RK 41). The period of temperatures where the maximum daily temperature exceeded 23°C is highlighted.

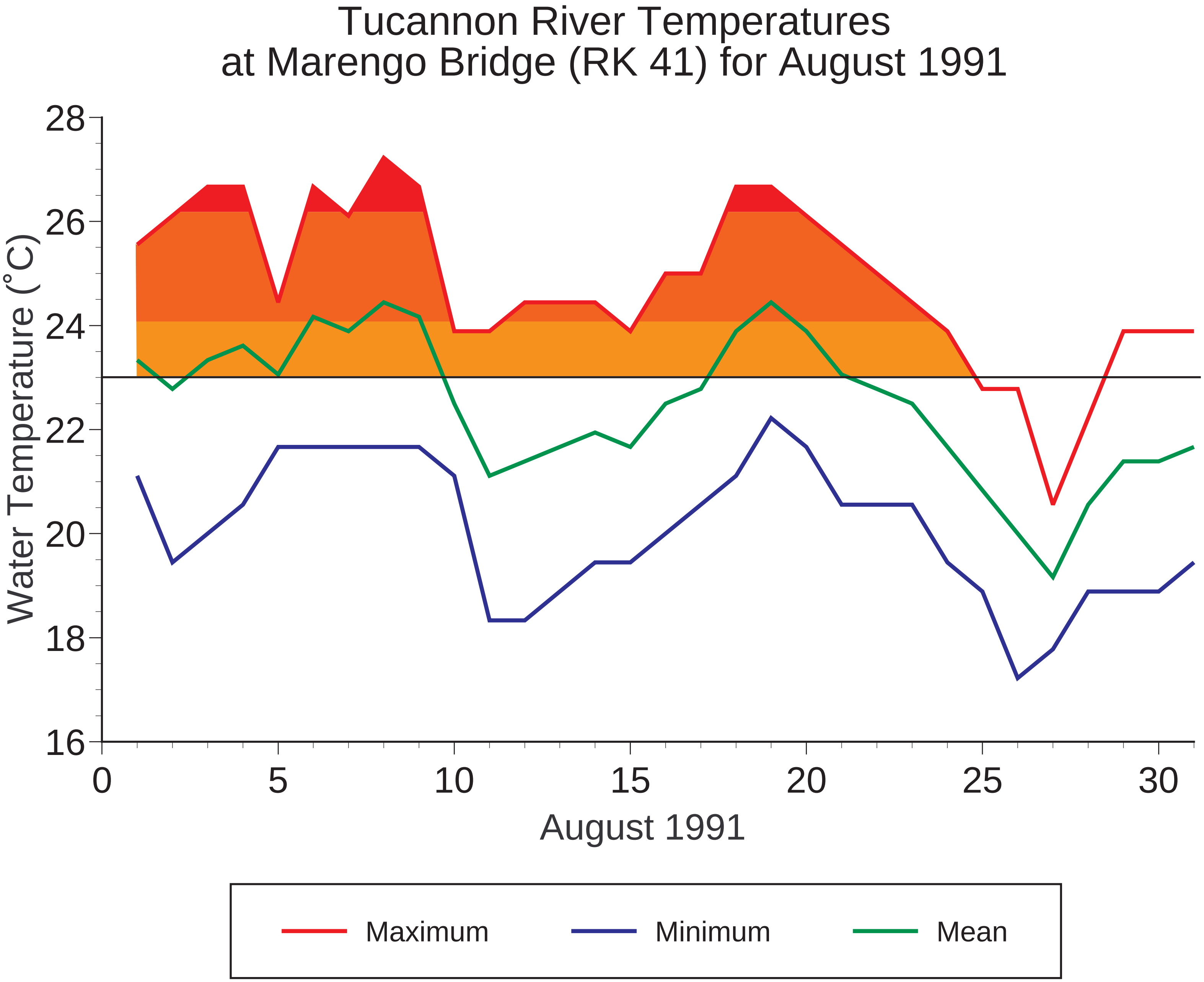

Tucannon River Temperatures
at Marengo Bridge (RK 41) for August 1991
Water Temperature (°C)
28
26
24
22
20
18
16
0
5
10
15
20
25
30
August 1991
Maximum
Minimum
Mean

Figure 12.

**Figure 13.** Tucannon River water temperatures (daily maximum, mean, and minimum) for August 1991 at the Deer Lake site (RK 62) as reported in Bugert et al. (1992).

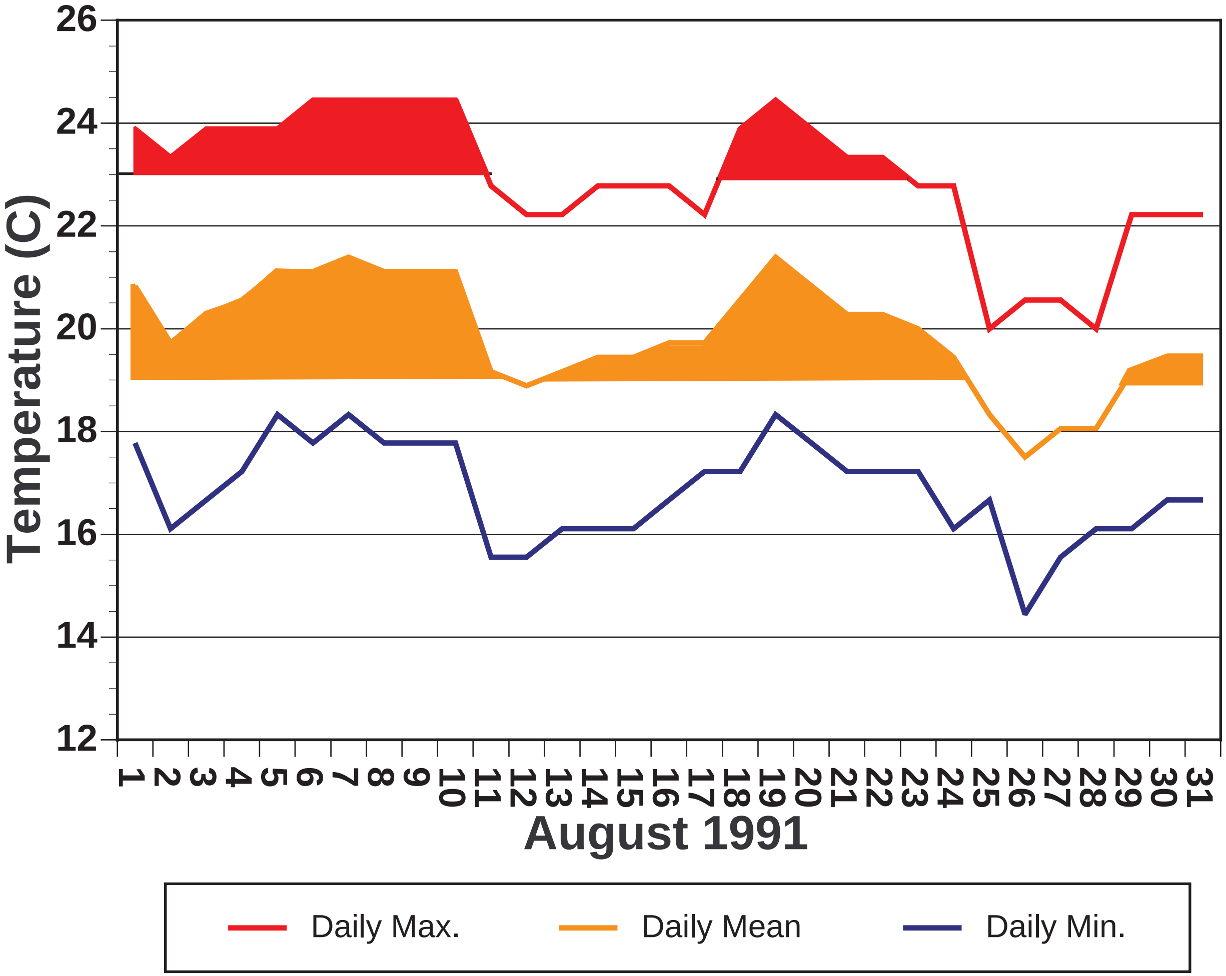

26
24
22
20
18
16
14
12
Temperature (C)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
August 1991
Daily Max.
Daily Mean
Daily Min.

Figure 13.

**Figure 14.** Tucannon River maximum daily water temperatures for the period July 1-September 30 at Cummings Creek for years 1986-1997. Data provided courtesy of Joseph Bumgarner, WDFW, Dayton, Washington.

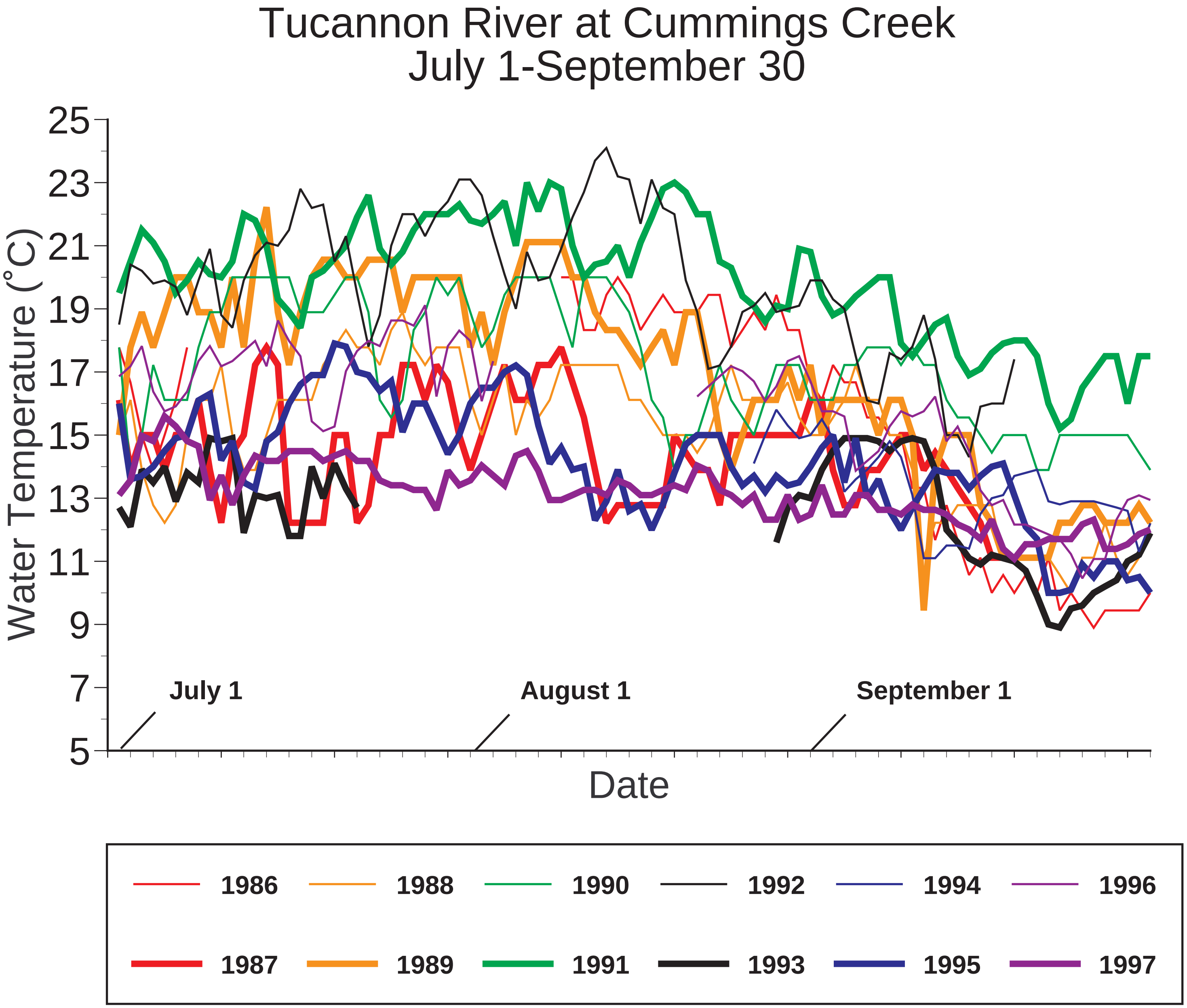

Tucannon River at Cummings Creek
July 1-September 30
Water Temperature (°C)
25
23
21
19
17
15
13
11
9
7
5
July 1
August 1
September 1
Date
1986
1988
1990
1992
1994
1996
1987
1989
1991
1993
1995
1997

Figure 14.

**Figure 15.** Tucannon River maximum daily water temperatures for the period July 1-September 30 at Marengo Bridge for years 1989-1997. Data provided courtesy of Joseph Bumgarner, WDFW, Dayton, Washington.

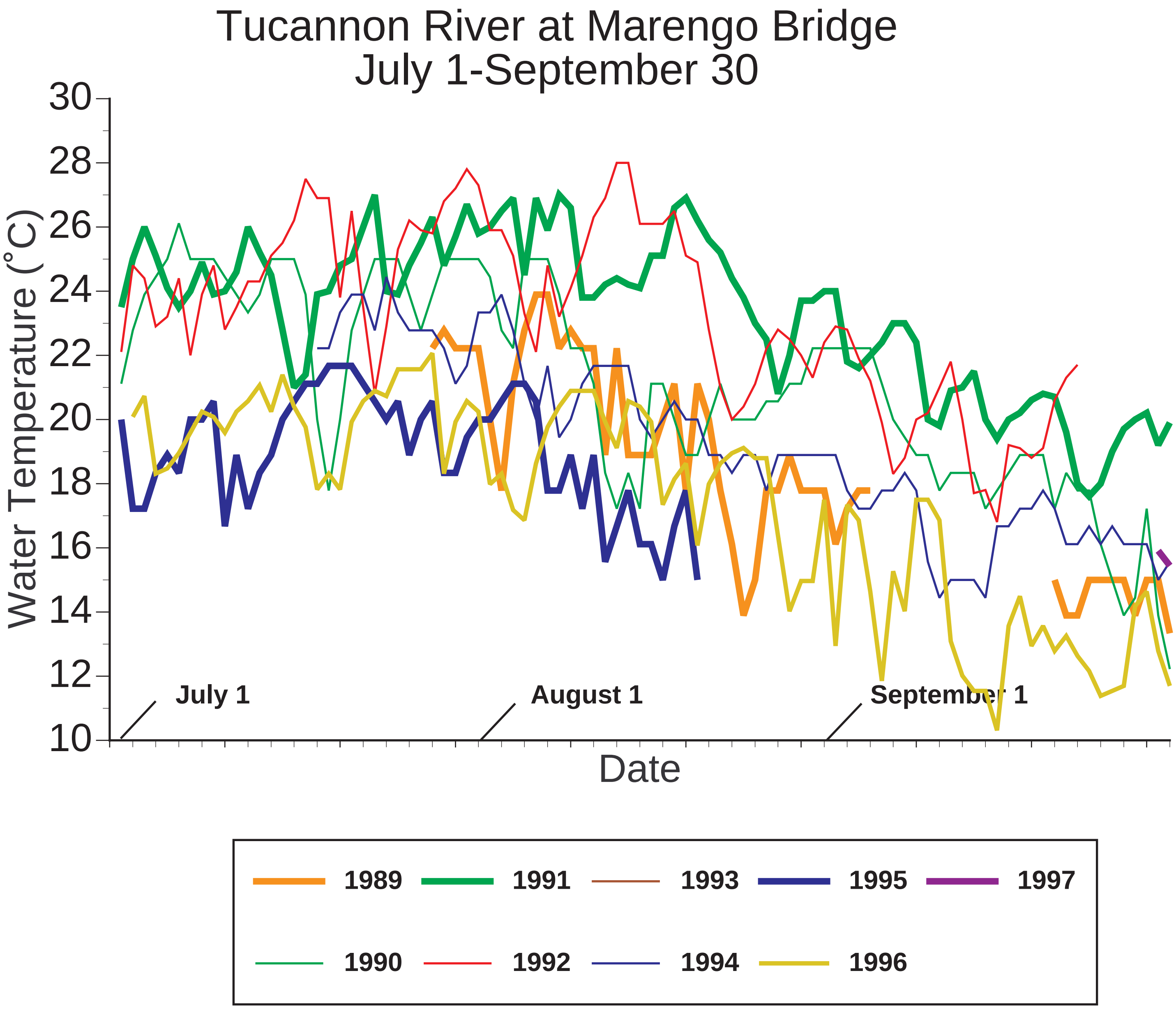

Tucannon River at Marengo Bridge
July 1-September 30
Water Temperature (°C)
30
28
26
24
22
20
18
16
14
12
10
July 1
August 1
September 1
Date
1989
1991
1993
1995
1997
1990
1992
1994
1996

Figure 15.

**Figure 16.** The percentage of days in July/August 1991 reaching maximum daily water temperatures at Marengo Bridge, Tucannon River.

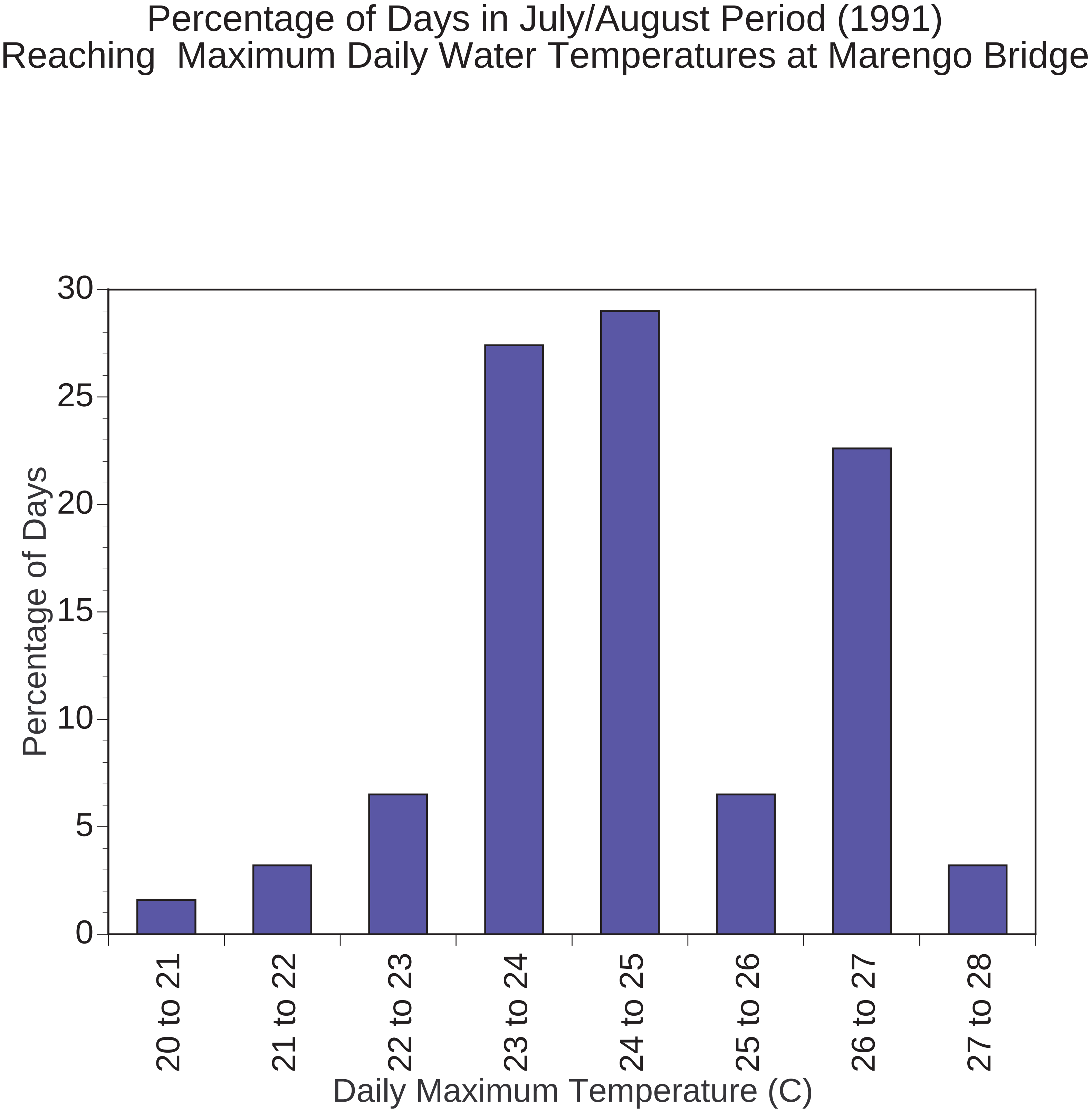

Percentage of Days in July/August Period (1991)
Reaching Maximum Daily Water Temperatures at Marengo Bridge
Percentage of Days
0
5
10
15
20
25
30
20 to 21
21 to 22
22 to 23
23 to 24
24 to 25
25 to 26
26 to 27
27 to 28
Daily Maximum Temperature (C)

Figure 16.

**Figure 17.** Tucannon River water temperatures (daily maximum, mean, and minimum; also 7-d moving mean of the maximum daily temperature and 7-d moving mean of the mean daily temperature) for July-August 1991 at the Marengo Bridge site (RK 41).

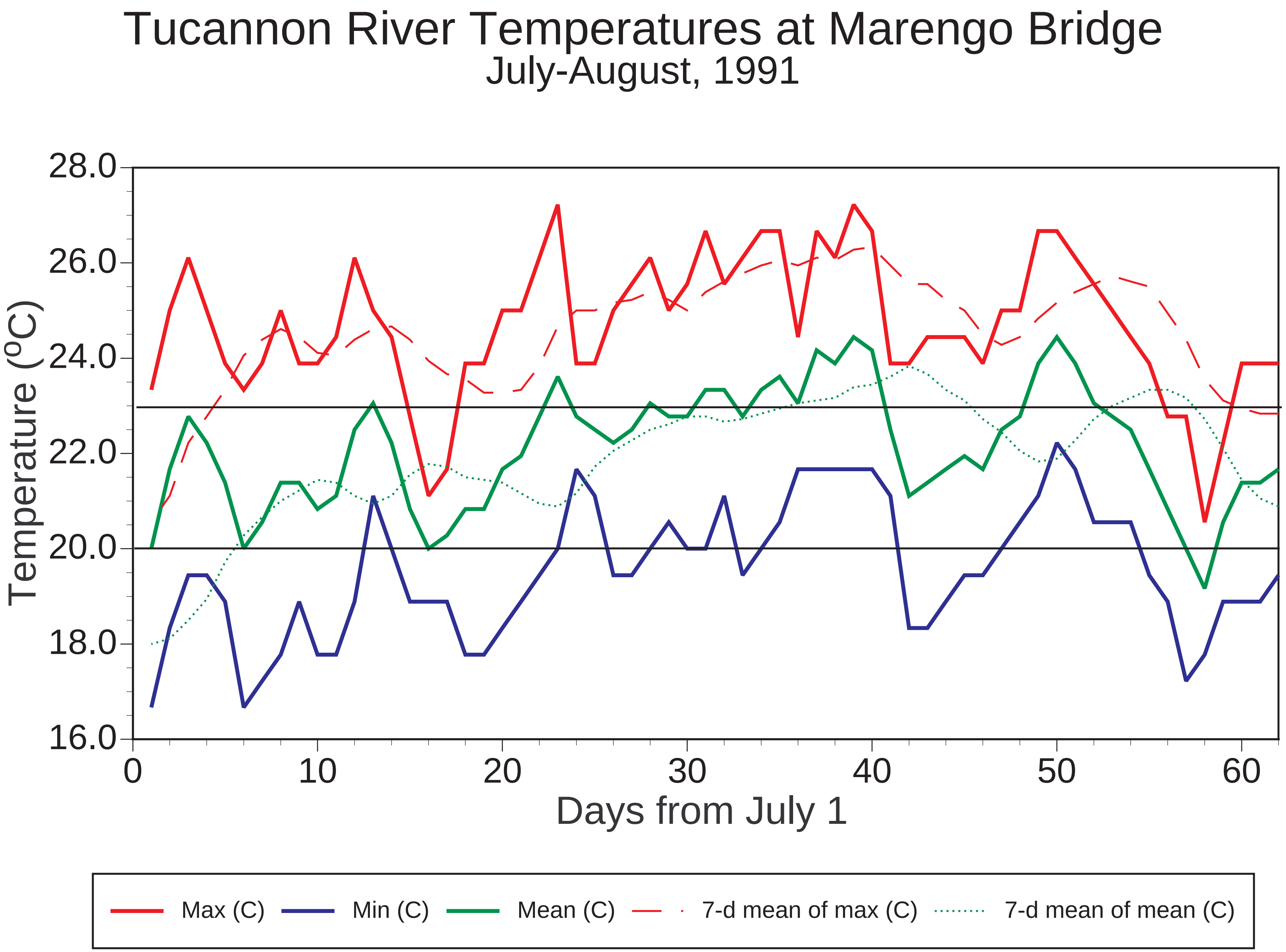

Tucannon River Temperatures at Marengo Bridge
July-August, 1991
28.0
26.0
24.0
22.0
20.0
18.0
16.0
Temperature (°C)
0
10
20
30
40
50
60
Days from July 1
Max (C)
Min (C)
Mean (C)
7-d mean of max (C)
7-d mean of mean (C)

Figure 17.

**Figure 18.** Tucannon River water temperatures (daily maximum, mean, and minimum; also 7-d moving mean of the maximum daily temperature and 7-d moving mean of the mean daily temperature) for September 1-30, 1991 at the Marengo Bridge site (RK 41).

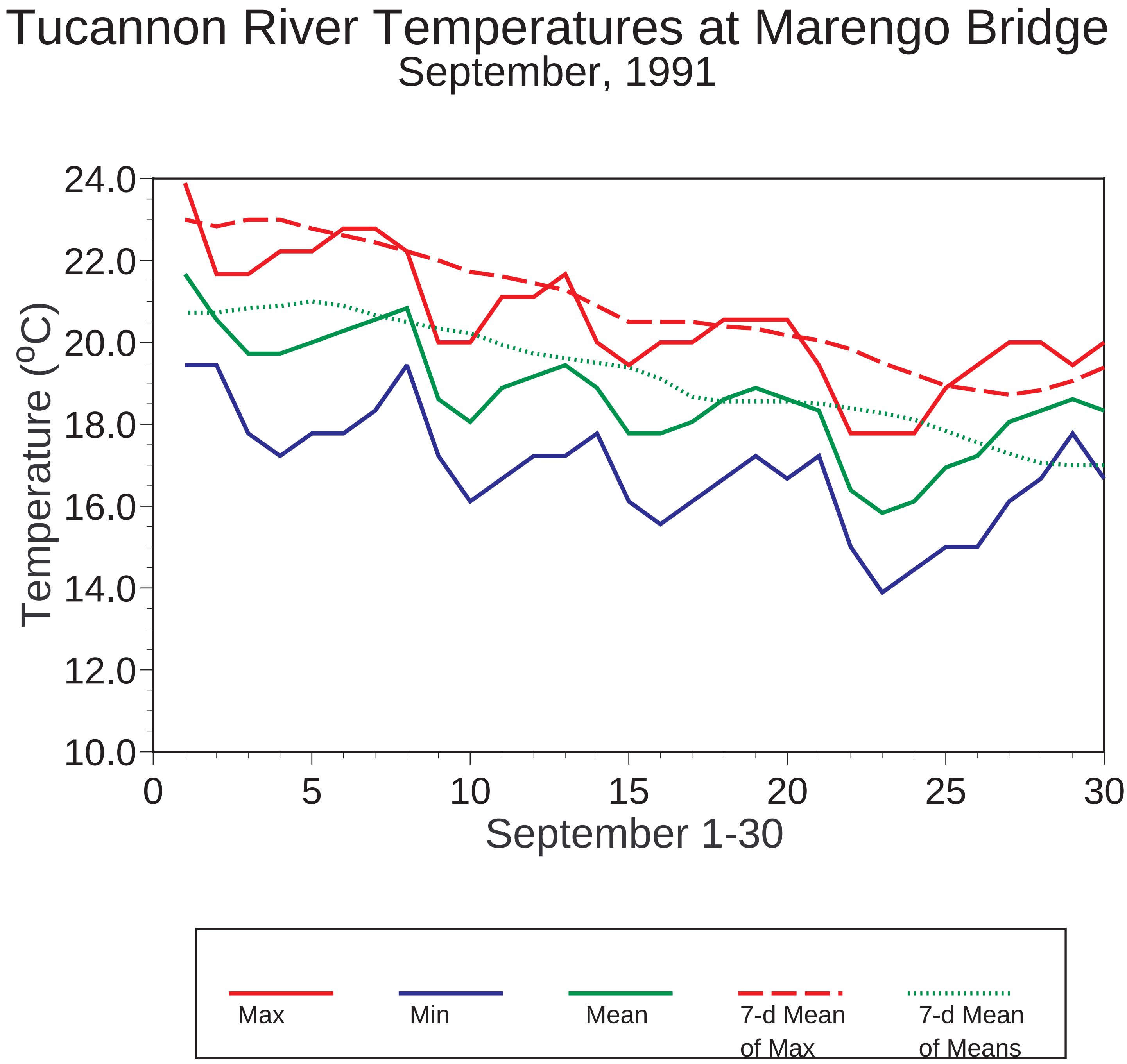

Tucannon River Temperatures at Marengo Bridge
September, 1991
Temperature (°C)
24.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
0
5
10
15
20
25
30
September 1-30
Max
Min
Mean
7-d Mean of Max
7-d Mean of Means

Figure 18.

**Figure 19.** Tucannon River water temperatures (daily maximum, mean, and minimum; also 7-d moving mean of the maximum daily temperature and 7-d moving mean of the mean daily temperature) for September 1-30, 1991 at the Cummings Creek site.

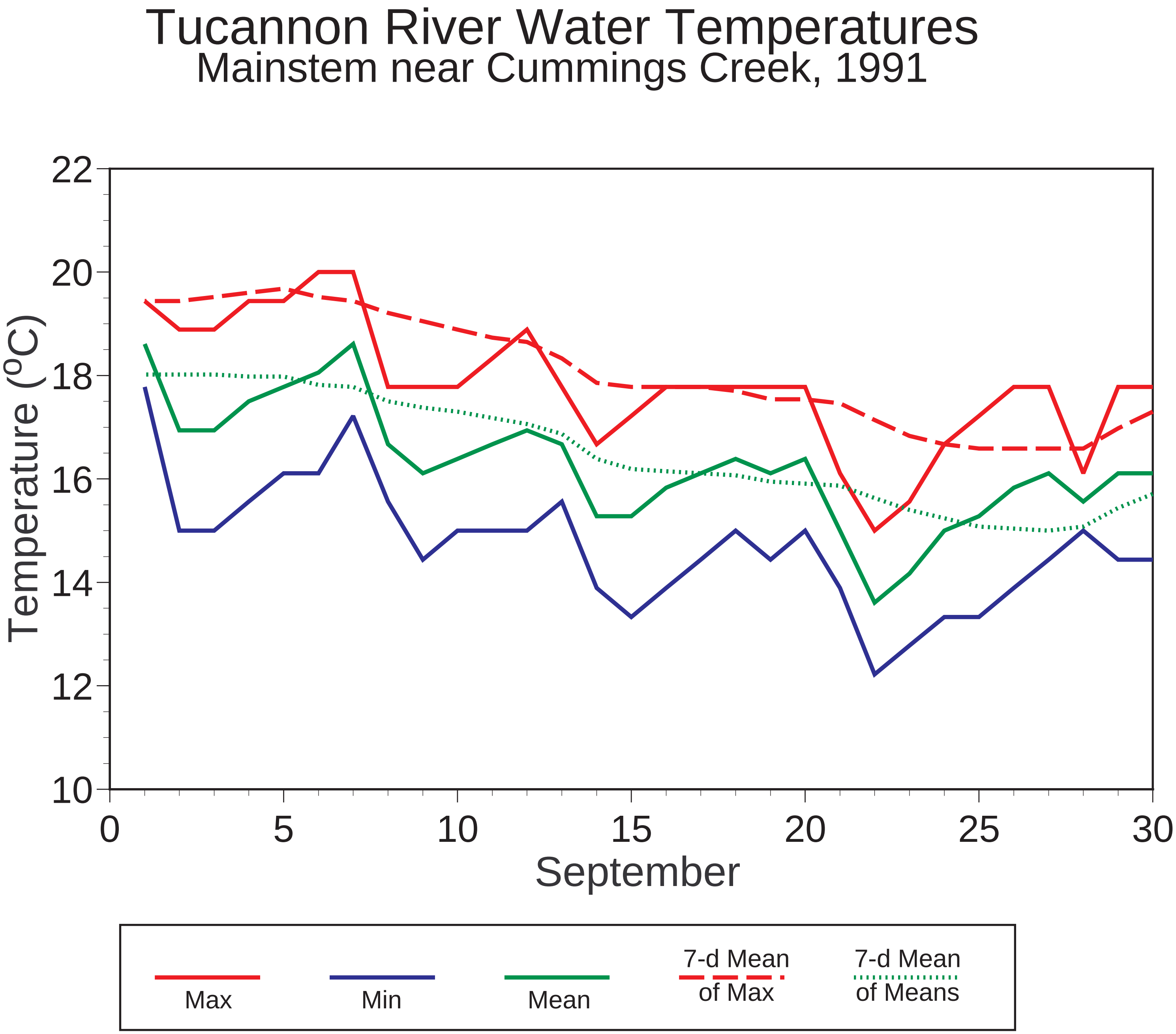

Tucannon River Water Temperatures
Mainstem near Cummings Creek, 1991

Figure 19.

**Figure 20.** Tucannon River average mean daily water temperatures for July estimated by use of stream segment temperature modeling (Theurer et al. 1985) for management alternatives ranging from the current condition to restored mainstem conditions (restoration of riparian vegetation and channel morphology).

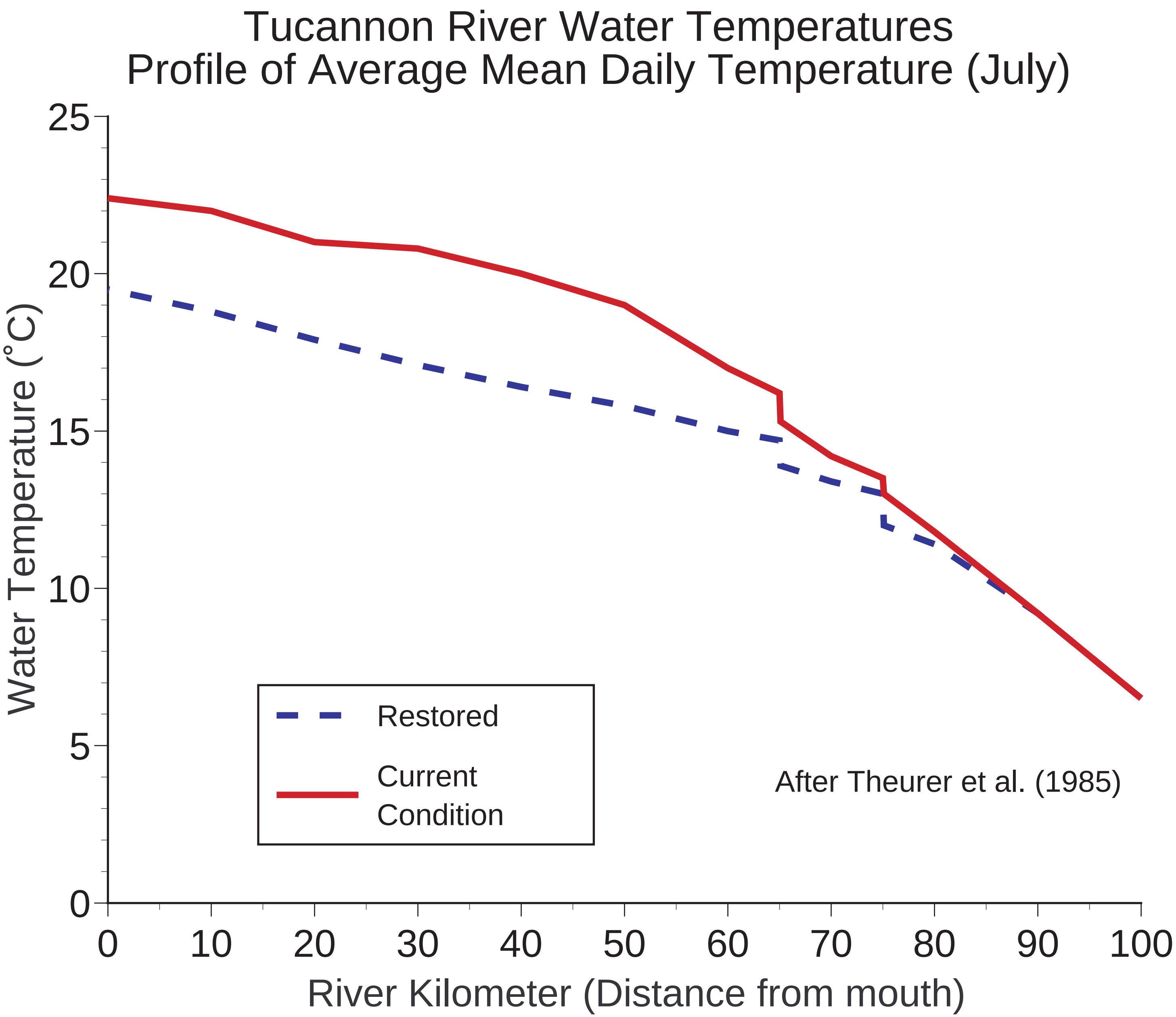

Tucannon River Water Temperatures
Profile of Average Mean Daily Temperature (July)
Water Temperature (°C)
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
100
River Kilometer (Distance from mouth)
Restored
Current Condition
After Theurer et al. (1985)

Figure 20.

**Figure 21.** Maximum daily air temperature at LaGrande, Oregon and maximum daily water temperature for the Tucannon River at Cummings Creek for August of 1988 and 1992.

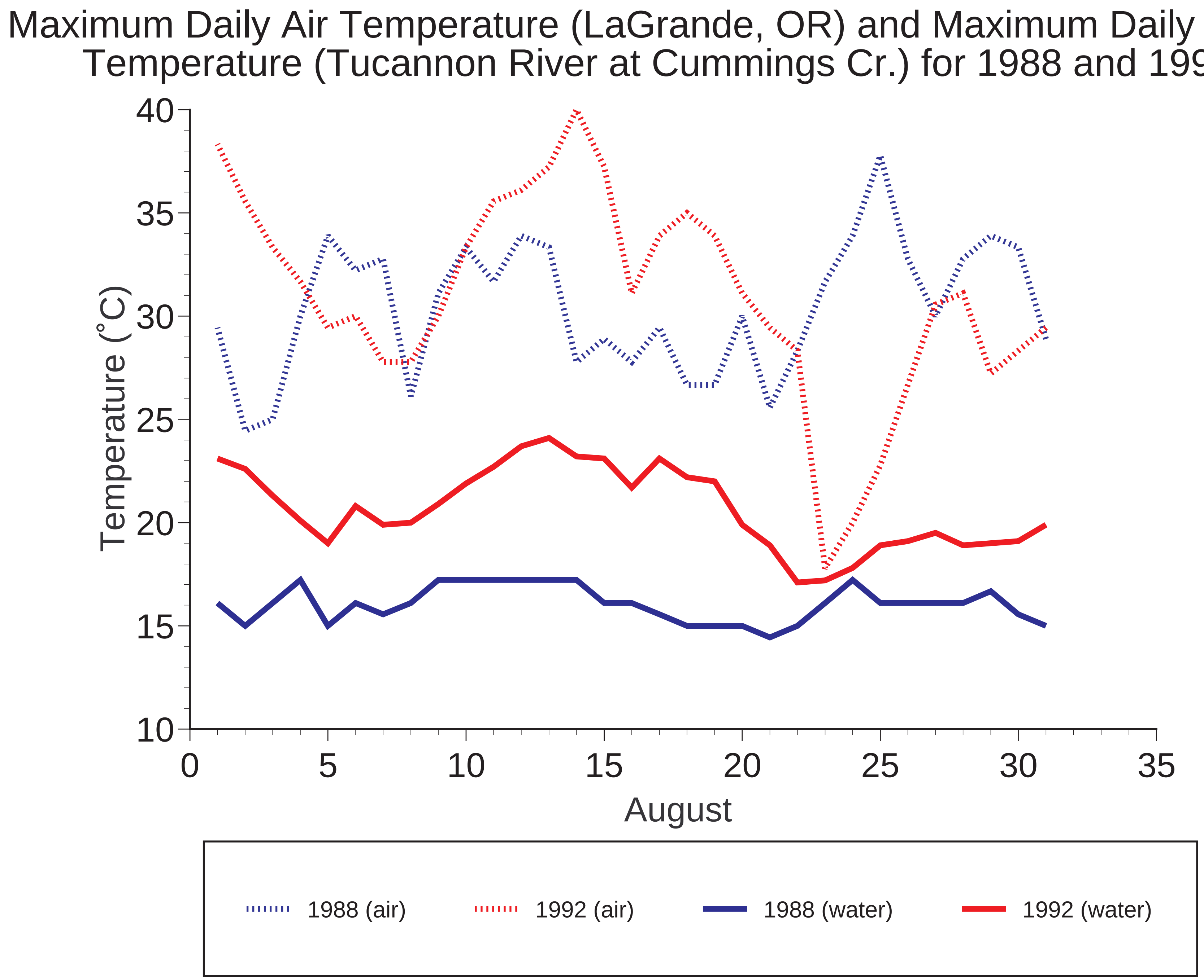

Maximum Daily Air Temperature (LaGrande, OR) and Maximum Daily Water Temperature (Tucannon River at Cummings Cr.) for 1988 and 1992
Temperature (˚C)
40
35
30
25
20
15
10
0
5
10
15
20
25
30
35
August
1988 (air)
1992 (air)
1988 (water)
1992 (water)

Figure 21.

**Figure 22.** Tucannon River (at Cummings Creek site) maximum daily water temperatures and the ratio of maximum daily air temperature to mean daily stream discharge for the period July-September, 1989. Air temperatures were taken from LaGrande, Oregon climatic station which is 125 km air distance from Cummings Creek.

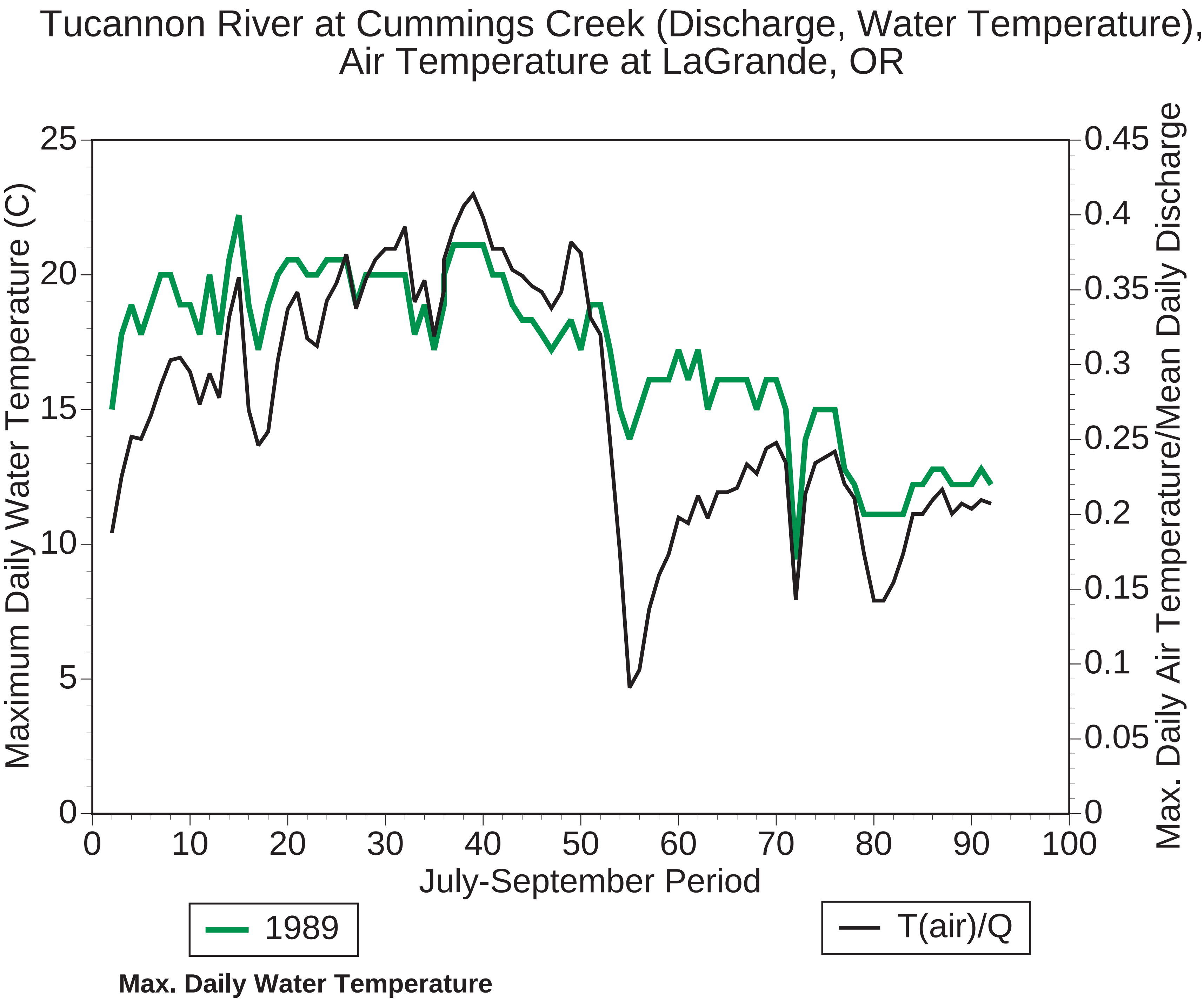

Tucannon River at Cummings Creek (Discharge, Water Temperature),
Air Temperature at LaGrande, OR
Maximum Daily Water Temperature (C)
0
5
10
15
20
25
Max. Daily Air Temperature/Mean Daily Discharge
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0
10
20
30
40
50
60
70
80
90
100
July-September Period
1989
T(air)/Q
Max. Daily Water Temperature

Figure 22.

# LITERATURE CITED

Adams, B.L., W.S. Zaugg, and L.R. McLain. 1973. Temperature effect on parr-smolt transformation in steelhead trout (Salmo gairdneri) as measured by gill sodium-potassium stimulated adenosine triphosphatase. Comp. Biochem. Physiol. 44A:1333-1339.

Adams, B.L., W.S. Zaugg, and L.R. McLain. 1975. Inhibition of salt water survival and Na-K-ATPase elevation in steelhead trout (Salmo gairdneri) by moderate water temperatures. Trans. Am. Fish. Soc. 104(4):766-769.

Alabaster, J.S. 1988. The dissolved oxygen requirements of upstream migrant chinook salmon, Oncorhynchus tshawytscha, in the lower Willamette River, Oregon. J. Fish Biology 32:635-636.

Alabaster, J.S. 1989. The dissolved oxygen and temperature requirements of king salmon, Oncorhynchus tshawytscha, in the San Joaquin delta, California. J. Fish Biol. 34(2):331-332.

Alabaster, J.S.and R. Lloyd. 1982. Water quality criteria for freshwater fish. 2nd edition. Food and Agriculture Organization of the United Nations. Butterworths, London. 361 p.

Alcorn, S.R. 1976. Temperature tolerances and upper lethal limits of Salmo apache. Trans. Am. Fish. Soc. 105(2):294-295.

Alderdice, D.F. and F.P.J. Velsen. 1978. Relation between temperature and incubation time for eggs of chinook salmon (Oncorhynchus tshawytscha). J. Fish Res. Board Can. 35(1):69-75.

Andrew, F.J., and G.H. Geen. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Int. Pac. Salmon Fish. Comm. Bull. XI: 259 p.

Armour, C.L. 1990. Guidance for evaluating and recommending temperature regimes to protect fish. U.S. Fish and Wildlife Service. Fort Collins. Biological Report 90(22). 13 p.

Averett, R.C. 1969. Influence of temperature on energy and material utilization by juvenile coho salmon. Ph.D. Thesis, Oregon State Univ., Corvallis, Oregon. 74 p.

Bailey, J.E. and D.R. Evans. 1971. The low-temperature threshold for pink salmon eggs in relation to a proposed hydroelectric installation. Fish. Bull. 69:587-593.

Baker, P.F., T.P. Speed, and F.K. Ligon. 1995. Estimating the influence of temperature on the survival of chinook salmon smolts (Oncorhynchus tshawytscha) migrating through the Sacramento-San Joaquin River Delta of California. Can. J. Fish. Aquat. Sci. 52:855-863.

Barans, C.A. and R.A. Tubb. 1973. Temperatures selected seasonally by four fishes from western Lake Erie. J. Fish. Res. Board Can. 30:1697-1703.

Bartholow, J.M. 1989. Stream temperature investigations: field and analytic methods. Instream flow information paper no. 13. Biological Report 89(17). U.S. Fish and Wildlife Service. Fort Collins, Co. library> 4512 McMurray Avenue, Fort Collins, CO 80525-3400

Bartholow, J.M. 1991. A modeling assessment of the thermal regime for an urban sport fishery. Environmental Management 15(6):833-845.

Barton, D.R., W.D. Taylor, and R.M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. N. Am. J. Fish. Manage. 5:364-378.

Beacham, T.D. 1988. A genetic analysis of early development in pink (Oncorhynchus gorbuscha) and chum salmon (O. keta) at three different temperatures. Genome 30:89-96.

Beacham, T.D. and C.B. Murray. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (Oncorhynchus keta) from the Nitinat River, British Columbia. Can. J. Fish. Aquatic Sci. 42(11):1755-1765.

Beacham, T.D. and C.B. Murray. 1986. Comparative developmental biology of chum salmon (Oncorhynchus kisutch) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43:252-262.

Beacham, T.D. and C.B. Murray. 1989. Variation in developmental biology of sockeye salmon (Oncorhynchus nerka) and chinook salmon (Oncorhynchus tshawytscha) in British Columbia. Can. J. Zool. 67:2081-2089.

Beacham, T.D. and C.B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Trans. Am. Fish. Soc 119(6):927-945.

Beacham, T.D. and T.P.T. Evelyn. 1992. Genetic variation in disease resistance and growth of chinook, coho, and chum salmon with respect to vibriosis, furunculosis, and bacterial kidney disease. Trans. Am. Fish. Soc. 121:456-485.

Beacham, T.D. and R.E. Withler. 1991. Genetic variation in mortality of chinook salmon, Oncorhynchus tshawytscha (Walbaum), challenged with high water temperatures. Aquacult. Fish. Manage. 22(2):125-133.

Beacham, T.D., R.E. Withler, C.B. Murray, and L.W. Barner. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. Trans. Am. Fisheries Society 117(2):109-126.

Beamish, F.W.H. 1978. Swimming capacity. p. 101-187. In: Fish Physiology. Volume VII. Academic Press, Inc.

Becker, C.D. 1973. Columbia River thermal effects study: reactor effluent problems. Water Pollution Control Federation 45(5):850-869.

Becker, C.D. and R.G. Genoway. 1979. Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater fish. Environmental Biology of Fishes 4(3):245-256.

Becker, C.D. and M.G. Wolford. 1980. Thermal resistance of juvenile salmonids sublethally exposed to nickel determined by the critical thermal maximum method. Environmental Protection 21:181-189.

Becker, C.D., R.G. Genoway, and M.J. Schneider. 1977. Comparative cold resistance of three Columbia River organisms. Trans. Am. Fish. Soc. 106(2):178-184.

Behnke, R.J. 1992. Native trout of western North America. American Fisheries Society Monograph 6. American Fisheries Society. Bethesda, Maryland. 275 p.

Bell, M.C. 1986. Fisheries handbook of engineering requirements and biological criteria. US Army Corps of

Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, Oregon.

Bell, M.C. 1991. Fisheries handbook of engineering requirements and biological criteria. US Army Corps of Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, Oregon.

Bennett, D.H., M.H. Karr, and M.A. Madsen. 1997. Thermal and velocity characteristics in the Lower Snake River reservoirs, Washington, as a result of regulated upstream water releases. U.S. Army Corps of Engineers final completion report. Project 14-16-0009-1579. 178 p.

Bennett, W.A., R.W. McCauley, and T.L. Beitinger. 1998. Rates of gain and loss of heat tolerance in channel catfish. Trans. Am. Fish. Soc. 127:1051-1058.

Berman, C.H. 1990. The effect of elevated holding temperatures on adult spring chinook salmon reproductive success. M.S. thesis. University of Washington. Seattle, WA.

Berman, C.H. and T.P. Quinn. 1990. The effect of elevated holding temperatures on adult spring chinook salmon reproductive success. Submitted to TFW Cooperative Monitoring, Evaluation, and Research Committee, Center for Streamside Studies, Fisheries Research Institute, Seattle, Washington.

Berman, C.H. and T.P. Quinn. 1991. Behavioral thermoregulation and homing by spring chinook salmon, Oncorhynchus tshawytscha (Walbaum), in the Yakima River. J. Fish Biology 39:301-312.

Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby, and T.D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. p. 191-231. In: E.O. Salo and T.W. Cundy, editors. Streamside mangement: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle. Contribution No. 57. Proceedings of a Symposium held at University of Washington, February 12-14, 1986.

Bidgood, B.F. and A.H. Berst. 1969. Lethal temperatures for Great Lakes rainbow trout. J. Fisheries Res. Board Can. 26:456-459.

Biesinger, K.E., R.P. Brown, C.R. Bernick, G.A. Flittner, and K.E.F. Hokanson. 1979. A national compendium of freshwater fish and water temperature data. Volume I: Data management techniques, output examples and limitations. EPA/600/3-79/056.

Biette, R.M. and G.H. Geen. 1980. Growth of underyearling sockeye salmon (Oncorhynchus nerka) under constant and cyclic temperatures in relation to live zooplankton ration size. Can. J. Fish. Aquatic Sci. 37(2):203-210.

Bilby, R.E. 1984. Characteristics and frequency of cool-water areas in a western Washington stream. J. Freshwater Ecol. 2(6):593-602.

Billard, R. 1985. Environmental factors in salmonid culture and the control of reproduction. p. 70-87. In: R.N. Iwamoto and S. Sower (eds.). Salmonid reproduction: an international symposium. Washington Sea Grant Program, Seattle, Washington.

Bilton, H.T. and H.D. Smith. 1973. Relationship between egg size and fish size in pink salmon (Oncorhynchus gorbuscha) from the lower Babine River in 1966 and 1967. Fish. Res. Board Can. Manuscr. Rep. No. 1235.

Binns, N.A. and F.E. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Trans. Am. Fish. Soc. 108(3):215-228.

Biro, P.A. 1998. Staying cool: behavioral thermoregulation during summer by young-of-year brook trout in a lake. Trans. Am. Fish. Soc. 127:212-222.

Bishai, H.M. 1960. Upper lethal temperatures for larval salmonids. J. Cons. Cons. Perm. Intern Explor. Mer 25:129-133.

Bisson, P.A. and G.E. Davis. 1976. Production of juvenile chinook salmon, Oncorhynchus tshawytscha, in a heated model stream. NOAA Fish. Bull. 74(4):763-774.

Bisson, P.A., J.L. Nielson, and J.W. Ward. 1988. Summer production of coho salmon stocked in Mount St. Helens streams 3-6 years after the 1980 eruption. Trans. Am. Fish. Soc. 117:322-335.

Bjornn, T.C. and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. Trans. Am. Fish. Soc. 93:70-76.

Bjornn, T.C. and D.W. Reiser. 1991. Habitat requirements of anadromous salmonids. Influences of forest and rangeland management on salmonid fishes and their habitats. Am. Fish. Soc. Special Publ. 19: 83-138.

Black, E.C. 1953. Upper lethal temperatures of some British Columbia fishes. J. Fish. Res. Board Can. 10:196-200.

Black, M.C., D.S. Millsap, and J.F. McCarthy. 1991. Effects of acute temperature change on respiration and toxicant uptake by rainbow trout, Salmo gairdneri (Richardson). Physiol. Zool. 64(1):145-168.

Bouck, G.R., G.A. Chapman, P.W. Schneider, and D.G. Stevens. 1975. Effects of holding temperatures on reproductive development in adult sockeye salmon (Oncorhynchus nerka). p. 24-40. In: J.R. Donaldson (ed.) 26th annual Northwest Fish Culture Conference, Otter Creek, Oregon.

Bowlby, J.N. and J.C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. Trans. Am. Fish. Soc. 115:503-514.

Brett, J.R. 1946. Rate of gain of heat tolerance in goldfish (Carassius auratus). Univ. Toronto Stud., Biol. Ser. No. 53, Publ. Ont. Fish Res. Lab. No. 64:9-28.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, genus Oncorhynchus. J. Fish. Res. Bd. Can. 9(6):265-323.

Brett, J.R. 1956. Some principles of the thermal requirements of fishes. Quarterly Review of Biology 31(2):75-87.

Brett, J.R. 1958. Implications and assessments of environmental stress. p. 69-83. In: P.A. Larkin (ed). Investigations of fish-power problems. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (Oncorhynchus nerka). Am. Zool. 11(1):99-113.

Brett, J.R. 1983. Life energetics of sockeye salmon, Oncorhynchus nerka. p. 29-63. In: W.P. Aspey and S.I. Lustick (eds.). Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press.

Brett, J.R. and N.R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Bd. Can. 30:379-387.

Brett, J.R. and J.E. Shelbourn. 1975. Growth rate of young sockeye salmon, Oncorhynchus nerka, in relation to fish size and ration level. J. Fish. Res. Board Can. 32:2103-3110.

Brett, J.R., W.C. Clarke, and J.E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon, Oncorhynchus tshawytscha. Can. Tech. Rep. Fish. Aquat. Sci. 1127. 29 p.

Brett, J.R., M. Hollands, and D.F. Alderdice. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. J. Fish. Res. Board Can. 15(4):587-605.

Brett, J.R., J.E. Shelbourn, and C.T. Shoop. 1969. Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd. Can. 26(9):2363-2394.

Brown, L.R. 1989. Temperature preferences and oxygen consumption of three species of sculpin (Cottus) from the Pit River drainage, California. Environmental Biology of Fishes 26:223-226.

Brungs, W.A. and B.R. Jones. 1977. Temperature criteria for freshwater fish: protocol and procedures. EPA-600-3-77-061. Environmental Research Laboratory-Duluth, Office of Research and Development, US Environmental Protection Agency. 136 p.

Bugert, R., C. Busack, G. Mendel, L. Ross, K. Petersen, D. Marbach, and J. Dedloff. 1991. Lower Snake River Compensation Plan. Tucannon River spring chinook salmon hatchery evaluation program. 1990 Annual report. Washington Department of Fisheries. Olympia, WA. AFF 1/LSR-91-14. 81 p.

Bugert, R., K. Petersen, G. Mendel, L. Ross, D. Milks, J. Dedloff, and M. Alexandersdottir. 1992. Lower Snake River Compensation Plan. Tucannon River spring chinook salmon hatchery evaluation program. 1991 Annual report. Washington Department of Fisheries. Olympia, WA. AFF 1/LSR-92-08. 91 p.

Bumgarner, J., G. Mendel, D. Milks, L. Ross, and J. Dedloff. 1995. Tucannon River spring chinook salmon hatchery evaluation program. 1994 Annual report. Washington Department of Fish and Wildlife, Olympia, Washington. Report H95-05 to US Fish and Wildlife Service, Cooperative Agreement 14-48-001-94544.

Bumgarner, J., G. Mendel, D. Milks, L. Ross, and J. Dedloff. 1996. Tucannon River spring chinook salmon hatchery evaluation. 1995 Annual report. Washington Department of Fish and Wildlife, Olympia, Washington. Report H96-07 to US Fish and Wildlife Service, Cooperative Agreement 14-48-0001-95572.

Bumgarner, J., G. Mendel, D. Milks, L. Ross, M. Varney, and J. Dedloff. 1997. Tucannon River spring chinook hatchery evaluation. 1996 Annual report. Washington Department of Fish and Wildlife Hatcheries Program Assessment and Development Division. Report #H97-07. Produced for US Fish and Wildlife Service, Cooperative Agreement 14-48-0001-96539.

Burck, W.A. 1994. Life history of spring chinook salmon in Lookingglass Creek, Oregon. Information Reports, Number 94-1. Oregon Department of Fish and Wildlife, Fish Division. 148 p.

Burck, W.A., R.B. Lindsay, B.J. Smith, and E.A. Olsen. 1980. Spring chinook studies in the John Day River. Federal Aid Progress Reports, Fisheries, Fish Research Project, Contract Number DEAC79-80BP18234. Oregon Department of Fish and Wildlife. 69 p.

Burger, C.V., R.L. Wilmot, and D.B. Wangaard. 1985. Comparison of spawning areas and times for two runs of chinook salmon (Oncorhynchus tshawytscha) in the Kenai River, Alaska. Can. J. Fish. Aquat. Sci. 42:693-700.

Burrows, R. 1963. Water temperature requirements for maximum productivity of salmon. p. 29-38. In: Water temperature influences, effects, and control. Proc. 12th Northwest Symp. Water Pollution Research. U.S. Department of Health, Education, and Welfare, Public Health Service, Pacific Northwest Water Laboratory, Corvallis, Oregon.

Burton, G.W. and E.P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26:182-194.

Cada, G.F., J.M. Loar, and M.J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. Trans. Am. Fish. Soc. 116:692-702.

California Department of Water Resources (CDWR). 1988. Water temperature effects on chinook salmon (Oncorhynchus tshawytscha) with emphasis on the Sacramento River: a literature review. Northern District Office Report, Red Bluff, California. 42 p.

Calow, P. 1985. Adaptive aspects of energy allocation. p. 13-31. In: P. Tytler and P. Calow (ed.). Fish energetics. Johns Hopkins University Press, Baltimore, Maryland.

Cech, J.J., Jr., S.J. Mitchell, D.T. Castleberry, and M. McEnroe. 1990. Distribution of California stream fishes: influence of environmental temperature and hypoxia. Env. Biol. Fishes 29:95-105.

Charlon, N., B. Barbier, and L. Bonnet. 1970. Résistance de la truite arc-en-ciel (Salmo gairdneri Richardson) a des variations brusques de température. Ann. Hydrobiol. 1(1):73-89.

Chen, Y.D. and H. Chen. 1993. Determining stream temperature changes caused by harvest of riparian vegetation: an overview. p. 313-323. In: Proceedings of the conference on riparian ecosystems in the humid U.S.: functions, values and management, Atlanta, GA, March 15-18, 1993.

Cherry, D.S., K.L. Dickson, and J. Cairns, Jr. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. J. Fish. Res. Board Can. 32(4):485-491.

Cherry, D.S., K.L. Dickson, J. Cairns Jr., and J.R. Stauffer. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J. Fish. Res. Board Can. 34:239-246.

Christie, G.C. and H.A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. 45:301-314.

Claire, E.W. and B.J. Smith. 1990. John Day fish district. Unpublished status report on wild spring chinook, wild summer steelhead, resident trout, smallmouth bass and channel catfish, bull trout, and cutthroat trout. Portland, Oregon.

Clapp, D.F., R.D. Clark, Jr., and J.S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Trans. Am. Fish. Soc. 119:1022-1034.

Clarke, W.C. 1978. Growth of underyearling sockeye salmon (Oncorhynchus nerka) on diel temperature cycles. Fish . Environ. Can. Fish. Mar. Serv. Tech. Rep. 780. 19 p. fluctuating

Clarke, W.C. and J.E. Shelbourn. 1977. Effect of temperature photoperiod and salinity on growth and smolting of underyearling coho salmon. Am. Zool. 17:957.

Clarke, W.C. and J.E. Shelbourn. 1985. Growth and development of seawater adaptability by juvenile fall chinook salmon (Oncorhynchus tshawytscha) in relation to temperature. Aquaculture 45:21-31.

Clarke, W.C., J.E. Shelbourn, and J.R. Brett. 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (Oncorhynchus kisutch), chinook (O. tshawytscha), and sockeye (O. nerka) salmon. Aquaculture 22:105-116.

Cleland, B. 1997. Clean Water Act Section 303(d)/Water quality limited streams and temperature. Presentation given at the Columbia/Snake River mainstem water temperature workshop. Integrated ecosystem management of the Columbia River basin. November 6-7, 1997. Portland State University, Portland, OR.

Colgrove, D.J. and J.W. Wood. 1966. Occurrence and control of Chondrococcus columnaris as related to Fraser River sockeye salmon. Progress report no. 15. International Pacific Salmon Fisheries Commission, British Columbia, Canada. 51 p.

Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148-1153.

Combs, B.D. 1965. Effect of temperature on the development of salmon eggs. Prog. Fish-Cult. 27(3):134-137.

Combs, B.D. and R.E. Burrows. 1957. Threshold temperatures for the normal development of chinook salmon eggs. Prog. Fish Cult. 19:3-6.

Coutant, C.C. 1970. Thermal resistance of adult coho (Oncorhynchus kisutch) and jack chinook (O. tshawytscha) salmon, and adult steelhead trout (Salmo gairdneri) from the Columbia River. Battelle Memorial Inst., Pac. Northwest Lab., Richland, WA. Rep. No. BNWL-1508, UC-48. 24 p.

Coutant, C.C. 1972. Water quality criteria. A report of the committee on water quality criteria. p. 151-170 (text) and Appendix II-C (p. 410-419). In: National Academy of Sciences, National Academy of Engineers, EPA Ecol. Res. Series EPA-R3-73-033, US Environmental Protection Agency, Washington, D.C. 594 p.

Coutant, C.C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Board Can. 30(7):965-973.

Coutant, C.C. 1977. Compilation of temperature preference data. J. Fish. Res. Board Can. 34:739-745.

Coutant, C.C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18(3):161-172.

Craigie, D.E. 1963. An effect of water hardness in the thermal resistance of the rainbow trout, Salmo gairdneri Richardson. Can. J. Zoology 41:825-831.

Craik, J.C.A. 1985. Egg quality and egg pigment content in salmonid fishes. Aquaculture 47:61-88.

Crisp, D.T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11:361-368.

Crisp, D.T. 1990. Water temperature in a stream gravel bed and implications for salmonid incubation. Freshwater Biology 23:601-612.

Crisp, D.T. and G. Howson. 1982. Effect of air temperature upon mean water temperature in streams in the north Pennines and English Lake District. Freshwater Biol. 12:359-367.

CRITFC. 1995. Wy-Kan-Ush-Mi Wa-Kish-Wit, Spirit of the Salmon. The Columbia River anadromous fish restoration plan of the Nez Perce, Umatilla, Warm Springs and Yakama Tribes. Volume I. Columbia River Inter-Tribal Fish Commission. Portland, OR.

Crone, R.A. and C.E. Bond. 1976. Life history of coho salmon, Oncorhynchus kisutch, in Sashin Creek, southeastern Alaska. National Marine Fisheries Service Fishery Bulletin 74:897-923.

Cunjak, R.A. and J.M. Green. 1986. Influence of water temperature on behavioural interactions between juvenile brook charr, Salvelinus fontinalis, and rainbow trout, Salmo gairdneri. Can. J. Zool. 64(6):1288-1291.

Dahlberg, M.L., D.L. Shumway, and P. Doudoroff. 1968. Influence of dissolved oxygen and carbon dioxide on swimming performance of largemouth bass and coho salmon. J. Fish. Res. Board Can. 25:49-70.

Danzmann, R.G. and M.M. Ferguson. 1988a. Developmental rates of heterozygous and homozygous rainbow trout reared at three temperatures. Biochem. Genet. 26(1/2):53-67.

Danzmann, R.G. and M.M. Ferguson. 1988b. Temperature-dependent genotypic selection and embryonic survival of rainbow trout. Biochem. Genet. 26(1/2):69-81.

Dauble, D.D. and D.G. Watson. 1997. Status of fall chinook salmon populations in the mid-Columbia River, 1948-1992. N. Am. J. Fisheries Management 17:283-300.

Daykin, P.N. 1965. Application of mass transfer theory to the problem of respiration of fish eggs. J. Fish. Res. Board Can. 22:159-171.

de Gaudemar, B. and E. Beall. 1998. Effects of overripening on spawning behaviour and reproductive success of Atlantic salmon females spawning in a controlled flow channel. J. Fish. Biol. 53:434-446.

DeHart, D.A. 1975. Resistance of three freshwater fishes to fluctuating thermal environments. M.S. Thesis. Oregon State University, Corvallis, Oregon.

DeLacy, A.C., S.P. Felton, and G.J. Paulik. 1956. A study to investigate the effects of fatigue and current velocities on adult salmon and steelhead trout. p. 126-138. In: Prog. Rep. on Fish. Eng. Res. Prog., N. Pac. Div., US Army Corps Eng., Portland, OR.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Can. J. Fish. Aquat. Sci. 54:1685-1698.

Dickson, I.W. and R.H. Kramer. 1971. Factors influencing scope for activity and active standard metabolism of rainbow trout (Salmo gairdneri). J. Fish. Res. board Can. 28:587-596.

Dimick, R.E. and F. Merryfield. 1945. The fishes of the Willamette River system in relation to pollution. Oregon State College Engineering Experiment Station Bulletin Series 20:7-55. Oregon State College, Corvallis, Oregon.

Dingman, S.L. 1972. Equilibrium temperatures of water surfaces as related to air temperature and solar radiation. Wat. Resour. Res. 8:42-49.

Dockray, J.J., S.D. Reid, and C.M. Wood. 1996. Effects of elevated summer temperatures and reduced pH on metabolism and growth of juvenile rainbow trout (Oncorhynchus mykiss) on unlimited ration. Can. J. Fish. Aquat. Sci. 53:2752-2763.

Donaldson, L.R. and F.J. Foster. 1941. Experimental study of the effect of various water temperatures on the growth, food utilization, and mortality rate, of fingerling sockeye salmon. Trans. Am. Fish. Soc. 70:339-346.

Dwyer, W.P. and R.H. Kramer. 1975. The influence of temperature on scope for activity in cutthroat trout, Salmo clarki. Trans. Am. Fish. Soc. 104:522-554.

Eaton, J.G., J.H. McCormick, B.E. Goodno, D.G. O'Brien, H.G. Stefany, M. Hondzo, and R.M. Scheller. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries 20(4):10-18.

Edwards, R.W., J.W. Densen, and P.A. Russell. 1979. An assessment of the importance of temperature as a factor controlling the growth rate of brown trout in streams. J. Anim. Ecol. 48:501-507.

Elliott, J.M. 1975a. The growth rate of brown trout (Salmo trutta L.) fed on maximum rations. J. Animal Ecology 44:805-821.

Elliott, J.M. 1975b. The growth rate of brown trout, Salmo trutta L., fed on reduced rations. J. Animal Ecology 44:823-842.

Elliott, J.M. 1981. Some aspects of thermal stress on freshwater teleosts. p. 209-245. In: Stress and fish. A.D. Pickering (ed.). Academic Press.

Elliott, J.M. 1994. Quantitative ecology and the brown trout. Oxford Series in Ecology and Evolution, Series editors R.M. May and P.H. Harvey. Oxford University Press, Oxford, England. 286 p.

Elliott, J.M. and J.A. Elliott. 1995. The effect of the rate of temperature increase on the critical thermal maximum for parr of Atlantic salmon and brown trout. J. Fish Biol. 47:917-919.

Environmental Protection Agency and National Marine Fisheries Service (EPA and NMFS). 1971. Columbia River Thermal Effects Study. Volume 1. Biological Effects Study. U.S. Environmental Protection Agency and National Marine Fisheries Service. 102 p.

Erman, D.C. and G.R. Leidy. 1975. Downstream movement of rainbow trout fry in a tributary of Sagehen Creek, under permanent and intermittent flow. Trans. Am. Fish. Soc. 104:467-473.

Espinosa, F.A., Jr., J.J. Rhodes, and D.A. McCullough. 1997. The failure of existing plans to protect salmon habitat on the Clearwater National Forest in Idaho. J. Env. Management 49(2):205-230.

Evans, D.O. 1990. Metabolic thermal compensation by rainbow trout: effects on standard metabolic rate and potential usable power. Trans. Am. Fish. Soc. 119:585-600.

Ewing, R.D., S.L. Johnson, H.J. Pribble, and J.A. Lichatowich. 1979. Temperature and photoperiod effects on gill (Na+K)-ATPase activity in chinook salmon (Oncorhynchus tshawytscha). J. Fish. Res. Board Can. 36:1347-1353.

Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (Salvelinus fontinalis) and other resident salmonids in streams? Physiology and Ecology Japan, Special Volume 1:303-322.

Fausch, K.D. and R.J. White. 1981. Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Can. J. Fish. Aq. Sciences 38:1220-1227.

Fausch, K.D. and M.K. Young. 1995. Evolutionarily significant units and movement of resident stream fishes: a cautionary tale. American Fisheries Society Symposium 17:360-370.

Fedorov, K.Ye. and L.S. Bogdanova. 1978. The growth and development of the larvae of the pink salmon, Oncorhynchus gorbuscha, under different temperature and feeding regimes. J. Ichthyol. 18(4):568-576.

Feldmeth, C.R. and C.H. Eriksen. 1978. A hypothesis to explain the distribution of native trout in a drainage of Montana's Big Hole River. Internationale Vereinigung fur theroetische und angewandte Limnologie Verhandlungen 20:2040-2044.

FEMAT. 1993. Forest ecosystem management: an ecological, economic, and social assissment. USFS, NMFS, USBLM, USFWS, USNPS, and USEPA. US Forest Service PNW Region, Portland, Oregon.

Ferguson, H.W. 1981. The effects of water temperature on the development of proliferative kidney disease in rainbow trout, Salmo gairdneri Richardson. J. Fish Dis. 4(2):175-177.

Ferguson, R.G. 1958. The preferred temperatures of fish and their midsummer distribution in temperate lakes and streams. J. Fish. Res. Board Can. 15:607-624.

Fields, R., S.S. Lowe, C. Kaminski, G.S. Whitt, and D.P. Philipp. 1987. Critical and chronic thermal maxima of northern and Florida largemouth bass and their reciprocal $F_1$ and $F_2$ hybrids. Trans. Am. Fish. Soc. 116:856-863.

Fish, F.F. 1944. The retention of adult salmon with particular reference to the Grand Coulee Fish Salvage Program. U.S. Fish and Wildlife Service Special Scientific Report No. 27.

Fish, F.F. 1948. The return of blueback salmon to the Columbia River. Scientific Monthly (Wash), 66:283-292.

Fish, F.F. and M.G. Hanavan. 1948. A report upon the Grand Coulee fish-maintenance project 1939-1947. U.S. Fish and Wildlife Service, Special Science Report 55. 63 p.

Fish, F.R. and R.R. Rucker. 1943. Columnaris as a disease of freshwater fishes. Trans. Am. Fisheries Society 73:32-36.

Flett, P.A., K.R. Munkittrick, G. Van Der Kraak, and J.F. Leatherland. 1996. Overripening as the cause of low survival to hatch in Lake Erie coho salmon (Oncorhynchus kisutch) embryos. Can. J. Zool. 74:851-857.

Folmar, L.C., W.W. Dickhoff, C.V.W. Mahnken, and F.W. Waknitz. 1982. Stunting and parr-reversion during smoltification of coho salmon (Oncorhynchus kisutch). Aquaculture 28:91-104.

Frissell, C.A., R.K. Nawa, and W.J. Liss. 1992. Water temperature and distribution and diversity of salmonid fishes in Sixes River Basin, Oregon, USA: changes since 1965-1972. p. 127-172. In: C.A. Frissell. 1992. Cumulative effects of land use on salmon habitat in southwest Oregon coastal streams. Ph.D. thesis, Oregon State University, Corvallis, Oregon.

Frost, W.E. and M.E. Brown. 1967. The trout. New Naturalist Series, Collins, St. James Place. London.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser., No. 55. Pub. Ont. Fish. Res. Lab., No. 68. 62 p.

Fry, F.E.J. 1957. The lethal temperature as a tool in taxonomy. Ann. Biol. 33:205-219.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. p. 1-98. In: W.S. Hoar and D.J. Randall (ed.). Fish physiology. Vol. VI: Environmental relations and behavior. Academic Press, Inc. San Diego, CA.

Fry, F.E.J. and M.B. Gibson. 1953. Lethal temperature experiments with speckled trout x lake trout hybrids. J. Hered. 44(2):56-57.

Fry, F.E.J., J.S. Hart, and N.F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout, Salvelinus fontinalis. Univ. Toronto Studies, Biol. Ser. 54, Ontario Fish. Res. Lab. Publ. 66:9-35.

Fryer, J.L. and K.S. Pilcher. 1974. Effects of temperature on diseases of salmonid fishes. US Environmental Protection Agency. Office of Research and Development, Ecological Research Series EPA-660/3-73-020. 114 p.

Fryer, J.L., K.S. Pilcher, J.E. Sanders, J. Rohovec, J.L. Zinn, W.J. Groberg, and R.H. McCoy. 1976. Temperature, infectious diseases, and the immune response in salmonid fish. U.S. Environ. Prot. Agency Ecol. Res. Ser. EPA-600/3-76-21. 70 p.

Fujihara, M.P. and F.P. Hungate. 1970. Seasonal distribution of Chondrococcus columnaris disease in river fishes: a procedure using antibody synthesis in fishes as a survey technique. Battelle Northwest, BNWL-SA-3563. SH 177 .C49 F854 1970.

Fujihara, M.P. and R.E. Nakatani. 1970. Antibody production and immune response of rainbow trout and coho salmon to Chondrococcus columnaris. October 1, 1970. Manuscript 43 prepared for Columbia River Thermal Effects Study by NMFS.

Fujihara, M.P., P.A. Olson, and R.E. Nakatani. 1971. Some factors in susceptibility of juvenile rainbow trout and chinook salmon to Chondrococcus columnaris. J. Fish. Res. Bd. Can. 28:1739-1743.

Gard, R. and G.A. Flittner. 1974. Distribution and abundance of fishes in Sagehen Creek, California. J. Wildlife Management 38:347-358.

Garling, D.L. and M. Masterson. 1985. Survival of Lake Michigan chinook salmon eggs and fry incubated at three temperatures. Prog. Fish-Culturist 47:63-66.

Garside, E.T. and J.S. Tait. 1958. Preferred temperature of rainbow trout (Salmo gairdneri, Richardson) and its unusual relationship to acclimation temperature. Can. J. Zool. 36:563-567.

Gibson, R.J. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. J. Fish. Res. Board Can. 23:1977-1980.

Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. Int. Pac. Salmon Fish. Comm. Bull. XXII: 51p.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Bull. Int. Pac. Salmon Fisheries Comm. 26: 62 p.

Goddard, C.I. and J.S. Tait. 1976. Preferred temperatures of $F_3$ to $F_5$ hybrids of Salvelinus fontinalis x S. namaycush. J. Fish. Res. Board Can. 33:197-202.

Godin, J-G. J. 1981. Migrations of salmonid fishes during early life history phases: daily and annual timing. p. 22-50. In: E.L. Brannon and E.O. Salo (ed.). Proceedings of the salmon and trout migratory behavior symposium. School of Fisheries, Univ. of Washington, Seattle, WA.

Golden, J.T. 1975. Immediate effects of logging on the freshwater environment salmonids: lethal temperatures for coastal cutthroat trout under fluctuating temperature regimes: job progress report, 1974-1975. Oregon Dept. Fish Wildlf. Fed. Aid Prog. Rep. Anadrom. Fish Proj. AFS-585: 7 p.

Golden, J.T. 1976. Lethal temperatures for coastal cutthroat trout under fluctuating temperature regimes. Federal Aid Progress Reports, Fisheries. Oregon Department of Fish and Wildlife. 14 p.

Golden, J.T. and C.B. Schreck. 1978. Effects of fluctuating temperatures on the thermal tolerance limits of coastal cutthroat trout Salmo clarki clarki). Unpublished m.s., Oregon Department of Fish and Wildlife. Corvallis, Oregon.

Grabowski, S.J. 1973. Effects of fluctuating and constant temperatures on some hematological characteristics, tissue glycogen levels, and growth of steelhead trout (Salmo gairdneri). Ph.D. dissertation, University of Idaho. 77 p.

Grande, M. and S. Andersen. 1991. Critical thermal maxima for young salmonids. J. Freshwater Ecology 6(3):275-279.

Graynoth, E. 1979. Effects of logging on stream environments and faunas in Nelson. New Zealand Journal Marine and Freshwater Research 13(1):79-109.

Gresswell, R.E. 1995. Yellowstone cutthroat trout. p. 36-54. In: M.K. Young (tech. ed.). Conservation assessment for inland cutthroat trout. USDA Forest Service, Gen. Tech. Report RM-GTR-256.

Griffiths, J.S. and D.F. Alderdice. 1972. Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. J. Fish. Res. Board Can. 29(3):251-264.

Groberg, W.J., Jr., R.H. McCoy, K.S. Pilcher, and J.L. Fryer. 1978. Relation of water temperature to infections of coho salmon (Oncorhynchus kisutch), chinook salmon (O. tshawytscha), and steelhead trout (Salmo gairdneri) with Aeromonas salmonicida and A. hydrophila. J. Fish. Res. Board Can. 35(1):1-7.

Groberg, W.J., Jr., J.S. Rohovec, and J.L. Fryer. 1983. The effects of water temperature on infection and antibody formation induced by Vibrio anguillarum in juvenile coho salmon (Oncorhynchus kisutch). J. World Maricult. Soc. 14:240-248.

Hahn, P.K.J. 1977. Effects of fluctuating and constant temperatures on behavior of steelhead trout (Salmo gairdneri). Ph.D. dissertation, University of Idaho. 142 p. Dissertation Abstracts Int. B Sci. Eng. 38(12):5668.

Hall, L.W., Jr., C.H. Hocutt, and J.R. Stauffer, Jr. 1978. Implication of geographic location on temperature preference of white perch, Morone americana. J. Fish. Res. Board Can. 35:1464-1468.

Hallock, R.J., R.F. Elwell, and D.H. Fry. 1970. Migrations of adult kind salmon Oncorhynchus tshawytscha in the San Joaquin Delta as demonstrated by the use of sonic tags. California Dept. Fish Game Fish Bull. 151. 92 p.

Hart, J.S. 1947. Lethal temperature relations of certain fish of the Toronto region. Trans. Roy. Soc. Can. Sec. 5(41):57-71.

Hart, J.S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. University of Toronto biology series no. 60. The University of Toronto Press, Toronto. 79 p.

Hartman, G.F., L.B. Holtby, and J.C. Scrivener. 1984. Some effects of natural and logging-related winter stream temperature changes on the early life history of the coho salmon (Oncorhynchus kisutch) in Carnation Creek, British Columbia. p. 141-149. In: W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.). Fish and wildlife relationships in old-growth forests; proceedings of a symposium. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Hartwell, S.I. and D.E. Hoss. 1979. Thermal shock resistance of spot (Leistomus xanthurus) after acclimation to constant or cycling temperature. Trans. Am. Fisheries Soc. 108:397-400.

Hatch, D., A. Wand, A. Porter, and M. Schwartzberg. 1993. The feasibility of estimating sockeye salmon escapement at Zosel Dam using underwater video technology. 1992 Annual progress report prepared for Public Utility District No. 1 of Douglas County. Columbia River Inter-Tribal Fish Commission, Portland, OR. 27 p.

Hawkins, C.P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Healey, M.C. 1991. Life history of chinook salmon (Oncorhynchus tshawytscha). p. 311-393. In: C. Groot and L. Margolis (ed.). Pacific salmon life histories. UBC Press, Vancouver. 564 p.

Healey, T. 1979. The effect of high temperature on the survival of Sacramento River chinook (king) salmon, Oncorhynchus tshawytscha), eggs and fry. California Department of Fish and Game, Anadromous Fisheries Branch, Administrative Report No. 79-10. 7 p.

Heath, W.G. 1963. Thermoperiodism in the sea-run cutthroat (Salmo clarki clarki). Science 142:486-488.

Hedrick, R.P., M.L. Kent, R. Rosemark, and D. Manzer. 1984. Proliferative kidney disease (PKD) in Pacific salmon and steelhead trout. J. World Maricul. Soc. 15:318-325.

Heming, T.A. 1982. Effecs of temperature on utilization of yolk by chinook salmon (Oncorhynchus tshawytscha) eggs and alevins. Can. J. Fish. Aquat. Sci. 39:184-190.

Henjum, M.G., J.R. Karr, D.L. Bottom, D.A. Perry, J.C. Bednarz, S.G. Wright, S.A. Beckwitt. 1994. Interim protection for late successional forests, fisheries, and watersheds: national forests east of the Cascade Crest, Oregon and Washington. The Wildlife Society, Bethesda, MD.

Hetrick, F.M., J.L. Fryer, and M.D. Knittel. 1979. Effect of water temperature on the infection of rainbow trout Salmo gairdneri Richardson with infectious hematopoietic necrosis virus. J. Fish. Dis. 2(3):253-257.

Hoar, W.S. 1988. The physiology of smolting salmonids. In: W.S. Hoar and D.J. Randall (eds.). Fish physiology. Vol XIB. p. 275-343. Academic Press, New York, NY.

Hoffmaster, J.L., J.E. Sanders, J.S. Rohovec, J.L. Fryer, and D.G. Stevens. 1988. Geographic distribution of the myxosporean parasite, Ceratomyxa shasta Noble, 1950, in the Columbia River basin, USA. J. Fish Diseases 11(1):97-100.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to seasonal temperature cycle. J. Fisheries Research Board of Can. 34(10):1524-1550.

Hokanson, K.E.F., C.F. Kleiner, and T.W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, Salmo gairdneri. J. Fish. Res. Board Can. 34(5):639-648.

Hokanson, K.E.F., J.H. McCormick, B.R. Jones, and J.H. Tucker. 1973. Thermal requirements for maturation, spawning, and embryo survival of the brook trout (Salvelinus fontinalis). J. Fish. Res. Board Can. 30:975-984.

Holt, R.A., J.E. Sanders, J.L. Zinn, J.L. Fryer, and K.S. Pilcher. 1975. Relation of water temperature to Flexibacter columnaris infection in steelhead trout (Salmo gairdneri), coho (Oncorhynchus kisutch) and chinook (O. tshawytscha) salmon. J. Res. Fish. Board Can. 32(9):1553-1559.

Holtby, B.L. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Science 45:502-515.

Holtby, L.B., T.E. McMahon, and J.C. Scrivener. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (Oncorhynchus kisutch) smolts and fry and chum salmon (O. keta) fry from Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 46:1396-1405.

Holtby, L.B. and J.C. Scrivener. 1989. Observed and simulated effects of climatic variability, clear-cut logging and fishing on the numbers of chum salmon (Oncorhynchus keta) and coho salmon (Oncorhynchus kisutch) returning to Carnation Creek, British Columbia. p. 62-81. In: C.D. Levings, L.B. Holtby, and M.A. Henderson (eds.). Proceedings of the national workshop on effects of habitat alterations on salmonid stocks. Canadian Special Publication of Fisheries and Aquatic Sciences 105, Ottawa, Ontario, Canada.

Horning, W.B. and R.E. Pearson. 1973. Growth temperature requirements and lower lethal temperatures for juvenile small bass (Micropterus dolomieui). J. Fish. Res. Board Can. 30:1226-1230.

Hostetler, S.W. 1991. Analysis and modeling of long-term stream temperatures on the Steamboat Creek Basin, Oregon: implications for land use and fish habitat. Water Resources Bull. 27(4):637-647.

Hubert, W.A. and W.A. Gern. 1995. Influence of embryonic stage on survival of cutthroat trout exposed to temperature reduction. Prog. Fish-Culturist 57:326-328.

Hubert, W.A., R.W. Stonecypher, Jr., Gern, W.A., and J. Bobbit. 1994. Response of cutthroat trout embryos to reduced incubation temperatures at different developmental stages. Prog. Fish-Culturist 56:185-187.

Humpesch, U.H. 1985. Inter- and intra-specific variation in hatching success and embryonic development of five species of salmonids and Thymallus thymallus. Arch. Hydrobiol. 104(1):129-144.

Hutchison, V.H. and J.D. Maness. 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. Am. Zool. 19:367-384.

Idler, D.R. and W.A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Prog. Rep., Int. Pac. Salmon Fish. Comm. 80 p.

Inskip, P.D. and J.J. Magnuson. 1983. Changes in fish populations over an 80-year period: Big Pine Lake, Wisconsin. Trans. Am. Fish. Soc. 112:378-389.

Iron, J.G., III, S.R. Ray, L.K. Miller, and M.W. Oswood. 1989. Spatial and seasonal patterns of streambed water temperatures in an Alaskan subarctic stream. p. 381-390. In: Headwaters Hydrology. American Water Resources

Association.

Jensen, A.J. 1990. Growth of young migratory brown trout Salmo trutta correlated with water temperature in Norwegian rivers. J. Anim. Ecol. 59(2):603-614.

Jensen, A.J., B.O. Johsen, and L. Saksgard. 1989. Temperature requirements in Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic char (Salvelinus alpinus) from hatching to intitial feeding compared with geographic distribution. Can. J. Fish. Aquat. Sci. 46:786-789.

Jobling, M. 1981. Temperature tolerance and final preferendum-rapid methods for the assessment of optimum growth temperatures. J. Fish Biology 19:439-455.

Jobling, M. 1993. Bioenergetics: feed intake and energy partitiioning. p. 1-43. In: J.C. Rankin and F.B. Jensen (ed.). Fish ecophysiology. Chapman and Hall. London.

Johnson, J. 1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. U.S. Fish. Wildl. Serv., Fish. Bull. 176:471-485.

Johnson, H.E. and R.F. Brice. 1953. Effects of transportation of green eggs, and of water temperature during incubation, on the mortality of chinook salmon. Prog. Fish-Culturist 15:104-108.

Johnston, C.E. and R.L. Saunders. 1981. Parr-smolt transformation of yearling Atlantic salmon (Salmo salar) at several rearing temperatures. Can. J. Fish. Aquat. Sci. 38(10):1189-1198.

Jowett, J.G. 1990. Factors related to the distribution and abundance of brown and abundance of brown and rainbow trout in New Zealand clear-water rivers. N.Z. J. Mar. Freshwat. Res. 24(3):429-440.

Karr, M.H., J.K. Fryer, and P.R. Mundy. 1998. Snake River water temperature control project. Phase II. Methods for managing and monitoring water temperatures in relation to salmon in the lower Snake River. Columbia River Inter-Tribal Fish Commission, Prepared for U.S. Environmental Protection Agency, Region 10, Contract No. X-990375-01-1. 209 p.

Karr, M., B. Tanovan, R. Turner, and D. Bennett. 1992. Interim report: model studies and 1991 operations. Water temperature control project, Snake River. Columbia River Inter-Tribal Fish Commission, US Army Corps of Engineers, and University of Idaho Fish and Wildlife Resources Department. 58 p.

Kaya, C.M. 1978. Thermal resistance of rainbow trout from a permanently heated stream, and of two hatchery strains. Prog. Fish-Culturist 40(4):138-142.

Kaya, C.M., L.R. Kaeding, and D.E. Burkhalter. 1977. Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. Prog. Fish-Culturist 39(1):37-39.

Keleher, C.J. and F.J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain Region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Trans. Am. Fish. Soc. 125(1):1-13.

Kellogg, R.L. and J.J. Gift. 1983. Relationship between optimum temperatures for growth and preferred temperatures for the young of the four fish species. Trans. Am. Fish. Soc. 112:424-430.

Kelsch, S.W. 1996. Temperature selection and performance by bluegills: evidence for selection in response to available power. Trans. Am. Fish. Soc. 125:948-955.

Kelsch, S.W. and W.H. Neill. 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optima. Trans. Am. Fish. Soc. 119:601-610.

Kilgour, D.M. and R.W. McCauley. 1986. Reconciling the two methods of measuring upper lethal temperatures in fishes. Environmental Biology of Fishes 17(4):281-290.

King, W. 1937. Notes on the distribution of native speckled and rainbow trout in the streams at Great Smoky Mountians National Park. J. Tenn. Acad. Sci. 12:351-361.

Konecki, J.T., C.A. Woody, and T.P. Quinn. 1993. Thermal adaptations of Washington coho salmon (Oncorhynchus kisutch)populations: incubation, preference and tolerance. School of Fisheries, Center for Streamside Studies, University of Washington WH-10, Seattle, WA. 34 p.

Konecki, J.T., C.A. Woody, and T.P. Quinn. 1995a. Critical thermal maxima of coho salmon (Oncorhynchus kisutch) fry under field and laboratory acclimation regimes. Can. J. Zool. 73:993-996.

Konecki, J.T., C.A. Woody, and T.P. Quinn. 1995b. Temperature preference in two populations of juvenile coho salmon, Oncorhynchus kisutch. Env. Biol. Fishes 44:417-421.

Konstantinov, A.S., V.V. Zdanovich, and D.G. Tikhomirov. 1989. Effect of temperature oscillation on the metabolic rate and energetics of young fish. J. Ichthyology 29( 6):1019-1027.

Kovacs, T.G. and G. Leduc. 1982. Acute toxicity of cyanide to rainbow trout (Salmo gairdneri) acclimated at different temperatures. Can. J. Fish. Aquat. Sci. 39:1426-1429.

Kwain, W. 1975. Effects of temperature on development and survival of rainbow trout, Salmo gairdneri, in acid waters. J. Fish. Res. Board Can. 32(4):493-497.

Kwain, W. and R.W. McCauley. 1978. Effects of age and overhead illumination on temperatures preferred by underyearling rainbow trout, Salmo gairdneri, in a vertical temperature gradient. J. Fish. Res. Board Can. 35(11):1430-1433.

Lattenmaier, D.P. and T.Y. Gan.1990. Hydrologic sensitivities of the Sacramento-San-Joaquin River Basin, California, to global warming. Water Resources Res. 26(1):69-86.

Lee, R.M. and J.N. Rinne. 1980. Critical thermal maxima of five trout species in the southwestern United States. Trans. Am. Fish. Soc. 109(6):632-635.

Leitritz, E. and R.C. Lewis. 1976. Trout and salmon culture. California Department of Fish and Game. Fish Bulletin 164. 197 p.

Li, H.W., G.A. Lamberti, T.N. Pearsons, C.K. Tait, J.L. Li, and J.C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Trans. Am. Fish. Soc. 123:627-640.

Li, H.W., T.N. Pearsons, C.K. Tait, J.L. Li, and R. Gaither. 1992. Approaches to evaluate habitat improvement programs in streams of the John Day Basin. Oregon Cooperative Fishery Research Unit, Department of Fisheries and Wildlife, Oregon State University. Completion Report.

Li, H.W., C.B. Schreck, C.E. Bond, and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. p. 193-202. In: Matthews, W.J. and D.C. Heins (eds.). Community and evolutionary ecology of North American stream fishes. Univ. of Oklahoma Press. Norman and London.

Lindsay, R.B., B.C. Jonasson, R.K. Schroeder, and B.C. Cates. 1989. Spring chinook salmon in the Deschutes River, Oregon. Information Reports, No. 89-4. Oregon Department of Fish and Wildlife. 92 p.

Lindsay, R.B., W.J. Knox, M.W. Flesher, B.J. Smith, E.A. Olsen, and L.S. Lutz. 1986. Study of wild spring chinook salmon in the John Day River system. 1985 Final Report. Oregon Department of Fish and Wildlife. Bonneville Power Administration, Division of Fish and Wildlife, Contract No. DE-A179-83BP39796, Project No. 79-4.

Lohr, S.C., P.A. Byorth, C.M. Kaya, and W.P. Dwyer. 1996. High-temperature tolerances of fluvial Arctic grayling and comparisons with summer river temperatures of the Big Hole River, Montana. Trans. Am. Fish. Soc. 125:933-939.

Lyons, J., and L. Wang, T.D. Simonson. 1996. Development and validation of an index of biotic integrity for coldwater streams in Wisconsin. N. Am. J. Fisheries Management 16(2):241-256.

Mabbott, L.B. 1982. Density and habitat of wild and introduced juvenile steelhead trout in the Lochsa River drainage, Idaho. Master's thesis. University of Idaho, Moscow.

Madison, D.M., R.M. Horrall, A.B. Stasko, and A.D. Hasler. 1972. Migrating movements of adult sockeye salmon (Oncorhynchus nerka) in coastal British Columbia as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 29:1025-1033.

Magnuson, J.J., L.B. Crowder, and P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool 19:331-343.

Mahnken, C.V.W. and F.W. Waknitz. 1979. Factors affecting growth and survival of coho salmon (Oncorhynchus kisutch) and chinook salmon (O. tshawytscha) in saltwater net-pens in Puget Sound. Proc. World Maricul. Soc. 10:280-305.

Major, R.L. and J.L. Mighell. 1967. Influence of Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of sockeye salmon. Fishery Bull. 66(1):131-147.

Mantelman, I.I. 1960. Distribution of the young of certain species of fish in temperature gradients. Fisheries Board of Canada Translation Series 257.

Margolis, L. and T.P.T. Evelyn. 1975. Ceratomyxa shasta (Myxosporida) disease in chum salmon (Oncorhynchus keta) in British Columbia. J. Fish. Res. Board Can. 32:1640-1643.

Margolis, L., T.E. McDonald, and D.J. Whitaker. 1992. Assessment of the impact of the myxosporean parasite Ceratomyxa shasta on survival of seaward migrating juvenile chinook salmon, Oncorhynchus tshawytscha, from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 49:1883-1889.

Marine, K.R. 1992. A background investigation and review of the effects of elevated water temperature on reproductive performance of adult chinook salmon (Oncorhynchus tshawytscha) with suggestions for approaches to the assessment of temperature induced reproductive impairment of chinook salmon stocks in the American River, California. Unpublished manuscript, prepared for the American River Technical Advisory Committee. Department of Wildlife and Fisheries Biology, University of California, Davis, California.

Marine, K.R. and J.J. Cech, Jr. 1998. Effects of elevated water temperatuare on some aspects of the physiological and ecological performance of juvenile chinook salmon (Oncorhynchus tshawytscha): implications for management of California's chinook salmon stocks. Stream temperature monitoring and assessment workshop. January 12-14, 1998. Sacramento, California. Forest Science Project, Humboldt State University, Arcata, California.

Marr, D.H.A. 1966. Influence of temperatuare on the efficiency of growth of salmonid embryos. Nature (Lond.)212(5065):957-959.

Marten, P.S. 1992. Effect of temperature variation on the incubation and development of brook trout eggs. The Progressive Fish-Culturist 54:1-6.

Martin, D.J., L.J. Wasserman, and V.H. Dale. 1986. Influence of riparian vegetation on posteruption survival of coho salmon fingerlings on the west-side streams of Mount St. Helens, Washington. N. Am. J. Fisheries Management 6(1):1-8.

Mather, D. and C.A. Silver. 1980. Statistical problems in studies of temperature preference of fishes. Can. J. Fish. Aquat. Sci. 37:733-737.

Mathur, D., R.M. Schutsky, E.J. Purdy, Jr., and C.A. Silver. 1981. Similarities in acute temperature preferences of freshwater fishes. Trans. Am. Fish. Soc. 110:1-13.

Mattax, B.L. and T.M. Quigley. 1989. Validation and sensitivity analysis of the stream network temperature model on small watersheds in northeast Oregon. p. 391-400. In: Woessner, W.W. and D.F. Potts (eds.). Am. Water Resour. Ass., Proc. of the Symp. on Headwaters Hydrology.

Matthews, K.R. and N.H. Berg. 1997. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. J. Fish Biology 50:50-67.

McCauley, R.W. 1958. Thermal relations of geographic races of Salvelinus. Can. J. Zool. 36(5):655-662.

McCauley, R.W. and W.L. Pond. 1971. Temperature selection of rainbow trout (Salmo gairdneri) fingerlings in vertical and horizontal gradients. J. Fish. Res. Board Can. 28:1801-1804.

McCauley, R.W., J.R. Elliot, and A.L.A. Read. 1977. Influence of acclimation temperature on preferred temperature in the rainbow trout, Salmo gairdneri. Trans. Am. Fish. Soc. 106:362-365.

McCormick, J.H. and J.A. Wegner. 1981. Responses of largemouth bass from different latitudes to elevated water temperatures. Trans. Am. Fish. Soc. 110:417-429.

McCormick, J.H., K.E.F. Hokanson, and B.R. Jones. 1972. Effects of temperature on growth and survival of young brook trout (Salvelinus fontinalis). J. Fish Res. Board Can. 29:1107-1112.

McCullough, D.A. 1975. Bioenergetics of three aquatic invertebrates determined by radioisotopic analyses. Idaho State University. 326 p.

McCullough, D.A. 1987. A systems classification of watersheds and streams. Ph.D. thesis. Oregon State University. 217 p.

McCullough, D.A. 1990. Classification of streams within a landscape perspective. 158 p. In: Coordinated Information System Project, Annual Progress Report, January 5, 1989- December 31, 1990. Prepared by Columbia River Inter-Tribal Fish Commission for Bonneville Power Commission.

McCullough, D.A. 1996. Stream carrying capacity and smolt production. p. 45-70. In: Proceedings from a workshop on ecological carrying capacity of salmonids in the Columbia River Basin: Measure 7.1A of the Northwest Power Planning Council's 1994 Fish and Wildlife Program. Report 3 of 4. Final report. US Department of Energy, Bonneville Power Administration. Project Number 93-012, Agreement Number DE-AI79-86BP62611.

McCullough, D.A. and F.A. Espinosa, Jr. 1996. A monitoring strategy for application to salmon-bearing watersheds. Tech. Report 96-5. Columbia River Inter-Tribal Fish Commission, Portland, Oregon. 170 p. + appendices.

McCullough, D.A., G.W. Minshall, and C.E. Cushing. 1979. Bioenergetics of a stream "collector" organism Tricorythodes minutus (Insecta: Ephemeroptera). Limnol. Oceanogr. 24(1):45-58.

McGeer, J.C., L. Baranyi, and G.K. Iwama. 1991. Physiological responses to challenge tests in six stocks of coho salmon (Oncorhynchus kisutch). Can. J. Fish. Aquat. Sci. 48:1761-1771.

McIntosh, B.A., D.M. Price, C.E. Torgersen, and H.W. Li. 1995a. Distribution, habitat utilization, movement patterns, and the use of thermal refugia by spring chinook in the Grande Ronde, Imnaha, and John Day Basins. Progress report to the Bonneville Power Administration, Project No. 88-108, FY-1995.

McIntosh, B.A., C.E. Torgersen, D.M. Price, and H.W. Li. 1995b. Distribution, habitat utilization, movement patterns, and the use of thermal refugia by spring chinook in the Grande Ronde, Imnaha, and John Day Basins. Annual report to the Bonneville Power Administration, Project No. 93-7000, FY-1995.

McIntyre, J.D. and B.E. Rieman. 1995. Westslope cutthroat trout. p. 1-15. In: M.K. Young (tech. ed.). Conservation assessment for inland cutthroat trout. USDA Forest Service, Gen. Tech. Report RM-GTR-256.

McMahon, T.E. and G.F. Hartman. 1988. Variation in the degree of silvering of wild coho salmon, Oncorhynchus kisutch, smolts migrating seaward from Carnation Creek, British Columbia. J. Fish Biol. 32:825-833.

McMahon, T.E. and G.F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (Oncorhynchus kisutch). Can. J. Fish. Aq. Sci. 46(9):1551-1557.

McRae, G. and C.J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for brook trout habitat. Trans. Am. Fish. Soc. 123:641-656.

Meisner, J.D. 1990 . Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. Trans. Am. Fish. Soc. 119:282-291.

Meisner, J.D., J.S. Rosenfeld, and H.A. Regier. 1988. The role of groundwater in the impact of climate warming on stream salmonines. Fisheries 13(3):2-8.

Mesa, M.G., T.P. Poe, A.G. Maule, and C.B. Schreck. 1998. Vulnerability to predation and physiological stress responses in juvenile chinook salmon (Oncorhynchus tshawytscha) experimentally infected with Renibacterium salmoninarum. Can. J. Fish. Aquat. Sci. 55:1599-1606.

Metcalfe, N.B. and J.E. Thorpe. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, Salmo salar L. J. Fish Biol. 41(Suppl. B):93-99.

Moore, A.M. 1967. Correlation and analysis of water-termperature data for Oregon streams. U.S. Geological

Survey Water-Supply Paper 1819-K. 53 p.

Moyle, P.B. 1976. Inland fishes of California. University of California Press. Berkeley, California. 405 p.

Moyle, P.B. and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. 114:695-704.

Mullan, J.W., K.R. Williams, G. Rhodus, T.W. Hillman, and J.D. McIntyre. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. U.S. Fish and Wildlife Service, Monograph 1. 187 p. plus appendices.

Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Science 38:137-145.

Murray, C.B. 1980. Some effects of temperature on zygote and alevin survival, rate of development and size at hatching and emergence of Pacific salmon and rainbow trout. M.S. thesis. University of British Columbia, Vancouver, B.C.

Murray, C.B. and T.D. Beacham. 1986. Effect of varying temperature regimes on the development of pink salmon (Oncorhynchus gorbuscha) eggs and alevins. Can. J. Zool. 64:670-676.

Murray, C.B. and T.D. Beacham. 1987. The development of chinook (Oncorhynchus tshawytscha) and chum salmon (Oncorhynchus keta) embryos and alevins under varying temperature regimes. Can. J. Zool. 65(11):2672-2681.

Murray, C.B., T.D. Beacham, and J.D. McPhail. 1990. Influence of parental stock and incubation temperature on the early development of coho salmon (Oncorhynchus kisutch) in British Columbia. Can. J. Zool. 68:347-358.

Murray, C.B. and J.D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (Oncorhynchus) embryos and alevins. Can. J. Zool. 66(1):266-273.

Murray, C.B., J.D. McPhail, and M.L. Rosenau. 1989. Reproductive and developmental biology of kokanee from Upper Arrow Lake, British Columbia. Trans. Am. Fish. Soc. 118:503-509.

Nakamoto, R.J. 1994. Characteristics of pools used by adult summer steelhead oversummering in the New River, California. Trans. Am. Fish. Soc. 123:757-765.

National Academy of Sciences (NAS). 1996. Upstream. Salmon and society in the Pacific Northwest. Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. National Academy Press.

National Academy of Sciences (NAS). 1972. Water quality criteria. Freshwater aquatic life and wildlife. Appendix II. EPA Ecol. Res. Series EPA-R3-73-033, US Environmental Protection Agency, Washington, D.C. 594 p.

Neitzel, D.A., M.J. Scott, S.A. Shankle, and J.C. Chatters. 1991. The effect of climate change on stream environments: the salmonid resource of the Columbia River basin. Northwest Environmental Journal 7:271-293.

Newsome, G.E. and G. LeDuc. 1975. Seasonal changes of fat content in the yellow perch (Perca flavescens) of two Laurentian Lakes. J. Fish. Res. Board Can. 32:2214-2221.

Nielsen, J.L., T.E. Lisle, and V. Ozaki. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Trans. Am. Fish. Soc. 123:613-626.

NMFS. 1998. Progress of species status reviews in NMFS Northwest Region. File 1pg898.pdf at NOAA website http://www.nwr.noaa.gov.

Northwest Power Planning Council (NPPC). 1986. Council staff compilation of information on salmon and steelhead losses in the Columbia River basin. NPPC, 850 S.W. Broadway, Suite 1100, Portland, Oregon 97205. 252 p.

Norton, D.J., M.A. Flood, B.A. McIntosh, N.J. Poage, P.J. LaPlaca, J.P. Craig, R.S. Karalus, J.R. Sedell, C.E. Torgerson, Y.D. Chen, S.C. McCutcheon, V. Duong, H. Puffenberger, J. Moeller, V. Kelly, E. Porter, and L. Shoemaker. 1996. Modeling, monitoring and restoring water quality and habitat in Pacific Northwestern watersheds. EPA GATF '95 Project. Abridged/unclassified version. April 1996.

Olsen, E., P. Pierce, M. McLean, and K. Hatch. 1993. Stock summary reports for Columbia River anadromous salmonids. Vol. I: Oregon. Coordinated Information System. Prepared for U.S. Department of Energy, Bonneville Power Administration, Division of Fish and Wildlife, Contract No. 88-108. DOE/BP 94402-1 and 94402-2.

Olson, P.A. and R.F. Foster. 1955. Temperature tolerance of eggs and young of Columbia River chinook salmon. Trans. Am. Fish. Soc. 85:203-207.

Ordal, E.J. and R.E. Pacha. 1963. The effects of temperature on disease in fish. p. 39-56. Proc. Twelfth Pacific Northwest Symposium on water pollution research. Corvallis, Oregon.

Oregon Department of Environmental Quality (ODEQ). 1995. 1992-1994 Water quality standards review. Department of Environmental Quality, Standards and Assessment Section. Final issues papers. Portland, Oregon.

Pacha, R.E. 1961. Columnaris disease in fishes in the Columbia River Basin. Univ. of Washington, Ph.D. Thesis. 332 p.

Pacha, R.E. and E.J. Ordal. 1970. Myxobacterial diseases of salmonids. p. 243-257. In: S.F. Snieszko (ed.). A symposium on diseases of fishes and shellfishes. Special Publication No. 5, American Fisheries Society, Washington, D.C.

Paladino, F.V., J.R. Spotila, J.P. Schubauer, and K.T. Kowalski. 1980. The critical thermal maximum: a technique used to elucidate physiological stress and adaptation in fishes. Rev. Can. Biol. 39(2):115-122.

Parker, F.L. and P.A. Krenkel. 1969. Thermal pollution. Status of the art report. Report Number 3, Department of Environmental and Water Resources Engineering, Vanderbilt University, Nashville, Tennessee. Prepared for the Federal Water Pollution Control Administration. Grant No. WP-01387-01.

Parrish, E.M. 1978. Evaluation of spring chinook salmon eigration, harvest and returns to Rapid River Hatchery, 1977. Idaho Department of Fish and Game. Annual Performance Report, Project No. IPC-17 and IPC-13.

Paulik, G.J. 1960. The locomotive performance of salmonids during upstream migration. p. 41-42. In: T.S.Y. Koo (ed.). Research in fisheries...1959. Contrib. No. 77. Univ. Wash., College Fish., Seattle, WA.

Paulik, G.J. and A.C. DeLacy. 1958. Changes in the swimming ability of Columbia River sockeye salmon during upstream migration. Univ. Wash., Sch. Fish., Tech. Rep. No. 46, p. 1-67.

Paulik, G.J., A.C. DeLacy, and E.F. Stacy. 1957. The effect of rest on the swimming performance of fatigued adult silver salmon. Univ. Wash., Sch. Fish., Tech. Rep. No. 31, p. 1-24.

Peterson, R.H. and D.J. Martin-Robichaud. 1989. First feeding of Atlantic salmon (Salmo salar L.) fry as influenced by temperature regime. Aquaculture 78(1):35-53.

Peterson, R.H., H.C.E. Spinney, and A. Sreedharan. 1977. Development of Atlantic salmon (Salmo salar) eggs and alevins under varied temperature regimes. J. Fish. Res. Board Can. 34:31-43.

Peterson, R.H., A.M. Sutterlin, and J.L. Metcalfe. 1979. Temperature preference of several species of/ Salmo/ and Salvelinus/ and some of their hybrids. J. Fish. Res. Board Can. 36(9):1137-1140.

Piper, R.G., I.B. McElwain, L.E. Orme, J.P. McCraren, L.G. Fowler, and J.R. Leonard. 1982. Fish hatchery management. US Department of Interior. Fish and Wildlife Service. Washington, D.C. 517 p.

Platts, W.S. 1974. Geomorphic and aquatic conditions influencing salmonids and stream classification. Surface Environment and Mining Program. 199 p.

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. Aq. Sci. 46:1805-1818.

Potter, I.C. and F.W.H. Beamish. 1975. Lethal temperatures in ammocoetes of four species of lampreys. Acta Zoologica 56:85-91.

Power, M. and G. Power. 1994. Modeling the dynamics of smolt production in Atlantic salmon. Trans. Am. Fish. Soc. 123:535-548.

Pratt, K. 1984. Habitat use and species interaction of juvenile cutthroat trout (Salmo clarki lewisi) and bull trout (Salvelinus confluentus) in the upper Flathead River Basin. M.S. thesis, University of Idaho, Moscow, Idaho.

Preall, R.J. and N.H. Ringler. 1989. Comparison of actual and potential growth rates of brown trout (Salmo trutta) in natural streams based on bioenergetic models. Can. J. Fish. Aquat. Sci. 46:1067-1076.

Priede, I.G. 1985. Metabolic scope in fishes. p. 33-64. In: P. Tytler and P. Calow (eds.). Fish energetics new perspectives. The John Hopkins University Press, Baltimore, Maryland.

Quinn, T.P. and D.J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77(4):1151-1162.

Quinn, T.P., S. Hodgson, and C. Peven. 1997. Temperature, flow, and the migration of adult sockeye salmon (Oncorhynchus kisutch) in the Columbia River. Can. J. Fish. Aquat. Sci. 54:1349-1360.

Rahel, F.J. and W.A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: biotic zonation and additive patterns of community change. Trans. Am. Fish. Soc. 120:319-332.

Raleigh, R.F., W.F. Miller, and P.C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: chinook salmon. U.S. Fish Wildl. Service Biol. Rep. 82(10.122). 64 p.

Ratliff, D.E. 1981. Ceratomyxa shasta: epizootiology in chinook salmon of central Oregon. Trans. Am. Fisheries Soc. 110:507-513.

Ratliff, D.E. 1983. Ceratomyxa shasta: longevity, distribution, timing, and abundance of the infective stage in central Oregon. Can. J. Fisheries and Aquatic Sciences 40:1622-1632.

Reeves, G.H., F.H. Everest, and J.D. Hall. 1987. Interaction between redside shiner (Richarsonius balteatus) and the steelhead trout (Salmo gairdneri) in western Oregon: the influence of water temperature. Can. J. Fisheries and Aquatic Sciences 44:1603-1613.

Reeves, G.H., J.D. Hall, and S.V. Gregory. 1997. The impact of land-management activities on coastal cutthroat trout and their freshwater habitats. p. 138-144. In: J.D. Hall, P.A. Bisson, and R.E. Gresswell (ed.). Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis.

Reiser, D.W. and T.C. Bjornn. 1979. Habitat requirements of anadromous salmonids. Gen. Tech. Rep. PNW-96. USDA Forest Service. Pacific Northwest Forest and Range Experiment Station. Portland, Oregon. 54 pp.

Reynolds, W.W. and M.E. Casterlin. 1979a. The role of temperature in the environmental physiology of fishes. In: M.A. Ali (ed.). Environmental physiology of fishes. Plenum Press, New York.

Reynolds, W.W. and M.E. Casterlin. 1979b. Behavioral thermal regulation and the 'final preferendum' paradigm. Amer. Zool 19:211-224.

Reynolds, W.W. and M.E. Casterlin. 1979c. Thermoregulatory behavior of brown trout, Salmo trutta. Hydrobiologia 62:79-80.

Rhodes, J.J., D.A. McCullough, and F.A. Espinosa, Jr. 1994. A coarse screening process for evaluation of the effects of land management activities on salmon spawning and rearing habitat in ESA consultations. Tech. Report 94-4. Columbia River Inter-Tribal Fish Commission, Portland, Oregon. 127 pp. + appendices.

Rice, G.V. 1960. Use of coldwater holding facilities in conjunction with king salmon spawning operations at Nimbus Hatchery. Inland Fisheries Administrative Report Number 60-3.

Ricklefs, R.E. 1973. Ecology. Chiron Press, New York. 861 p.

Rodgers, D.W. and J.S. Griffiths. 1983. Effects of elevated thermal regimes on survival of rainbow trout (Salmo gairdneri) alevins. J. Great Lakes Res. 9(3):421-424.

Ryder, R.A., W.B. Scott, and E.J. Crossman. 1964. Fishes of northern Ontario, north of the Albany River. R. Ont. Mus., Life. Sciences Contribution 60. 30 p.

Sadler, S.E., G.W. Friars, and P.E. Ihssen. 1986. The influence of temperature and genotype on the growth rate of hatchery-reared salmonids. Can. J. Anim. Sci. 66:599-606.

Sandercock, F.K. 1991. Life history of coho salmon (Oncorhynchus kisutch). p. 395-445. In: C. Groot and L. Margolis (ed.). Pacific salmon life histories. UBC Press, Vancouver. 564 p.

Sanders, J.E., K.S. Pilcher, and J.L. Fryer. 1978. Relation of water temperature to bacterial kidney disease in coho salmon (Oncorhynchus kisutch), sockeye salmon (O. nerka), and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 35(1):8-11.

Sauter, S.T. and A.G. Maule. 1997. The role of water temperature in the smolt physiology of chinook salmon. Presentation given at the Columbia/Snake River mainstem water temperature workshop. Integrated ecosystem management of the Columbia River basin. November 6-7, 1997. Portland State University, Portland, OR.

Scarnecchia, D.L., A. Isaksson, and S.E. White. 1989. Oceanic and riverine influences on variations in yield among Icelandic stocks of Atlantic salmon. Trans. Am. Fish. Soc. 118:482-494.

Schreck, C.B., J.C. Snelling, R.E. Ewing, C.S. Bradford, L.E. Davis, and C.H. Slater. 1994. Migratory behavior of adult spring chinook salmon in the Willamette River and its tributaries. Oregon Cooperative Fishery Research Unit, Oregon State University, Corvallis, Oregon. Project Number 88-160-3, Prepared for Bonneville Power Administration, Portland, Oregon.

Schurmann, H., J.F. Steffensen, and J.P. Lomholt. 1991. The influence of hypoxia on the preferred temperature of rainbow trout Oncorhynchus mykiss. J. Exp. Biol. 157:75-86.

Scott, W.B. and E.J. Crossman. 1985. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa, 1973. Bull. 184. The Bryant Press Limited. 966 p.

Servizi, J.A. and J.O.T. Jensen. 1977. Resistance of adult sockeye salmon to acute thermal shock. Progress report no. 34. International Pacific Salmon Fisheries Commission, British Columbia, Canada. 51 p.

Servizi, J.A. and D.W. Martens. 1991. Effect of temperature, season, and fish size on acute lethality of suspended sediments to coho salmon (Oncorhynchus kisutch). Can. J. Fish. Aquat. Sci. 48:493-497.

Shepard, B.B., S.A. Leathe, T.M. Weaver, and M.D. Enk. 1984. Monitoring levels of fine sediment within tributaries to Flathead Lake and impacts of fine sediment on bull trout recruitment. Proceedings of the Wild Trout III Symposium. Yellowstone Nat. Park, WY.

Shepherd, B.G., G.F. Hartman, and W.J. Wilson. 1986. Relationships between stream and intragravel temperatures in coastal drainages, and some implications for fisheries workers. Can. J. Fisheries and Aquatic Sciences 43:1818-1822.

Slater, D.W. 1963. Winter-run chinook salmon in the Sacramento River, California with notes on water temperature requirements at spawning. U.S. Fish and Wildlife Service, Special Scientific Report, Fisheries No. 461. 9 p.

Smith, C.E., W.P. Dwyer, and R.G. Piper. 1983. Effect of water temperature on egg quality of cutthroat trout. Prog. Fish-Cult. 45(3):176-178.

Snake River Subbasin Plan. 1990. Snake River subbasin (Mainstem from mouth to Hells Canyon Dam). Salmon and steelhead production plan. September 1, 1990. Northwest Power Planning Council and Columbia Basin Fish and Wildlife Authority, Portland, Oregon.

Snieszko, S.F. 1964. Remarks on some facets of epizootiology of bacterial fish diseases. Devel. Indust. Microbiol. 5:97-100.

Snieszko, S.F. 1974. The effects of environmental stress on outbreaks of infectious diseases of fishes. J. Fish. Biol. 6:197-208.

Sonski, A.J. 1983a. Heat tolerance of redband trout. Annu. Proc. Tex. Chap. Am. Fish. Soc. 5:66-76.

Sonski, A.J. 1983b. Culture of redband trout at a warm-water hatchery. p. 21-40. Proceedings of Fish Farming Conference and Annual Convention of Catfish Farmers of Texas. Texas A&M University.

Sonski, A.J. 1984. Comparison of heat tolerances of redband trout, Firehole River rainbow trout, and Wytheville rainbow trout. Annu. Proc. Tex. Chap. Am. Fish. Soc. 6:27-35.

Spence, B.C., G.A. Lomnicky, R.M. Hughes, R.P. Novitzki. 1996. An ecosystem approach to salmonid conservation. TR-4501-96-6057. ManTech Environmental Research Services Corp., Corvallis, OR.

Spigarelli, S.A., M.M. Thommes, and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. Trans. Am. Fish. Soc. 111(2):199-209.

Spigarelli, S.A., M.M. Thommes, W. Prepejchal, and R.M. Goldstein. 1983. Selected temperatures and thermal experience of brown trout, Salmo trutta, in a steep thermal gradient in nature. Environ. Biol. Fishes. 8(2):137-149.

Stabler, D.F. 1981. Effects of altered flow regimes, temperatures, and river impoundment on adult steelhead trout and chinook salmon. M.S. thesis, University of Idaho, Moscow, Idaho. 84 p.

Stauffer, J.R., Jr. 1980. Influence of temperature on fish behavior. p. 103-141. In: C.H. Hocutt, J.R. Stauffer, Jr., J.E. Edinger, L.W. Hall, Jr., R.P. Morgan II. (eds.). 1980. Power plants. Effects on fish and shellfish behavior. Academic Press, New York.

Stauffer, J.R., J. Cairns, Jr., K.L. Dickson, and D.L. Cherry. 1976. The potential and realized influence of temperature on the distribution of fishes in the New River, Glen Lyn, Va. Wildlife Monographs 50:1-40.6.

Stauffer, J.R., Jr., E.L. Melisky, and C.H. Hocutt. 1984. Interrelationships among preferred, avoided, and lethal temperatures of three fish species. Arch. Hydrobiol. 100(2):159-169.

Stearns, S.C. 1981. On measuring fluctuating environments: predictability, constancy, and contingency. Ecology 62:185-199.

Stefan, H.G. and E.B. Preud'homme. 1993. Stream temperature estimation from air temperature. Water Resour. Bull. 29:27-45.

Stonecypher, R.W., Jr., W.A. Hubert, and W.A. Gern. 1994. Effect of reduced incubation temperatures on survival of trout embryos. Prog. Fish-Culturist 56:180-184.

Stoneman, C.L. and M.L. Jones. 1996. A simple method to classify stream thermal stability with single observations of daily maximum water and air temperatures. N. Am. J. Fisheries Management 16:728-737.

Sullivan, K., J. Tooley, K. Doughty, J.E. Caldwell, and P. Knudsen. 1990. Evaluation of prediction models and characterization of stream temperature regimes in Washington. Timber/Fish/Wildlife Rep. No. TFW-WQ3-90-006. Washington Department of Natural Resources, Olympia, Washington. 224 p.

Sylvester, R.O. 1958. Water quality studies in the Columbia River Basin. U.S. Fish Wildlife Service Spec. Sci. Rep. Fish. No. 239. 134 p.

Tang, J., M.D. Bryant, and E.L. Brannon. 1987. Effect of temperature extremes on the mortality and development rates of coho salmon embryos and alevins. Prog. Fish-Cult. 49(3):167-174.

Taniguchi, R., F.J. Rahel, D.C. Novinger, and K.G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Can. J. Fish. Aquat. Sci. 55:1894-1901.

Taylor, B.R. and B.A. Barton. 1992. Temperature and dissolved oxygen criteria for Alberta fishes in flowing waters. Prepared for Alberta Fish and Wildlife Division, Edmonton, Alberta by Environmental Management Associates, Calgary, Alberta. 72 p.
Taylor, E.B. 1990. Environmental correlates of life-history variation in juvenile chinook salmon, Oncorhynchus tshawytscha (Walbaum). J. Fish Biology 37:1-17.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185-207.

Thedinga, J.F. and K.V. Koski. 1984. The production of coho salmon, Oncorhynchus kisutch, smolts and adults from Porcupine Creek. p. 99-108. In: W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.). Fish and wildlife relationships in old-growth forests; proceedings of a symposium. Juneau, Alaska, 12-15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Theurer, F.D., I. Lines, and T. Nelson. 1985. Interaction between riparian vegetation, water temperature, and salmonid habitat in the Tucannon River. Water Resources Bull. 21(1):53-64.

Thomas, R.E., J.A. Gharrett, M.G. Carls, S.D. Rice, A. Moles, and S. Korn. 1986. Effects of fluctuating temperature on mortality, stress, and energy reserves of juvenile coho salmon. Trans. Am. Fish. Soc. 15:52-59.

Thompson, K. 1974. Chapter 7: Salmonids. p. 85-103. In: K. Bayha and C. Koski. (ed.). Anatomy of a river. Pac. Northwest River Basins Comm., Vancouver, WA.

Threader, R.W. and A.H. Houston. 1983. Heat tolerance and resistance in juvenile rainbow trout acclimated to diurnally cycling temperatures. Comp. Biochem. Physiol. 75A:153-155.

Tiffan, K.F., R.D. Garland, and P.G. Wagner. 1996. Osmoregulatory performance, migration behavior, and marking of subyearling chinook salmon at McNary Dam to estimate adult contribution. p. 99-128. In: D.W. Rondorf and K.F. Tiffan (ed.). Identification of the spawning, rearing, and migratory requirements of fall chinook salmon in the Columbia River basin. 1994 Annual report to Bonneville Power Administration, Contract DE-AI79-91BP21708, Portland, Oregon.

Torgerson, C.E. 1997. Multiscale assessment of thermal patterns and the distribution of chinook salmon in the John Day River Basin, Oregon. M.S. thesis. Oregon State University, Corvallis, Oregon. 99 p.

Torgersen, C.E., D.M. Price, H.W. Li, and B.A. McIntosh. 1995. Thermal refugia and chinook salmon habitat in Oregon: applications of airborne thermal videography. p. 167-171. In: Proceedings of the 15th biennial workshop on color photography and videography in resource assessment, May 1995, Terre Haute, Indiana. American Society for Photogrammetry and Remote Sensing.

Tucannon River Subbasin Plan (TSP). 1990. Salmon and steelhead production plan. Prepared by the Washington Department of Fisheries, Confederated Tribes of the Umatilla Indian Reservation, Nez Perce Tribe of Idaho, and Washington Department of Wildlife. Northwest Power Planning Council and Columbia Basin Fish and Wildlife Authority. 98 p.

U.S. Environmental Protection Agency (USEPA) 1992. Columbia River Basin water quality summary report: an ecosystem assessment. Prepared for the Northwest Power Planning Council, Portland, Oregon, by C. Kelly, J. Gabrielson, J. Malek, G. Hayslip. June 26, 1992.

Udey, L.R., J.L. Fryer, and K.S. Pilcher. 1975. Relation of water temperature to Ceratomyxosis in rainbow trout (Salmo gairdneri) and coho salmon (Oncorhynchus kisutch). J. Fish. Res. Board Can. 32(9):1545-1551.

U.S. Geological Survey (USGS). 1968. Water temperatures in the lower Columbia River. Geological Survey Circular 551. 45 p.

van den Berghe and M.R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: Oncorhynchus kisutch). Evolution 43(1):125-140.

Vannote, R.L. and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Am. Nat. 115:667-695.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vaux, W.G. 1962. Interchange of stream and intragravel water in a salmon spawning riffle. US Fish Wild. Serv. Spec. Sci. Rep. Fish. No. 405. 11p.

Vigg, S. and D.L. Watkins. 1991. Temperature control and flow augmentation to enhance spawning migration of salmonids in the Snake River, especially fall chinook salmon. Manuscript. Bonneville Power Administration, Portland, Oregon. 11 p.

Vigg, S.C. and D.L. Koch. 1980. Upper lethal temperature range of Lahontan cutthroat trout in waters of different ionic concentration. Trans. Am. Fish. Soc. 109(3):336-339.

Vronskiy, B.B. 1972. Reproductive biology of the Kamchatka River chinook salmon [Oncorhynchus tshawytscha (Walbaum)]. J. Ichthyol. 12:259-273.

Wade, M. 1986. The relative effects of Ceratomyxa shasta on crosses of resistant and susceptible stocks of summer steelhead. Information Reports, Number 86-8. Oregon Department of Fish and Wildlife, Fish Division.

Wagner, H.H. 1974. Photoperiod and temperature regulation of smolting in steelhead trout (Salmo gairdneri). Can. J. Zool. 52:219-234.

Wangila, B.C.C. and T.A. Dick. 1988. Influence of genotype and temperature on the relationship between specific growth rate and size of rainbow trout. Trans. Am. Fish. Soc. 117(6):560-564.

Warren, C.E. 1971. Biology and water pollution control. W.B. Saunders Co. Philadelphia. 434 p.

Warren, C.E. 1979. Toward classification and rationale for watershed management and stream protection. U.S.E.P.A. Corvallis, Oregon. EPA-600/3-79-059. 143 p.

Watenpaugh, D.E. and T.L. Beitinger. 1985. Temperature tolerance of nitrite-exposed channel catfish. Trans. Am. Fish. Soc. 114:274-278.

Weatherley, A.H. 1963. Zoogeography of Perca fluviatilis (Linnaeus) and Perca flavescens (Mitchill) with special reference to the effects of high temperature. Proc. Zool. soc. London 141:557-576.

Wedemeyer, G. 1973. Some physiological aspects of sublethal heat stress in the juvenile steelhead trout (Salmo gairdneri) and coho salmon (Oncorhynchus kisutch). J. Fish. Res. Board Can. 30(6):831-834.

Wedemeyer, G.A. 1980. Effects of environmental stressors in aquacultural systems on quality, smoltification and early marine survival of anadromous fish. Proc. No. Pac. Aquaculture Symp., Anchorage, Alaska.

Wedemeyer, G.A. and D.J. McLeay. 1981. Methods for determining the tolerance of fishes to environmental stressors. p. 247-275. In: A.D. Pickering (ed.). Stress and fish. Academic Press, London.

Wedemeyer, G.A., R.L. Saunders, and W.C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42 (6):1-14.

White, D.S., C.H. Elzinga, and S.P. Hendricks. 1987. Temperature patterns within the hyporheic zone of a northern Michigan river. J. North Am. Benthological Society 6:85-91.

Williams, I.V., U.H.M. Fagerlund, J.R. McBride, G.A. Strasdine, H. Tsuyuki, and E.J. Ordal. 1977. Investigation of prespawning mortality of 1973 Horsefly River sockeye salmon. Progress report no. 37. International Pacific Salmon Fisheries Commission, British Columbia, Canada. 51 p.

Wilson, W.J., M.D. Kelley, and P.R. Meyer. 1987. Instream temperature modeling and fish impact assessment for a proposed large-scale Alaska hydro-electric project. p. 183-206. In. J.F. Craig and J.B. Kemper (eds.). Regulated streams. Plenum Press, New York. 431 p.

Wissmar, R.C., J.E. Smith, B.A. McIntosh, et al. 1994. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1800s-1900s). Northwest Science. Special 68:1-36.

Withler, R.E. and T.P.T. Evelyn. 1990. Genetic variation in resistance to bacterial kidney disease within and between two strains of coho salmon from British Columbia. Trans. Am. Fish. Soc. 119(6):1003-1009.

Wurtsbaugh, W.A. and G.E. Davis. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of Salmo gairdneri, Richardson. J. Fish. Biol. 11:87-98.

Young, M.K. 1994. Mobility of brown trout in south-central Wyoming streams. Can. J. Zoology 72(12):2078-2083.

Young, M.K. 1995. Colorado River cutthroat trout. p. 16-23. In: M.K. Young (tech. ed.). Conservation assessment for inland cutthroat trout. USDA Forest Service, Gen. Tech. Report RM-GTR-256.

Zaugg, W.S. and L.R. McLain. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (Oncorhynchus kisutch). Comp. Biochem. Physiol. 54A:419-421.

Zaugg, W.S. and H.H. Wagner. 1973. Gill ATPase activity related to parr-smolt transformation in steelhead trout Salmo gairdneri: influence of photoperiod and temperature. Comparative Biochemistry and Physiology 45:955-965.

Zinn, J.L., K.A. Johnson, J.E. Sanders, and J.L. Fryer. 1977. Susceptibility of salmonid species and hatchery strains of chinook salmon (Oncorhynchus tshawytscha) to infections by Ceratomyxa shasta. J. Fish. Res. Board Can. 34:933-936.