AN ANALYSIS OF THE EFFECTS OF TEMPERATURE ON SALMONIDS OF THE PACIFIC NORTHWEST WITH IMPLICATIONS FOR SELECTING TEMPERATURE CRITERIA

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Kathleen Sullivan

Sustainable Ecosystems Institute
Portland, Oregon

Douglas J. Martin

Martin Environmental
Seattle, Washington

Richard D. Cardwell

Parametrix Inc.
Kirkland, Washington

John E. Toll

Parametrix Inc.
Kirkland, Washington

Steven Duke

Weyerhaeuser Company
Tacoma, Washington

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ABSTRACT

To administer the Clean Water Act, the U.S. Environmental Protection Agency and state water quality agencies throughout the nation have adopted numeric and qualitative criteria that establish environmental conditions known to protect aquatic life from adverse effects. Pacific Northwest states have adopted temperature criteria designed specifically to protect fish with emphasis on salmonid species because water temperature plays a role in virtually every aspect of salmon life. Adverse levels of temperature can affect growth, behavior, disease resistance, and mortality. In recent years, the EPA and National Academies of Science and Engineering have promoted risk assessment techniques to develop water quality criteria, including formal protocols that have been peer reviewed nationally. Risk assessment is designed to combine the information from biological studies with an analysis of each population's exposure to quantified effects. Risk occurs when the stress' magnitude, frequency and duration exceed the species' ability to deal with that stress. A risk-based approach seems ideally suited to developing criteria for and assessing temperature risk to fish because exposure has been well documented through temperature monitoring and extensive research on the lethal and sublethal effects on salmon physiology has been conducted over the past 40 years. Nevertheless, risk-based approaches have not yet been used to establish temperature criteria in recent state agency reviews of water quality standards.

In this paper we develop a risk-based approach to analyze summertime temperature effects on juvenile salmon species. We use available research findings to quantitatively evaluate the biological effects of temperature in combination with measured stream temperature ranging from very cold to very warm. Many currently exceed Washington's temperature standard. Acute risk to high temperatures was assessed using laboratory-derived values of mortality in relation to duration of exposure. Despite warm temperatures, the risk analysis found that direct mortality from temperature is unlikely in the range of temperature in study streams because temperatures high enough to cause mortality are either never observed, or occur over too short of periods of time to cause death. The analysis suggested that there is little or no risk of mortality if annual maximum temperature is less than 26°C, although site-specific analyses are suggested when annual maximum temperature exceeds 24°C to affirm this result in local river conditions. Short-term occurrence of temperatures sufficient in duration and magnitude to cause mortality is feasible, within parts of the Pacific Northwest region, and therefore streams in other geographic areas or streams with known temperature extremes should be individually evaluated with the method. Chronic exposure to temperature was based on the growth potential of fish as assessed using a simplified bioenergetics approach developed in the report. This analysis found that growth predicted from ambient temperatures is somewhat less than the maximum potential growth in all streams regardless of temperature regime, because no stream experienced temperatures that fully optimized growth all of the time during the summer rearing period. Generally the effect of temperature regime on growth was small in the range of streams studied, but growth effects were evident at higher temperatures. The results suggest that quantitative analysis of growth effects can be determined with reasonably simple methods that can be applied at specific sites or at a region scale to identify appropriate temperature thresholds. Assuming a 10% growth loss represents an appropriate risk level, an upper threshold for the 7-day maximum temperature of 16.5^{o}C is appropriate for coho and 20.5^{o}C is appropriate for steelhead. Criteria derived in this manner are somewhat lower than those developed in a U.S.E.P.A. paper in 1977 and close to, but not identical, to those currently specified in Washington and Oregon criteria.

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SECTION 1   INTRODUCTION AND OBJECTIVES

Maintaining the quality of aquatic environments that allow fish and other organisms to grow and prosper is a primary objective of the Clean Water Act adopted by Congress in 1972. To administer the Act, the U.S. Environmental Protection Agency (EPA) and state water quality authorities throughout the nation have adopted numeric and qualitative criteria that establish environmental conditions known to protect aquatic life from adverse effects. Historically, physical environmental characteristics have been used to indicate the minimum requirements for biological health. The criteria address naturally occurring conditions that may be affected by human activities (e.g., temperature, sediment, dissolved oxygen, pH, and nutrients) and numerous exogenous pollutants introduced by manufacturing and agricultural activities. Water quality criteria are often a single value defining thresholds of favorable or adverse conditions (Suter et al. 1993). The public and the regulatory system have accepted simple physical criteria as indicators of biological health, although natural systems are dynamic and often exhibit a range of water quality conditions over time in response to many non-anthropogenic factors. Thus, even though criteria are often an over-simplification of real biological response, they have generally been accepted as necessary to effectively administer the regulatory system.

The Environmental Protection Agency and other agencies have conducted water quality research over the years to accomplish two major objectives: 1) develop sound cause-and-effect relationships between water quality conditions and biological response, and 2) develop repeatable methodologies that use research findings to craft regulatory water quality criteria grounded in sound science. A primary technique used by researchers is to subject fish and other aquatic organisms to pollutants in a controlled laboratory setting to determine the relationships between dosage, length of exposure and biological responses such as growth loss, stress, altered behavior, disease, or death. Such laboratory-based research has been a cornerstone of fisheries science during this century and its validity has been confirmed in field-based studies (Brett 1971, Shuter et al. 1980, Baker et. al. 1995, Filbert and Hawkins 1995). Conversely, field observations alone are often not reliable for deriving water quality criteria because of variability in the natural environment and the complexity of factors controlling natural systems and habitat response. Brett (1971) observed that "it is inherently difficult to examine existing conditions and deduce the important biological factors which have occurred in the past to explain the present." Laboratory studies were the basis for EPA recommended temperature criteria (U.S. EPA 1977), and field studies have been used mainly for validating the appropriateness of water quality criteria (Hansen 1989, Mount et al. 1984).

Most water quality criteria were originally adopted in the 1970s (e.g., U.S. EPA 1980) with relatively little revision since implementation (Hansen 1989). In recent years, water quality agencies in the Pacific Northwest have conducted scheduled reviews of criteria to reassure their effectiveness or change them if necessary (ODEQ 1995, WDOE 1999). Interest in the validity of temperature criteria has been particularly keen because of concern that temperature is one of the habitat elements that has contributed to the decline in certain runs of salmon and trout in the region (NAS Committee on Protection and Management of Pacific Northwest Anadromous Salmonids 1996). Within the home range of salmon in Washington, Oregon, and Idaho, over 2500 streams are currently listed on Clean Water Act section 303(d) lists, many for exceeding summer temperature criteria. High summertime temperatures in these streams are due in part to a variety of land use

and manufacturing activities that have historically impacted temperature regimes (Sullivan et al. 1990), as well as natural phenomenon that affect stream temperature.

The risk to salmon and trout populations associated with temperature is perceived to be high because: 1) the potential for biological effects exists according to laboratory-derived results; and, 2) many populations are already exposed to temperatures exceeding those believed to induce negative biological consequences. Water temperature plays a role in virtually every aspect of salmon life (Brett 1995; Weatherly and Gill 1995), and adverse levels of temperature can affect behavior (e.g. migration delays and timing), disease resistance, growth, and mortality (Brett 1956). Such concerns have led agencies to reconsider temperature requirements and tolerances of these species, with emphasis on those listed as threatened or endangered: chinook and coho salmon, steelhead trout, and bull trout. Recent reviews have called for lowering of temperature criteria to levels thought to be more desirable (less stressful) for these species (e.g. ODEQ 1995; WDOE 1999, U.S. EPA in preparation).

The scientific justification for these recommendations relies largely on review of the scientific literature and application of a number of implicit assumptions concerning the temperatures that occur and those that cause adverse effects. They also include safety factors to ensure that adverse effects and exposures are not underestimated. These assumptions and safety factors are usually developed using best professional judgment. A more objective risk assessment technique, where adverse effects are placed in an exposure context to identify population risk, has not yet been applied in these temperature criteria reviews, despite its accepted value for establishing criteria (Suter and Mabrey 1994) and risk for other pollutants (U.S. EPA 1995).

Risk assessment involves comparing effects and exposure periods to achieve probability of adverse effects for the defined exposure. This process includes: 1) biological effects characterization, 2) exposure characterization, and 3) a risk characterization that combines the two. The effects characterization requires a quantitative measure of the biological effects of temperature, and the exposure characterization requires a quantitative measurement of the temperatures occurring in the fish's environment. These quantitative measures are expressed as probabilities for the risk characterization, where the in situ temperature regime is related to the temperature biological effects relationships to estimate the likelihood of adverse biological impacts.

A risk-based approach seems ideally suited to developing criteria for and assessing temperature risk to aquatic life. Fish are constantly exposed to temperatures that vary by minutes, hours, days, weeks, and months depending on celestial forces that guide the earth around the sun. Fish are thermoconformers; that is, they cannot maintain body temperatures much different from the water in which they occur. Thus their exposure is variable, ranging over the full array of optimal and suboptimal temperatures. Considerable laboratory study has been conducted on a variety of salmon and trout species to characterize their responses to temperature; these data may be sufficient to characterize the responses of some species and life stages. Finally, temperature is easy to measure and there is an abundance of data available in Washington and elsewhere to characterize temperature regimes and to evaluate exposure with considerable precision.

The objectives of this paper are (1) to review relevant temperature research and (2) to evaluate the biological risks associated with ambient temperature regimens on populations of two species of juvenile salmonids using a probabilistic risk assessment. This

assessment is based on laboratory data concerning the effects of temperature on growth and mortality. The analyses concentrate on the summer rearing life history phase of species within the Salmonidae family that dwell in stream environments, namely juvenile coho salmon and steelhead trout. There has also been considerable study of the thermal requirements of chinook, sockeye, pink, and chum salmon, but since these species are not typically found in western Washington streams during the summer months, they will not be directly considered here. This analysis illustrates the use of risk analysis for objectively deriving temperature criteria; similar techniques could be applied to other species, stocks, and life history phases (Hokanson 1977). We also use results to evaluate the biological effects of existing and proposed temperature criteria in the context of risk assessment techniques.

This report contains:

- A review of the scientific literature regarding the effects of water temperature on direct acute mortality and growth of fish, with emphasis on salmonids during fresh water rearing (Section 2)

- A description of the temperature data collected from a variety of stream conditions in Washington used in the quantitative analyses, with a discussion of temperature indices (Section 3).

- A synthesis of available scientific information into a quantitative, risk-based approach to evaluating biological response to acute or lethal temperatures in natural streams (Section 4),

- A comprehensive development of a new, quantitative approach to assessing fish growth in response to long-term exposure to temperatures in natural streams (Section 5),

- A synthesis of the risk-based approaches to suggest temperature criteria for coho and steelhead (Section 6),

- A discussion of the use of scientific information, including methods developed in this report, to identify temperature standards in federal and state regulatory approaches (Section 7).

- A brief summary of key findings and a synthesis of information for policy-makers and scientists (Section 8).

SECTION 2 REVIEW OF THE PHYSIOLOGIC RESPONSE OF FISH TO ENVIRONMENTAL TEMPERATURE

ABSTRACT

In this section, the biological effects of temperature on fish are briefly reviewed, with emphasis on the fresh water rearing phases of salmonids. Lethal and non-lethal effects are discussed.

Key findings:

- Many of the lethal and non-lethal effects of temperature on salmonids are well understood and in many cases have been quantitatively established.

- Both lethal and sub-lethal effects of temperature depend on its magnitude in relation to duration of exposure.

- Fish have behavioral and physiological mechanisms to tolerate temporary excursions into stressful temperature levels. If exposure and magnitude limits are exceeded, mortality can occur.

- Growth has been widely used to evaluate the sub-lethal response of fish to temperature.

INTRODUCTION

Temperature is a dominant factor affecting aquatic life within the stream environment (Hynes 1970). Temperature influences all aspects of fish life, as well as those of the macroinvertebrates (Sweeney and Vannote 1986) and primary producers (algae, bacteria etc.) that dwell within the stream and serve as food for fish (Hynes 1970). As summarized by Brett (1956 pg. 76):

"Because of the all-pervading nature of environmental temperature, the fundamental thermal requirement of fishes is an external environmental temperature most suitable to their internal tissues... Temperature sets lethal limits to life; it conditions the animal through acclimation to meet levels of temperature that would otherwise be intolerable; it governs the rate of development; it sets the limits of metabolic rate within which the animal is free to perform; and it acts as a directive factor resulting in the congregation of fish within given thermal ranges, or movements to new environmental conditions."

Quantitatively defining the effects of temperature on key biological functions is essential for understanding how temperature contributes to fish success as well as how it places species at risk. Temperature effects have been extensively studies for all aspects of fish life. Although review of all temperature effects are beyond the scope of this report, we note that there are excellent references where temperature effects are discussed more fully (e.g., Groot et al. 1995), or where specific species are reviewed in detail (e.g. McCullough

1999 on chinook salmon). We narrow our review to aspects of temperature affecting the rearing of salmonid species in the fresh water environment.

Two important elements of temperature affect the growth and survival of fish: 1) the relationship between temperature, metabolism, and food conversion efficiency over long periods, and 2) the thermal tolerance of fish to lethal temperatures over relatively short periods. Both aspects are important because ambient stream temperature may vary from very low levels in winter to occasionally high peaks in summer (e.g., Beschta et al. 1987; Sullivan et al. 1990).

The thermal tolerance to temperature has been the focus of considerable laboratory testing for many fish species, including salmonids, beginning early in this century and continuing today (see reviews by Fry 1967, NAS/NAE 1973, Coutant 1977). Much of the available laboratory research on temperature tolerances was performed prior to 1980 and was stimulated principally by the need to assess the impact of heated effluent from power plants, dams and other facilities (Hokanson 1977). Since that time, temperature research has focused on studying additional species and refining the understanding of contributing factors such as the effect of acclimation temperatures, daily diurnal temperature fluctuations, food rations, and the interaction of temperature with other pollutants (e.g., Elliott 1976, Wurtsbaugh and Davis 1977, Brett et al. 1982, Thomas et al 1986, Coutant and Talmage 1977).

These and other studies show that fish respond to temperature through physiological and behavioral adjustments that depend on the magnitude and duration of temperature exposure. Upper and lower temperature extremes that cause death after exposures ranging from minutes to 96 hours are termed acute temperature effects. Temperatures causing thermal stress after longer exposures, ranging from weeks to months, are termed chronic temperature effects. Endpoints of exposure to temperature over longer periods (chronic
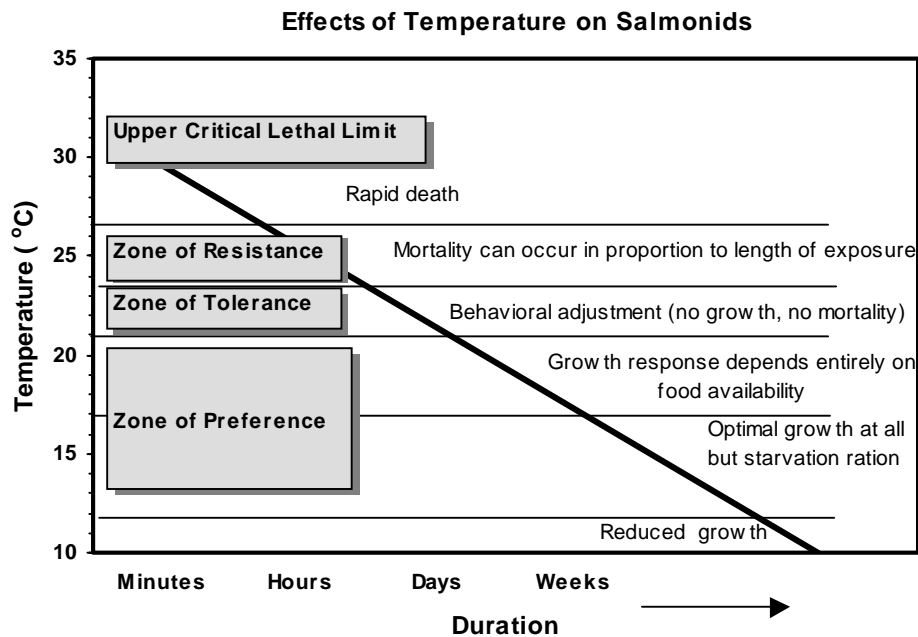
Figure 2.1 General biological effects of temperature on salmonids in relation to duration and magnitude of temperature.

effects) are sublethal and may include growth, competitive interactions, change in behavior, or disease. Temperature ranges defined by acute and chronic temperature effects are referred to as the zones of thermal resistance and tolerance (Elliott 1981, Jobling 1981). The range of physiological response relative to temperature is summarized in Figure 2.1. The range of temperature over which feeding occurs without signs of abnormal behavior is referred to as the optimum temperature range (Elliott 1981).

ACUTE TEMPERATURE EFFECTS

The acute effects of temperature are frequently expressed as effects on survival that result from exposure to elevated temperatures for specified time periods. Mortality, expressed as the median lethal time (LT50), and the ultimate upper incipient lethal threshold (Brett 1952) have been the most common endpoints measured. The median lethal time is the duration eliciting 50% mortality at a specific temperature. The ultimate upper incipient lethal limit is the temperature at which acute mortality does not increase with any further increase in the temperature.

Laboratory studies repeatedly show that salmon have the ability to extend their temperature tolerance through acclimation. Brett (1956) reports that the rate of increase in ability to tolerate higher temperatures among fish is relatively rapid, requiring less than 24 hours at temperatures above 20°C (e.g., Figure 2.2). Acclimation to low temperatures (less than 5°C) is considerably slower (Brett 1956). Studies of the acute temperature effects on salmonids have yielded remarkably consistent results between studies and among salmon species (Brett 1956; Lee and Rinne 1980), indicating temperature's influence on fish with similar biochemistry and physiology. The upper lethal limit, that is the temperature at which death occurs within minutes, ranges from 27° to 30°C for salmonids (Jobling 1981). Fish

Figure 2.2 Example of a relationship between the time (min) for 50% mortality of brown trout (Salmo trutta, and the lethal temperature (oC) at different acclimation temperatures. (From Elliott 1981).

acclimated at cold temperatures can have upper lethal limits 3° to 4°C lower. Many species of fish have considerably higher upper thermal levels than members of the Salmonidae family, which are classified in cold water temperature guilds (Magnuson et al. 1979). At temperatures below the upper lethal limit, fish can tolerate each successively lower temperature for exponentially increasing intervals of time.

Behavioral mechanisms may allow fish in situ to resist short-term extreme temperature, and acclimation will promote resistance to high temperature, although there is an upper

limit to the temperature to which fish can acclimate (Jobling 1981). This resistance to the lethal effects of thermal stress enables fish to make excursions for limited times into temperatures that would eventually be lethal (Brett 1956; Elliott 1981). The period of tolerance prior to death is known as the "resistance time" and the duration-temperature is termed the "zone of resistance" (Figure 2.1) (Hokanson 1977, Jobling 1981). Laboratory studies have repeatedly found that salmon can spend very lengthy periods in streams of 24°C or less without suffering mortality.   Thus temperature as a direct cause of death generally ceases at temperatures less than 24° C (Brett 1956). Acute effects are not generally considered below this level, because continuous long duration exposure to temperature of this magnitude is not likely to occur in natural environments within the species' normal geographical range. Laboratory studies testing daily fluctuations in temperature as large as 13.5°C did not shown effects on growth or mortality of salmonids, although lethal levels were never exceeded (Thomas et. al. 1986).
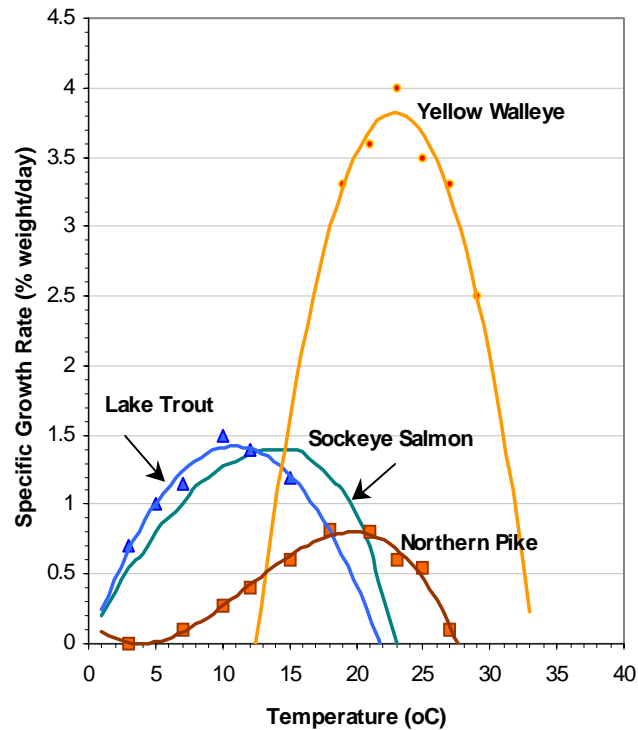
Figure 2.3 Example of a multi-family specific growth rate curves (after Christie and Regier 1988)

SUBLETHAL TEMPERATURE EFFECTS

Chronic exposure to sublethal temperatures can have a broad range of effects on the various functions of fish. Brett (1971) described 25 physiological responses for sockeye salmon and, similarly, Elliott (1981) identified 19 similar characteristics for brown trout. The relationship between these responses and temperature follow two general patterns: either the response (e.g., standard metabolic rate, active heart rate, gastric evacuation) increases continuously with rise in temperature, or the response (e.g., growth rate, swimming speed, feeding rate) increases with temperature to maximum values at optimum temperatures and then decreases as temperature rises (Brett 1971, Elliott 1981). In the latter case, the form of the responses to temperature and the optimum temperatures are not always the same for different functions, and the optimum temperature for a response may change if there is an alteration in another factor such as energy intake (Elliott 1981).

Based on this theory, fish rarely occur within a temperature regime that is optimal for all functions given the natural diel and seasonal variability in water temperature. Consequently, fish have developed mechanisms to survive various levels of thermal stress both above and below optimal ranges to maintain the health and survival of a population.

Several studies have indicated that growth under fluctuating temperatures is essentially the same as that under constant temperature if the fluctuating temperature is expressed as the time-weighted mean[1] (Thomas et al. 1986; Brett 1971; Everson 1973; Iverson 1972; Wurtsbaugh and Davis 1977).

Fish are poikilothermic and temperature plays a key role in regulating their metabolic functions. Fish tolerate suboptimal temperatures by metabolic adjustment and behavioral thermoregulation (Elliott 1981). For example, as temperatures increase above the optimum for feeding, the feeding rate declines and is completely inhibited at temperatures several degrees below the incipient lethal level (e.g, at 22°C for brown trout, Elliott 1981; and 24°C for sockeye and chinook salmon, Brett 1971). Similarly, the metabolic rate of and scope for activity declines, reducing the overall energy expenditure, which helps to conserve energy and reduce thermal stress. Behavioral adjustments, such as movements to cooler refuge sites, also enable fish to avoid thermal stress. Numerous observers have reported significant changes in salmonid activity at or near 22°C (Donaldson and Foster 1941; Griffiths and Alderdice 1972; Wurtsbaugh and Davis 1977; Lee and Rinne 1980; Bisson et. al. 1988; Nielsen et al. 1994, Tang and Boisclair 1995; Linton et al. 1997; Biro 1998). This temperature is consistent with a sharp drop in food consumption and conversion efficiency observed in laboratory studies (Brett et al. 1982). At very low temperatures, salmonids have been observed to cease feeding and seek cover under banks or within stream gravels (Everest and Chapman 1972).

How large fish grow is fundamentally determined by environmental and population factors that determine the availability of food. Temperature, however, regulates how much growth can occur with the food that is available. Growth is dependent on the energy consumed by the fish balanced by its energy expenditures to meet basic demands such as metabolism and swimming. What is left over can be used to grow body mass and reproductive capability. The long-term exposure of salmonids to environmental temperature during their freshwater rearing phase has an important influence on the size fish achieve and potentially the timing at which they reach readiness for smolting (Weatherly and Gill 1995).

The size of salmonids during juvenile and adult life stages influences survival and reproductive success. Although the large majority of anadromous salmonid growth occurs in the ocean environment, growth of juveniles in natal streams is especially important for anadromous salmonids that must reach minimum sizes before they can smolt (Weatherly and Gill 1995). Holtby and Scrivener (1989) and Quinn and Peterson (1996) demonstrated that the size achieved by juvenile coho at the end of their first summer growing period was a strong determinant of their later success in overwintering and smolting. Larger size generally conveys competitive advantage for feeding in the freshwater environment (Puckett and Dill 1985, Nielsen 1994) for both resident and anadromous species. Mason (1976) and Keith et al. (1998) found that the smaller fish tend to be those that are lost from rearing populations. Brett et al. (1971) described the freshwater rearing phase of juvenile sockeye as one of restricted environmental conditions and generally retarded growth. This synopsis is also generally true for salmonid species that dwell in stream and river environments for lengthy periods of time.

To explore the effects of prolonged exposure to temperature, numerous investigators have found growth to be a reliable and measurable integrator of a variety of physiological

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[1] The maximum temperature studied cannot be high enough to elicit mortality.

responses (Brett 1971, 1995; Iverson 1972; Brungs and Jones 1977; Wurtsbaugh 1973). Growth rate is the most frequently reported measure of fish health from laboratory studies and occasionally from field studies. Growth can be viewed as the net effect of the environment on the relation between food consumption, metabolism, and activities of an organism (Warren 1971). Growth integrates a host of specific physiological responses to temperature, including metabolic rate (basal and active), feeding and digestion, and swimming performance or the ability to hold position with the current (Brett 1995; Weatherly and Gill 1995).

Laboratory studies demonstrate that virtually all fish, including salmonids, grow best within a range of temperatures. Optimal growth generally occurs at a midpoint of temperatures where the fish live, and it declines in waters that are warmer or cooler. The range of temperature at which

Figure 2.4 Basic relationship between temperature, ration and growth of 7-12 month-old sockeye salmon (from Brett et. al. 1969).

growth occurs is generally wide, and usually reflects the ambient temperatures likely to be found within the natural range of the specie's habitats (Hokanson 1977). Significant differences in growth curves exist among fish families (Figure 2.3), from Christie and Regier 1988), but growth curves are often similar for species within the same genera and family. Because all salmonids have a similar biokinetic range of tolerance, performance, and activity, they are classified as temperate stenotherms (Hokanson 1977) and are grouped in the cold water guild (Magnuson et al. 1979).

The effect of temperature on growth varies significantly with the ration of available food (Figure 2.4). For example, in Figure 2.4, sockeye salmon held at optimum temperature and fed satiation rations achieved 600% more growth than fish held at optimum temperature with starvation rations. As ration increases from maintenance level (no net growth) to satiation or excess level (more than is needed for growth, metabolism, and all physiological functions), the optimum temperature for growth shifts progressively to higher temperatures. This response is consistent for all salmonids where laboratory studies are available (Brett 1971; Everson 1973; Iverson 1972; Wurtsbaugh and Davis 1977).

The relationship between food and temperature must be taken into account when considering the productivity of fish populations (Filbert and Hawkins 1995). Many studies have observed an increase in the growth and productivity of fish populations in streams when temperature (and correspondingly) food is increased. This tends to occur even in the cases where temperatures exceed preferred and sometimes lethal levels (Murphy et al. 1981, Hawkins et. al., 1983, Martin 1985, Wilzbach 1985). This situation indicates that starved fish require somewhat lower temperature, although the low environmental temperature tends to create conditions of low food supply (Weatherly and Ormerod 1990).

The forgoing discussion indicates that the optimum temperature for fish extends over a broad range depending on the function and the presence of other interacting factors. This optimum (preferred) range is defined by Elliott (1981) as the range over which feeding occurs and there are no external signs of abnormal behavior, i.e., thermal stress is not obvious. This delineates a wider range than the peak optimal temperatures where growth is maximized.

Within the optimum temperature range, research has identified a preferred temperature range, which is defined as the temperature around which all individuals will ultimately congregate regardless of their prior temperature exposure history (Fry 1947). Some investigators specifically define the optimal temperature as the temperature at which maximum growth occurs, and refer to the range of temperature where growth occurs as "preferred" temperatures. Determining this range, however has resulted in considerable variability within the same species due to different experimental test procedures and the multiplicity of environmental factors that affect fish preference (Elliott 1981, Jobling 1981). This uncertainty has led Elliott (1981) to conclude that the optimum temperature range defined based on physiologic response is a more realistic concept for studies on thermal stress then definitions based on concepts of "preference". Different uses of the terminology can create confusion.

Elliott's optimum temperature definition fits well with the behavioral response of fish to natural temperature regimes. For example, Brett (1971) showed how behavioral thermoregulation by juvenile sockeye resulted in energy conservation.   Vertical movements in a thermally stratified lake over the course of a day enabled the juveniles to maximize the efficiency of food conversion into growth by controlling energy intake and metabolism as temperature followed the solar cycle. The sockeye salmon exhibited varied behavior in selecting temperatures that did not solely reflect the preferred temperature available to them within the lake. Other field studies have also documented salmonid utilization of temperatures outside of the preferred range when those within or near the preferred level were readily accessible (e.g. Matthews et al. 1994, Brett 1971, Biro 1998).

Metabolic characteristics are not the only response, but they are the most important and most easily quantifiable. Less quantifiable in a dose-response context are relationships involving temperature and disease resistance, and temperature effects on sensitivity to toxic chemicals and other stressors. It is well recognized that temperature can decrease disease resistance in the most sensitive individuals within each species' population and influence their sensitivity to certain toxic chemicals (e.g., Cairns et al. 1978). However, the study of Cairns et al. (1978) concluded that "temperature-toxicity interactions are far more complex than earlier literature has indicated," and increased temperature does not necessarily lead to increased sensitivity to toxic chemicals. For example, Linton et al. (1997) found that sublethal levels of ammonia enhanced growth at higher temperatures and Dockray et al. (1996) found better performance at high temperature when pH was

low. For temperature to affect the occurrence of disease, disease-causing organisms must be present, and either those organisms must be affected by temperature or fish must be in a weakened state due to the effect of temperature. In addition, some diseases may be more prevalent at high temperature, others are more prevalent at low temperature, and some are not apparently related to temperature. Therefore, for disease and pollutants, the specific nature and local presence of the disease-causing organism or pollutant influences its interaction with temperature.

The response of fish to temperature in natural streams is not only based on physiological functions but also on the overall interaction with other ecological factors (e.g., predators, prey abundance, and competitors). Differences among species can confer competitive advantages in relation to environmental variables that are reflected by the species' distribution (Brett 1971, Baltz et. al. 1982, Reeves et al. 1987, DeStaso and Rahel 1994). Natural stream environments nearly universally have increasing temperature from headwaters to their mouths (Hynes 1970), largely reflecting systematic changes in a variety of critical environmental factors that control heat transfer processes (Sullivan et al. 1990). Systematic changes in the occurrence or dominance of species within river systems in part reflects these temperature patterns.

ASSOCIATING BIOLOGICAL EFFECTS AND STREAM TEMPERATURE

Identification of appropriate temperature criteria to protect fish is complicated by the highly variable nature of temperature at stream sites, coupled with the differing temperature requirements of fish species. Water temperature at individual sites varies
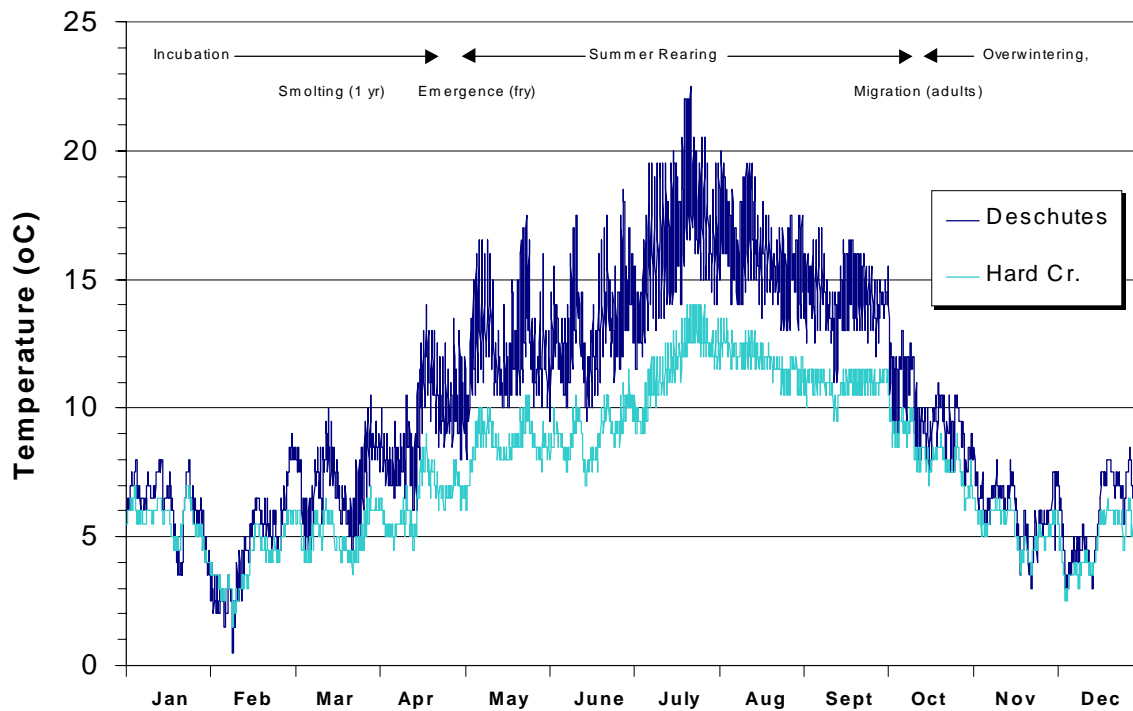
Figure 2.5 Annual temperature regime of the Deschutes River (148 km2) and Hard Creek (2.3 km2), a headwater tributary, near Vail, Washington. Data are hourly measurements.

significantly with time, ranging from lows in winter to highs in summer, with daily fluctuations depending on stream and climatic characteristics (Figure 2.5). The life history phases of salmonids are generally adapted to the prevalent temperature as illustrated for two stream sites in Figure 2.5, although species and stocks have specific life history timing (Weatherly and Gill 1995). Growth of alevins within the gravel bed and as fry and resident adults within the stream is a function of temperature; the timing of movement of alevins, fry and adults also depends, in part, on temperature.

The intent of temperature criteria is to index or describe key characteristics of the temperature regimen that have important measurable impacts on individuals or populations. Many authors favor identification of criteria appropriate for each life history phase (Bell 1973, Reiser and Bjornn 1979, Armour 1991) that reflect the temporal variability of temperature through the year. Hokannson (1977) described a quantitative means of establishing criteria for each life history phase of percids (perch, walleye) in a procedure he termed the "Envelope Method." Quantitative estimates of fish response to temperature for maturation cycles, spawning times, migrations, activity and spatial distribution are compared to seasonal changes in temperature. In Hokannson's example, natural history observations supplement experimental data where available. Temperature ranges that indicate optimal, sub-optimal, and lethal temperatures are plotted or tabulated for each life stage period (e.g., migration, spawning, incubation, rearing) to show the range and temporal distribution of temperature preference/tolerance regimes (temperature envelopes) during the hydrologic year.

Recent development of temperature standards in Oregon and Washington have also endorsed life history-based criteria for salmonid and char species, and promoted reach- and watershed-based approaches for determining criteria (ODEQ 1995; WDOE 1999). The intent is to identify a series of criteria that can be applied to limit impact on all species and life stages that may exist in a stream reach at that time of year. There has been some interest in "tailoring" criteria to specific time of the year, species, and even individual stream reaches. However, reach-, species-, or temporally-specific criteria can create enormous data collection and management issues.

Table 2.1 Characteristics of temperature regimes relevant to temperature criteria.

Regime Characteristic	Variables	
Temperature Threshold	❑	Acute
	❑	Sub-lethal
Temperature Fluctuation Characteristic	❑	Maximum
	❑	Mean
	❑	Minimum
	❑	Fluctuation (maximum-minimum)
Averaging Period	❑	Instantaneous maximum
	❑	7-Day average
	❑	Monthly or seasonal average

Criteria that can be applied on a regional basis require indices of the key characteristics of temperature regimes that are biologically meaningful, measurable without extraordinary means, and sensitive to human-caused effects. Factors to consider when reducing the variable summer temperature regime to simpler indices include: 1) the temperature threshold that reflects biological effects (e.g., usually a maximum but can be a minimum);

2) the temperature statistic within the amplitude of fluctuation (e.g., maximum, mean or minimum); and 3) the averaging period that characterizes temperature exposure (e.g., hourly, daily, or weekly) (Table 2.1).

ESTABLISHING WATER QUALITY CRITERIA

In recent years, the EPA and National Academies of Science and Engineering have promoted risk assessment techniques to develop water quality criteria, including formal protocols that have been peer-reviewed nationally (Parkhurst et al. 1996, U.S. EPA 1995). Risk assessment is designed to enhance understanding of the potential adverse effects of a pollutant on species by combining the information from biological studies with an analysis of each population's potential exposure to those effects. Risk occurs when the stress' magnitude, frequency, and duration exceed the species' ability to deal with that stress. Risk has little to do with the organisms' or species' sensitivity to a stress or to the concentration or level of environmental stress; risk depends entirely on whether the combination of exposure and sensitivity exceeds the organism's ability to withstand or adapt to the stress (Suter et al. 1993; U.S. EPA 1992).

Recent risk assessment techniques use more available data and disclose more uncertainties than assessments based on comparing a number denoting an effect, criterion or an exposure (Parkhurst et al. 1996; Solomon et al. 1996). Exposures and potential effects may be represented as probabilities of occurrence. Uncertainties about exposures and effects can also be expressed (e.g., as 95% confidence limits) and used in decision-making. Risk assessment techniques have been used to derive water quality criteria for aquatic life (U.S. EPA 1993), wildlife, and human health, and are being considered as one of the site-specific water quality criteria tools (Spehar and Adams, 1998). They can be used to evaluate broad effects if general patterns of exposure are known or to develop stream-specific criteria.

To derive a meaningful biological measure for specific life phase requirements, careful consideration must be given to both magnitude and duration of temperature, since these factors together have great effect on the risk that temperature poses to fish. In the remainder of this report, we will use a risk assessment approach to quantitatively estimate acute and chronic effects of temperature on salmonids. Risk assessment requires a quantitative analysis of fish response to temperature, and a quantitative assessment of the exposure to temperature that a fish may experience during the period of interest. The overlap between effects and exposure determines the risks associated with temperatures experienced in the aquatic environment.

CONCLUSIONS

The implications of this research to the question of establishing temperature criteria are:

- The effects of temperature on physiologic functions during the freshwater phase of salmonid life history are reasonably well understood, and in many cases have been quantitatively established in a laboratory setting.

- Salmon and trout have physiological and behavioral mechanisms that resist death at high and low temperatures unless extreme maximums are achieved.

Establishing temperature criteria for water quality standards is benefited by consideration of both duration and magnitude of temperature within these extremes.

- The effects of temperature on other factors, such as resistance to disease or pollutants, are more variable, depending on site conditions, and are less well characterized.

SECTION 3   TEMPERATURE CHARACTERISTICS OF STREAMS USED IN ANALYSIS

Abstract

Temperature data collected during the summer months from a number of streams and rivers in Washington are used for biological analysis in following sections of this report. In this section, we introduce these data and summarize the site and temperature statistics for each of the monitoring stations, and compare them among sites and with previous temperature studies. Temperature data span a range of temperatures from cold to warm, and many stream sites exceed current temperature criteria.   Sites are shown to be broadly representative of temperatures observed in many Washington streams. Temperature indices, including annual maximum, 7-day maximum, and 7-day mean temperature are closely related at each site, and any can be used to index stream temperature measured over longer periods.

KEY FINDINGS INCLUDE:

- The data used in this report are broadly representative of stream temperatures in fish-bearing streams found in forested, rural, and urban streams in Washington. Temperature patterns are also probably representative of many streams throughout the Pacific Northwest.

- Temperatures span a range of temperatures, from 12° to 26°C in the annual maximum water temperature. This temperature range is within the range that salmonids may experience growth and lethal effects from short and long-term exposure.

- There is year-to-year variation in temperatures at sites, which affects short-duration temperature indices.

- Various temperature indices such as annual maximum, 7-day maximum, and 7-day mean are closely related to one another.

TEMPERATURE DATA

Analysis of the biological effects of temperature that follows in Sections 4, 5 and 6 is based on temperature recorded at 19 stream sites in the Chehalis, Deschutes, and Toutle river watersheds, located in the Coast Range and the west slopes of the Cascade Mountains in Washington. Temperature has been monitored over the years for various monitoring and research projects. All sites are located on portions of the river systems where forestry is the dominant land use. Sites with hourly temperature records varying from very cool headwater streams that support cutthroat steelhead, and coho populations to warm river mainstems with more diverse fish communities were selected.

Three sites are located in the mainstem of the headwaters of the Chehalis River near the town of PeEll and represent the largest river in our analysis. Bankfull stream widths

average 30 to 60 meters. The amount of shade varies with stream width, ranging from low to high. The river and its tributaries flow through second growth forests, and riparian areas are in various stages of regrowth following past logging-related disturbance. Eight tributaries to the headwaters of the Chehalis River were monitored. Each is approximately 5-10 meters in width at their confluence with the mainstem. Tributary streams were logged to the stream banks, and in some cases cleaned of woody debris, in the 1970's. Most are now well shaded with second-growth alder and Douglas-fir plantations. The mainsteam of the Chehalis River supports fall chinook nearly as far upstream as site 3. The lower portions of the tributaries support steelhead and coho spawning, incubation and rearing. Several of these streams are the location of marine nutrient and fish carcass supplementation research previously reported in the literature (Bilby et al., 1996, 1998). Porter Creek is a tributary to the lower Chehalis River flowing from the Capitol Forest near Olympia. It is well shaded with a predominantly alder overstory. This stream was the site of a woody debris addition study (Cederholm et al. 1997).

Four sites in the Deschutes River basin were monitored, including the mainstem, near the town of Vail and at the downstream end of the forest land use zone. A 2000-ha tributary, Thurston Creek, and two small streams (<300 ha) in the headwaters (Hard and Ware Creeks) have been monitored since 1974. Previous monitoring information is available in Sullivan et al. (1987). The smallest tributaries support cutthroat trout populations, while coho use the lower tributaries and mainstem. Anadromous fish are excluded from the upper tributaries by a barrier falls.

Two sites are located in the Mt. St. Helens blast zone. These streams have experienced vegetative recovery since the eruption in 1980, and currently support populations of steelhead and coho, that at times are supplemented by hatchery fish. Previous research on the interaction of temperature and fish production has been reported by Bisson et al. (1988).

Sites represent a range of small to large streams with shade varying from 0 to 100%. Maximum potential shade naturally varies among the sites with stream width. However, current shade is lower than potential at many sites due to past forest practices or natural disturbance.

Water temperature was sampled to the nearest 0ºC each hour by an electronic temperature recording device (HoboTemp® or Omnidata®) calibrated at the time of deployment and field-checked at least once each month. The temperature recorded by the instrument was the average temperature for the hour. Water temperature probes were placed in the stream near the bank and out of direct exposure to sunlight.

Temperature Characteristics

Temperatures span a range from predominantly cold to predominantly warm as indexed by the annual maximum temperature (the single highest hourly temperature during the year) (Table 3.1, Figure 3.1). Multiple years of data were available at some sites. The selection of years to include in the analysis was arbitrary, largely reflecting the ready access to data in the archives. Although additional years or sites could have been included, data would fall entirely within the range of data observed at the example sites. We did not feel that is was as important to include a large number of sites in this temperature analysis, as it was to select sites that span the range of temperatures likely to occur within Washington to the extent possible with the data available to us.

Table 3.1 Basin and temperature characteristics of 18 stream sites used in acute (Section 4) and growth risk analysis (Section 5). These sites are referenced as temperature study sites in the text.

Site	Watershed	Basin Area (km^2)	7-Day Maximum[a] ^{o}C	7-Day Mean[b] ^{o}C	Annual Maximum[c] ^{o}C	Season Median[d] ^{o}C	Year Measured
Deschutes River mainstem	Deschutes	145.0	21.0	18.4	22.5	15.0	1994
Thurston Creek	Deschutes	9.1	14.9	14.1	15.5	12	1994
Hard Creek	Deschutes	3.0	14.0	13.0	14.0	11.0	1994
Ware Creek	Deschutes	2.8	17.5	16.1	18.3	12.9	1994
Huckleberry Creek	Deschutes	5.3	18.4	17.6	18.5	15.5	1991
Chehalis River mainstem (Site 1)	Chehalis	181.8	21.1	18.9	22.1	15.6	1997
Chehalis River mainstem (Site 2)	Chehalis	57.5	22.1	18.2	23.2	14.5	1997
Chehalis River mainstem (Site 3)	Chehalis	29.5	20.6	18.6	21.4	14.3	1997
Crim Creek	Chehalis	22.0	18.8	16.9	19.4	14.3	1997
Lester Creek	Chehalis	10.4	18.4	16.3	19.0	14.2	1997
Thrash Creek	Chehalis	16.7	15.3	14.3	15.8	12.3	1997
Rogers Creek	Chehalis	13.1	15.7	14.1	16.1	12.6	1997
Big Creek	Chehalis	9.0	16.5	14.6	16.9	12.5	1997
Sage Creek	Chehalis	5.3	16.5	14.6	16.9	12.5	1997
Salmon Creek	Chehalis	8.9	15.8	14.2	16.2	12.3	1997
Mack Creek	Chehalis	2.8	12.9	12.5	13.1	11.7	1997
Porter Creek	Chehalis	25	17.5	16.3	18.6	14.4	1990
Hoffstadt Creek	Toutle	25.6	24.5	18.4	26.0	14.0	1988
Harrington Creek	Toutle	8	19.1	16.7	20.5	13.3	1988

[a] maximum value of the 7-day moving average of the daily maximum temperature
[b] maximum value of the 7-day moving average of the daily mean temperature
[c] instantaneous maximum
[d] median of daily mean temperature from June 1 to September 15

The coolest measured stream was Mack Creek. The temperature never exceeded 13°C at any time during the summer (Figure 3.1). The warmest temperatures recorded in the temperature study occurred in Hoffstadt Creek located within the Mt. St. Helens blast zone, although this stream continues to cool with vegetation regrowth since previous studies (Bisson et al. 1988). The mainstem of the Chehalis River (sites 1, 2 and 3) experienced the longest duration of high temperature at or above 20°C. The Chehalis River is among the warmest rivers in Washington and well exceeds existing state temperature standards. The contrast in seasonal temperature regime between a consistently warm and a consistently cool site within the same time period and watershed is shown in Figure 3.2. Except for Hoffstadt Creek, the temperatures of the other sixteen sites fell somewhere between these two.   All streams that exceed 16°C annual maximum temperature exceed current Washington water quality temperature standards.

The minimum temperatures observed during the period between June 1 and September 15 were between 7 and 9 ^{o}C in all streams (Figure 3.3). This temperature is close to groundwater temperature and was typically experienced early in June. The maximum temperature observed reflects site characteristics such as openness to the sky, stream depth, and the extent of groundwater inflow (Sullivan et al. 1990). Despite large differences in the annual maximum temperatures among sites (Figure 3.1), most streams also spent a considerable amount of time at the same temperatures, most notably in the range between 12 and 17 ^{o}C. This temperature is coincident with the optimal temperature range of many salmonids.

Temperature Study Sites
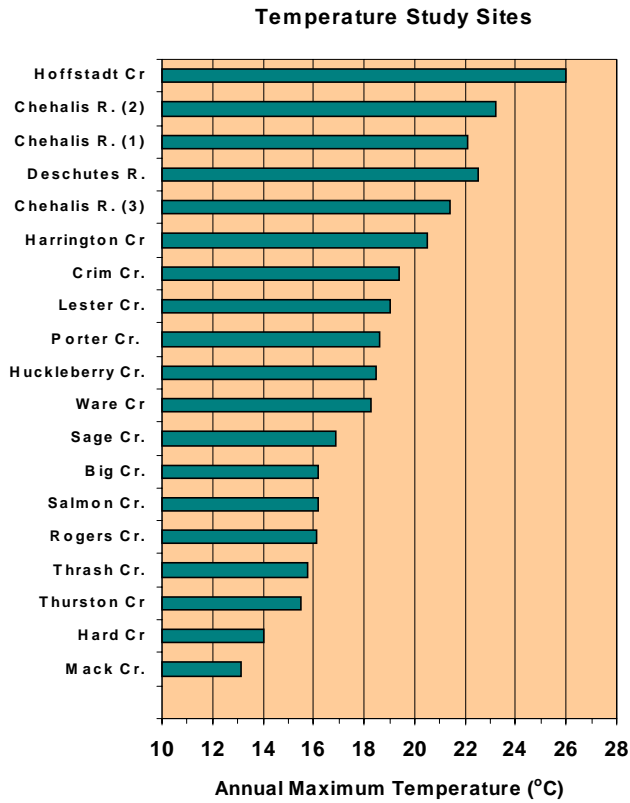
Figure 3.1 Annual warmest temperature at the 19 temperature study sites included in the temperature risk assessment.
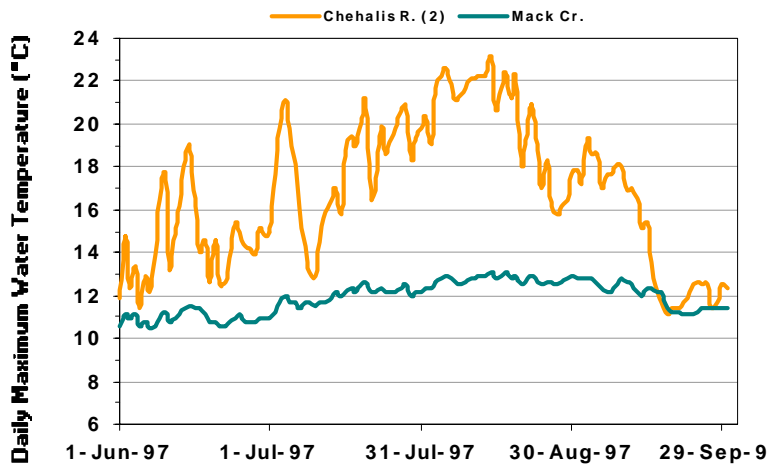
Figure 3.2 Daily maximum temperature at one of the warmest sites (Chehalis River site 2), and one of the coolest sites (Mack Creek).

Hourly Temperature Distribution
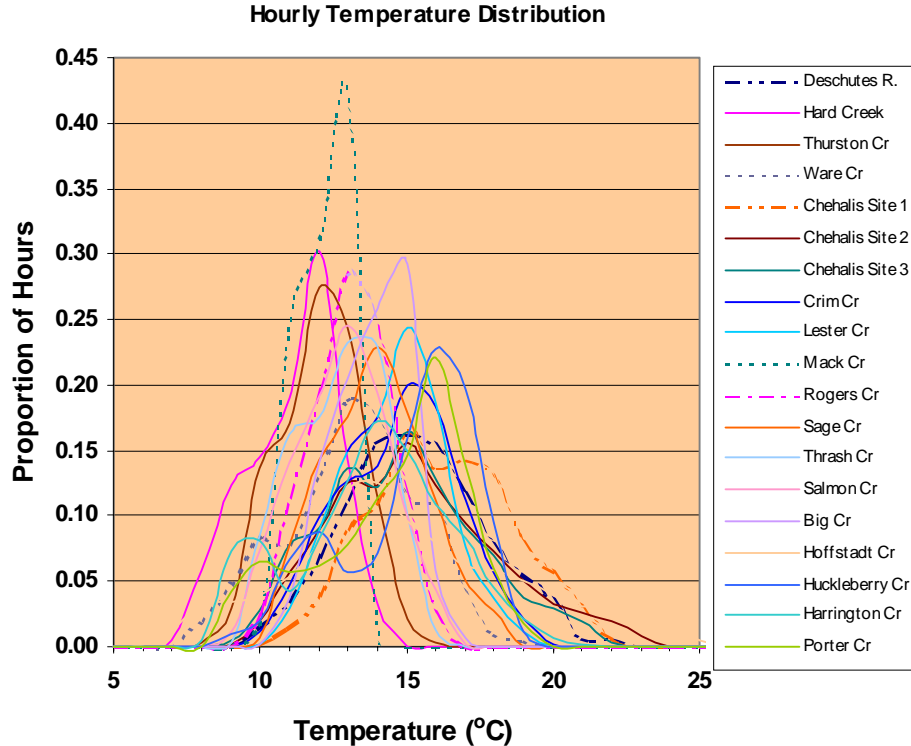
Figure 3.3 Proportion of 2567 hourly temperature observations by temperature at 19 temperature study sites measured between June 1 and September 15.

Comparison of Study Sites to Other Temperature Studies in Washington, Oregon and Idaho

Stream temperatures at the nineteen sites are representative of most other streams and rivers in Washington, and probably elsewhere in the Pacific Northwest as well. As an indication of how well the example data span the range of temperatures, we compare the relative occurrence of annual maximum temperature at sites included in other large-scale temperature studies that have been conducted in Washington. The 19 risk analysis sites represent temperature patterns in the same range as the 89 streams included in the 1990 Timber/Fish/Wildlife statewide temperature study; the earlier statewide, multi-agency study represented a broad range of stream conditions found primarily in forests located throughout Washington (Sullivan et al. 1990). Using the annual maximum temperature to index long-term temperature, the distribution of temperature at sites were similar between the two studies, although this analysis includes a few more warm sites and a few less cold sites (Figure 3.4). Temperatures from seven sites included in both studies tended to be warmer than expected with mature riparian vegetation, due in part to past land use or recent natural disturbance. The 1990 study contained a number of undisturbed sites.

Figure 3.4 also includes the cumulative distribution of maximum temperatures measured in a synoptic study of 570 urban/rural streams throughout the Puget Sound region coordinated by the University of Washington Center for Urban Studies. Temperature data were collected by volunteers within a 2-hour interval in the afternoon of August 19, 1998. Data from this study do not necessarily represent the hourly maximum temperature since temperatures did not necessarily coincide with the hottest hour of the year. However, the data are representative of the long-term average daily maximum for August (Derek Booth, pers. com.) and are likely to be within a few degrees of the annual maximum (Sullivan et al., 1990). Streams tended to be small tributary streams. Stream temperatures at these sites tended to be slightly cooler than risk analysis sites, and no streams were as warm as those included in this analysis.

Figure 3.4 Cumulative distribution of the annual maximum temperature at temperature study sites included in this study in comparison to the 89 sites included in the statewide study of temperature conducted by Sullivan et al. (1990) and the 570 sites included in the University of Washington Center for Urban Studies synoptic survey of urban and rural streams in the Puget Sound area. The 1990 TFW study included sites located throughout Washington.

In further consideration of how the risk sites represent the range of high temperatures observed throughout the Pacific Northwest region, we examined published U.S. Geological Survey temperature records from Washington, Oregon and Idaho. We selected the year 1978-79 for several reasons: there were more sites recording temperature in the 1970's and 1980's than are operative today, and this was a period of rather high temperature throughout the region due to the 1977-78 drought. The annual maximum temperatures are shown by state in Figure 3.5. (Note differences in the number of sites in each state.) The U.S.G.S. sites are primarily on larger rivers, although some smaller streams are also included. For example, the Columbia River mainstem is represented 6 times in the Washington data and 3 times in the Oregon data. Rivers such as the Columbia, Skagit, Yakima, Snake, Deschutes (OR), Willamette, Rogue, and Umpqua, to name a few, are included in this data set. (See Appendix A for a listing of U.S.G.S. sites.) None of the sites in the Timber/Fish/Wildlife study, University of Washington survey, or the risk sites (Table 3.1) were located within the zone of influence of dams. Dams often cause local heating or cooling depending on the release depth from the upstream reservoir. A few of the U.S. Geological Survey sites were located below dams. These sites were generally colder than expected given the size of the river at these locations.

Of the 129 U.S.G.S. sites, 11 (8.5%) had an annual maximum temperature greater than 26°C, the highest temperature observed at the risk analysis sites. One of those was in Washington (Yakima River), 1 was observed in Idaho (Snake River) and 9 were observed in Oregon. The John Day River in eastern Oregon reached temperatures as high as 31°C. The remainder of the Oregon sites exceeding 26°C were concentrated in the southwestern corner of the state, including the Applegate, Siuslaw, N. and S. Fork Umpqua, Calapooia River, and Elk Creek.

The four sources of data cited in this report provide perspective on the temperatures of small forested and urban streams and moderate to large size rivers in both the dry interior and wet coastal zones. The sites included in the risk analysis are broadly representative of temperatures of moderate to small size streams (all sites had basin area less than 200 km^2). Larger rivers tend to fall within the temperature ranges observed in the smaller rivers. However, it is appropriate to recognize that the largest rivers, and those in some geographic areas, have different temperature regimes than most Pacific Northwest streams, and if temperature is of concern, these should be specifically evaluated to determine whether the duration of specific temperatures exceeds adverse levels.

Regional Temperature, U.S.G.S. 1979

● Washington (n=34) □ Oregon (n=78) ▲ Idaho (n=17)
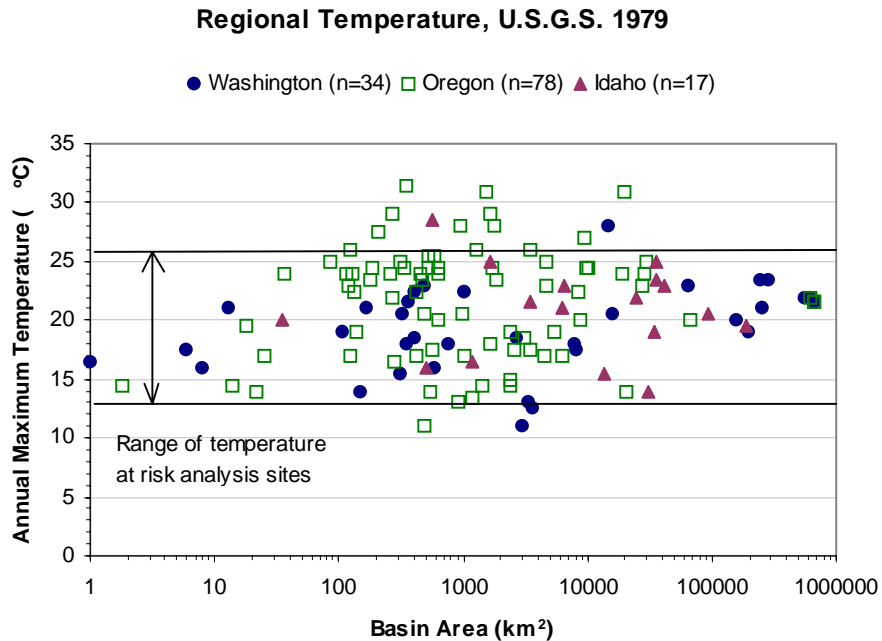
Figure 3.5. Annual maximum temperature for all stream and river sites listed in the U.S.Geological Survey Water resources data for Washington, Oregon, and Idaho for the year 1978-79.

The data from the University of Washington website, the statewide Timber/Fish/Wildlife study, and the U.S. Geological Survey are presented merely to establish how well the 19 risk analysis sites used in this report (Table 3) represent the streams found in a variety of geographic and land use settings that occur in the Pacific Northwest region. Only the records from the 19 sites are used for the analyses of acute and chronic temperature effects that follow in Sections 4,5, and 6 of this report.

We had no hourly temperature records for comparable time intervals from the coldest streams (e.g., <12°C). These are most likely to occur in well-shaded, small headwaters streams (Black, 2000). When well-shaded, these streams tend to hover near groundwater temperature (typically 6°-10°C during the summer, depending on geographic location) with little, if any, daily fluctuation. Such patterns were evident in Norwegian Creek (western Washington) and Cee Cee Ah Creek (eastern Washington) as examples taken from the TFW statewide study in 1990 (Sullivan et al. 1990). To represent this type of stream, we assigned constant temperatures through the summer. All temperature indices, including daily mean and daily maximum were set to 10°C for "Ten Site" and 8°C for "Eight Site".
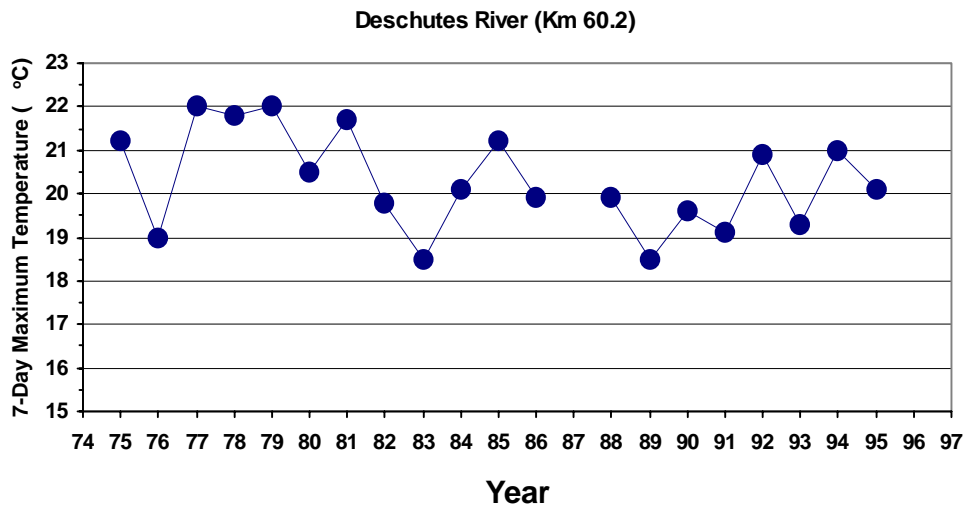
Figure 3.6 Annual maximum temperature of the Deschutes River near Vail, Washington from 1975-1995.
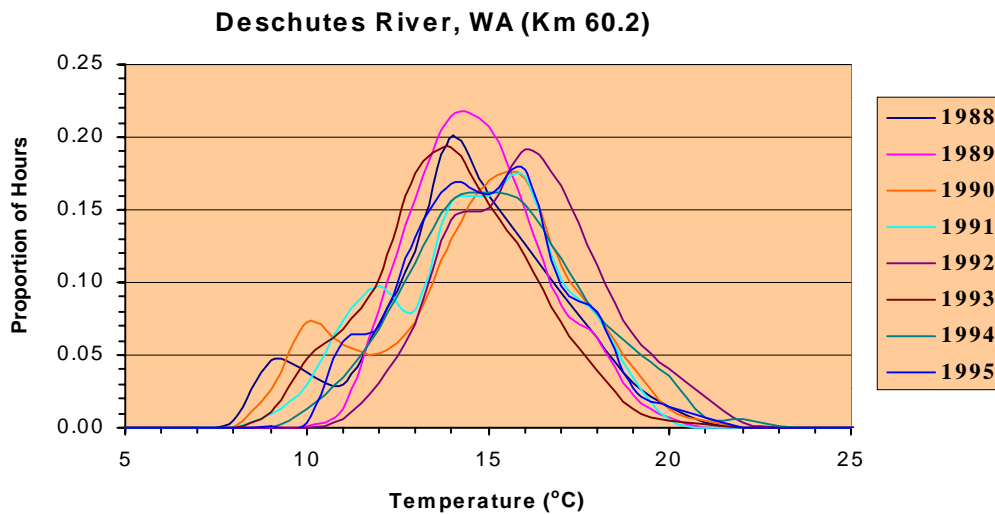
Figure 3.7 Frequency distribution of hourly temperature for 8 years in the Deschutes River near Vail, WA.

Temporal Variation at a Site

Temperature regimes at sites often vary somewhat from year to year due to climatic factors. Annual variation is illustrated in the 7-day maximum temperature at the Deschutes River mainstem (Figure 3.6). The long-term mean at this site was 20.3^{o}C averaged over 20 years but the upper temperature ranged $\pm1.25^{o}$C the average. The shape of the frequency distribution, available in hourly increments for eight years since 1988, was similar from year to year, but tended to shift up or down the temperature scale (Figure 3.7). Therefore, the time-averaged characteristics of temperature are likely to vary on an annual basis at a site. However, the relationship between the indexing characteristics such as maximum 7-day temperature and the overall distribution of temperature during the same summer period should remain consistent.

Temperature Indices

Later in this report (Sections 6 and 7), we will discuss the temperature indices that have been used to characterize the complex long-term temperature regime experienced by the biological community inhabiting streams (e.g., Figures 2.5 and 3.2) in ways that are meaningful ecologically. These indices or metrics are considered necessary as per Clean Water Act requirements to establish temperature criteria that are protective of salmonids or other designated uses. When water quality criteria are exceeded in water bodies, activities that contribute to or cause the exceedances to those water bodies may be restricted. Many streams and rivers are currently identified as exceeding water quality criteria according to the 305b reports from the states in the Pacific Northwest region, with a large number of them listed for temperature impairment. Therefore, the temperature criteria take on significant legal and economic meaning, and their appropriateness is of great concern to the public, scientists, and regulators.

Temperature criteria generally specify a temperature threshold calculated over an averaging period (Table 2.1). For example, Washington's current criteria, sometimes also referred to as standards, specifies the annual maximum temperature, expressed as the maximum hourly temperature that occurs each year. Oregon specifies the average of the daily <u>maximum</u> temperature of the 7 warmest consecutive days (ODEQ 1995). The U.S. EPA (1977) recommends the average of the daily <u>mean</u> temperature of the 7 warmest consecutive days (MWAT). Each of these measures for each temperature site is listed in Table 3.1.

There is an implicit assumption with these indices that they are representative of temperatures that is biologically meaningful in some way. The relationship between short-term indices and acute temperatures, which are typically expressed for short intervals, may be direct as discussed in Section 4. However, the threshold values associated with state water quality criteria appear to be selected to prevent long-term chronic effects as discussed in Sections 5 and 6. Therefore, there is an implicit assumption that short-term indices, based on temperature measured for only a few hours each year, represent the effects of long-term exposure. This assumption is worthy of evaluation. Furthermore, there is no consensus on how to report stream temperature with meaningful but simplified measures: laboratory and field studies use a wide variety of methods, and seemingly, no two are alike. Lack of standardized methods for reporting temperature among both the physical and biological sciences makes comparison among

studies difficult, and the selection of temperature criteria based on field ecological and laboratory studies tenuous.

Our analyses of acute and chronic biological effects associated with natural stream temperatures that follow in Sections 5 and 6 of this report rely on hourly records summarized only to average daily temperature. These analyses are therefore not limited by the lack of consensus on methodology to compress long-term temperature regimes into very short duration indices. We will, however, use results based on detailed temperature records in Section 6 to evaluate whether short-term indices are reliable indictors of at least some long-term biological responses.

Nevertheless, although there is some debate as to whether short-term indices are appropriate to represent long-term exposure, it appears that all of the short-term indices are closely related to one another (Figure 3.8). This makes selection among them a matter of procedural and logistical questions, rather than a biological question, since all similarly index the characteristics of the upper tail of the distribution of the temperatures sampled.

Perhaps a more important question is how well the short-term measures correlate with temperature characteristics occurring over longer periods. The median temperature for the period from June 1 to September 15, a long-term measure, is shown in relation to the three short-duration indices in Figure 3.9. Although more variable, the short-term indices are well correlated with the season median, indicating that short-duration measures can meaningfully characterize seasonal temperature patterns, albeit with some loss of precision. Not surprisingly, the 7-day mean temperature (MWAT) is best correlated with the season median, probably because each is respectively characterizing the central tendency of the temperature within the daily and seasonal period.
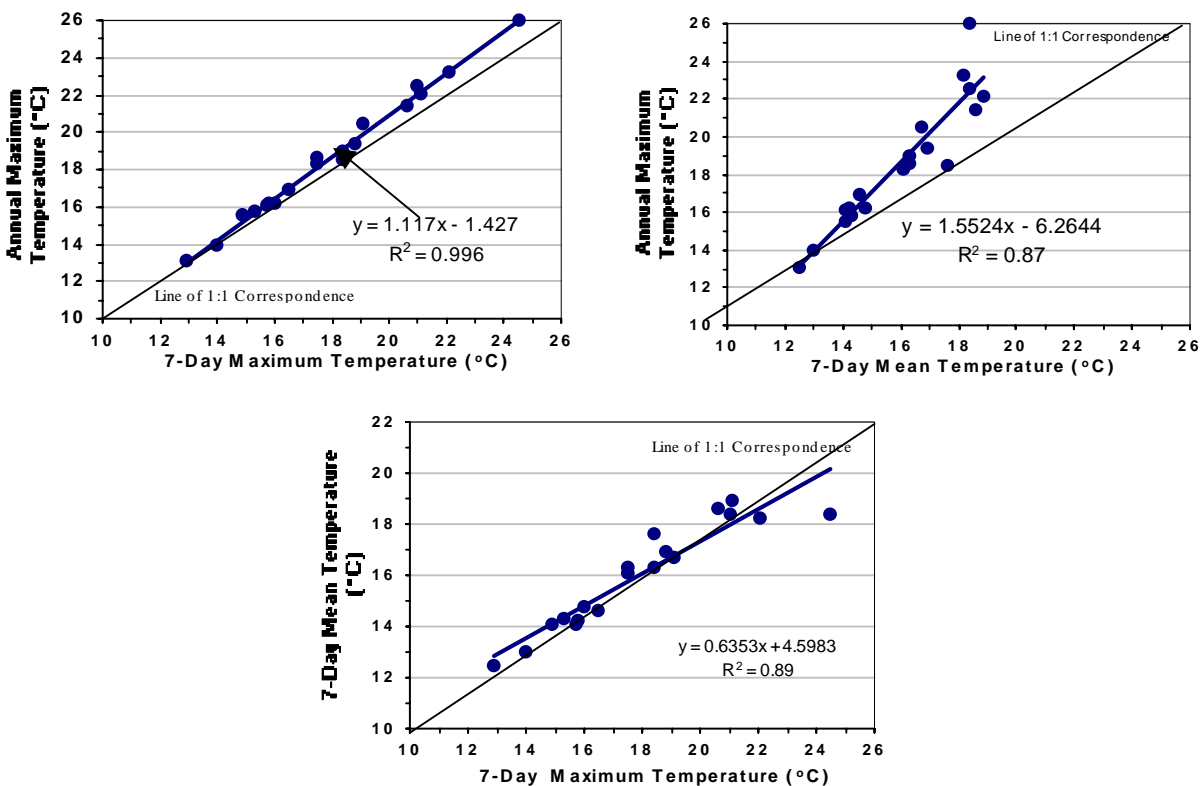
Figure 3.8 Relationships between temperature indices including annual maximum, 7-day mean (MWAT), and 7-day maximum.

3-10
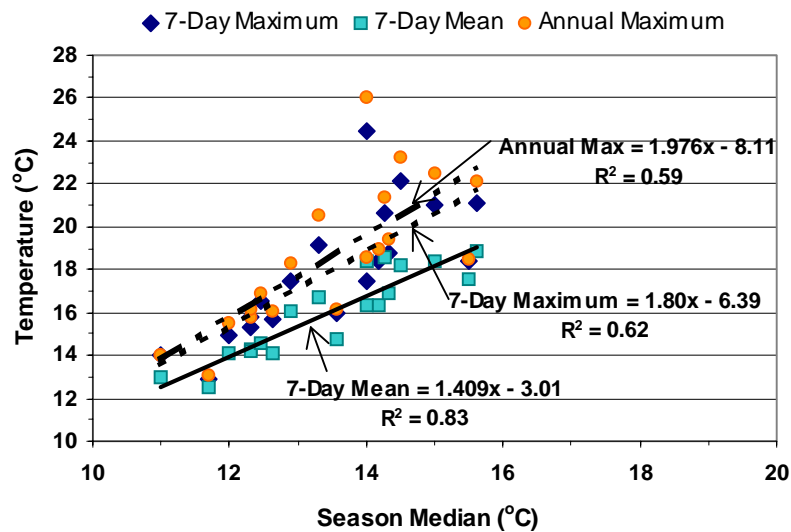
Figure 3.9 Relationship between season median temperature (June 1-Sept 15) with short duration indices.

CONCLUSIONS

- The data used in this report are broadly representative of stream temperatures in fish-bearing streams found in forested, rural, and urban streams in Washington. Their temperatures also appear to be representative of many streams throughout the Pacific Northwest, based on comparisons of data from other sources in the region.

- Observed temperatures at study sites span a range of temperatures, from 13° to 26°C in the annual maximum water temperature. This range encompasses most of the temperatures where salmonids may experience acute and chronic effects from short and long-term exposure.

- Various temperature indices such as annual maximum, 7-day maximum, and 7-day mean that are often used in temperature criteria are closely related to one another and can be compared or used interchangeably with the appropriate correlation relationships.

- Measures representing long duration exposure, such as the median temperature observed over the summer period are related to short-term measures.

- There is year-to-year variation in temperatures at stream sites, which is reflected in short-duration temperature indices.

SECTION 4   ASSESSMENT OF RISK OF SALMON SPECIES TO ACUTE TEMPERATURE IN STREAMS AND RIVERS

Abstract

In this section, we examine temperature records from streams and rivers in Washington spanning a range of summertime maximum temperatures to determine whether acute lethal temperature conditions exist, and if they could be associated with water quality temperature criteria. A relationship between temperature and duration of exposure sufficient to cause mortality was established based on previously published research. Hourly temperature records were scanned for occurrences of sufficient continuous duration, defined for each level of temperature to cause mortality within salmonid populations. Although at least one stream had temperature as high as $26^{o}C$, a temperature that can be lethal to salmonids, the length of exposure was not sufficient to cause mortality. We found no occurrence of acute lethal temperature conditions in any of the stream sites, which are broadly representative of streams and rivers in the Pacific Northwest.

Key findings of this chapter:

- ❑ There is sufficient information to quantitatively define the lethal effects of temperature on salmonids.

- ❑ No occurrences of acute lethal temperatures were observed at stream sites with a wide range of temperatures including many with annual maximum temperatures that well exceed current water quality standards.

- ❑ Nevertheless, lethal level temperatures of sufficient duration to cause mortality have been reported in the Pacific Northwest. Therefore, although not a common occurrence, attention should be paid to local site conditions that can lead to acute mortality.

- ❑ A temperature threshold of $26^{o}C$ is suggested to prevent mortality of salmon and trout species in natural rivers and streams. Further analysis of temperature to determine exposure is suggested for streams where annual maximum temperature is between 24° and $26^{o}C$.

INTRODUCTION

Temperature duration and lethality relationships have been established through laboratory study for most salmon species. Acute effects of temperature typically have been assessed as effects on survival that result from continuous exposure to elevated temperatures for specified periods of time (usually from 1 to 96 hours). Mortality has been commonly expressed as the duration eliciting mortality of some specified portion of the population at a specific temperature (Brett 1952). This is a measure of mortality from temperatures occurring within the zone of resistance (Figure 2.1) (Fagerlund et al. 1995); that is, where the temperature must be experienced for some duration greater than 1 hour before

mortality occurs. These temperatures are more likely to occur than the ultimate lethal thresholds where mortality of most or all of the population occurs within a very brief time.

Risk analysis is performed by quantitatively relating key temperature characteristics with specific measures of probable population response to those temperatures. We examined the likelihood that exposure to temperature is of sufficient magnitude and duration that it causes direct mortality within the fish population using conventional probabilistic risk assessment procedures (Parkhurst et al. 1996). Laboratory mortality data available from the literature were used to develop temperature effects relationships. Temperature data from streams monitored continuously during the summer months were used to assess exposure. Acute effects would most likely be associated with the occasional spikes of warm temperature that may induce mortality.

ACUTE THERMAL EFFECTS CURVES ASSOCIATED WITH 50% MORTALITY

Past research has emphasized the exposure duration causing 50% mortality in the population at a given temperature, as the most common lethality measure. Data from several sources were used to generate curves showing the relationship between temperature and duration to 50% mortality (EPA 1977, Brett 1952, and Golden 1978). Each curve estimates the length of time that 50% of a population can survive at some temperature above its upper incipient lethal temperature. This temperature is referred to as the LT50. At each successively lower temperature, the duration of exposure must be longer to achieve the same amount of mortality (Figure 2.2).

EPA (1977, page 11 of text and page 38 of Appendix C) provides a regression equation relating exposure time (in minutes) to the LT50 (in °C):

$$\log_{10} t = a + b \cdot LT50 \tag{4.1}$$

where t is the exposure time, and *a* and *b* are coefficients of the relationships. Equation 4.1 can be arranged to

$$LT50 = (\log_{10} t - a)/b \tag{4.2}$$

The regression coefficients, *a* and *b*, are provided in EPA (1977) for many fish species, including all those identified above, except cutthroat trout (pages 55-58 of Appendix B). From the coefficients provided, curves can be generated for selected species of salmon and trout: pink salmon, chum salmon, coho salmon, sockeye salmon, and chinook salmon. The coefficients in EPA (1977) were gathered from many different sources, including Brett's 1952 paper summarizing his study of lethal temperatures for the five salmon species. It is a necessary assumption of this analysis that the data from these laboratory studies conducted on a small number of fish and a few stocks are representative of the species, and that these relationships correctly characterize the mortality/temperature relationships. Golden (1978, Figure 4 on page 14) provides regression coefficients for cutthroat trout. Steelhead LT50 curves were generated using data from Alabaster and

Table 4.1 Regression coefficients for the relationship between duration and percent mortality of the sample population for laboratory studies on salmon and trout species. Most of the data are taken from a summary U.S.E.P.A document (1977). Studies report LT50, unless otherwise noted.

Species	Acclimation Temperature (°C)	Source	Age/Size	a	b	N	R	Notes
Coho salmon	15	Brett 1952	Juvenile	20.4066	-0.6858	6	-0.9681	
	20	"	"	20.4022	-0.6713	4	-0.9985	
	23	"	"	18.9736	-0.6013	5	-0.9956	
	17	Coutant 1970	Adult	5.9068	-0.1630	5	-0.9767	Reported acclimation temp. was the Columbia River temp (at Priest Rapids) during fall migration.
Rainbow trout	15	Alabaster and Downing 1966	Juvenile	15.650	-0.5000	2	-	
(Steelhead)	18	Alabaster and Welcomme 1962	"	18.4654	-0.5801	5	-0.9787	D.O. at 7.4 mg/l
	18	"	"	13.6531	-0.464	5	-0.9742	D.O at 3.8 mg/l
	20	Alabaster and Downing 1966	"	19.6250	-0.6250	2	-	
	20	Craigie 1963	Yearling	14.6405	-0.4470	3	-0.9787	Raised in soft water, tested in soft water
	20	"	"	15.0392	-0.4561	3	-0.9917	Raised in soft water, tested in hard water
	20	"	"	15.1473	-0.4683	3	-0.9781	Raised in hard water, tested in soft water
	20	"	"	12.8718	-0.3837	3	-0.9841	Raised in hard water, tested in hard water
Cutthroat trout	23	Golden 1978	Juvenile	18.092	-0.56523	?	-0.996	Hatchery fish only
	13-25 (fluctuating)	"	"	22.543	-0.71999	?	-0.999	Hatchery fish only
	23	"	"	18.3166	-0.5723	?	-0.999	Hatchery and wild fish pooled
	13-25 (fluctuating)	"	"	18.1515	-0.5723	?	-0.992	Hatchery and wild fish pooled
Chinook salmon	20	Blahm and McConnell	Juv (spring run)	21.3981	-0.7253	3	-0.9579	50% mortality
	20	Unpub.data	"	22.6664	-0.7797	4	-0.9747	10% mortality
	20	"	"	20.9294	-0.7024	3	-0.9463	90% mortality
	20	"	Juv (fall run)	22.2124	-0.7526	4	-0.9738	50% mortality
	20	"	"	21.6756	-0.7438	4	-0.9550	10% mortality
	20	"	"	20.5162	-0.6860	3	-0.9475	90% mortality
Sockeye salmon	15	Brett 1952	Juvenile	15.8799	-0.5210	7	-0.9126	
	20	"	"	19.3821	-0.6378	5	-0.9602	
	23	"	"	20.0020	-0.6496	4	-0.9981	
	20	McConnell and Blahn 1970	Juv/underyearling	16.7328	-0.5473	6	-0.9552	
	20	Unpublished data	"	17.5227	-0.5861	6	-0.9739	10% mortality
	20	"	"	15.7823	-0.5061	6	-0.9539	90% morality

Downing (1966) and Alabaster and Welcomme (1962), as cited in the EPA document. Data were combined where studies were reasonably comparable. Coefficients for each species are provided in Table 4.1 for experiments that tested a range of acclimation temperatures. Generally, the higher the acclimation temperature, the higher the LT50 temperature.

The acute thermal effects curves were generated in Excel® using regression coefficients provided in EPA (1977) and Golden (1978) for a range of exposure times. While the equations provided in EPA (1977) were based on exposure times measured in minutes, we converted them to hours in order to be consistent with temperature measurements at field sites. To generate the hourly curves, equation 4.2 was modified to

$$LT50 = ((\log_{10} t \cdot 60) - a)/b \qquad\qquad (4.3)$$

Although it was assumed that the regression coefficients in Appendix B of EPA (1977) were correct, one appeared to be in error. The value for a was given as 16.2444 for pink salmon at an acclimation temperature of 20°C from Brett's study (1952). The resulting curve did not match the one presented in Figure 5 of Brett (1952). To generate a curve more representative of Brett's (1952) figure, a value of 13.2444 was used for a instead.

A few of the studies included in EPA (1977) were excluded from the analysis. These were studies in which the fish being tested showed signs of gas bubble disease or other effects of gas supersaturation.

COMPARISON OF LT50 and LT10 MORTALITY RELATIONSHIPS

Most of the available information on thermal effects is based on 50% survival. We felt that it was appropriate to use a more conservative population measure for risk assessment. Therefore, we also expressed acute effects as the duration of time needed to elicit 10% mortality (LT10) for each temperature and species studied. LT10 was selected because it is the amount of mortality considered acceptable in the control groups for acute toxicity tests (ASTM 1997), and 90% (100% - 10%) is a recommended protection level for species populations (SETAC 1994; Solomon et al. 1996).

In the EPA (1977) document, two unpublished studies provided regression coefficients for both 50% and 10% (LT10) mortality curves at acclimation temperatures of 15°C or higher. McConnell and Blahm (1970) calculated regression coefficients for sockeye salmon; and Blahm and McConnell (1970) calculated regression coefficients for both spring and fall runs of chinook salmon. Using the regression coefficients generated from these studies, LT50 and LT10 values for sockeye (Table 4.2) and chinook (Table 4.3) were calculated for a range of time periods, along with their ratio.

For the range of exposure times, the LT10 values were 98.0 to 99.7% of the LT50 values. This is consistent with Brett (1958, page 76 and Figure 4), who indicated that differences between temperatures for 50% mortality and those for <50% mortality are relatively small. This "implies that temperatures of this order have only to increase slightly to cause a large difference in mortality." Based on visual inspection of the LT50 and LT10 curves, the slopes were similar. That is, on the log-time scale, the differences between the LT50 and LT10 curves were approximately constant. (There was insufficient information

Table 4.2 Relationship between LT50 and LT10 for sockeye salmon. Acclimation temperature is 20°C. Data from McConnel and Blahm (1970), unpublished data (cited in U.S. EPA 1977).

Time (hrs)	LT50 (°C)[&]	LT10 (°C)[#]	LT10/LT50 Ratio (%)	Delta T (°C)
.1	29.2	28.6	98	0.6
.25	28.4	27.9	98.12	0.5
.5	27.9	27.4	98.21	.0.5
1	27.3	26.9	98.31	0.5
2	26.8	26.3	98.41	0.4
3	26.5	26.0	98.47	0.4
4	26.2	25.8	98.52	0.4
6	25.9	25.5	98.58	0.4
8	25.7	25.3	98.63	0.4
12	25.4	25.0	98.7	0.3
16	25.1	24.8	98.74	0.3
20	24.9	24.6	98.78	0.3
24	24.8	24.5	98.81	0.3
32	24.6	24.3	98.86	0.3
40	24.4	24.1	98.9	0.3
60	24.1	23.8	98.98	0.2
80	23.8	23.6	99.03	0.2

& regression coefficients a=16.7328, b=-0.5473

regression coefficients a=17.5227, b=-0.5861

Table 4.3 Relationship between LT50 and LT10 for chinook salmon. Acclimation temperature is 20°C. Data from McConnel and Blahm (1970), unpublished data (cited in U.S. EPA 1977).

Type	Time (hrs)	LT50 (°C)[&]	LT10 (°C)[#]	LT10/LT50 Ratio (%)	Delta T (°C)
Spring run[a]	0.1	28.4	28.1	98.74	0.4
	0.25	27.9	27.6	98.86	0.3
	0.5	27.5	27.2	98.95	0.3
	2	26.6	26.4	99.13	0.2
	4	26.2	26.0	99.23	0.2
	6	26.0	25.8	99.28	0.2
	8	25.8	25.6	99.33	0.2
	10	25.7	25.5	99.36	0.2
	16	25.4	25.2	99.43	0.1
	24	25.1	25.0	99.49	0.1
	40	24.8	24.7	99.57	0.1
	60	24.6	24.5	99.64	0.1
	80	24.4	24.3	99.68	0.1
	100	24.3	24.2	99.72	0.1
Fall run[b]	0.1	28.5	28.1	98.65	0.4
	0.25	28	27.6	98.6	0.4
	0.5	27.6	27.2	98.56	0.4
	2	26.8	26.3	98.49	0.4
	4	26.4	25.9	98.44	0.4
	6	26.1	25.7	98.42	0.4
	8	26	25.5	98.4	0.4
	10	25.8	25.4	98.39	0.4
	16	25.6	25.1	98.36	0.4
	24	25.3	24.9	98.33	0.4
	40	25	24.6	98.3	0.4
	60	24.8	24.4	98.27	0.4
	80	24.6	24.2	98.25	0.4
	100	24.5	24.1	98.24	0.4

&regression coefficients LT50:a=21.3981, b=-0.7253   lT10: a=22.6664, b=-0.7797

regression coefficients   LT50:s a=22.2121, b=-0.7526   LT10 a=21.6756, b=-0.7438

presented in Appendix B of the EPA (1977) document to statistically compare the slopes.) Had the differences not appeared constant, the application of a singe adjustment factor would not have been appropriate.

ACUTE THERMAL EFFECTS CURVES AT 10% MORTALITY

The adjustment factor estimated from the McConnell and Blahm (1970) and Blahm and McConnell (1970) data for sockeye and chinook salmon was assumed to be appropriate to use in estimating LT10 curves for the other salmon and trout species. For the other studies from which LT50 curves were generated, LT10 curves were estimated by applying a factor of 0.98 to each LT50 curve. The equation used to calculate the estimated LT10 values is

$$LT10 = \frac{(\log_{10}(t*60)-a)}{b} \cdot 0.98 \qquad (4.4)$$

The estimated LT10 curves for 15°C acclimation for four salmon species are provided in Figure 4.1. (Relationships for all species and acclimation temperatures are graphically depicted in Appendix C, under separate cover.)

The resulting LT10 lethal curves are very similar among salmon species although cutthroat trout have higher tolerance to high temperature than the other species (Figure 4.1). We note that using the relationship based on fluctuating acclimation temperature (Golden 1978) produced higher LT50's than when tested at constant temperature. Continuous exposures of 3 to 30 hours are necessary to cause mortality at temperatures between 24° to 26°C, varying by species. The duration of time necessary to cause mortality decreases sharply with small increments of temperature above approximately 26°C. Short duration excursions (less than two hours) above 27°C are very likely to cause mortality of some individuals in the population because only one hour duration is necessary
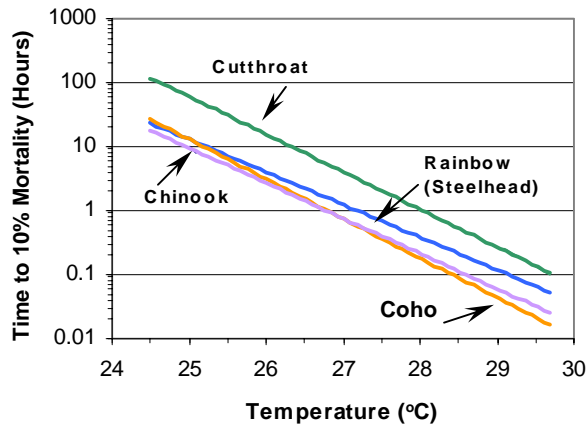
Figure 4.1 Duration curve for the LT10 acute effects of temperature for coho and chinook salmon and cutthroat and steelhead trout, acclimated at 15°C. (Data from Brett 1952, Alabaster and Downing 1966, Golden 1978; see Appendix C).

ACUTE EXPOSURE CHARACTERIZATION

The maximum temperatures juvenile salmonids experienced *in situ* were determined through exposure characterization, (U.S. EPA 1992). Summertime temperatures for sites described in Section 3 (Table 3.1) were assembled for this study. The occurrence of potentially lethal temperatures was determined by examining the <u>hourly</u> temperature record at each of the 19 temperature sites for exposure periods defined as the number of continuous hours at or above the exposure temperature (temperature was rounded to the nearest ^{o}C). We used a lower level of 16°C since it approximates the <u>optimum</u> temperature for several salmon species (Weatherly and Gill 1995) although it is important to note that acute mortality does not commence until 24ºC under naturally fluctuating conditions. Exposure was based on hourly temperatures so that we could capture relatively short duration effects and the LT10 data were expressed in hours.

An exposure period is the number of consecutive hours each temperature (measured to the nearest 1.0°C) occurred within a period when the temperature was at or above 16°. For example, if the temperature increased from below 16° to 16.6°, a count of one was added to 16°C. If the next hourly temperature was 18.5ºC, then a count of one was added to16^{o}, 17° and 18ºC. If the following hourly temperature decreased back to 17ºC, then a count of one was added to 16°, and 17°, and so forth. As soon as the next temperature retreated below each temperature degree category, the counting (i.e., duration of exposure) for that temperature ceased. When temperatures dropped below 16ºC, the entire exposure period was concluded. In the example above, there was one exposure period where temperature reached 16° for 3 hours, 17° for two hours, and 18° for one hour.

Exposure to temperatures above 16°C varied significantly among sites. Table 4.2 lists the number of exposure periods for temperatures greater than 16°C and the number of hours by temperature category for the warmest continuous exposure period at each site. At some sites there were no exposure periods at any time during the summer months, while at others both the magnitude and duration of exposure were relatively large. Hoffstadt Creek in the Mt. St. Helens Blast Zone experienced the warmest temperature (26.0^{o}C) which lasted one hour (Figure 4.3A and 4.4). This stream is shallow, and it heats and cools rapidly over the course of the day. The deeper Chehalis River sites (Figure 4.3B) did not reach quite as high a temperature (22°C), but experienced higher temperatures over much longer continuous periods.

Table 4. 4 Number of exposure sequences where temperature was continuously greater than or equal to 16° C for one or more hour at each of the sites and the duration of continuous exposure (hours) at each temperature for the warmest period.

Number of Hours by Temperature for the Maximum Sequence at the Site

Site	Total Number of Sequences	_16_	_17_	_18_	_19_	_20_	_21_	_22_	_23_	_24_	_25_	_26_
Big Creek	6	4	0	0	0	0	0	0	0	0	0	0
Chehalis River Main 1	49	455	70	21	16	12	8	2	0	0	0	0
Chehalis River Main 2	69	44	33	26	21	16	1	6	1	0	0	0
Chehalis River Main 3	62	44	32	23	17	11	0	0	0	0	0	0
Crim Creek	54	22	14	7	3	0	0	0	0	0	0	0
Deschutes River Main	70	139	65	17	14	10	7	5	0	0	0	0
Hard Creek	0	0	0	0	0	0	0	0	0	0	0	0
Harrington Creek	36	25	17	12	9	5	0	0	0	0	0	0
Hoffstadt Creek	83	19	16	15	13	12	7	8	7	5	5	1
Huckleberry Creek	34	405	65	12	0	0	0	0	0	0	0	0
Lester Creek	47	14	8	5	0	0	0	0	0	0	0	0
Mack Creek	0	0	0	0	0	0	0	0	0	0	0	0
Porter Creek	30	21	15	9	0	0	0	0	0	0	0	0
Rogers Cr.	1	2	0	0	0	0	0	0	0	0	0	0
Sage Cr.	17	7	0	0	0	0	0	0	0	0	0	0
Salmon Cr.	2	3	0	0	0	0	0	0	0	0	0	0
Thrash Cr.	0	0	0	0	0	0	0	0	0	0	0	0
Thurston Cr.	0	0	0	0	0	0	0	0	0	0	0	0
Ware Cr.	24	34	23	13	0	0	0	0	0	0	0	0

ACUTE RISK CHARACTERIZATION

To assess acute risk to lethal temperature, the periods when duration of temperature equaled or exceeded the LT10 curve (e.g. Figure 4.1) were examined to determine if the duration of exceedance was of sufficient length to cause mortality. If the time spent at any temperature equaled or exceeded the time necessary to elicit mortality at the LT10 level, then an exceedance occurred. If an exceedance occurred, we assumed that 10% of the population died. The number of exceedances that occurred during the summer interval was counted. It follows that if 10% of the population died at each exposure, then the cumulative risk to the population (Lethal Risk) could be calculated using the number of exceedances (*n*) experienced by the population:

$$\text{Lethal Risk} = \left[1.0 - (1.0 - 0.10)^n\right] \hspace{2cm} (4.5)$$

where lethal risk is defined as the proportion of the population that dies due to the temperature exposure. For example, if a stream's temperature exceeded an LT10 once, the cumulative total mortality risk would be $[1.0-(0.90)^1]$ or 10%; if it exceeded an LT10 four times, the total mortality risk would be $[1.0-(0.90)^4]$ or 34%.

There were no indicated periods of acute exposure for chinook, coho, steelhead, or cutthroat at any of the stream locations despite higher temperatures at some sites. The warmest period of exposure at each of the 19 temperature study sites in relation to species' LT10 exposure curves is shown in Figure 4.2. Some sites did not exceed optimal temperature (approximately 16°C) at any time during the summer and do not appear on the figure. For those that exceeded acute lethal temperatures (24°C or greater), the exposure was generally much less than required to cause mortality.

The only site that exceeded 24°C (the temperature zone where mortality depends on duration of exposure) was Hoffstadt Creek, which peaked at 26.0^{o}C for one hour (Figure 4.2 and 4.3A). Hoffstadt Creek had an additional two exposure periods reaching 25°C (three-hour duration) and twelve reaching 24°C (five-hour duration). Although the one-hour maximum temperature approached the magnitude and duration that could elicit mortality at this site, the duration of exposure at 24°, 25°, and 26°C for Hoffstadt Creek was too short to directly cause mortality (Figure 4.3A). The Chehalis

Figure 4.2 Hours of continuous exposure at temperature sites (see Table 4.1) and LT10 lethality relationships for fish species.

River mainstem experienced much longer duration at higher temperatures (Figure 4.3B), but never came close to lethal temperatures.

No acute risks were identified since none of the water temperatures persisted long enough to exceed the lethal thresholds (LT10s) of salmonid species likely to occur in these streams. Since *n* equaled 0 at all sites, the probability of acute effects was 0.
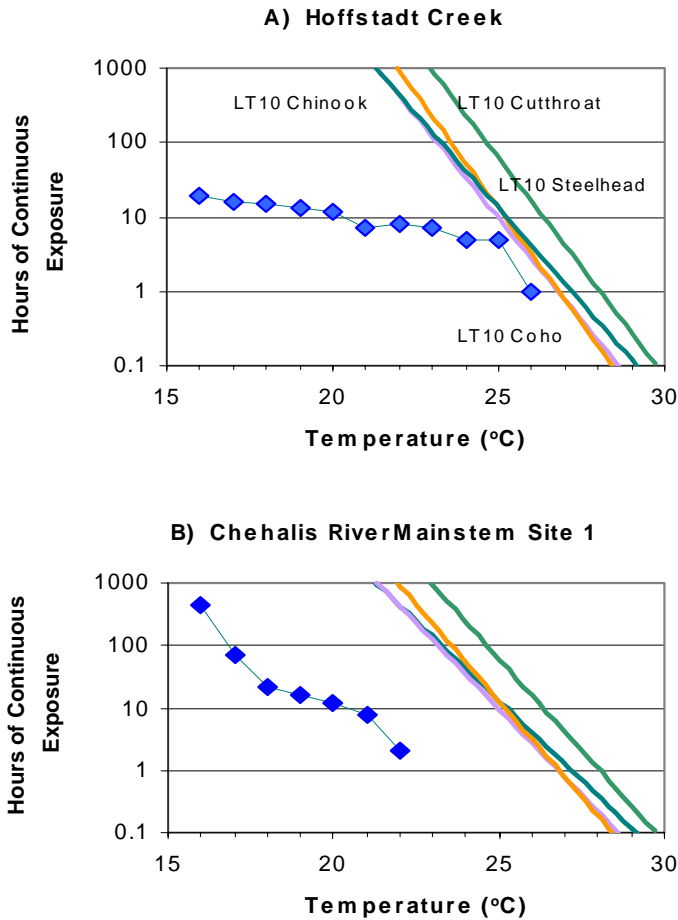
Figure 4.3 Example of how acute exposures were summarized: maximum number of sequential hours at each temperature for A) Chehalis River mainstem (site 1) and B) Hoffstadt Creek sites. Diamonds are the exposure for each temperature for the warmest period at each site.

Small to moderate size streams and rivers have sufficient fluctuation in the daily temperature that water does not spend long continuous duration at lethal temperature. The daily fluctuation is strongly dependent on stream depth (Adams and Sullivan, 1990, Sullivan and Adams, 1990). Within much of the Pacific Northwest, relatively shallow streams and rivers may be capable of achieving temperatures that can cause mortality within a few hours. Their shallowness, however, will generally preclude them from maintaining high lethal temperatures for more than a few hours during the day, and temperatures can fluctuate widely over the solar cycle (Brown 1969). For example, Figure 4.4 shows Hoffstadt Creek during its warmest 7-day period in 1990. The duration of lethal temperature is short.

Conversely, large deep rivers may maintain higher average temperature, but the daily fluctuation is smaller. For example, for much of the summer and its length, the Columbia River maintains an average temperature of 22°C with a daily fluctuation of 0.5 °C. In the U.S.G.S. water resource records discussed in Section 3, the S. Umpqua River in southern Oregon reached 30°C annual maximum temperature. Nevertheless, the daily minimum temperature on the hottest days did not exceed 21° to 23.5°C, indicating that duration of extreme temperature was short, and probably within lethal thresholds. Thus, duration of exposure at higher temperatures can be significant, but lethal temperatures that cause mortality in a few hours are not likely to occur in most cases. The dependence of daily fluctuation on stream depth makes the case that very large, deep rivers are different than most of the streams and rivers in the region (Section 3), and those rivers with extreme temperatures should probably be analyzed individually to fully understand their local site conditions.

Table 4.5 shows the calculated temperature for 1-hour and 6-hour exposure that would cause mortality of 10% of the population based on relationships provided in Table 4.1, and the calculation methods described in this section.
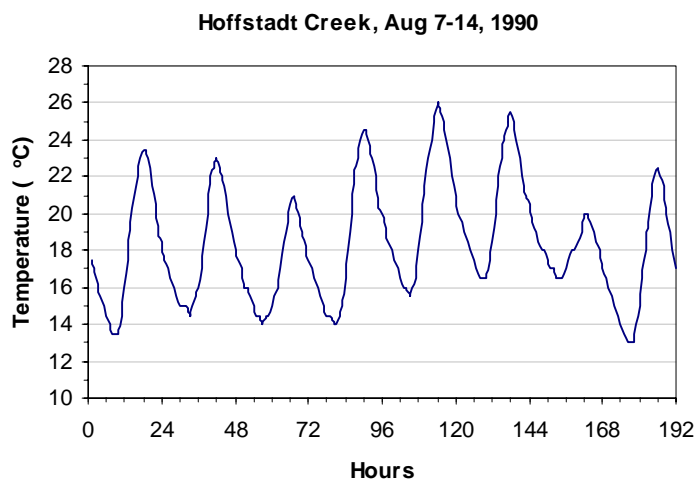
Figure 4.4 Hourly temperature during the warmest 7-day period at Hoffstadt Creek in 1990.

The temperatures at which mortality occurs at exposures of 1 hour and 6 hours if very similar among species. This temperature is between 25.4°C and 27.4°C, averaging 26.4°C. There is a low probability that the 6-hour duration temperature occurring in most natural streams in Washington, as suggested by Table 4.1. Therefore, an acute temperature for salmon of approximately 26°C in the annual maximum temperature is suggested to prevent mortality with a margin of safety. We also suggest that a site-specific analysis of temperature be performed when annual maximum temperature is between 24° and 26°C, to determine whether duration is sufficient to cause mortality. It would appear that in most cases it will not, but until more analyses are completed over a broader geographic range this will not be known with certainty. Site specific analyses would also be warranted at sites of thermal pollutant sources that alter the normal daily temperature fluctuation.

Table 4.5. Temperature of 1-hour and 6-hour duration that will cause mortality of 10% of the population for salmon and trout species.

Species	Age/size	Acclimation Temp (°C)	1-Hour Temperature (°C)	6-Hour Temperature (°C)
Coho salmon	juvenile	15	26.6	25.5
		20	27.2	26.1
		23	28.0	26.8
Rainbow trout	juvenile	15	27.2	25.7
		18	27.5	26.9
		20	28.0	26.8
Rainbow trout	yearling	20	28.2	26.5
		20	28.5	26.8
		20	28.0	26.3
		20	28.3	26.3
Cutthroat trout	juvenile	23	28.3	27.1
		13-25 (fluctuating)	28.5	27.9
		23	28.3	26.3
		13-23 (fluctuating)	28.0	26.7
Chinook salmon	juvenile	15	26.8	25.4
		20	27.5	26.8
	jacks	19	30.1	27.1
	juvnile spring	20	26.5	25.5
		20	26.8	25.8
	Juvenile fall	20	26.6	25.6
		20	26.8	25.7
Sockeye salmon	juvenile	15	26.5	25.1
		20	26.0	25.9
		23	27.5	26.3
	underyearling	20	26.8	25.4
Chum salmon	juvenile	15	26.3	24.9
		20	27.8	25.9
		23	28.2	26.6

Discussion

We conclude that direct mortality from temperature is unlikely to affect populations living in streams with temperatures similar to those evaluated in this paper.

Mortality associated with acute lethal temperatures has been previously reported from streams similar to those in this study. In both cases, natural and logging-related disturbance caused complete denudation of the watershed, including all riparian vegetation and in-channel cover. In the years immediately following the1980 eruption of Mt. St.

Helens, temperatures of streams within the blast zone were extreme relative to those typically recorded in the Pacific Northwest. Bisson et al. (1988) and Martin et al. (1986) reported temperatures in Hoffstadt Creek and other moderate size streams in the blast zone that exceeded 29°C for short daily intervals several times during the summer. The lethality curve suggests that even short duration exposure to such warm temperatures could cause mortality of individual fish and repeated exposures could have a measurable effect on salmon populations. In this case, the acute effects analysis would have predicted mortality, although we do not have temperature data from these earlier studies to calculate the cumulative mortality. Populations of juvenile coho salmon successfully survived the temperature episodes exceeding lethal levels (Bisson et al. 1988). However, Martin et al. (1986) also reported significant mortality of juvenile coho within populations in the same streams as Bisson et al. (1988) that was proportional to the magnitude of daily temperature fluctuations (maximum fluctuation of 17°C) when temperatures exceeded 26°C.

Temperatures have since sufficiently declined with vegetation re-growth that mortality is not expected at temperatures existing eight years after the eruption and beyond. Hall and Lantz (1969) reported no reduction in numbers of coho, and a 25% reduction in cutthroat trout, when summertime temperatures reached 30°C in a small Oregon stream (Needle Branch) after clearcut logging and severe burning.

Elsewhere in the Pacific Northwest, water temperatures greater than 24°C are measured relatively rarely in streams and rivers (see Section 3). Based on the foregoing analysis, one can conclude there is low risk of acute lethality to salmonid species juveniles from temperatures observed at the nineteen sites in this risk assessment. The temperatures at these sites are representative of the potentially lethal temperature of most of the natural streams up to 5th order found in the Pacific Northwest, including many with disturbed riparian forest cover (Sullivan et al. 1990). Streams in this analysis include many sites affected by land use and catastrophic natural disturbance. Nevertheless, if temperatures should reach as high as 28°C for as little as an hour, mortality of some portion of the population can be expected.

CONCLUSIONS

- There is sufficient information to quantitatively define the lethal effects of temperature on salmonids.

- No occurrences of acute lethal temperatures were observed at stream sites with a wide range of temperatures including many with annual maximum temperatures that well exceed current water quality standards.

- Nevertheless, lethal level temperatures of sufficient duration to cause mortality have been reported in the Pacific Northwest. Therefore, although not a common occurrence, attention should be paid to local site conditions that can lead to acute mortality.

- A temperature threshold of 26°C is suggested to prevent mortality of salmon and trout species in natural rivers and streams. Further analysis of temperature to determine exposure is suggested for streams where annual maximum temperature is between 24° and 26°C.

SECTION 5 DEVELOPMENT AND CORROBATION OF A BIO-ENERGETICS –BASED APPROACH TO EVALUATING SALMON GROWTH IN RELATION TO ENVIRONMENTAL TEMPERATURE

Abstract

Growth is an important biologic function for juvenile salmonids rearing in streams and rivers. In this section, we develop a quantitative method to evaluate the effects of the long-term temperature on the growth of salmonids. The mathematical model considers the effects of temperature and food consumption on daily growth rate. When applied over time to measured stream temperature regimes, the model simulates the weight gain of salmon species, and can be used to assess the importance of the cumulative or chronic effects of temperature on growth. At present, the model is formulated to assess the growth of juvenile salmonid species during the summer months with variable temperatures. Previous researchers have used similar approaches, although this specific method has not been explicitly described previously. We use well-established bioenergetics principles and models available in the scientific literature to help develop it.

The relatively simple formulation appears to predict weights well according to a number of comparisons of observed and predicted growth at stream sites where fish populations had been sampled. The method is sensitive to temperature, making it a useful tool for evaluating salmon response to temperature in natural streams, and it allows direct comparisons among sites and species if desired. Application of bioenergetics principles to field observations using this tool suggests ecological adaptation to environmental temperature and food supply. The model may prove useful for helping field investigators sort out the complex relationships between population dynamics, environmental temperature, and food supply that control growth in natural streams.

Because the model is central to determining the effects of temperature on fish growth in relation to temperature, the mathematical approach is developed in detail in this section. If the scientific basis for the growth analysis is not of interest, the reader is urged to move directly to Section 6, where the method is applied to develop temperature criteria.

Key findings include:

❑   Methods of predicting growth based on quantitative bioenergetics principles can be applied to streams to assess the effects of temperature on juvenile salmonid growth, with results that are consistent with observed wild fish population growth patterns.

❑   The method is sensitive to temperature and can be applied to the daily temperature regime making it a useful tool for assessing the biological impacts of temperature in natural streams.

INTRODUCTION

Of primary interest in selecting temperature criteria is the prevention of adverse effects of long-term exposure to temperatures detrimental to fish. To explore the effects of prolonged exposure to temperature, numerous investigators have found growth to be a reliable and measurable integrator of a variety of physiological responses (Brett 1971, 1995; Iverson 1972; Brungs and Jones 1977; Wurtsbaugh 1973). Growth rate is the most frequently reported measure of fish health from laboratory studies and occasionally from field studies. By corollary, the weight a fish gains over a time interval is, in part, determined by the ambient temperature of the water in which it lives.

The size of salmonids during juvenile and adult life stages influences survival and reproductive success. Although the large majority of anadromous salmonid growth occurs in the ocean environment, growth of juveniles in natal streams is especially important for anadromous salmonids that must reach minimum sizes before they can smolt (Weatherly and Gill 1995). Holtby and Scrivener (1989) and Quinn and Peterson (1996) demonstrated that the size achieved by juvenile coho at the end of their first summer growing period was a strong determinant of their later success in overwintering and smolting. Larger size also conveys competitive advantage for feeding in the freshwater environment (Puckett and Dill 1985, Nielsen 1994) for both resident and anadromous species. Mason (1976) and Keith et al. (1998) found that the smaller fish tend to be those that are lost from rearing populations. Brett et al. (1971) described the freshwater rearing phase of juvenile sockeye as one of restricted environmental conditions and generally retarded growth. This synopsis is generally true for salmonid species that dwell in stream and river environments for lengthy periods of time.

Growth can be viewed as the net effect of the environment on the relation between food consumption, metabolism, and activities of an organism (Warren 1971). The bioenergetics of many fish species, including salmonids, has been widely studied and quantified (reviewed by Adams and Breck 1990, Brett 1995, and others). The food fish consume is allocated to maintaining basic metabolic functions, growth and waste. The most generalized representation of bioenergetics is of the form:

$$\text{Consumption} = \text{Metabolism} + \text{Growth} + \text{Wastes}$$

Researchers have developed mathematical relationships for the rate functions for various energetic processes (summarized in Brett 1995). We propose that a bioenergetics approach can be used to assess the effects of temperature exposure because many of the energetic relationships are based on temperature and the energy balance determines growth.

Bioenergetics models vary in their formulations of specific functions and in the complexity with which they attempt to characterize the details of each (Ney 1993). The most comprehensive bioenergetics models consider all modes of energy intake and expenditures including consumption, respiration, active metabolism, specific dynamic action (swimming), wastes (including egestion and excretion), and growth (including body tissue and gonads) (Kitchell et al. 1974, Hewett and Johnson 1992). Bioenergetics models combine these relationships into an energy balance where the energy consumed and the energy expended to all functions must sum to one. Elliott's (1976) relationships for brown trout are also widely cited. Bioenergetics models have been developed for a number of applications in fisheries management and their uses are many and varied (Hansen et al. 1993, Ney 1993). They have been used routinely to manage the rearing of fish in hatcheries (McLean et al. 1993) and populations in natural environments (Hanson et al. 1997). Increasingly,

they have been used to explore ecological responses to environmental conditions (Filbert and Hawkins 1995, Preall and Ringler 1989, Railsback and Rose 1999).

J.F. Kitchell and colleagues at the University of Wisconsin have made bioenergetics analysis available to a wide variety of scientists and managers. They have summarized research for many fish species, including salmonids, and packaged the energy functions in software for easier use of the multiple mathematical statements required for the energy balance (Kitchell et al. 1974, Hewett and Johnson 1992, Hansen et. al. 1997). In practice, model users are urged to supply data to calibrate model parameters and to validate population growth. There are a variety of data needs in conducting full bioenergetics analysis. The Wisconsin models require a relatively large number of parameters (15-30), some of which are measured from the population and environment of interest (Hanson 1997). Default values are supplied if the user is unable to develop local data, often times borrowed from similar species that have received greater laboratory and field study. The proliferation of parameters, each with its own estimation error, has led some to criticize bioenergetic models for being insensitive statistically and difficult to apply (Hansen et al. 1993).

For practical applications, it is often desirable to construct the simplest model possible that can capture the key environmental or biological effects of interest (Kitchell et al. 1974). Moreover, Ney (1993) has suggested that elaborate energetic characterizations may not be necessary to provide satisfactory answers to some bioenergetics questions. Although grwoth is only one of the bioenergetic functions, many authors argue that it integrates a host of specific physiological responses to temperature, including metabolic rate (basal and active), feeding and digestion, and swimming performance or the ability to hold position with the current (Brett 1995; Weatherly and Gill 1995). For example, Brett et al. estimated weight gain of sockeye (1971) and chinook (1982) in relation to environmental temperature assuming that the relationship between temperature, food consumption and growth rate, such as illustrated in Figure 2.4, adequately integrates the organism's response to temperature. Mallet et al. (1999) applied a temperature-modified form of a von Bertalanffy growth model, which has no explicit of energetics, to estimate the growth of grayling in a European River. Up to 25 to 30% of the energy consumed by salmonids is allocated to growth and the remainder is allocated to the other energy demands (Brett et al. 1982, Brett 1995). With the exception of respiration, the pattern of response of all of the energetic functions to temperature is similar to that of growth rate, with maximums and minimums of activity peaking and declining at similar optimal temperatures (e.g. Brett et al. 1971, Hansen et al. 1997). Energy consumed by respiration continually increases reaching maximums at temperatures coincident with shut down of other metabolic functions, including growth (e.g., 24°C for salmonids, Brett 1995).

Growth, or more precisely, gain in weight for our purpose, is one of the few energetic functions that can be readily measured in natural environments, and it perhaps is the quality of greatest interest for juvenile salmonids. Because bioenergetic functions respond similarly to growth, the approach of Brett et al. (1982) assumes that the other components of the energy equation can be ignored yielding a modeling approach that requires only a few parameters.

In this section, we develop a mathematical approach to predict growth from temperature and food consumption, using realistic estimates of food supply. It follows the approach of Brett et al. (1971, 1982) in that only growth rate as mediated by temperature and food consumption are accounted for in the energy balance. However, we use the bioenergetics approach to estimate the interaction of food consumption with temperature. We develop the rationale for each of the components of the growth model, and parameterize them based on laboratory and field studies of fish populations. We then compare model simulation results with fish population weight gain at a number of stream

sites to evaluate model performance. This analysis considers growth during summer rearing because high water temperatures are of a particular concern in how they may restrict growth. The analysis focuses primarily on coho and steelhead species because 1) they occur widely in Pacific Northwest streams, penetrating well into the headwaters, and 2) necessary biological data were available for constructing the model and evaluating its performance. The growth model is then used in Section 6 to explore methods for quantifying growth response to identify biologically-based water quality criteria.

GROWTH MODEL

The basis for the mathematical formulation for daily weight gain in juvenile salmonids is its relationship to temperature and food consumption. This relationship has been graphically depicted for sockeye and chinook salmon by Brett and colleagues (summarized in Brett 1995 and Weatherly and Gill 1995). The relationship for sockeye salmon is shown in Figure 2.4 of this report.

The change in weight is calculated for defined scenarios of temperature, food availability, and species size characteristics on a daily basis, and summed through the growth period. Weight gain is determined by multiplying the daily specific growth rate by the body weight:

$$\Delta w_i = g_i \cdot w_i \tag{5.1}$$

where:

Δw_i = current day's growth, day i (gram $_{growth}$ /day)

g_i = specific growth rate, day i (gram $_{growth}$ /gram $_{body\ weigh\ t}$ · day)

w_i = body weigh t, day i (gram $_{body\ weigh\ t}$)

Next day's weight is computed by adding the daily growth to the current day's weight:

$$\begin{aligned} w_{i+1} &= w_i + \Delta w_i \\ &= \left(1 + g_i\right) \cdot w_i \end{aligned} \tag{5.2}$$

Weight at some time t can be computed as a function of an initial weight w_0 and daily growth rate coefficients:

$$w_t = w_0 \cdot \prod_{i=0}^{t-1} \left(1 + g_i\right) \tag{5.3}$$

The daily specific growth rate is a function of the water temperature to which the fish are exposed that day and daily food consumption:

$$g_i = f_g(T_i, C_i) \tag{5.4}$$

where:

T_i = temperatur e, day i (°C)

C_i = daily consumptio n day i (gram $_{food}$ /gram $_{body\ weigh\ t}$ · day)

In turn, the consumption is a function of the water temperature to which the fish are exposed that day, the weight of the fish, and the food supply (R_i):

$$C_i = f(T_i, W_i, R_i) \tag{5.5}$$

Looking at equations 5.1, 5.4 and 5.5, one can see that growth is being modeled as a function of water temperature, consumption, and size of the fish. The interaction of these terms is discussed in detail as the mathematical relationships are developed. The fact that consumption is both a dependent and an independent variable of temperature introduces some complexity into the growthcalculation that must be addressed.

The growth model is developed in two parts. First, the relationship between consumption, temperature and weight (equation 5.5) is estimated following the approach discussed by Stewart and Ibarra (1991), and used, for example, in the Wisconsin bioenergetics model (Hewett and Johnson 1992, Hanson 1997). Second, the relationships between specific growth rate, temperature and consumption (equation 5.4) are developed for several salmon species. We draw from previously published laboratory experiments to establish these relationships. These studies exposed juvenile salmonids for periods sufficiently long to determine the rate of growth (e.g., change in weight from one interval to the next) of the sample population at a given temperature and food consumption. Experimental data for coho salmon (*Oncorhynchus kisutch*) were obtained from Everson (1973) and for steelhead trout (*Oncorhynchus mykiss*) from Wurtsbaugh and Davis (1977). We assumed that these experimental data are representative of the species' response to temperature and consumption in the natural environment. (Data from these experiments is provided in Appendix A.)

Consumption. There is a maximum level of food consumption for each species that constitutes satiation or fullness. There is also a minimum consumption required to maintain standard metabolism. Consumption is generally expressed as a proportion of food mass to fish body mass consumed each day (g g_{bw} $^{-1}d^{-1}$), or alternatively, as a percent of body mass per day.   Within the range of consumption between satiation and minimum maintenance, the growth rate varies with consumption as illustrated for sockeye salmon in Figure 2.4.

The consumption rate at satiation, (C_s), and by corollary, at lesser amounts of food, varies with temperature and changes systematically with the fish's weight (Brett 1995). Salmonids respond physiologically to temperature by altering food consumption and the efficiency with which food is converted to growth (Weatherly and Gill 1995). C_s is at a maximum at optimal temperature and declines at colder and warmer temperatures (Brett 1971), yielding the characteristic shape of growth/temperature response (e.g., Figure 2.4). For example, coho consumption was 40% greater at 21°C than at 11°C in the laboratory experiments (Everson 1973), but dropped off sharply above 22°C (Brett et al. 1982). Consumption at satiation also declined with increasing fish weight (Brett 1995). The rate of consumption of Everson's (1973) experimental fish at 3.6 grams was 45% of that of fish weighing 2.0 grams at the same temperature.

There is a maximum consumption rate for each species, (C_{max}), a key benchmark established in laboratory studies at optimum temperature, low weight, and unlimited food supply. Generally, the

consumption at 1 gram of weight and optimum temperature is the highest consumption likely to be observed for the species (C_{max}), and serves as an important reference point for growth computations (Hanson 1997, Beauchamp et al. 1989, Hewett and Johnson 1987). The maximum consumption at satiation rations for other temperatures and weights (C_s) is less than C_{max}, and can be calculated as a proportion of maximum (p) according to equation 5.6.

$$p = \frac{C_s}{C_{max}} \hspace{4cm} (5.6)$$

where:

p = normalized consumptio n (dimensionl ess)
C_{max} = satiation ration at reference weight and optimum temperatu re

(gram of food gram of body weigh t^{-1} day $^{-1}$, g g $_{bw}$ $^{-1}$d $^{-1}$)

C_{max} varies by species (sockeye: Brett 1971; chinook: Brett et al. 1982; coho: Everson 1973, steelhead: Wurtsbaugh and Davis 1977).

To appropriately estimate growth rate (g), it is necessary to establish the consumption at each weight (C_w) and temperature (C_T). We follow the approach used in the Wisconsin bioenergetics model (Hanson 1997) where consumption equations are of the basic form:

$$C_T = C_{max} \cdot p \cdot f(T) \hspace{3.5cm} (5.7)$$
$$C_w = CA \cdot W^{CB} \hspace{3.8cm} (5.8)$$

We develop equations for each independently, and then we will bring the two effects together by referencing consumption relative to C_{max} and calculating the reduction from that benchmark due to each of the two factors. Hanson (1997) notes that developing a set of parameters for these relationships may be accomplished by deriving them from published reports, estimating them from specifically designed field or laboratory experiments, or borrowing parameters from closely related species.

The allometric relationship between consumption and weight (eq. 5.8) generally has the form of a negative power function (Ricker 1975) whose terms are the intercept, CA, and the coefficient, CB. The intercept value of CA is the consumption of a 1-gram fish and has units of grams per gram of body mass per day (g g^{-1} $_{bw}$ d^{-1}). These terms must be estimated from *ad libit*um feeding experiments conducted at the optimum temperature. There are relatively few such laboratory studies reporting values for salmonid species of interest in this report, although several other salmon species have been extensively studied. The laboratory studies of juvenile growth for coho (Everson 1973) and steelhead (Wurtsbaugh and Davis 1977) were not designed specifically to determine the allometric relationship of consumption to weight. However, in both studies, a series of one-month long feeding trials were conducted on individuals drawn from a population of fish that was maintained in a natural stream between experiments over a year-long period. Thus, the fish grew at natural rates between experiments and represented a range of weights from 1 to 4 grams, which is within the range of size expected for salmonids in natural streams in the first year.

We examined the laboratory data of Everson (1973) and Wurtsbaugh and Davis (1977) to estimate *CA* and *CB* for coho and steelhead looking only at trials where: 1) fish weights were reasonably near 1 gram; 2) rations were considered to be at satiation; and 3) temperatures were optimal, as suggested by high growth rates.   Data matching these criteria were limited and some of our selected data values only marginally fit these criteria. Nevertheless, a relationship between consumption and weight at satiation ration followed an allometric relationship with *CB* equal to –0.254 for coho (R^2=0.19) and –0.311 for steelhead (R^2=0.41), albeit the R^2 is relatively low. (The poor fit in the relationship could be because some of the experimental data points did not match the criteria as closely as desirable). Stewart and Ibarra (1991) and the Wisconsin user's manual recommend values for *CB* of   –0.275 for coho, based on the work of Beauchamp et al. (1989), and –0.30 for steelhead based on Rand et al. (1993). Although these studies were conducted with larger fish, the results are very similar. Calibrating predictions of weight gain of populations in natural streams, as described later, we found that selecting values for *CB* of –0.275 for both coho and steelhead, as suggested by other researchers, produced satisfactory modeling results. Setting *CB* at –0.3 for steelhead slightly but consistently underestimated growth, suggesting that consumption was not declining at quite this high of a rate in natural populations.

Maximum consumption observed in a few of the laboratory trials suggested values for the intercept, *CA,* of 0.11 and 0.16 g g^{-1}d^{-1} for coho and steelhead, respectively. The allometric relationship developed from all trial data suggested *CA* equaled 0.083 and 0.16 for coho and steelhead, respectively. Calibrating the model predictions in natural streams suggested that *CA* was closer to 0.10 for coho (10% body weight per day). The User's Manual for the Wisconsin model (Hanson 1997) recommends values of *CA* between 0.15 and 0.35, which are higher than those we derived using the laboratory data. We selected values for *CA* of 0.10 and 0.16 for coho and steelhead respectively. These are also the values of C_{max} for each species.

Bartell et al. (1986), Beauchamp et al. (1989) and Hanson et al. (1997) have noted that the allometric parameters for the dependence of consumption on body mass (CA and CB) are among the parameters that have the greatest influence on bioenergetics predictions. In subsequent model predictions, described later in this section, we found this to be true. Within the narrow range of values separating adult from juvenile studies, there was relatively little effect of CB on weight predictions, and we selected the widely cited values. However, the laboratory studies of juvenile fish did not support CA values greater than we selected. Growth predictions are sensitive to this parameter.

Food consumption in relation to weight as calculated with the allometric parameters is shown in Figure 5.1. There are significant differences in consumption levels between these two species.

The proportion of consumption at each weight (C_w) relative to C_{max} , is defined by the slope of the allometric equation (CB) and can be calculated as:

$$p_w = W^{CB} \tag{5.8}$$

Consumption at Satiation
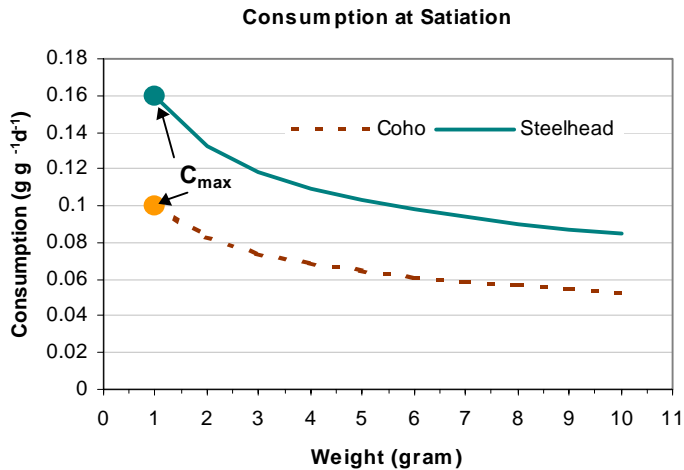
Figure 5.1 Consumption at satiation in relation to weight as modeled by selected parameters for CA and CB described in text.

To determine the effects of temperature on food consumption, a number of authors have used the Thornton and Lessem algorithm (1978) (Beauchamp et al. 1989, Stewart and Ibarra 1991, Hanson et al. 1997). The algorithm estimates the maximum consumption at each temperature, expressed as the proportion of the maximum consumption at the optimal temperature (p_t). The algorithm fits two sigmoid curves to specified parameters, which include the optimal temperature and the upper and lower temperatures where consumption nears zero. Thus, the general shape of the relationship between temperature and consumption is assumed and key temperatures must be known or estimated to fit the proper shape of the curve for each species. The user's manual for the Wisconsin bioenergetics model (Hanson 1997) suggests values for the key parameters of the Thornton and Lessem algorithm drawn from Stewart and Ibarra (1991) and Rand et al. (1993). We began with those parameters, but then calibrated them to fit the experimental data for coho (Everson 1973) and steelhead (Wurtsbaugh and Davis 1977) (Figure 5.2). Small adjustments to the suggested parameters appeared to slightly improve the fit compared to the laboratory observations, although our final curve for coho is very similar to that presented by Stewart and Ibarra (1991). The parameter values we derived are provided in Table 5.1 and the fitted relationships are shown in Figure 5.2. The Thornton and Lessem equation is awkward to use in an EXCEL® spreadsheet format. We fit a polynomial regression to the
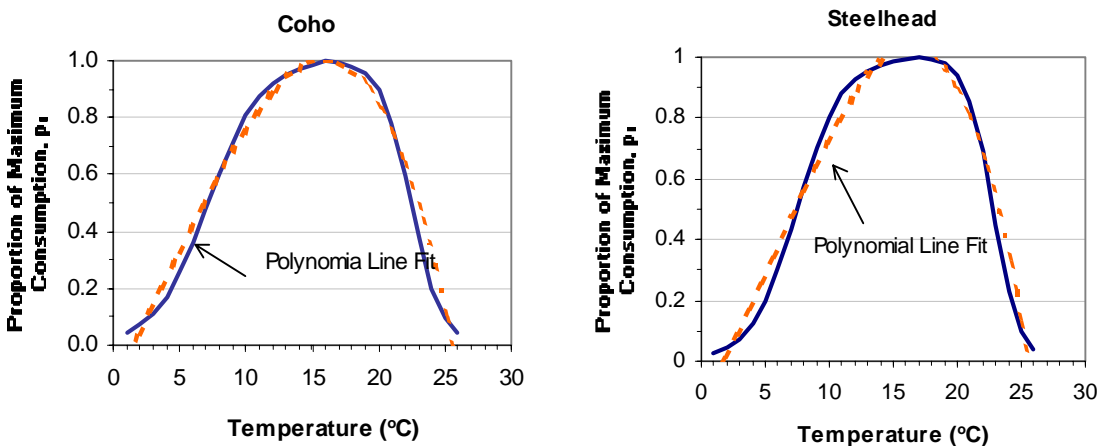
Figure 5.2 Maximum consumption in relation to temperature computed with the Thornton and Lessem algorithm (1978).

Thornton and Lessem algorithm results to provide an equation for calculating p_t at each temperature (Figure 5.2).

$$p_t = \lambda_0 + \lambda_1 \cdot T + \lambda_2 \cdot T^2 + \lambda_3 \cdot T^3 \qquad (5.9)$$

The fit was quite close (Figure 5.2), especially in the range of temperatures likely to be observed during the summer, when the relationship was used for growth modeling. The polynomial terms describing the equations are provided in Table 5.1.

We now have mathematical expressions that account for the influence of weight (p_w), and temperature (p_t) on consumption at satiation where each is expressed in proportion to C_{max}. The maximum consumption rate, p_s, at each combination of weight and temperature expressed relative to C_{max}, (a constant value for each species) is calculated according to equation 5.10:

$$p_s = p_w \cdot p_t \qquad (5.10)$$

and ranges between 0 and 1. The actual amount of food consumed (C_s), expressed in grams of prey mass in relation to grams of body mass per day, (g $g_{bw}^{-1}d^{-1}$), is equal to:

$$C_s = p_s \cdot C_{max} \qquad (5.11)$$

Table 5.1 Estimated physiological parameter values used in equations calculating consumption for coho and steelhead.

Relationship	Parameter	Coho	Steelhead
Allometric	CA	0.10	0.16
	CB	-0.275	-0.275
Thornton and Lessem function for temperature dependence (1978)[φ]	CQ	7	5
	CK1	0.4	0.2
	CTO	15.6	14.0
	CTM	18	17.9
	CTL	24	24
	CK4	0.2	0.1
Regression fit to Thornton and Lessem algorithm generated by above parameters	λ_0	-0.1419	-0.1229
	λ_1	0.0544	0.0607
	λ_2	0.0061	0.0055
	λ_3	-0.0003	-0.0003

φ Terminology as used by Hanson et al. (1995), see Appendix B

The value of C_s computed over a range of temperature and weight is illustrated for coho in Figure 5.3. As expected from the formulation, the highest levels of consumption occur near optimal temperatures and at lowest weight. The deepest shades on the contour map represent starvation. Falling below the minimum maintenance consumption (approximately 0.03 g $g_{bw}^{-1}d^{-1}$ for coho juding from the laboratory trials) for extensive periods of time should result in no growth, or even
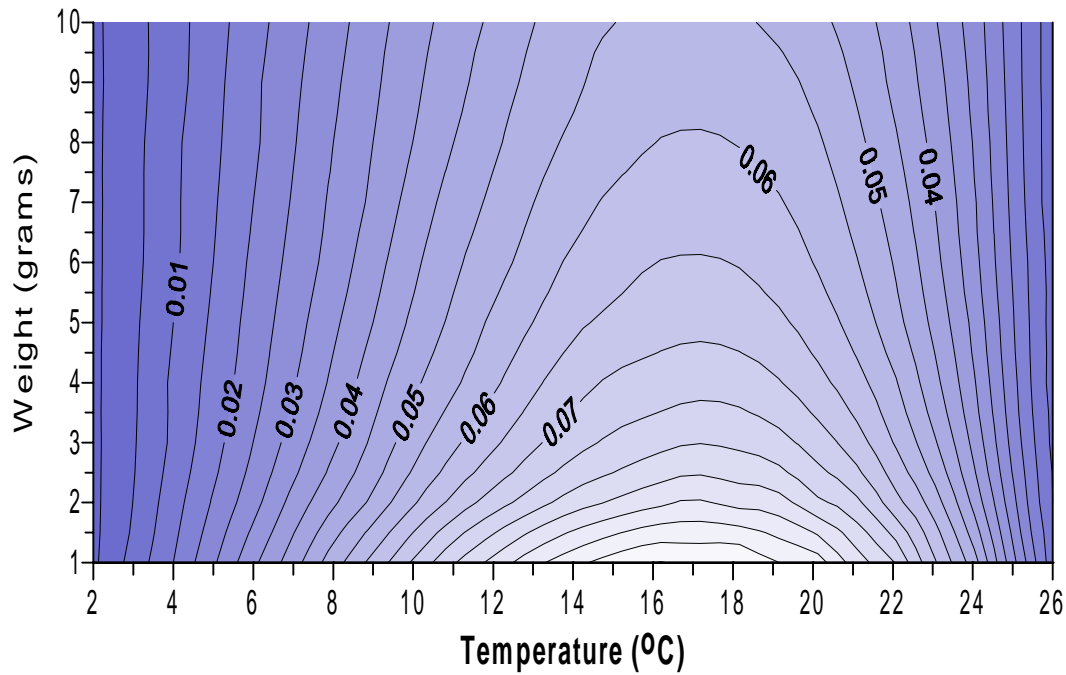
Figure 5.3 Illustration of the relationship of the maximum food consumption at satiation with temperature and coho weight. Contours are the daily consumption rate, C_s, expressed in prey mass per fish body mass per day (g g_{bw}^{-1} d^{-1}). This figure illustrates the maximum potential consumption where food supply is not limited and fish can eat to satiation.

weight loss. The maximum potential consumption is relatively moderate for most of the temperatures and weights that juveniles are likely to encounter in the freshwater growth phase of their life history due to the interaction of the temperature and weight. However, consumption is severely limited only at high and low temperatures at all weights. Consumption approaches the maximum potential (0.10 g $g_{bw}^{-1}$$d^{-1}$ for coho) only for a relatively few combinations of weight and temperature, and therefore for probably relatively little time during the life of a fish. Maximum consumption at all weights is achieved at optimal temperature (T_{opt}), where growth rate is greatest for each level of consumption (approximately 17°C for coho).

The food consumption illustrated in Figure 5.3 represents the upper maximum controlled by the physiology of the fish at each combination of weight and temperature. We refer to this as the maximum potential consumption. In the natural stream environment, as well as in the laboratory, the amount of food available to consume may be less than the maximum that the fish can potentially consume and the fish may experience some degree of hunger. We distinguish consumption, which we use to refer to the physiological response controlling food intake, from ration, which we use to refer to the food supply. Ration, which we express as % satiation, is 100% satiation at the maximum consumption (C_s) at each weight and temperature.

Consumption in natural streams depends on food supply, competition for food, and the size of the fish based on the past regime of water temperature. The Wisconsin model accounts for ecological constraints on the maximum consumption rate (C_s) by imposing an additional proportionality (P-value) that can also range from 0 to 1 at rations less than the physiological maximum (p_s). Thus, when modeling consumption at less than satiation for each temperature and weight, C_i may be calculated as

$$C_i = P_{value} \cdot p_s \cdot C_{max} \tag{5.12}$$

It's important to note that, on any given day, field consumption may be limited by either the physiological limits imposed by temperature or weight or by the food supply. Consumption in streams must be determined from in situ observations of feeding, or inferred from weight gain.

Specific Growth Rate. The specific growth rate (g) is the daily growth rate in relation to temperature and consumption, expressed in proportion of body weight per day. Specific growth rate functions ("growth curves") are defined with data from the laboratory studies. This relationship was established for sockeye by Brett (1971), and for chinook by Brett et al. (1982). Both Brett (1995 pp. 28-29) and Weatherly and Gill (1995) recently reaffirmed this relationship, some form of which appears to apply to all species of salmonids.

Growth rate curves for coho and steelhead have not been previously published, although the requisite laboratory studies were available to develop them. Experiments on growth of juvenile coho reported by Everson (1973) were conducted at temperatures between 11.1° and 22.5°C and rations between satiation and starvation. Experiments on steelhead growth reported by Wurtsbaugh and Davis (1977) were conducted at temperatures between 6.9° and 22.5°C and the full range of rations. Growth rate of the population during the experimental period, represented by the average population weights, was calculated as:

$$g = \frac{(w_e - w_0)}{(0.5 \cdot (w_e + w_0) \cdot t)} \tag{5.13}$$

where w_e and w_0 are the weights at the end and beginning of the experiment, respectively, and t is the number of days (generally 25) in each trial. Dry weights were used to calculate the growth rates because the moisture content of fish is similar to that of their prey in natural streams (Winberg, 1971) and thus the dry weight relationships would appropriately match growth curves of fish living in natural environments to their natural food supply.

We used standard linear regression to build mathematical expressions for the growth rate g (g g_{bw}^{-1}d^{-1}) from food consumption, C, (g g_{bw}^{-1}d^{-1}), temperature, T, ($^{\circ}$C), and initial weight, w_o, for coho and steelhead. To reduce multicollinearity problems during the model building process, the independent variables were centered by subtracting each sample value from the population mean. The models were built with the Reg procedure in SAS® Version 6.12 (SAS Institute Inc., 1989). The general form of the model is:

$$g = \chi_0 + \chi_1 \cdot T + \chi_2 \cdot T^2 + \chi_3 \cdot C + \chi_4 \cdot C^2 + \chi_5 \cdot C \cdot T + \chi_6 \cdot W \tag{5.14}$$

The relationship for coho includes squared and linear terms for temperature and consumption and has high R^2 (0.93) and low root mean square error (0.0023). Similarly, the relationship for steelhead includes squared and linear terms for temperature and consumption as well as a linear term accounting for weight of the fish. This relationship also has high R^2 (0.97), and low root mean square error (0.0021). Statistically determined coefficients for these relationships are provided in Table 5.3. It is essential to note that the growth rate equation (eq 5.14) will compute erroneous growth rates if the consumption term is not appropriately constrained for each weight and temperature as described earlier. Thus, the use of this model always requires a two step process where consumption level is estimated and then growth rate is selected.

The growth curves for coho and steelhead resulting from the full growth model formulation calculated at a weight of 1 gram are shown in Figure 5.4. They show the familiar form of sockeye and chinook that have been previously published by Brett and others (Brett 1969, Brett et al. 1982, Weatherly and Gill 1995), although the curves in Figure 5.4 are derived mathematically. Brett et al. (1982) discussed how optimum temperature declines with decreasing ration, thus skewing the growth rate curves towards cooler temperature with less food. The mathematical formulation of equation 5.14 also produces skew in optimal temperature with declining consumption. The cross-product (χ_5) between temperature and consumption determines this shape.

The growth curves for each species are similar, but differ in details such as optimal temperatures, growth rate, and consumption levels at which growth rates are achieved. One can see that the growth rate varies widely with the temperatures and food availability that salmon are likely to encounter in the natural environment of Pacific Northwest streams and rivers, suggesting that fish size should be strongly influenced by these two parameters.

In natural streams, temperature varies over the course of the day and some temperature value must be chosen to represent the daily temperature. Laboratory tests have noted that the daily average temperature approximates the constant exposure test conditions. Experiments where temperatures were fluctuated to mimic daily temperature regimes have found either no effect from variable temperature (Thomas et al. 1986, Dickerson and Vinyard 1999) or an improvement in growth (Spigarelli et al. 1982, Weatherly and Gill 1995). Water temperature fluctuated with natural stream temperatures in the experiments of Everson (1973) and Wurtsbaugh and Davis (1977). We select the daily mean temperature as appropriate to represent the temperature related to daily growth rate.

Table 5.2 Coefficients for specific growth rate relationship to temperature (T) and consumption (*C*). Coho data are from Everson (1973), Steelhead data are from Wurtsbaugh and Davis (1977).

Variable	Coho	Steelhead
χ_0	-0.010649	0.00631
χ_1	0.00096624	-0.0007403
χ_2	-0.00008312	-0.00003909
χ_3	0.450620	0.4302104
χ_4	-3.02056	-1.43765
χ_5	0.01677	0.00735
χ_6	NA	-0.00517
χ_7	NA	NA
Regression R-square	0.93	0.97

Figure 5.4. Specific growth rate curves for coho salmon, steelhead trout at 1 gram weight. Coho growth curves based on Everson (1973), steelhead curves based on Wurtsbaugh and Davis (1977). Each line is the ration is expressed in % satiation, p_s.

Growth Model

Substituting equations 5.13 and 5.11 back into equation 5.3 gives a model for computing weight as a function of initial weight and the time series of daily water temperatures and food supply to which a fish is exposed:

$$w_t = w_0 \cdot \prod_{i=0}^{t-1} (1 + \chi_0 + \chi_1 \cdot T_i + \chi_2 \cdot T_i^2 + \chi_3 \cdot C + \chi_4 \cdot C_i^2 + \chi_5 \cdot C_i \cdot T_i + \chi_6 \cdot w_{i-1})$$
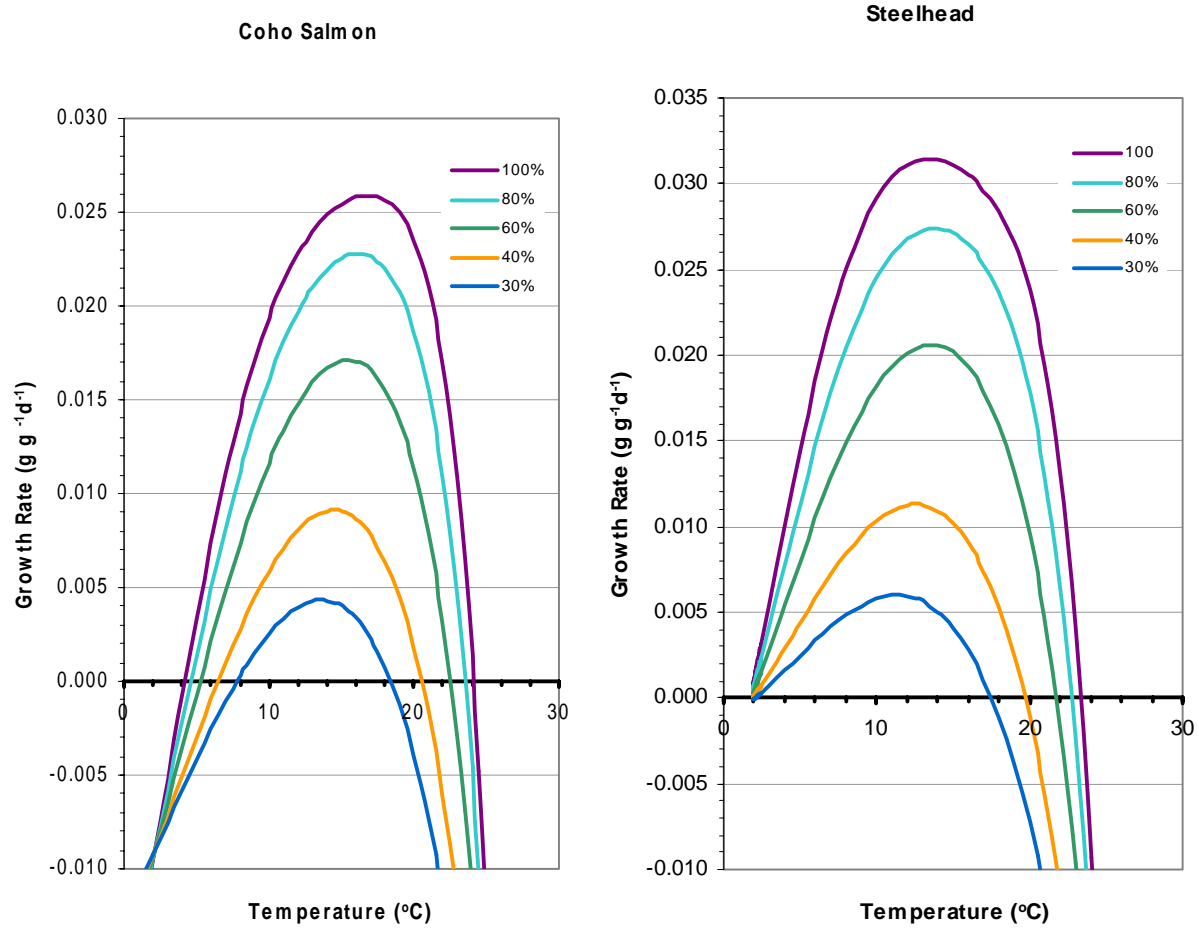
(5.15)

The model simulates the change in mass of an individual fish or a cohort of specified size. We define a cohort as a group of similar aged fish of the same species experiencing identical environmental conditions (Hanson et al. 1997). Cohort weights may be represented by the average population weight. It is important to recognize that the estimates of weight gain do not consider population interaction effects (Walters and Post 1993). Thus, they do not account for changes in population density that can also affect the average weight and biomass of populations. Measuring growth as the difference in a cohort's weight between two dates is subject to biases from any size-dependent movement and mortality (Railsback and Rose 1999). Our estimates only address temperature and food effects with the assumption that changes in number or weight are unbiased by size.

The growth formulations (equations 5.7-5.12) were easily programmed into an EXCEL® spreadsheet to perform the calculations of growth over time. To estimate weight gain of populations in natural streams, three parameters must be determined: initial weight (w_0), temperature (T) and the food consumption (C_i) that must reflect the food supply.

APPLICATION OF THE METHOD FOR PREDICTING GROWTH IN NATURAL STREAMS

In the remainder of this section, we apply the growth model to fish populations observed in natural streams to demonstrate model behavior and corroborate its predictions. We show a number of simulations where the three input parameters were known with varying degrees of certainty. No new experiments to determine food consumption or to validate the growth model's ability to accurately predict weight gain were conducted. Instead, model performance is examined using data from a number of previously reported studies.

The parameters required by the model are rather modest. Daily mean temperature is known with certainty at any site where temperature is continuously recorded, and we restrict growth simulations to sites where this condition was met. Initial weight and food consumption must be determined from fish population characteristics observed in streams or from known food consumption amounts. Of these two variables, the consumption characteristics of juvenile salmonids in natural streams are by far the least well quantified (Filbert and Hawkins 1995, Railsback and Rose 1999) and difficult to obtain (e.g., Martin 1985). For this reason, we begin simulations with data from a field experiment where food was well known and the assumptions about the 3 input parameters were limited.

Mason's Feeding Experiment. Mason (1976) reported an experiment where juvenile coho in a natural stream on Vancouver Island, British Columbia were fed to satiation for a 2-month summer period. Data from this experiment were ideal for comparing observed with predicted growth since environmental limitations on food supply were reduced, if not

eliminated, for most of the individuals in the population. Thus errors associated with estimating consumption were minimized and the other two input parameters were well known.

Mason (1976) reported that temperatures were between 12° and 13^oC during the study. We used a constant 12.5^oC temperature for the simulation. Mason (1976) provided information on individual fish size within the population. We modeled three cases where the initial weight was set to the weight of the largest, average, and smallest fish at the start of the experiment. (Figure 5.5). Fish were feed daily at what Mason calculated was a satiation ration for the population. For this simulation, growth was predicted at the maximum potential consumption determined by the weight and temperature (eq. 5.11),
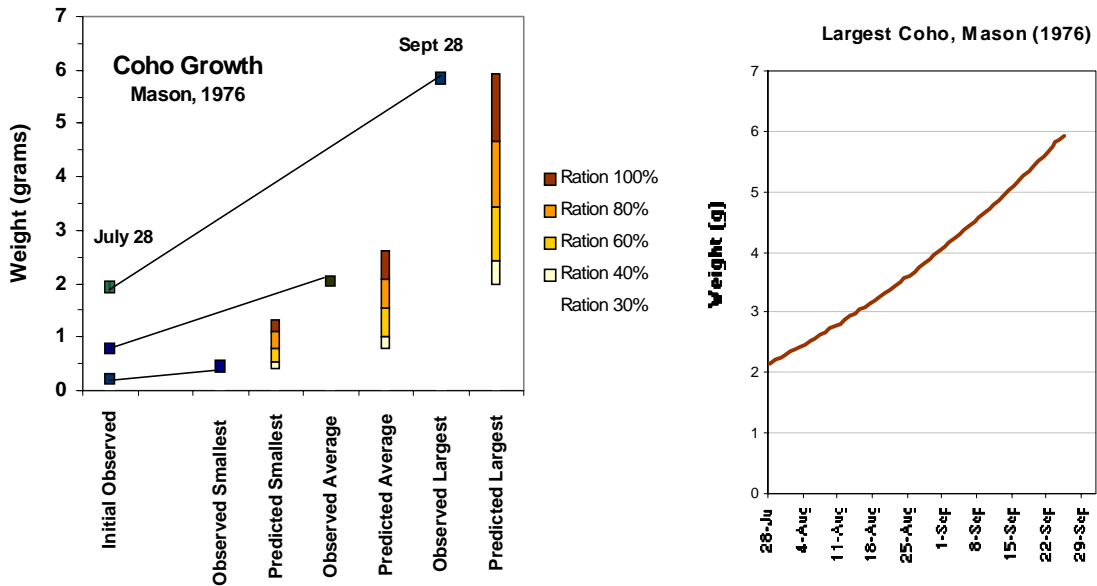
Figure 5.5. Observed and predicted growth of coho in an experimental feeding study in a natural channel in British Columbia (Mason 1976). The growth of the smallest, average and largest fish at the start of the feeding trial were modeled for the full range of satiation (shown in bars). Weight of the smallest, average and largest fish at the end of the experiment are shown relative to growth simulations. The predicted daily weight of the largest size fish is shown at right.

assuming that the available rations supplied 100% of the potential consumption and there was no food limitation. We also modeled the full range of rations (p_s) expressed as percentage of satiation of shown in increments of 80, 60, 40, and 30% in Figure 5.5.

After simulating growth for the two-month period, the estimated weights of the largest and average fish, computed at high food ration, were very similar to their observed weights (Figure 5.5). The largest fish in the population increased its weight by 286% (2 g to 5.9 g) during this period. The predicted weight for that fish, assuming 100% satiation, was within 2% of its observed weight. These results appear to corroborate growth predictions and confirm Mason's conclusion that some of the fish obtained satiation rations. Progressively smaller individuals within the population apparently ate at lesser rations than the largest individual. (It should be noted that it is not known whether the fish that held these ranks at the end of the study were the same individuals as those at the start.) The weight of the average size fish was consistent with growth predictions at 80% ration. The smallest fish did not fare nearly as well, achieving little weight gain consistent with

subsistence at minimum maintenance rations. Mason (1976) observed that the smaller fish tended to be those dying or migrating downstream, emphasizing the importance of larger size providing survival benefit through more effective feeding strategies (Puckett and Dill 1985, Nielsen 1994).

Overall, Mason (1976) observed many large fish remaining after the feeding experiment; moreover, the average population weight increased significantly. This has been taken as evidence that coho growth in streams tends to be limited by food supply. Other field experiments have showed improved growth resulting from activities that increased light (and temperature) in streams, presumably improving the food resources (Hawkins et al. 1983, Martin 1985, Bisson et al. 1988).

Fish Populations Living in Natural Stream Conditions. As they grow during the summer, juvenile fish living in streams in the Pacific Northwest experience temperatures that are relatively low in spring after emergence from the gravel, warm during the summer, and cool again in the fall after mid-September. Food resources may be limited and the manner in which natural populations regulate their numbers to match individual and population growth needs with available food supply is complex and largely unknown (Walters and Post 1993).

In the next set of simulations we estimate the average growth of a cohort of age 0 coho and steelhead in natural streams having natural and unknown food supplies. Fish population data were available from sites representing a number of treatments and controls in experiments previously reported in the literature (Table 5.3). Physical habitat characteristics varied among sites. Like many streams within the region, the stream segments where fish were sampled generally contained low amounts of large woody debris (LWD) and varying amounts of shade. The examples include sites with water temperature spanning very warm to cool (but not cold, e.g., less than 12°C). Porter Creek was the site of a habitat improvement experiment where LWD was added to increase pool habitat (Cederholm et al. 1997). Several sites were severely impacted by the Mount St. Helens eruption in 1980, but have since experienced recovery of vegetation (Bisson et. al 1988). A dam-break flood scoured portions of Huckleberry Creek and its floodplain in 1990 after several years of population monitoring during a feeding experiment (Fransen et al. 1993). Bear Creek is a tributary to the Bogachiel River, above a barrier falls, that flowed through undisturbed old growth forest (Martin 1985).

Although the experimental objectives and study designs differed, fish populations in these stream segments were sampled routinely in a similar way providing comparable data sets to draw from. Populations were sampled by electrofishing using the three-pass removal method (Young and Robson 1978, Bisson et al. 1988). The lengths of all captured fish were measured, while weights were sub-sampled. We selected a number of cases from the available data where fish populations were sampled at the beginning and end of the summer. A few sites were sampled mid-season. Early season sampling was conducted between March and July while end of season sampling was conducted between September and November. Coho occurred at all six sites and steelhead were found at four. The time periods encompassed by the temperature and fish population data did not always overlap at all sites, and, in a few cases, daily temperatures were not available.

Table 5.3. Characteristics of fish populations as determined by field surveys.

		Data Sources				Temperature Characteristics			Fish Population Surveys					Model Predictions	
Species	Site	Experiment	Reference	Year	Regime	Season median (°C)	Annual maximum (°C)	Dates sampled	Days (t)	Initial weight (g)	End weight (g)	Increase in weight (%)	Ave. Daily Growth Rate (g g⁻¹d⁻¹)	Estimated weight (g)	Difference from observed (%)
Coho	Huckleberry	Artificial feeding	Fransen et al. 1993	1987	Cool	12.5	15.5	7/13-10/1	80	3.0	3.6	16	.0064	5.2	+44
				1988	Cool	11.6	15.0	5/12-10/24	163	0.6	4.2	600	.0114	3.8	-10
				1989	Cool	12.0	14.5	7/16-7/28	101	2.0	4.1	105	.0063	3.8	-7
		Dam-break flood		1991	Warm	15.5	18.5	5/15-10/9	147	0.9	3.2	240	.0082	3.1	-3
		altered valley		1991	Warm	15.5	18.5	6/20-10/9	113	4.1	6.3	54	.0082	5.8	-8
				1998	Warm	14.0	18.0	6/23-9/15	84	2.7	4.0	57	.0072	5.0	+16
	Porter	Placement of large woody debris	Cederholm et al. 1997	1988	Warm	13.5	18.0	6/28-9/28	92	3.0	6.1	103	.0069	5.7	-7
				1989	Warm	14.0	17.0	6/19-9/18	91	3.4	6.0	76	.0069	6.4	+7
				1990	Warm	14.6	18.6	6/18-8/27	70	3.7	6.5	76	.0085	6.6	+2
				1991	Warm	12.8	17.3	6/4-9/30	118	2.5	5.4	116	.0080	6.4	+19
	Harrington	Volcanic eruption	Bisson et al. 1988	1984φ	Very warm	16.5δ	29.0	6/24-10/9	108	1.3	6.3	380	NA	NA	NA
		Vegetation regrowth		1990	Very warm	13.3	20.5	6/22-9/20	88	3.3	6.0	82	.0066	5.8	-2
	Hoffstadt	Volcanic eruption	Bisson et al. 1988	1984φ	Very warm	16.7δ	29.5	6/26-10/3	100	2.4	5.6	133	NA	NA	NA
		Vegetation regrowth		1990	Very warm	15.0	26.0	6/21-9/20	88	3.6	6.1	69	.0054	5.9	-5
	Big	Salmon carcass enhancement	Bilby et al. 1996, 1998	1994	Cool	12.9	16.1	7/13-9/8	57	4.6	6.0	30	.0093	6.9	+15
	Salmon	Salmon carcass enhancement	Bilby et al. 1996, 1998	1994	Cool	12.6	16.2	7/20-9/8	50	3.6	5.5	53	.0069	5	-9
Steelhead	Porter	Placement of large woody debris	Cederholm et al. 1997	1988	Warm	13.5	18.0	6/28-9/28	92	0.8	3.5	338	.0173	3.9	+11
				1989	Warm	14.0	17.0	6/19-9/18	91	0.6	3.3	450	.0210	3.6	+9
				1990	Warm	14.6	18.6	6/18-8/27	70	0.6	3.2	433	.0235	3.1	-3
				1991	Warm	12.8	17.3	6/4-9/30	118	0.4	3.4	750	.0191	3.8	+12
	Harrington	Volcanic eruption	Bisson et al. 1988	1984	Very warm	16.5δ	29.0	6/24-10/3	102	0.7	2.9		.0228		NA
		Vegetation regrowth		1990	Very warm	13.3	20.5	6/22-9/14	84	0.5	3.7	640	.0076	4.2	+14
	Hoffstadt	Vegetation regrowth	Bisson et al. 1988	1990	Very warm	15.0	26.0	6/21-9/20	91	2.1	5.5	162	.0180	4.2	-24
	Salmon	Salmon carcass enhancement	Bilby et al. 1996, 1998	1994	Cool	12.6	16.2	7/20-9/8	50	1.4	3.2	129		3.4	+6
Cutthroat	Bear	Control for riparian buffer experiment	Martin, 1985	1978	Cool	12.2θ	14δ	7/6-11/11	128	2.2	3.4	54		NA	NA

φContinuously recorded temperature data not available; population weights not simulated with model.

δEstimated from annual maximum temperature by relationship found in Section 3.   θThrough September

Consumption Rates in Natural Streams. Ideally, consumption rates in natural populations are determined by observation of food intake or availability (e.g., Martin 1985, Filbert and Hawkins, 1995). Such data are rare. In lieu of direct measurement, consumption can be approximated by examining the pattern of growth over the growing period (Beauchamp et al. 1989, Hanson et al. 1997). Consumption may be inferred by estimating how much food must have been consumed, given the prevailing temperature regime, to have maintained growth at the observed rate (Hanson et al. 1997). To estimate consumption indirectly, populations should be sampled several times over the summer duration, because consumption rates should decline through time as fish grow, based on the expected allometric effect. Such data are also rare.

A naturally-spawned coho population was sampled multiple times during the summer of 1991 at Huckleberry Creek. We selected 1991 data because fish were sampled a number of times over a long period from March to October, and we focused on the lower of two sites on the same stream because the population was naturally spawned fish with no augmentation. Coastal cutthroat trout were sampled multiple times at Bear Creek in 1978 (Martin 1985). We assume that the cutthroat trout sampled at this site are representative of steelhead trout, for the purposes of establishing feeding patterns only. We use these two sites to evaluate food consumption patterns and to establish the relationships used to estimate ration for growth simulation of the other populations in our study.

The consumption of food by cutthroat trout at Bear Creek was measured using stomach evacuation techniques (Martin 1985). In situ measurements of food consumption were computed by the modified Bajkov method (1935).

At Huckleberry Creek, neither food consumption nor food supply was measured. Apparent food consumption by coho between each sampling was derived using the growth rate curve. First, growth rate was computed for the full range of consumption from maintenance to satiation at the mean temperature and population weight for each interval. Consumption was then inferred by selecting the value from the computed

Weight, Growth, and Food Consumption for Age 0 Coho

Weight, Growth and Food Consumption for Age 0 Cutthroat

Figure 5.6. Mean weight and estimated consumption and growth rates for age 0 coho at Huckleberry Cr. , lower site, and age 0 cutthroat trout at Bear Creek.

range that corresponded most closely to the observed growth rate. Important assumptions accompany this analysis; only food and temperature influence the observed data, our growth equations capture these factors correctly, there are no effects from population dynamics and there are no sampling errors. Therefore, this approach is only an approximation and it is preferable to establish consumption estimates by direct measurement of food supply or intake, such as was done for cutthroat.

Average population weight and estimated (coho) and measured (cutthroat) growth and consumption rates for the two populations are shown in Figure 5.6. Growth rate was calculated using equation 5.13 assuming a linear growth rate between each sampling interval. Weight gain slowed late in the season and growth rate and consumption declined from initially higher rates for both species (Figure 5.6). This pattern is consistent with what would be expected for an allometric consumption relationship, where consumption declines with increasing weight. However, it can also suggest diminishing food supply that may accompany increasing size in an environment where food supply is fixed.

Consumption for Age 0 Coho

Consumption for Age 0 Cutthroat
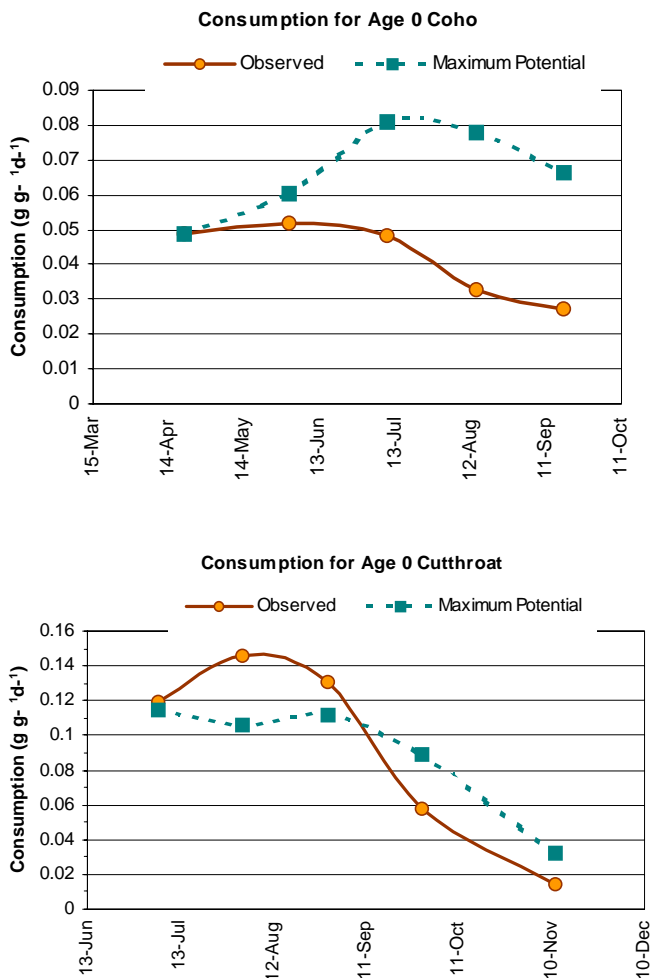
Figure 5.7. Maximum potential consumption based on temperature and weight for the period in relation to observed consumption.

The pattern of consumption observed at the sites is of particular interest with regard to its implications, vis-à-vis the physiological limits of temperature and weight versus food supply. Maximum potential consumption (C_s) was computed using the mean temperature and weight for each interval. It is plotted with apparent consumption in Figure 5.7. The apparent consumption was greatest during the early half of the summer and declined through the later half for both species. (Note that the time intervals differ for the two sites).

An important implication of the observations in Figure 5.7 is that the observed consumption of both species was remarkably similar to each species's physiologically-determined potential consumption. This was true for coho from soon after emergence from the gravels until the end of June or early July and into September for cutthroat trout. Cutthroat trout actually showed greater consumption than estimated during this period, but values were probably within the error range due to estimates of

average temperature and because the maximum potential is based on steelhead specific growth curves. During these periods, the data suggest that the physiological factors were controlling consumption and the average size fish was eating at satiation. That is, even if there were more food, the individual fish represented by the average population weight would not eat it. Later in summer, the apparent consumption was less than maximum potential for both species. The difference between the apparent and maximum potential consumption estimates suggests the degree of food limitation in the streams. The closer the observed lines are to potential, the closer available ration is to satiation.

It is interesting to note that it is during the early summmper period that the number of individuals in a population following emergence is determined, suggesting that population density adjusts to match the food supply (Chapman 1966). Carl (1983) observed that the number of coho in a population adjusted in response to population density, but that their daily growth rates were not dependent on density during the period when population adjustment after emergence occurred (May to July). Similarly, rainbow trout growth rate was not correlated with their population density. Carl's (1983) observations of population dynamics and growth are consistent with results from our analysis of consumption.

For coho, the difference between apparent and potential consumption was much larger than for cutthroat in the later half of the summer. Apparent consumption declined to near starvation ration by the end of the summer, while estimated potential consumption remained relatively high because both temperature and weight were moderate. Potential consumption actually increased during part of this period reflecting favorable (closer to optimum) temperatures. Declining food supply for coho during this period could be explained by increasing size of individuals in the population and limited food supply. Although the effects of size on consumption are not great, the absolute volume consumed by each fish must increase since the consumption is expressed as a proportion of body weight each day (Hanson 1997). The same food supplies that may have been adequate for the population at small size may represent a much smaller proportion as the fish grow. The decline could also reflect a change in the food supply. Studies generally show fairly steady or increased food availability during the summer, depending on habitat conditions (e.g., under forested vs. open riparian canopies, Hetrick et al. 1998).

Observed and maximum potential consumption were similar during the entire period for cutthroat trout (Figure 5.7). During the time period coincident with coho, cutthroat were apparently consuming at or near maximum potential (satiation) and food supply did not appear to be a major factor limiting the food consumption by this species. The decline in potential consumption in the fall can largely be attributed to lower temperature. One reason that consumption is nearer the maximum for much of the summer period may be that the cutthroat fry emerge later and are smaller than the coho in late summer. Thus, satisfying juvenile food demands is less challenging.

The apparent consumption patterns observed in populations inhabiting natural streams have important implications for the growth simulations. When consumption can be assumed to equal maximum potential (eq 5.11) there is no need to calibrate the consumption estimates to account for the ecological constraints on food supply (eq 5.12). This appears to be a reasonable assumption for age 0 cutthroat throughout the summer. We assume that age 0 steelhead have similar feeding patterns as cutthroat, and therefore, we assume that we can use the maximum potential consumption to represent age 0 steelhead. This also appears to be a reasonable assumption for coho until the end of June.

A)

Maximum Potential Consumption, C$_s$

B)

Relative Consumption, p$_s$
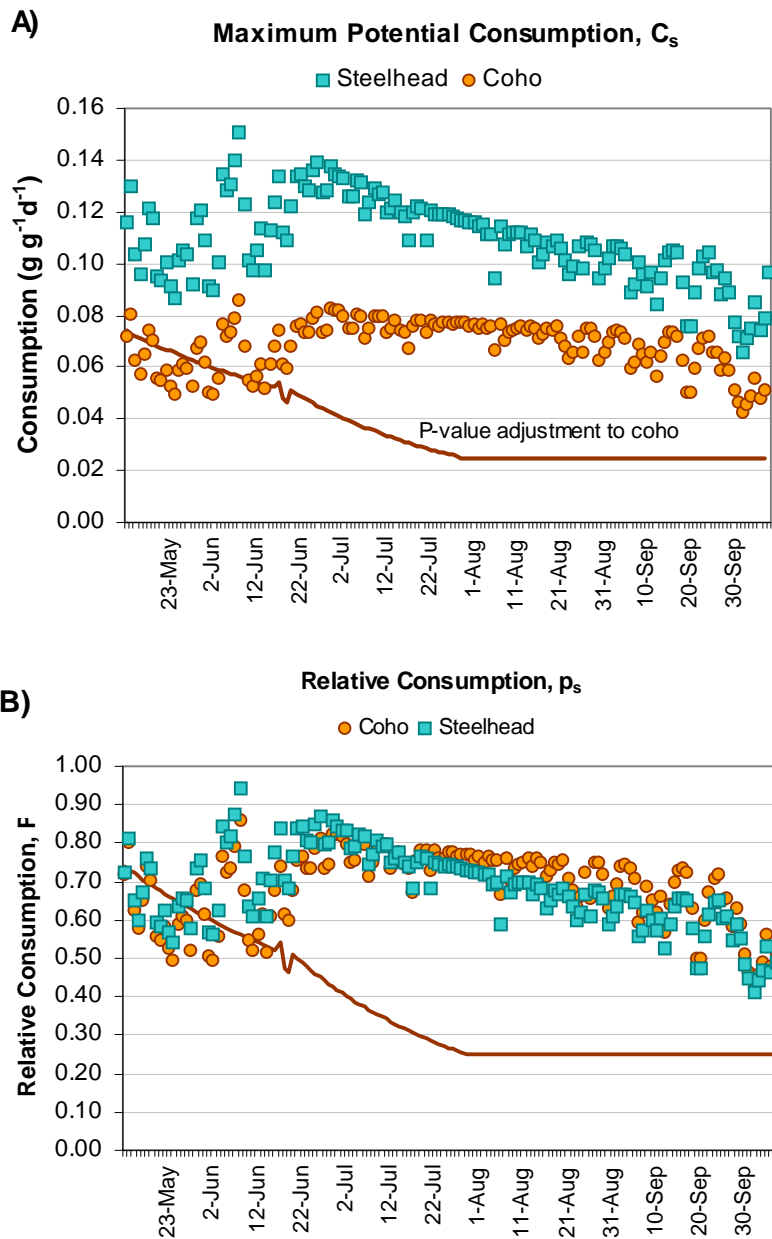
Figure 5.8 Estimates of consumption at Huckleberry Creek. Data points are estimates of maximum potential consumption based on temperature and weight: A) Consumption as a proportion of body mass; B) Relative consumption, calculated as daily consumption divided by *Cmax* generated by the consumption equations. The line is the P-value for coho that adjusts consumption based on field observations suggesting ecological constraints on food supply.

After June, apparent consumption by coho declined significantly relative to maximum potential and the consumption estimate must be modified by a factor reflecting food limitation (P-value in the Wisconsin model terminology). To do so for coho, we fit a linear regression to the apparent coho consumption from July to October (Figure 5.7)

5–21

using a dated time step. Maximum consumption values and the ecological adjusted relationship are shown in Figure 5.8A. For readers familiar with the Wisconsin model, the relative consumption for each day, (p_i), is also shown in Figure 5.8B. During growth simulation, each consumption value is calculated in the defined time frame (site adjusted P-Value and maximum potential) and the value that is lower is selected. (During the spring and early part of the summer, the P-value is not calculated since the continuation of the calculation outside the time interval on which it is based may estimate unrealistic values, although it does appear to fit the data during this interval as well.) Ideally, population weight data would be available at each site where the growth simulations are conducted, at least for coho. However, this information was not available at other sites (Table 5.4) since it is common to measure populations only at the beginning and end of the summer. Therefore, all population growth simulations for coho and steelhead that follow use the consumption estimates developed at Lower Huckleberry Creek, depicted in Figure 5.8A, to estimate consumption.

Comparison of Model Predictions to Observed Fish Growth

The apparent consumption estimates were used to simulate growth of the fish populations listed in Table 5.3, using initial weights and temperature recorded over the period between the initial and final sampling of populations. We first simulated coho population growth at the two sites at Huckleberry Creek where the coho consumption estimates were developed (Figure 5.8). Presumably, errors would be less here than at sites where consumption was not calibrated site-specifically. The simulation results and observed population weights at the two sites are shown in Figure 5.9

Between the first and last sampling time, the naturally-spawned coho at the lower site increased in weight more than threefold from 0.9 to 3.2 grams. The predicted weight was within 3% (0.1 g) of the observed weight at the end of the summer. The predicted and observed values are so close that the simulation line appears to connect the observations. The model correctly predicted the ending population weight and those observed at each mid-season sampling. This is perhaps not a surprising result given that the food consumption estimates (Figure 5.8) were developed at this site. However, the simulation shows that, when food intake is calibrated at a given location, the model can accurately predict weight gain.
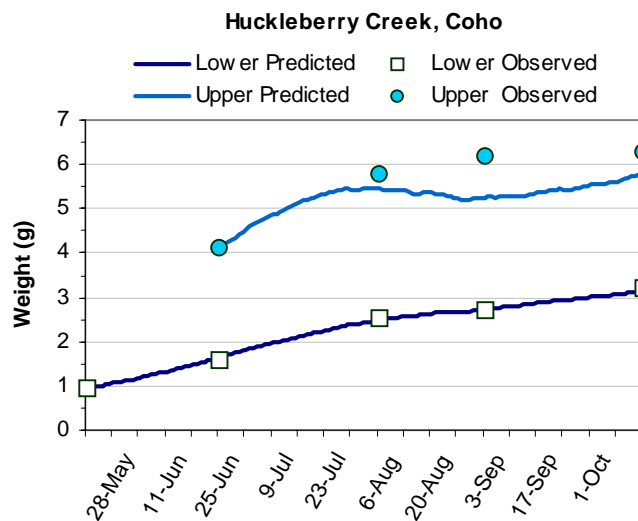
Figure 5.9 Observed and simulated weight gain at the lower and upper sites at Huckleberry Creek.

Importantly, the model simulations are sensitive to the consumption estimates. For example, increasing daily consumption by 10, 20 and 30% above the values shown in Figure 5.8 through the simulation period yields final weights of coho at the lower Huckleberry site of 4.0, 4.9, and 6.0 grams respectively (+25, +53 and +88% greater than observed). Thus, errors have a cumulative effect since they are applied over time. Interestingly, this relatively moderate increase in consumption results in increased population weights that are proportionately consistent with those observed in field studies that found improved production in streams where shade had been removed, and presumably, food had increased. (Hawkins et al. 1983, Hetrick et al. 1998). These results suggest that food supply doesn't have to increase by a large amount to significantly affect the weight that fish achieve over the course of the summer.

Predicted weight at the upper Huckleberry site was also close to that observed, but predictions were not as accurate (-8%) (Figure 5.9). The upper site had a large influx of larger fish between the May and June sampling dates, so the simulation was initiated in June after the population was determined. The upper site had a slightly different P-value at the end of the summer, and the value was used to model this site only (not shown). Growth of this population was low during the latter part of the summer and the rate of decline of the P-value was greater at this site than the lower site, possibly because of the larger size of fish in the population. Nevertheless, despite nearing minimum maintenance ration at the end of the season, the large size of the population was maintained into the fall and no weight loss was observed. The model prediction was actually more accurate at the end of the season than at some of the mid-points, where it tended to underestimate the weight.

In the next set of simulations, we applied the model to the rest of the populations listed in Table 5.3, except those where continuously recorded temperature data were not available. The consumption estimates established for the population at the lower site at Huckleberry Creek in 1991 were used for all of the coho simulations. We would expect that applying these assumptions to other sites could be a significant source of error, since presumably food supply differs among sites and the growth estimates are sensitive to this parameter. Furthermore, errors accumulate due to the effect of weight on consumption. We show the simulation for coho and steelhead at Porter Creek (1988) in Figure 5.10. Porter Creek is exemplified because the prediction accuracy was average for both coho and steelhead (Table 5.3), the site was far removed from Huckleberry Creek, the simulation period was long, and both species were present. Predicted weights closely approximated observed weights for both species (Coho: -7%, Steelhead:+11%).
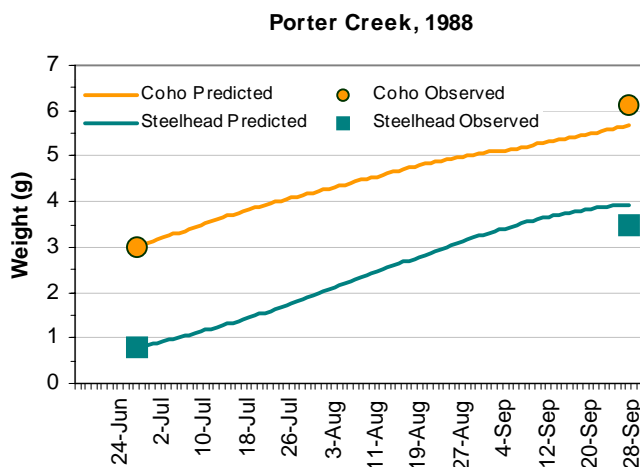
Figure 5.10 Weight prediction and observed fish weights for coho and steelhead populations at Porter Creek, 1988.

Predicted relative to observed weights at the end of the simulation period are shown for all of the site by year data sets in Figure 5.11 and listed in Table 5.3. The accuracy of the growth simulations was estimated by calculating the sum of unexplained residual variations between observed and simulated length for each cohort of coho (n=14) and steelhead (n=7) through the following equation:

$$ SCE = \frac{1}{n} \sum_{i=1}^{n} \frac{(W_{predicted_i} - W_{observed_i})^2}{W_{predicted_i}} \qquad \text{(eq. 5.16)} $$

SCE for both coho and steelhead was 0.08 of the observed for both, while the average gain
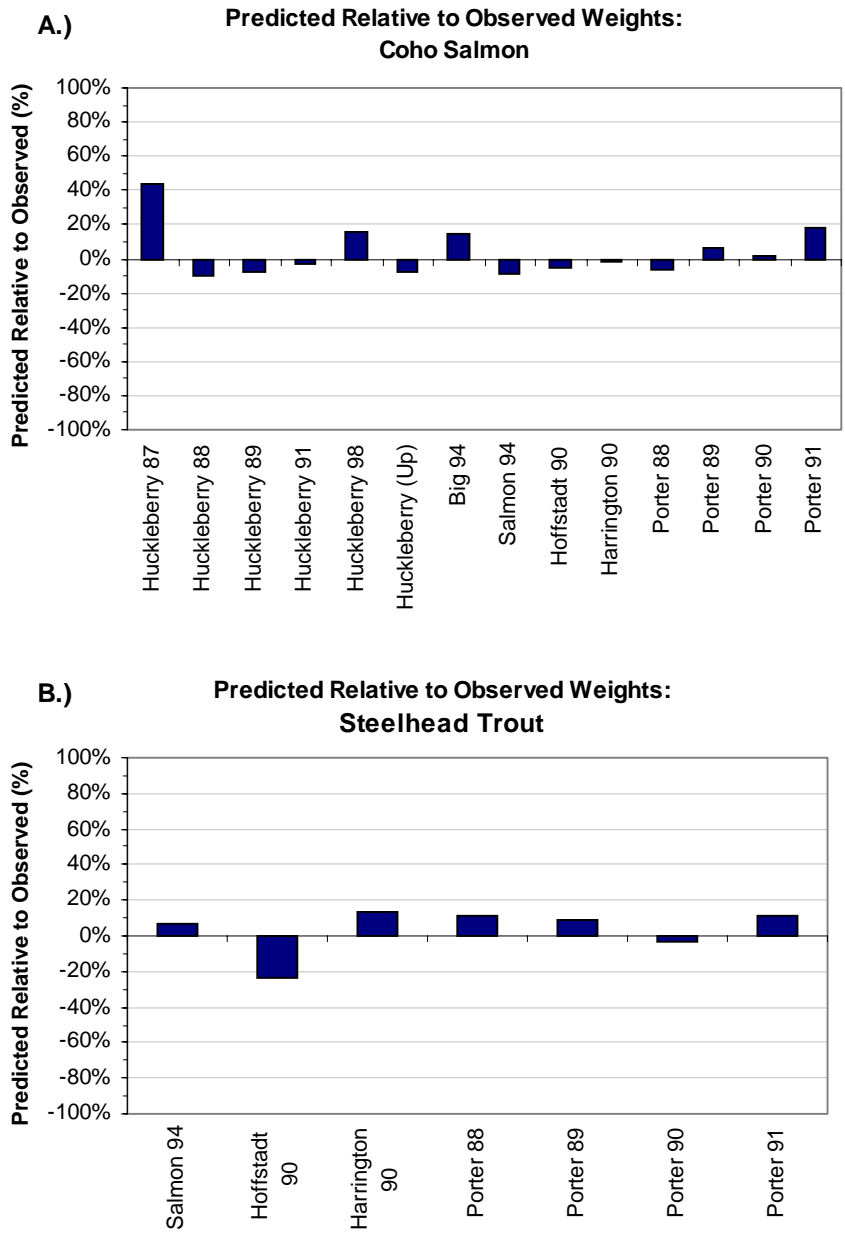
Figure 5.11. Differences between predicted and observed average weights of fish populations.

in weight during the period was 1.25 and 4.14 times initial weight, respectively. Some predictions were above and some were below the observed weights, with no apparent patterns. Model predictions averaged within 4% of observed for both species considering the sign of the difference between observed and predicted, and 11% when averaging its absolute value. The largest prediction error occurred at Huckleberry Creek in 1987 (+44%). There was very little weight gain at this site during this year and our consumption estimates were clearly too high. As another example, the steelhead population at Hoffstadt Creek was under-predicted by 24%, perhaps because the population was augmented by hatchery fish. Since there are no assumptions about food supply used to model steelhead, this error suggests that one or more of the model parameters were probably incorrect for this population and year. Our unexplained error is consistent with, but somewhat less than achieved by Mallet et al. (1999) for grayling in a European river where they used a similar approach for accounting for temperature but did not consider consumption.

The close correspondence of observed and predicted weights was welcome, if not somewhat surprising, given potential errors associated with using consumption estimates extrapolated from other streams in the case of coho, or from other species (cutthroat), albeit closely related, in the case of steelhead. While the physiological-based estimates of consumption should be broadly applicable to the species as formulated in this paper, varying perhaps by genetics among races, the ecological constraints on food supply can vary significantly among sites. Many factors potentially influence food supply; population dynamics and competition for food, (Walters and Post 1993), riparian, in-channel habitat characteristics that control primary and secondary production (Hawkins et al. 1983, Bilby and Bisson 1988, Hetrick, Murphy 1998, Railsback and Rose 1999) and even the energy content of prey (Stewart and Ibarra 1991). Information about these riparian, in-channel habitat and population characteristics are not directly measured, but are integrated by growth rate in the time series of daily temperatures, consumption and body weights. The average growth rate as a function of annual maximum temperature is shown in Figure 5.12. Railsback and Rose (1999) observed that measured growth rates of trout in the Sierra Nevada, and those predicted by the Wisconsin model, varied from year

Growth Rate of Fish Populations
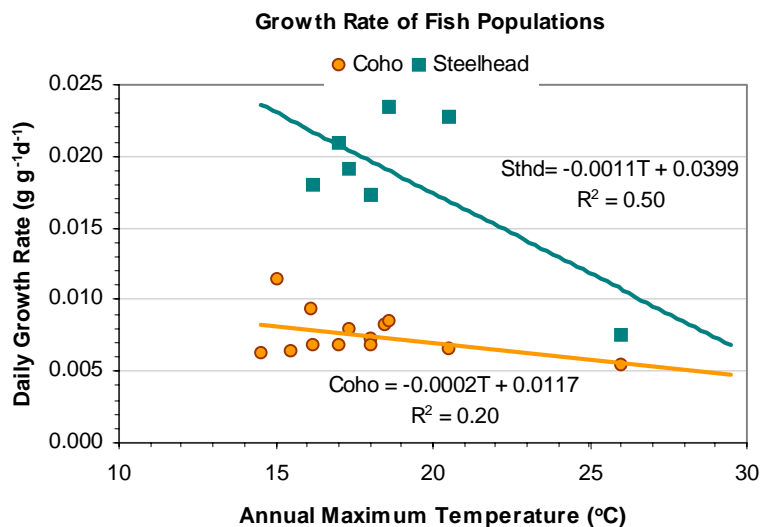
Figure 5.12 Growth rate calculated by the model averaged for the sampling period in relation to annual maximum temperature at each site.

to year and with site characteristics such as flow. We observed similar variation in the sites sampled in multiple years (Table 5.3), although we did not attempt to account for differences other than those caused by differences in temperature.

For the final two simulations, we examined how modeling weight over the full range of rations and weights of individuals within the population would relate to estimates based on averages. Presumably, individuals are feeding over the range of possible rations, from minimum maintenance to satiation, with consumption limited by their hierarchical position within the population (Puckett and Dill 1985, Nielsen 1994). In theory, some fish
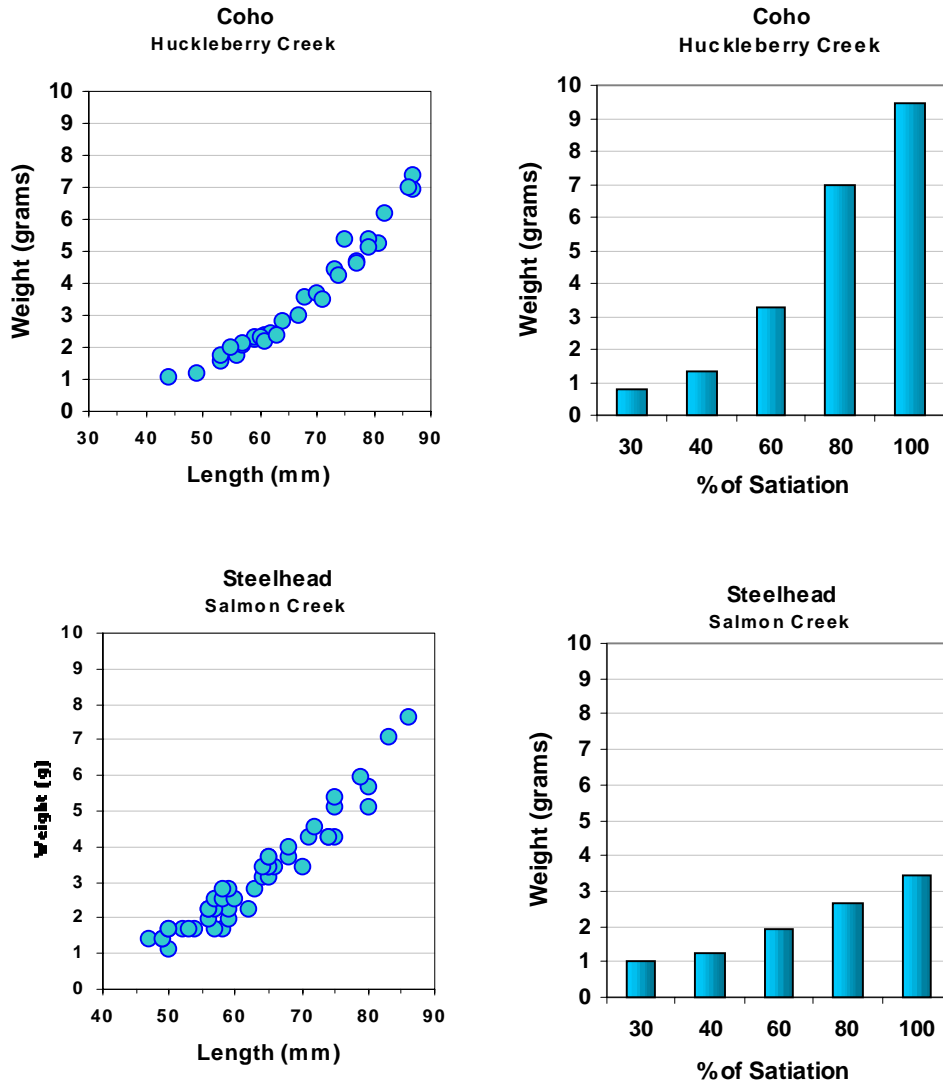
Figure 5.13. Examples of length-weight relationships for coho salmon population at the end of summer growing season at Huckleberry Creek and the steelhead trout population at Salmon Creek. Also shown are the predicted weight for each ration for Huckleberry Creek and Salmon Creek, calculated with the site's temperature from the period between population sampling, and a starting weight as observed at the site at the initial sampling.

may be feeding at satiation ration, although population density controls could prevent fish from achieving this level of ration (Brett 1995). Individuals feeding at less than minimum maintenance ration over extended periods of time are likely to be lost from the population due to starvation.

Weight gain was simulated for the coho population at lower Huckleberry Creek (1991) and the steelhead population at Salmon Creek (1994) for the intervals between fish population samplings, with weight initialized at the observed average population weight. The maximum potential consumption was computed each day based on temperature and fish weight, then categorized into 5 rations between 100% satiation and minimum maintenance (30, 40, 60, 80 and 100%). A minimum of 30% satiation was chosen because this is very near starvation but still allows some growth at some temperatures.

Predicted ending weight at each ration level is shown in comparison to the range of individual weights observed in the population on the final sampling date in Figure 5.13. The range of weights observed within the two populations near the end of the summer was wide, but typical of what is usually observed: the largest fish were 4 to 6 times larger than the smallest fish for both species. There was a range of weight among individuals within the population early in the season, although it was considerably narrower than it was at the end of the summer (Figure 5.14). The growth model predicted a range of weights that was similar to observed. Model predictions suggested that coho as large as 9.5 grams could occur at 100% satiation ration and the largest fish observed was 7.4 grams, a weight consistent with high consumption, but less than satiation. For steelhead, the largest predicted individual was about 3.5 grams, considerably smaller than the largest individual in the population assigned to the 0 age class by the field biologist. Seventy-five percent of the steelhead individuals were within the predicted range. The steelhead that are larger than the 100% ration prediction could actually be yearling fish since scale analysis was not performed, and it can be difficult to distinguish age of the fish from observation alone.

Exact correspondence in individual weights was not expected since the average population weight was used to initialize the simulation. If we apply the same analysis of the growth of the largest, average and smallest fish in the coho population at Huckleberry Creek as we did earlier for Mason's population, we estimate the average degree of satiation for each ranked fish (Figure 5.14). During this period there was only a small change in the number of fish in the population, although we do not know if the fish that held these ranks at the end of the summer were the same one's that held them at the beginning. As in Mason's experiment, the largest fish ate at a higher satiation level than smaller fish in the population. The largest fish is estimated to have eaten at 73% satiation, the average fish at 62%, and the smallest fish at 45% satiation, averaged over the growth period. These results are consistent with Fausch (1983), who found that dominant fish obtained more energy during natural feeding.

Modeling individuals within the range of population sizes produced qualitatively similar results as modeling the average fish for the range of rations, in terms of the range of weights predicted and the average consumption. Perhaps this is because the average population ration was in the mid-range of rations. Nevertheless, the growth model suggested a plausible range of weights at the individual scale using a range of rations, and the model closely approximated the average population weight and at the population scale using average weights and field-calibrated ration (Figure 5.11)
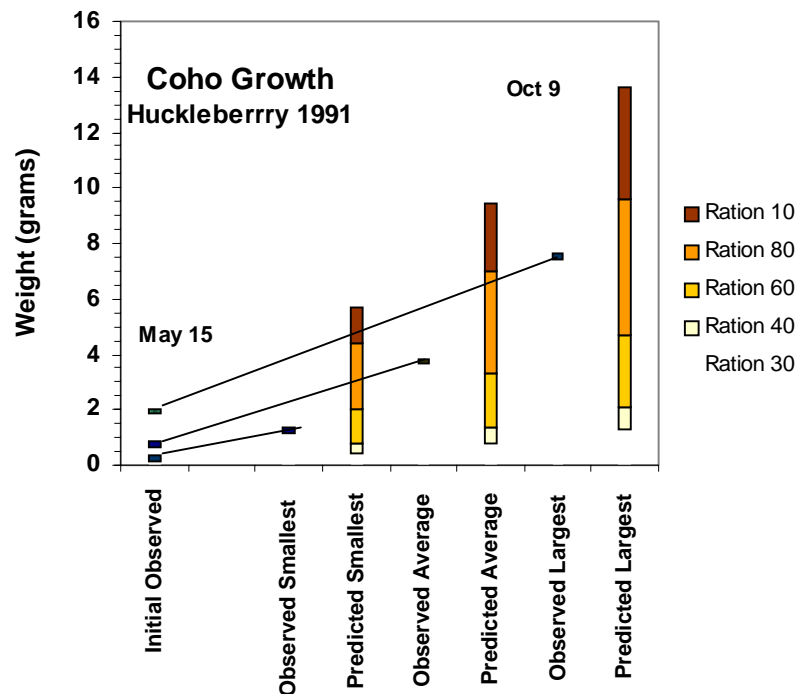
Figure 5.14 Observed and predicted weight of coho in Huckleberry Creek (1991). The growth of the smallest, average, and largest fish at the start of the summer (May 15) were modeled for the full range of satiation (shown in bars). Weight of each class at the end of the period (Oct 9) are shown at the end of the summer relative to growth simulations.

Finally, we conducted a brief sensitivity analysis to demonstrate model behavior over a range of temperatures and food consumption levels. Weight gain was simulated using the same time interval, starting weight, and range of rations from satiation to minimum maintenance, allowing only the temperature to vary for each site. June 1 to Sept 15 was selected to represent the primary growth period for coho and steelhead since both species should have emerged from the stream bed by this date, and our data set from temperature sites was complete during this interval. A representative initial weight was estimated by regressing weight of all the populations sampled early in the summer season with time. Steelhead tended to be very similar in weight early in the season, despite differences in sample dates, averaging 0.5 grams on June 1 (julian day 152). Coho weight varied more, and in some cases, included some sites with hatchery-raised fish. Coho averaged 1.4 grams on June 1. Temperature simulations included site temperature, which varied

through the season, as well as constant temperature for the period (Figure 5.15). Simulated weights based on each site's temperature regime are plotted as circles; constant temperature predictions are the solid parabolic lines at each ration, and the observed fish population weights are plotted as squares. The solid lines computed at constant temperature follow the growth rate curves on which they are based, but they reflect the effect of long-term exposure while compensating for effects of increasing weight on
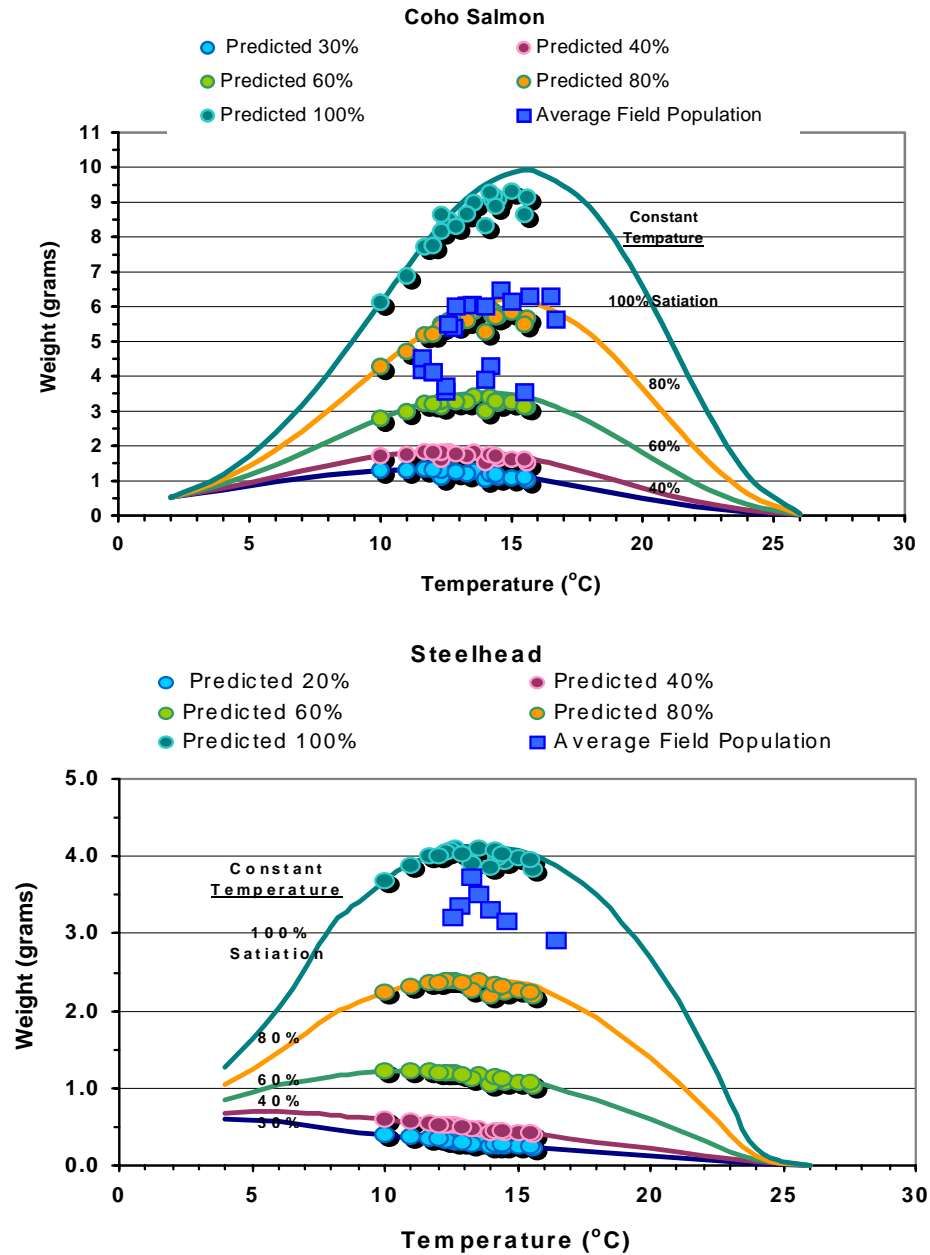
Figure 5.15. Summary of observed and predicted weights for coho salmon and steelhead trout. Solid lines are the weight predicted at constant temperature for 106-day simulation (June 1-Sept 15). Circles are the predicted weights at each site and ration based on the daily temperature regime for the period. Squares are the average weight of observed populations. Initial weight was 1.4 grams and 0.5 grams for coho and steelhead, respectively.

consumption.

Weight can be strongly affected by both the prevailing temperature and the amount of food available to fish. Either factor can have the same level of effect, although maximum weight can only occur when prevailing temperatures are near the species' physiological optimum temperature and food supply is high. Low to moderate weight can result from many combinations of temperature and food supply, perhaps helping to explain why it is difficult to determine whether food or temperature is limiting growth in natural streams from empirical field observations alone.

Weight is maximized when temperature over the course of the summer is closer to optimal temperature (Figure 5.15). Washington streams and rivers tended to be near optimal, despite significant differences in the temperature patterns at the sites when indexed by the annual extremes such as annual temperature (Figure 3.1). The effects of temperature are more pronounced at higher levels of food. Interestingly, observed weights of coho and steelhead populations show patterns consistent with those simulated across the range of temperatures, although food supply at sites was not well known. The biomass of fish populations measured at the study streams is moderate to high relative to those reported from the coastal areas of the Pacific Northwest and Alaska (Bisson and Bilby 1998). At very low levels of food, growth is very low, but is somewhat better at cooler temperatures.

The weights predicted using observed temperatures do not deviate far from those calculated with a constant temperature (Figure 5.15). Thus, since there is little loss of information using the constant temperature, these simulations suggest that the weight gain at sites much warmer and colder than those available in our data sets are realistic. The constant temperature can be represented by the median temperature of the period. Figure 5.13 suggests that the model is sensitive to temperature, and would estimate significantly different weights for significantly different temperature profiles. The similarity in the weights predicted with the growth simulation methods at many of the sites (Figure 5.15) does not appear to reflect lack of sensitivity of the model, but rather the relatively narrow range of average temperature at streams within the sample. Population weights should be less in streams with predominantly warmer or colder than occur in our data sets.

DISCUSSION

We have developed a bioenergetics-based approach to assessing the effects of temperature on growth of salmonids. At this time, it has only been applied to age 0 steelhead trout and coho salmon living in natural streams. Growth of other salmonids could easily be modeled with the same approach if the basic consumption and growth functions can be established.

There are many examples of growth modeling based on bioenergetics principles available in the literature. Most use similar methods for estimating consumption terms but provide more comprehensive evaluation of energetic functions in addition to growth (Beauchamp et al. 1989, Kitchell et al. 1974, Hewlett and Johnson 1987, Beauchamp et al. 1989, Hanson et al. 1997.). Our formulation differs from these in that energy consumed by growth, as evidenced by observed growth rate, is the only energy function considered, and we make no attempt to close the energy balance between intake and expenditure. Thus, we view our approach as bioenergetics-based but not a true bioenergetics model. However, the growth model developed here shares many key elements with bioenergetic

models, and therefore its application enjoys many of the same challenges and criticisms (Ney 1993, Hansen et al. 1993).

In a review of bioenergetics models, Ney (1993) noted that corroborative studies of bioenergetics models showed a number of deficiencies that appear to compromise their ability to estimate consumption and growth of non-captive fish accurately. Some critics feel the models are overly complex (Ney 1993) and prone to errors in parameter estimation (Boisclair and Leggett 1989). A comprehensive model of energy functions results in the proliferation of parameters, which may create difficulties in adequately informing a number of the input variables, and defining some of the energetic relationships. Hansen et al. (1993) comment that bioenergetics models having 20 or more input parameters, each with its own estimation error, can lead to estimates of consumption or growth that, in some circumstances may have to differ by 100% or more to be judged statistically different (Boiscalir and Leggett 1989.) This poses particular problems for trying to use these models to sort out complex ecological interactions. Beauchamp et al. (1989) noted that bioenergetics models are used more frequently to predict consumption than growth because of the additional errors associated with bringing in other equations. To the contrary, Hanson (1997) argues that forcing a balance of the energy budget acts to limit error propagation (Bartell et al. 1986).

The growth model developed in this paper is relatively simple, especially in field application, but the errors are unconstrained. Our model shares some of the same relationships that are most sensitive to the errors that are found in full bioenergetics models. Specifically, the consumption terms that apply to the physiologic controls of temperature and allometry, as well as the food supply, are both important in estimating growth (Stewart et al. 1983, Beauchamp et al. 1989, Bartell et al. 1986, Hanson et al. 1993). The physiologic relationships appear to be reasonably well established for salmonid species, given the similarity of parameter values developed from different studies (Hanson et al. 1997). We achieved good modelling results using these values.

There have been questions as to whether such laboratory study results can be used for predicting response of fish living in natural environments. Laboratory studies have unique conditions of food, environment, and population pressures that themselves may create stresses that may not be observed in natural settings. In our analyses, the gain in weight of fish living in stream environments was closely approximated by relationships derived from laboratory studies. This suggests that laboratory studies can be used with some confidence to predict responses in more natural ecological settings.

Achieving a quantitative understanding of the cause and effect linkage between food consumption and temperature in natural environments is a significant challenge, as suggested by Figure 5.14, where different conditions can produce similar population weight. Field studies are labor intensive and field estimates are laden with their own assumptions and subject to their own errors (Ney 1990). Trying to discern such relationships by empirical observation alone is problematic, given the multivariate and dynamic nature of the interaction and the difficulty of measuring some of the key fundamental relationships in natural environments (Brett 1971, Boisclair and Leggett 1991, Railsback 1997). While the growth model can not solve these problems, it can help field investigators to develop physiologically-based hypotheses that may help them understand the responses they observe.

We found that our simplified application of bioenergetics principles provided some useful structure to the analysis of field observations of environmental temperature and food supply that appeared to address some of the complexity of the interactions. This could lead to greater insight into their inter-relationships when compared to empirical observation alone. For example, our results suggest that food limitation existed for some species and not for others (at least at this age), and that food limitation varies in time in ways that have important implications for population dynamics. Additional study of food consumption and supply in natural streams, where data are extremely limited, would be very useful, given the importance of these factors in determining fish productivity and response to temperature. It seems clear from this analysis that there is more opportunity to affect productivity (population weight and density) by changing food supply than by changing temperature within the range of temperature observed in the study streams, at least during the summer months. This interpretation is consistent with field studies that have shown increased productivity with canopy removal, despite increases in temperature that at times have appeared to be adverse (Hawkins et al. 1983, Bisson et al. 1988).

Importantly, the hypotheses presented by the model can be explicitly tested in field experimentation, and rejected if model results fail to predict observed responses. In this first application, the model hypotheses were confirmed, but more carefully implemented field experiments would be beneficial. We caution that these results corroborate the utility of the model, but do not constitute a rigorous test of the model or its underlying assumptions (Hansen et al. 1993). Validation would best be achieved by field and laboratory experiments to confirm the growth curves and allometric functions and to independently determine food availability, rather than estimate consumption from observed change in average population weight through time (e.g. Filbert and Hawkins 1995, Martin 1985). Such tests would help refine the input parameters, as well as reveal whether our assumption that energetic functions, other than those captured in the allometric and growth rate functions, can be ignored in estimating growth effects of environmental temperature at a necessary level of precision.

It was somewhat surprising that we were able to achieve such good predictions of weight gain compared to observations of fish populations given the sparse amount of data used to develop consumption estimates. Weight estimates for populations of juvenile salmonids were generally within 11% of observed following growth over several months during a rapid growth phase. However, the model is always likely to perform best using site-specific estimates for food consumption. Nevertheless, extrapolated estimates proved satisfactory for our purposes.

We conclude that the methods developed in this section perform well for the purpose of assessing the effects of environmental temperature on juvenile salmonid growth. Ney (1993) concluded that, in their present state of development, bioenergetics models are best suited for making relative rather than absolute predictions such as comparing outcomes of different habitat and food availability scenarios. This is how we emphasize use of this method. The method is used in Section 6 to evaluate the effects of temperature regime on salmonid growth relative to temperature thresholds that could be used as water quality criteria.

Conclusions

❑ Methods of predicting growth based on quantitative bioenergetics principles can be applied to streams to assess the effects of temperature on juvenile salmonid growth, with results that are consistent with observed fish population growth patterns.

❑ The method is sensitive to temperature and can be applied to the daily temperature regime making it a useful tool for assessing the biological impacts of temperature in natural streams.

SECTION 6 QUANTIFYING GROWTH EFFECTS IN RELATION TO TEMPERATURE THRESHOLDS

Abstract

In Section 5, we developed a method to estimate the effects of temperature and food consumption on the gain or loss of weight of coho salmon and steelhead trout during the summer months. In this section, we use the methodology specifically to identify temperature indices, including the duration and magnitude of threshold temperatures that minimize the negative growth effects of the temperatures that occur over long periods of time. The analysis provides an objective method to establish temperature criteria based on protecting the opportunity for growth, rather than avoiding catastrophic impacts.

Analyses demonstrated that some effects from the ambient temperature occurred at all sites, because no stream spends all of its time at a fish's optimal temperature for growth. Sites with both chronically high and chronically low temperatures were estimated to experience significant growth loss. Using the 7-day maximum temperature, and allowing 10% growth loss, the upper threshold for coho salmon was found to be 16.5^{o}C and the lower limit was 13.0^{o}C. The range for steelhead was wider at 14.5 to 21°C. Many sites included in the analyses exceed current temperature criteria for Washington (annual maximum of 16°C). Streams that far exceed the criteria also were predicted to have high growth loss. Those near the threshold criteria ($\pm1^{o}$C) appeared to experience the best temperatures for growth. Streams with lower temperature ($<13^{o}$C) also had higher growth loss and temperature less than 10°C were adverse to growth of both coho and steelhead. The method could be used to identify thresholds for other temperature indices such as annual maximum and 7-day mean, or other levels of growth loss.

Key findings include:

- ❑   It is feasible to apply a risk-based approach that uses data without safety factors and produces an estimate of cumulative risks. This technique is a true quantitative benchmark that is measurable and testable.

- ❑   The majority of temperatures experienced by salmonids are generally suboptimal for growth, and these exert some cost on the maximum potential growth.

- ❑   Colder water temperatures are not necessarily better for rearing salmonids, and warmer water temperatures are not necessarily worse. Concepts of safety factors in selecting thresholds need to be exercised with some caution. Thresholds that are too low can also negatively effect growth.

- ❑   Despite what appear to be large differences in temperature among sites, especially with regard to the warmest temperatures that occur each summer, there was less of a difference in the predominance of temperatures that are important to growth. Sites with significantly different temperature regimes often have similar predicted growth risk.

❑ An upper threshold for the 7-day maximum temperature of 16.5^{o}C minimizes growth losses for coho. A 7-day maximum temperature or 20.5^{o}C minimizes growth losses for steelhead, based on an analysis that does not consider population dynamics.

Introduction

One of the most important aspects of temperature in natural environments is its effect on growth. Growth is regulated by a complex interrelationship between food supply, population dynamics, and the physiologic responses of the fish to temperature (Weatherly 1972). Trying to discern such relationships by empirical observation alone is problematic, given the multivariate and dynamic nature of the interaction and the difficulty of measuring some of the key fundamental relationships in natural environments (Brett 1971, Boisclair and Leggett 1991, Railsback 1997). The physiological responses, including energy consumption and expenditures are generally studied under laboratory conditions, and have been quantified for many species of salmonids (Weatherly and Gill 1995, Brett 1995). Field studies are labor intensive and they are laden with their own assumptions and subject to their own errors (Ney 1990). Consequently, there are relatively few field studies that have successfully established the linkage (Martin 1985, Filbert and Hawkins 1995). A combination of field and laboratory study offers the best hope for establishing a quantitative understanding of the cause and effect linkage between growth and temperature in natural environments (Hansen et al. 1993).

Laboratory studies have produced quantitative relationships between energy consumption and expenditure mechanisms. The rate at which most energetic functions proceed is mediated by ambient environmental temperature. Bioenergetics models have been developed to help manage understanding of the multitude of physiologic responses to temperature (Kitchell et al.1974), accounting for energy consumption and expenditures. Some have been packaged into software programs (Hewlett and Johnson 1992, Hanson et al. 1997), and have been proven to be useful tools for a number of applications in fisheries management (Hansen et al. 1993). These include the rearing of fish in hatcheries (McLean et al. 1993), and populations in natural environments (Hanson et al. 1997). The downside to such models is that they often require many parameters to inform a number of energetic functions, most of which are difficult to quantify in natural environments. Thus their application to explore ecological responses to environmental temperature are more limited, although researchers have recently found them promising for this purpose (Filbert and Hawkins 1995, Preall and Ringler 1989, Railsback and Rose 1999).

In Section 5, we developed and corroborated a bioenergetics-based approach that can be used to evaluate the effects on growth of the variable temperatures that occur over the juvenile rearing period in natural stream environments. The model treats the population as a cohort, and does not account for population density effects. Thus, the method allows us to focus on temperature differences among streams while minimizing biological data requirements. The mathematical model simulates weight gain over a specified duration, and requires only three input parameters (temperature, initial weight, and daily food consumption). The method is sufficiently simple that it can be applied in field experimental studies. Only the food consumption term is difficult to assess in streams (Filbert and Hawkins 1995). To our knowledge, no simple methodology for assessing food availability has been developed.

The ecological constraints on food supply can vary significantly among sites, and they are potentially influenced by many factors: population dynamics and competition for food, (Walters and Post 1993), riparian, in-channel habitat characteristics as they control primary and secondary production (Hawkins et al. 1983, Bilby and Bisson 1988, Hetrick, Murphy 1998, Railsback and Rose 1999) and the energy content of food prey (Stewart and Ibarra 1991). Information about these riparian, in-channel habitat and population characteristics is embodied in the time series of daily temperatures, consumption and body weights of fish as they grow in natural environments over time.

Despite difficulties in establishing *in situ* food consumption, we were able to generate estimates of consumption for juvenile coho and steelhead from observations of fish growth over time that produced close correspondence between simulated and observed weight gain, even when parameters were extrapolated among streams. Weight gain predicted for 16 populations of coho and 8 populations of steelhead were generally within 11% of the observed, during a rapid growth period where weight gain ranged from 67 to 415%. Based on corroboration with observed population growth, we concluded that the method is a useful tool for quantifying the effect of temperature regime on growth, though not biomass until population effects are accounted for.

In this section, we use the model to perform a series of relative comparisons of growth effects from observed stream temperatures from a number of stream sites with widely varying temperature profiles. We pay particular attention to interpreting results relative to temperature thresholds that are often used for water quality criteria.

Growth Simulation Method

The growth model was used to simulate weight gain for coho and steelhead using standard timelines, initial weights, and consumption estimates for each species (Table 6.1). Only the temperature varied, according to measured daily temperature at the 19 sites. Thus, this assessment isolated the effects of the long-term temperature on growth. Temperature profiles at the sites varied from very warm to cold (Table 6.2, and further described in Section 3), and many exceed the current Washington Department of Ecology temperature criteria. The temperature data set did not include very cold streams (12°C or less). These typically occur in the extreme headwaters, and are small and non-fish-bearing in this region (Black 2000). To represent these streams, we also conducted two simulations using a constant temperature of 8° and 10°C.

Growth of coho and steelhead populations was characterized by the average population weight according to the parameters identified in Table 6.1. Simulations were run from June 1 through September 15

Table 6.1 Input variables for growth simulations. See Section 5 for a full description of the growth model and the determination of parameters.

Input Variables	Coho	Steelhead
Simulation Period	June 1-Sept 15	June 1-Sept 15
Initial Weight (g)	1.4	0.5
Food Consumption (g g^{-1}d^{-1})	Declines through time with ecological constraint (see Section 5, Figure 5.8)	Assumed at maximum potential calculated by temperature and weight (see Section 5, Figure 5.8)
Temperature (^{o}C)	Daily mean calculated from hourly temperature measurements	Daily mean calculated from hourly temperature measurements

because we had a complete temperature record for all of the sites and this period encompasses most, if not all, of the growth occurring during the summer rearing period.

The consumption was varied according to observed or estimated rates inferred from growth of fish between time periods as described in Section 5. The analysis found that there are important differences between fish species in their consumption patterns. Age 0 steelhead appear to have no environmental constraint on food supply, subject only to physiological constraints imposed by temperature and weight. Coho show ecological constraint on food supply beginning in late June that lasts through the summer season. Fausch (1984) observed similar patterns, concluding that these differences are likely to influence the species' response to temperature.

Coho

Steelhead
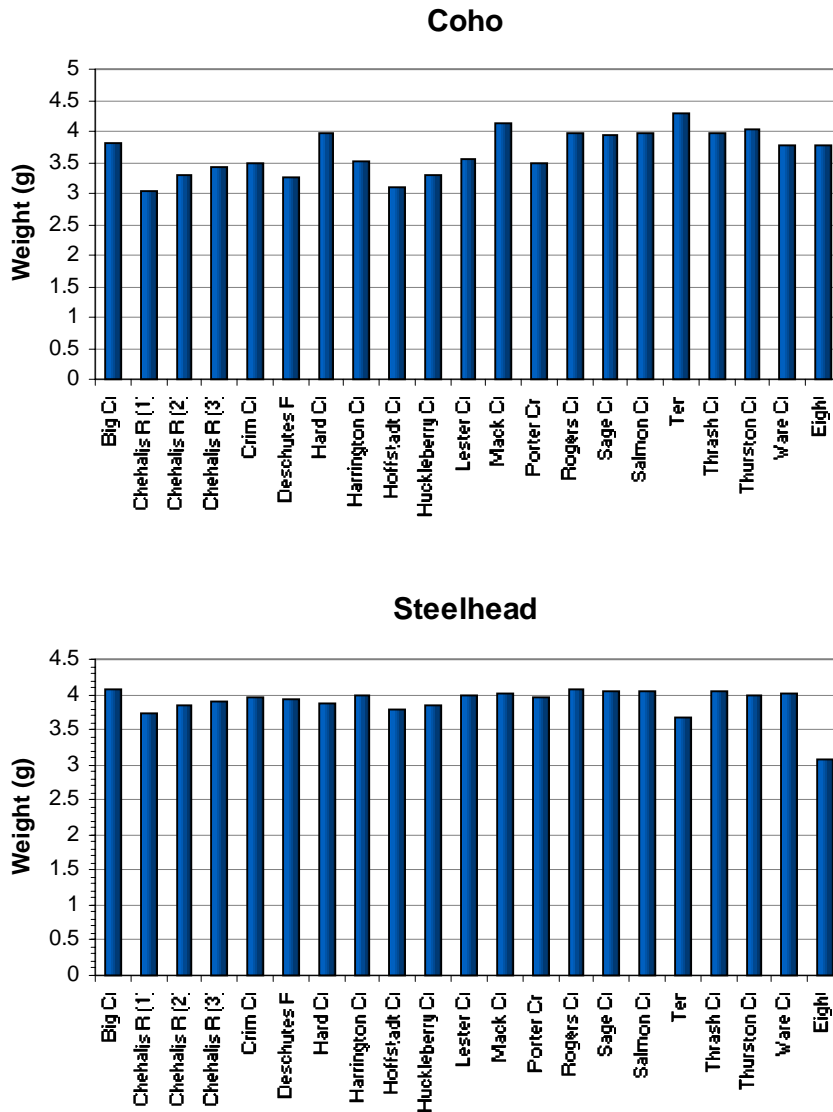
Figure 6.1 Estimated weight after 106-day growth period using the same initial weight and food consumption assumptions at each site.

Temperature Effects on Weight Gain

The predicted weights after 107 days of simulated growth are shown in Figure 6.1. Because the initiating assumptions are the same, the predicted weights are similar. Any differences in observed weight are due to the temperature at each of the sites. Coho vary up to 1.2 grams (31% of the mean), and cooler sites generally had greater weights. The predicted weights of steelhead vary by only 0.5 grams among sites (12% of the mean), despite large differences in the temperatures.

Relative Temperature Effects on Growth

Our approach to evaluating the effects of temperature on salmonid growth is to estimate the weight gain achieved during the summer according to the observed temperature regimes and estimates of food availability, then compare that growth to a reference point. Our reference point is the growth the fish would have achieved if temperatures had been at optimal for growth, and at the same level of food consumption. Brett (1971), Brett et al. (1982), Railsback and Rose (1997), Preall and Ringler (1989) used a similar reference approach, and growth models as a basis for prediction.

Establishing Optimal Temperature and Growth. Previous studies have established a maximum potential growth as the point of reference. Many have used the size calculated at constant optimal temperature and maximum consumption (a reference only observed at optimal temperature and low weight). (See Section 5 for a full discussion of this point). This represents the maximum possible growth that fish could achieve, and it is probably only observed in the laboratory setting where both of those parameters can be maintained at required levels and for a short period in a fish's life.

It's important to note that optimal temperature is not static but varies with weight and ration (Stewart and Ibarra 1991, Brett et al. 1971, Brett 1995). The change in optimal temperature with rations between the minimum required for basic metabolic functions and the maximum at satiation is shown for coho and steelhead in Figure 6.2. Note that consumption rates differ for the two species, as does the range of optimal temperatures.
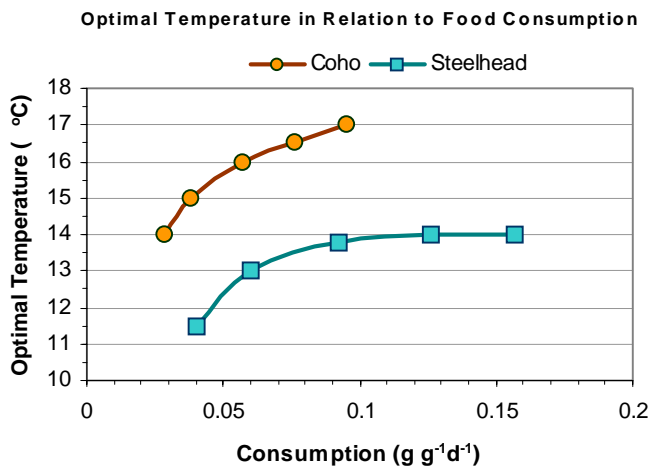
Figure 6.2 Optimal temperature in relation to food consumption. Consumption is expressed as grams of prey per gram of body mass per day. The range displayed is from satiation to minimum maintenance for each species.

There are also changes in consumption rates as the fish gain weight, referred to as allometric relationships (Brett 1995, Stewart and Ibarra 1991). In the optimal growth simulations, we reduce consumption according to fish weight and any ecological constraints on the food supply. Optimal temperature is then reduced accordingly. This yields realistic estimates of optimal growth reflecting well-documented allometric effects. By adjusting optimal temperature with consumption, we believe the reference optimal growth simulation realistically

represents the potential effects of temperature. It is not clear if previous researchers who have used optimal growth benchmarks have performed this adjustment.

In the second scenario, weight is calculated allowing the daily growth rate (g_i) to vary with temperature according to the specific growth curves in Figure 5.4, and food consumption assumptions (as illustrated in Figure 5.8). We express growth in terms of the *Reduction In Maximum Growth* (RMG). RMG is defined as the percentage of reduction in growth for the site specific temperature compared to the maximum growth achieved at the optimum temperature for each ration.

RMG (%) is calculated according to:

$$RMG \ = \ (1 - \frac{W_t}{W_{t=optimal}}) \, x100 \tag{6.1}$$

A sketch of the calculation is provided in Figure 6.3. Since no stream had optimal temperature all of the time, the gain in weight with varible temperature should be less than that for the optimal case. The RMG is expressed as a percentage of the maximum weight. The lower the value of RMG, the less the deviation from the optimal growth rate. A RMG value of 0% suggests there is no growth loss due to the temperature at the site.

The reduction in maximum growth due to temperature varied among species (Table 6.2). It is clear that fish spent only a portion of their time in the optimal temperature range during their growth period, since RMG was greater than zero at all sites for both species. Consequently, there was some cost to growth for salmonids living in Pacific Northwest streams due to their temperatures during the rearing growth phase (Table 6.2). However, the RMG were generally within 20% for both species at all sites.
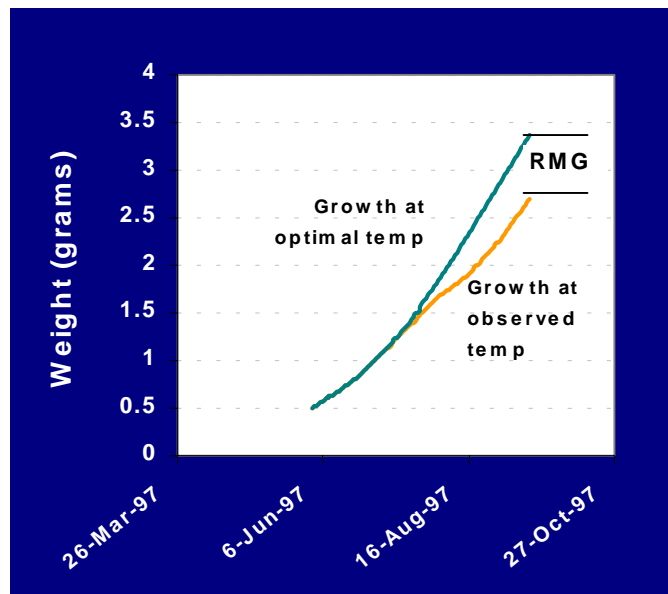
Figure 6.3 Illustration of the reduction in maximum growth based on two temperature scenarios; growth at constant optimal temperature and with the variable growth rate based on the site's temperature regime.

Table 6.2 Location and temperature characteristics of temperature sites used in reduction in growth analysis.

Site	Watershed	Basin Area (km^2)	Year	7-Day Maximum[a] ^{o}C	7-Day Mean[b] ^{o}C	Annual Maximum[c] ^{o}C	Season Median[d] ^{o}C	Coho	Steelhead
	Site characteristics			**Temperature characteristics**				**Reduction from maximum growth (%)**	
Deschutes River mainstem	Deschutes	145.0	1994	21.0	18.4	22.5	15.0	13.5	11.4
Thurston Creek	Deschutes	9.1	1994	14.9	14.1	15.5	12	10.0	9.5
Hard Creek	Deschutes	3.0	1994	14.0	13.0	14.0	11.0	19.2	13.7
Ware Creek	Deschutes	2.8	1994	17.5	16.1	18.3	12.9	14.7	8.7
Huckleberry Creek	Deschutes	5.3	1991	18.4	17.6	18.5	15.5	18.1	12.7
Chehalis River mainstem (Site 1)	Chehalis	181.8	1997	21.1	18.9	22.1	15.6	16.8	16.0
Chehalis River mainstem (Site 2)	Chehalis	57.5	1997	22.1	18.2	23.2	14.5	15.3	13.1
Chehalis River mainstem (Site 3)	Chehalis	29.5	1997	20.6	18.6	21.4	14.3	13.8	11.2
Crim Creek	Chehalis	22.0	1997	18.8	16.9	19.4	14.3	11.6	9.9
Lester Creek	Chehalis	10.4	1997	18.4	16.3	19.0	14.2	9.3	8.5
Thrash Creek	Chehalis	16.7	1997	15.3	14.3	15.8	12.3	8.8	8.1
Rogers Creek	Chehalis	13.1	1997	15.7	14.1	16.1	12.6	6.4	7.0
Big Creek	Chehalis	9.0	1997	16.5	14.6	16.9	12.5	6.2	6.9
Sage Creek	Chehalis	5.3	1997	16.5	14.6	16.9	12.5	9.1	7.7
Salmon Creek	Chehalis	8.9	1997	15.8	14.2	16.2	12.3	8.1	7.7
Mack Creek	Chehalis	2.8	1997	12.9	12.5	13.1	11.7	6.2	9.0
Porter Creek	Chehalis	25	1990	17.5	16.3	18.6	14.4	17.1	10.5
Hoffstadt Creek	Toutle	25.6	1990	24.5	18.4	26.0	14.0	24.6	15.1
Harrington Creek	Toutle	8	1990	19.1	16.7	20.5	13.3	16.5	9.5
Eight (Constant)	NA	NA	NA	8	8	8	8	28.1	35.4
Ten (Constant)	NA	NA	NA	10	10	10	10	7.1	18.3

[a] maximum value of the 7-day moving average of the daily maximum temperature
[b] maximum value of the 7-day moving average of the daily mean temperature
[c] instantaneous maximum
[d] median of daily mean temperature from June 1 to September 1
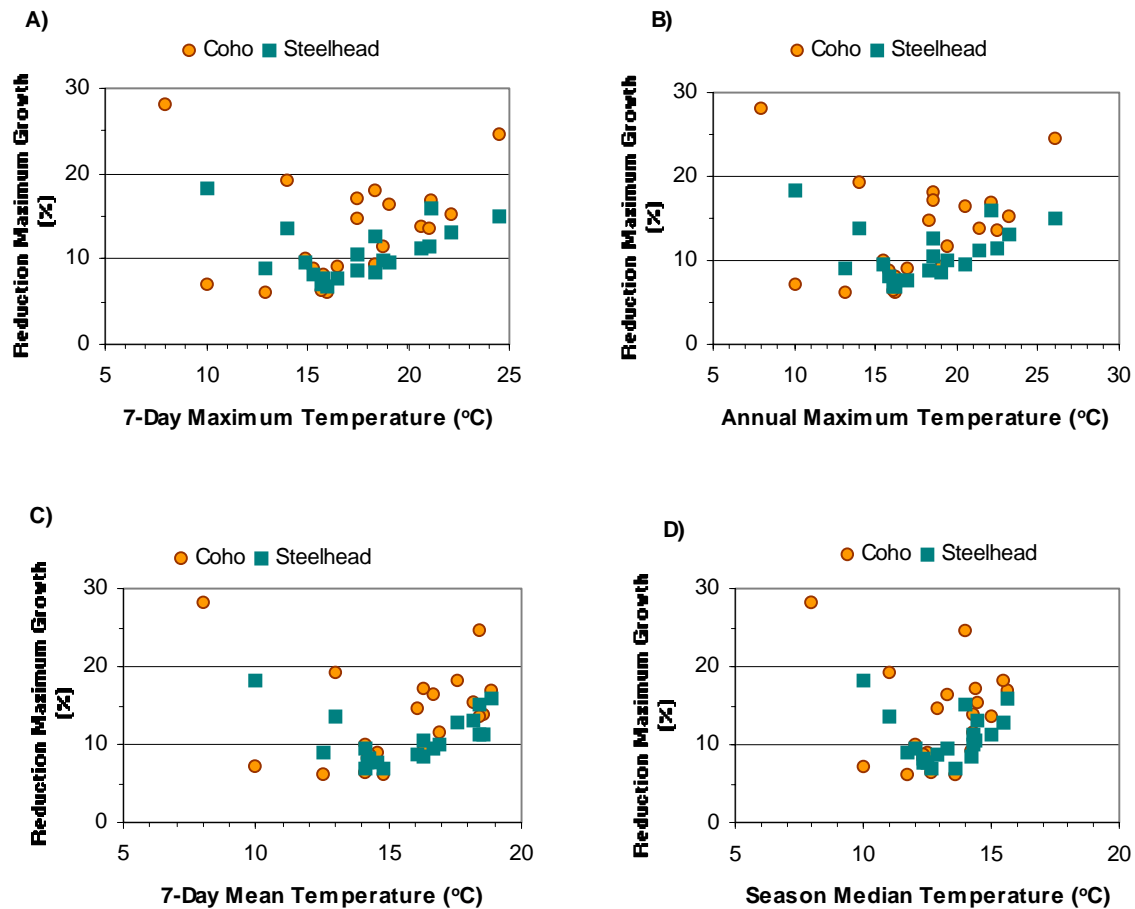
Figure 6.4 Estimated growth risk at temperature study sites in relation to several time-averaged temperature metrics: A) 7-day maximum, B) annual maximum, C) 7-day mean, and D) median temperature for the simulation period.

Temperature criteria for water quality standards are generally applied for time-averaged characteristics of temperature such as the warmest 7-day average of daily maximum and mean temperature, or the annual maximum temperature (instantaneous measure) (see Section 3). Growth reduction (RMG) is shown relative to various time-averaged temperature indices in Figure 6.4. RMG was at a minimum when the stream's temperature index most closed approximated the species'optimal temperature. All streams had some growth loss due to its long-term temperature, since no stream had RMG equal to 0. RMG tended to increase for streams significantly warmer or colder than the optimum or lowest point of the growth curves. Generally, the sites with lowest growth loss had indexing mean temperatures within the range of optimal temperatures (e.g., Figure 6.2). These are 14° to 17°C for coho and 11.5^{o} to 14°C for steelhead using the 7-day maximum measure. Both species showed steep response in growth loss at higher and lower temperatures than their optimal range. There was significantly growth loss for both coho

and steelhead when the 7-day maximum temperature was less than 10°C and greater than 24°C. The patterns are similar for both species, although coho predictions are more variable with site temperature than steelhead. These two species often cohabit the same streams, and with the growth simulation method, they are predicted to have similar level of response at approximately the same temperatures, despite fundamental differences in their specific growth rate/temperature curves (Section 5).

The general patterns in RMG described for the 7-day maximum temperature also held true for all of the time-averaging periods (Figure 6.4). Of course, the range of temperature where growth was optimized varies with each of the temperature indices. The relationship with the least scatter was the 7-day mean temperature, suggesting it may be the best for temperature criteria.

While the species have similar patterns of response, there were also important, non-intuitive, differences in simulation results. Although the optimal temperatures for coho are higher than steelhead (Figure 6.2), their growth was maximized within a narrower and lower range of temperatures. Steelhead maximized growth at a wider and somewhat higher range of temperatures. We believe that these differences reflect the food supply with which each species is modeled. Because no food limitation was assumed for steelhead, their optimal temperatures were on the high end of the optimal range. This gave steelhead a broader temperature range where growth was not compromised by temperature. Coho had a narrower range of temperature where growth was optimized, and this range was consistent with the optimal growth range indicated by their specific growth curves. Assumptions of food supply restrictions helped ensure that the optimal growth for coho would include those temperatures associated with low consumption (13 to16.5 ^{o}C).

The short-duration indices appear to be useful for characterizing the long-term temperature pattern in a way that is meaningful to fish growth. In Figure 6.5, the daily mean temperature for the entire simulation period is shown for three sites. Some sites
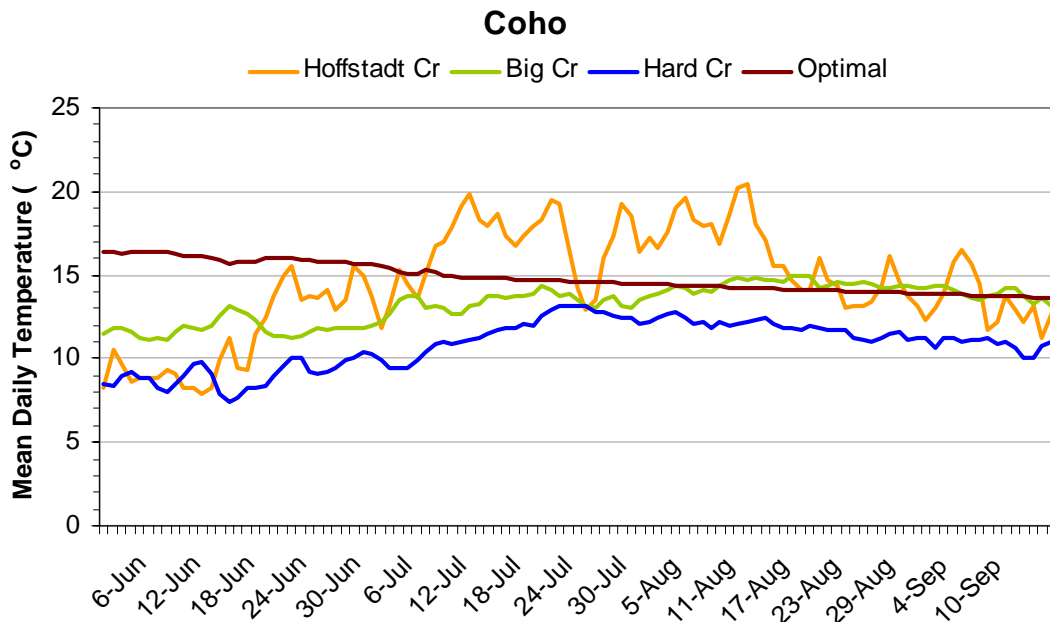
Figure 6.5 Temperature regime at selected sites with estimated optimal temperature.

spend a lot of time above optimal temperature (e.g., Hoffstadt Creek), and some spend all or most of the time below optimal (e.g. Hard Creek). Growth is impacted in both these cases by approximately 20%. The sites where temperature was close to optimal for the longest time (e.g., Big Creek), had the least effects on growth. Most site temperatures tended to be well below optimal early in the summer growing season when growth rates are maximized, partly because fish were smaller. Better growth early in the season appeared to compensate somewhat for very warm temperatures later in the season. Figure 6.5 also illustrates how optimal temperature declines through time with decreasing food consumption due to weight gain.

Since the sites span a range of temperature regimes, the site with the lowest growth loss represents the temperature profile that best encourages growth for that species. In a sense, this site fits the concept of an "index" stream, although in this case, the reference is defined by fish growth rather than its naturalness or lack of disturbance. Interestingly, Big Creek had the most optimal temperature for both coho and steelhead. This site has an annual maximum temperature of 16.9^{o}C, nearly 1 degree over the Washington water temperature criteria.

Risk Associated with Growth Limitation

Holtby and Scrivener (1989) and Quinn and Peterson (1996) found that coho size at the end of summer was a primary factor influencing overwintering survival and smolting. Holtby and Scrivener (1989) provided an equation relating probabilities of overwintering success to coho length. We translated this relationship to an equation based on weight using a population length/weight relationship (Ricker 1975). The relationship between weight and the probability of overwintering success from these two studies are shown in Figure 6.6. Holtby and Scrivener (1989) found a large increase in overwintering success with increased size, possibly because the coho were so small at Carnation Creek (generally less than 2 grams). According to their relationship, weight of about 6 grams or more yields an 80% or better probability of successfully overwintering. Note that we have extended Holtby and Scrivener's relationship beyond the limits of their data to cover the larger fish sizes at our sites. Quinn and Peterson (1996) found more modest improvement in overwintering success at Big Beef Creek with fish size, although the fish in this stream were significantly larger than Carnation Creek. These authors found

Figure 6.6 **Probability of success for coho overwintering survival (from Holtby and Scrivener 1989) based on end of summer fish size. Data from Quinn and Peterson (1996) are also shown. The two points were connected with a linear regression.**

that the probability of successfully overwintering was about 50% for fish >89 mm (approximately 8 grams) and only 17% for fish <60 mm (approximately 2.5 grams). These values agree more closely with fish sizes in our study streams. We connect the two lines to determine a relationship of overwintering success with weight.

We use both of the relationships to illustrate the potential effect of growth reduction on overwintering success. The probability of success for each individual in the population at Salmon Creek was calculated based on its weight (shown as actual weight in Figure 6.7). Quinn and Peterson's data are used in Figure 6.7A and Holtby and Scrivener's relationship is used to calculate Figure 6.7B. Despite the large differences in estimated probabilities with the two relationships, both produce similar relative results. There is a reduction in overwintering success with lower weight; the magnitude of change is approximately equal to the percentage change in weight. That is, a 10% reduction in growth calculated for the population results in an average reduction in overwintering success of 9%.

The important outcome of this analysis is the suggestion that the relatively small changes in weight that we calculate due to temperature (e.g. Figure 6.1) are sufficient to affect individual and population overwintering success to some extent. A 10% reduction in growth would be difficult to statistically detect given the typical range of sizes in natural populations. However, a 20% reduction should be detectable, especially when field experiments are guided by

A) Probability of Overwintering Success Quinn and Peterson

B) Probability of Overwintering Success Holtby and Scrivener

Figure 6.7 Histogram of probability of overwintering survival based on weight of individuals within the population and simulated effects with redcution in weight due to temperature. Probability calculated based on Quinn and Peterson results from Big Beef Creek, WA (A) and from Holtby and Scriverner's from Carnation Creek (B).

hypotheses generated from the growth model. Brett et al. (1982) suggested a 20% upper limit for change in weight due to temperature for chinook populations living in the Nechako River. This appears to be somewhat high for coho, based on implications for loss of overwintering success. However, it should be noted that many factors affect the survival of salmon in the marine environment.

Use of either relationship extends them beyond the original data or application developed by the authors. Therefore, even though we use both relationships to estimate the effect of growth reduction from temperature on overwintering success, we acknowledge uncertainty in this analysis. Additional research quantifying the effect of size on success at later life history stages would increase confidence in the analysis of risk to growth loss

due to temperature. This, in turn, creates uncertainty regarding the choice of 10% as the growth reduction limit. It appears clear that at least 5% growth loss can be expected at all sites due to long duration exposure, even when the bulk of temperatures are near optimal. The difference in temperature thresholds selected at 10 and 20% RMG is quite significant. Increased understanding of the role of juvenile size in determining success at later life history stages would improve confidence in selecting an appropriate limit to growth loss.

In the Carnation Creek study, improved growth of steelhead fry with increased temperature after logging did not translate to larger smolts after two to three years of rearing (Hartman and Scrivener 1990). Steelhead will usually spend at least one additional year in the stream regardless of size achieved in the first year. Thus the impacts on growth from temperature are shown to be small in this analysis, which is consistent with observations at Carnation Creek. The negative or positive effects on growth are not great enough to change weight sufficiently to change migratory patterns, that is, to speed up or delay them by one year.

This is in contrast to coho at Carnation Creek, where temperature increased growth sufficiently to bring some fish to smolting size in one year. It should be noted that Southern British Columbia represents the most northerly locale where coho are typically able to reach smolting size in one year (Sandercock 1991). Coho at Carnation Creek typically migrate at 2-years rather than one, presumably due to lower temperatures. In this case, increasing the temperature accelerated growth to the point where the coho outmigrated after the first season. This was interpreted as negative for the species, because the timing of their migration made them more susceptible to predation in the estuary and ocean environment. Where fish typically migrate in one year (e.g., Washington and Oregon), growth improvement would probably benefit their success by producing fish of larger size, according to Quinn and Peterson (1995).

Growth Loss and Temperature Criteria

We translate the RMG data (Figure 6.4) to zones of reduction in maximum growth to facilitate identifying thresholds of growth response in Figure 6.8. The range of temperatures was determined by ordering the site temperature data and estimating the temperature where the 10 and 20% boundaries occurred. The range of 20% reduction encompasses most of the stream temperatures typically observed in the region. The range of temperature where there was relatively little effect less than 10%) was fairly narrow for both species. It should be noted that at temperatures above and below the ranges illustrated, there is high growth loss due to temperature (30% or more).

Discussion

The temperature assessment approach provides a method for indexing the relative effects of stream temperature regimes on salmonid growth. A value of the approach is that the relative effects of temperature and food consumption can be evaluated independently of other habitat or population characteristics, and each other. Results can be also be used to directly compare growth effects among species. Because these factors are assumed constant in this analysis, the growth estimates only account for the direct effects of temperature, and do not account for population dynamics.
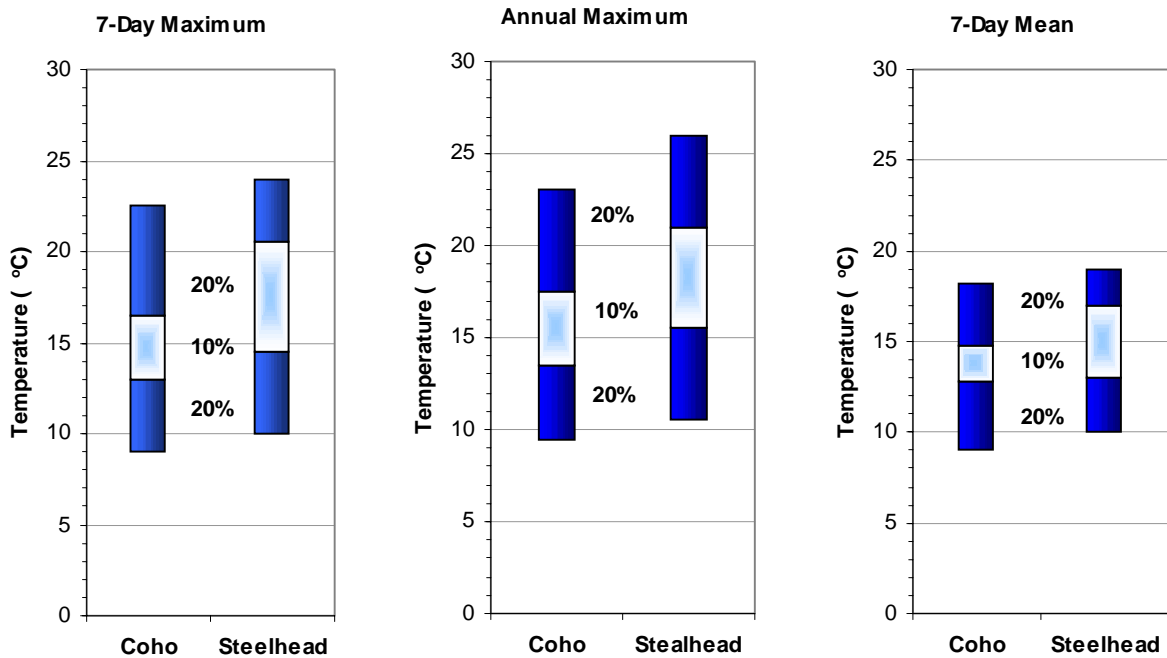
Figure 6.8 Ranges of temperature where reduction from maximum growth is 0-10% and 11-20%. At temperatures above and below these ranges RMG exceeds 20%.

Species were similar in their range of response. However, coho were more temperature sensitive, and steelhead tended to grow somewhat better at warmer temperatures than coho. If bioenergetics relationships are correct, this can be explained by differences in food supply. This, in turn, may reflect the different foraging strategies that each species utilizes when coexisting in the same streams (Bisson et al. 1988b). Selection of temperature criteria in management situations may be most useful if they reflect the most sensitive species (coho) when both species are present.

Fish were predicted to be growing near optimal within many streams, including a number that exceed current water quality standards. The temperature ranges observed at the sites included in this analysis are representative of current conditions in Washington streams and rivers. The vegetative overstory of many has been disturbed within the last 50 years, and therefore streams may be currently warmer than they have been at other times in their history. However, the range of temperature represented at these sites is likely to be representative of the range that has occurred historically, given the history and frequency of fire disturbance in the region (Agee 1993).

The patterns of biological growth response in relation to all of the time-averaged temperature regime metrics demonstrates that they can be used to index the temperature regimes of sites in biologically meaningful ways. Short averaging periods such as 7-day and even the annual instantaneous maximum temperature are strongly indicative of the long-term temperature regime that partially controls fish growth during the summer.

CONCLUSIONS

❑ It is feasible to apply a risk-based approach that uses data without undefined safety factors and produces an estimate of cumulative risks. This technique is a true quantitative benchmark that is measurable and testable.

❑ Modeled growth using measured temperature suggest that the majority of temperatures experienced by salmonids are generally suboptimal for growth, and these exert some cost on the maximum potential growth.

❑ Despite what appear to be large differences in temperature among sites, especially with regard to the warmest temperatures that occur each summer, there is considerable similarity in the predominance of temperatures that are important to growth. Sites with significantly different temperature regimes can have similar predicted effects on growth.

❑ An upper threshold for the 7-day maximum temperature of 16.5^{o}C minimizes growth losses for coho. A 7-day maximum temperature or 20.5^{o}C minimizes growth losses for steelhead.

❑ Concepts of safety factors in selecting temperature thresholds defined for salmonids need to be exercised with some caution. Thresholds that are both too low and too high can negatively affect growth.

❑ The criteria above assume 10% growth loss as the acceptable level of risk. There is uncertainty associated with this number, since there are relatively few quantitative data to base it on. Further research could help confirm acceptable risk levels.

SECTION 7   RELATIONSHIP BETWEEN EXISTING AND PROPOSED TEMPERATURE CRITERIA AND RISK ASSESSMENT FINDINGS

Abstract

Understanding the biological effects of temperature on fish is essential for effectively managing stream temperature under the Clean Water Act.   One of the key elements of water quality management is to establish temperature criteria (e.g., water quality standards) that will limit human-caused impacts to the beneficial uses of the stream (e.g., fish). Ideally, criteria are based on an understanding of the interaction of fish physiology and ecology (biological effects) and the physical watershed and climatic processes that control the temperature of streams (exposure). Scientific understanding of these factors should then lead to criteria that are realistic and appropriate in assigning a temperature threshold that appropriately reflects temperature. In this section, we review and compare methods of determining temperature criteria used to select criteria, including those developed in this report.

Key findings of this chapter are:

❑   Risk assessment allows the effects of magnitude, duration and frequency of temperature on fish growth and survival to be quantified in an objective and repeatable manner.

❑   The U.S. EPA (1977) temperature criteria were found to be the most objectively defined and consistent with risk analysis results. They generally appear to allow up to 20% reduction in growth due to temperature.

❑   Criteria derived from review of scientific literature without quantitative synthesis are generally consistent with risk assessment and U.S.EPA methods, although they tend to overestimate the benefits of cold temperatures and slightly underestimate the positive growth effects at temperatures somewhat higher than optimum.

Introduction

From a scientific basis, methods for deriving temperature criteria should be explicitly defined and based on sound scientific data that pass data quality screening criteria (ASTM 1997). A criteria derivation protocol needs to have:

❑   clearly defined, transparent and repeatable methodology;

❑   data quality objectives, attributed data sources, and quality control screens;

❑   defined levels of protection for species populations, communities or ecosystems;

❑   stated assumptions, safety factors, and data extrapolation factors; and

❑   temperature criteria that incorporate magnitude, frequency, and duration as decision variables.

In previous sections of this report we: reviewed the scientific literature elucidating the growth and acute lethal response of salmon to temperature during the rearing life history phase (Section 2); explored relationships between long-term and short-term temperature indices (Section 3); performed risk analysis on the effects of temperature on mortality of salmon (Section 4); developed a quantitative method to asses effects of long-term exposure to temperature on growth (Section 5); and established temperature threshold criteria (Section 6).   In this section we evaluate water quality temperature criteria derived from several methods that have been adopted or proposed by various authors and agencies relative to their biological effects, including the analyses developed in this report.

Criteria and Methods To Derive Them

Review of scientific literature and agency policy documents identified a number of different approaches to derive water temperature criteria for the summer maximum temperature. Methods fall into three general categories:

❑   criteria derived from experimental temperature tolerance studies;

❑   criteria derived from field observations of fish occurrence under different temperature regimes; and

❑   criteria derived from professional review of temperature information.

The degree of objectivity or subjectivity by which the information is synthesized into recommended criteria, the degree to which data forms the basis for the criteria, and the extent to which population effects can be probabilistically determined varies between methods.

Experimental Information-based Method (EPA)

The EPA has published temperature criteria for a number of fish species based on a review of laboratory-based research on the thermal tolerance of fish (Brungs and Jones, 1977, also cited as U.S.E.P.A. 1977). Brungs and Jone's method includes identification of acute and chronic threshold values, definition of averaging time of specific daily temperature characteristics, and explicit treatment of safety factors to ensure the recommended criteria control population level effects. Temperature criteria are based on temperature tolerance studies that generally follow the protocols developed by the NAS/NAE (1973). These protocols include procedures to derive specific temperature criteria for both chronic and acute exposure. Criteria for chronic exposure are derived from incipient lethal temperature and physiological (bioenergetic) performance (e.g., growth optima) data. The temperature assessment methods described in Sections 4,5 and

6 of this report are based on similar data such as the acute lethal and growth temperature/ration relationships.

From the perspective of selecting temperature criteria, some very simple principles can be derived from the growth curves that are meaningful (Figure 5.4). Beginning with the coolest temperatures (0°C), growth increases with temperature up to the temperature up to optimal where the maximum growth rate is achieved without any increase in ration (approximately 16°C). This improved growth is due to increased food conversion efficiency and consumption. At temperatures above the maximum growth rate, growth rates cannot be maintained because consumption declines and metabolic energy costs increase. Further increases or maintenance of growth rate must come from increased food, if possible within satiation limits. Because the shape of growth curves is broad at the maximum, there is little or no negative effect of temperature several degrees above optimum.

Brungs and Jones (1977) describe an objective method for developing threshold criteria based on optimal temperature and the range of preferred temperatures from laboratory derived growth curves available at the time. The criterion for chronic exposure is expressed as the maximum seasonal 7-day moving average of the daily mean temperature. Brungs and Jones (1977) refer to this metric as the "maximum weekly average temperature" (MWAT). This value may be derived for different seasons and life stages (e.g., summer rearing or fall/winter incubation). The scientific rationale for using the MWAT as a temperature limit is based on data showing that moderate temperature fluctuations can be tolerated as long as the incipient lethal temperature is not exceeded for long periods. The method also assumes that optimum temperatures are neither necessary nor realistic at all times to maintain viable fish populations (NAS/NAE 1973).

Criteria for protection from exposure to extreme temperatures are based on thermal tolerance data. Regression equations of median survival times (LT50) (e.g., Figure 2.2) are used to predict the upper incipient lethal temperature for a 24-hour exposure, and a 2°C safety factor is subtracted to derive a short-term criterion that will provide 100% survival (Brungs and Jones 1977). Since LT10's and LT50's are very close, the safety factor is sufficient to preclude effects on any fraction of the population.

Protocols for deriving criteria based on experimental temperature tolerance studies have not changed since being proposed by the Environmental Protection Agency (Brungs and Jones 1977). Various authors continue to recommend this method as an option for protecting fish habitat (Armour 1991).

The acute and chronic temperatures for the EPA protocol were computed for the rearing stage of seven native salmonids in Washington using the experimental temperature tolerance data that could be found in the literature (Table 6.1). This includes relevant data reported by the NAS/NAE (1973) and any newer data that could be found. Original criteria reported by Brungs and Jones (1977) are shown for comparison with the updated numbers. Note, the latter results are slightly different than criteria reported by Brungs and Jones (op cit) for the same species because our values are based on data from individual studies and not on the average of several studies. The results from multiple evaluations of the same species produced similar results (usually within 1°C), and differences among salmonid species were relatively small.

Table 7.1 Water temperature criteria (maximum weekly average temperature and acute exposure maximums during growth season) for salmonids based on the EPA methodology (Brungs and Jones 1977). Values reported by Brungs and Jones are shown for comparison.

Species	temp. (°C)	lethal level (°C)[a]	Median Survival Time		optimum	Source	Temperature criteria		
			intercept (a)	slope (b)			(°C)	maximum (°C)	data
Oncorhynchus clarki	13-23 fluctuating	25.5	18.1515	-0.5723	--	(a) Golden 1978	18.50		a, d
cutthroat trout	23	25.7	--	--	--	(b) Golden 1978	18.57		b,d
	16	22.6	--	--	--	(c) Vigg and Koch 1980		24.20	a
	constant	--	--	--	15	(d) Dwyer and Kramer 1975			
Oncorhynchus gorbuscha	24	23.9	14.7111	-0.4459	--	(e) Brett 1952	17.97		e,t
pink salmon								23.91	e
Oncorhynchus keta	23	23.8	15.3825	-0.4721	--	(f) Brett 1952	17.93		f,t
chum salmon	9	23.2	15.9272	-0.5575	--	(g) Blaham and Parente, unpublished in: NAS/NAE 1973	17.73		g,t
								23.89	f
								20.90	g
Oncorhynchus kisutch	23	25.0	18.9736	-0.6013	--	(h) Brett 1952	19.67		h,k
coho salmon	23	25.0				(hh) Dehart 1975			
	10	23.5	18.4136	-0.641	--	(i) Blaham and McConnel, unpublished in: NAS/NAE 1973	19.17		l,k
	10-13 fluctuating	26.0	--	--	--	(j) Thomas et al. 1986	20.00		j,k
	constant	--	--	--	17	(k) Averett 1968		24.30	h
								21.80	l
						Brungs and Jones (1977) estimate	18.00	24.00	
Oncorhynchus mykiss	18	26.5	18.4654	-0.5801	--	(l) Alabaster and Welcomme 1962	20.30		l,o
rainbow/steelhead	20	--	19.625	-0.625	--	(m) Alabaster and Downing 1966	19.17		l,p
	16	25.6	--	--	--	(n) Hokanson et al. 1977	19.83		l,q
	constant	--	--	--	17.2	(o) Hokanson et al. 1977	20.30		n,o
	fluctuating	--	--	--	15.5	(p) Hokanson et al. 1977	18.87		n,p
	fluctuating	--	--	--	16.5	(q) Wurtsbaugh and Davis 1977	19.53		n,q
								24.39	l
								24.35	m
						Brungs and Jones (1977) estimate	19.00	24.00	
Oncorhynchus nerka	23	24.8	20.002	-0.6496	--	(r) Brett 1952	18.27		
sockeye salmon	20	23.5	16.7328	-0.5473	--	(s) McConnel and Blahm, unpublished in: NAS/NAE 1973	17.83		
	constant				15	(t) Brett et al. 1969		23.93	
					15	(u) Shelbourn et al. 1973		22.80	
						Brungs and Jones (1977) estimate	18.00	22.00	
Oncorhynchus tshawytscha	20	25.1	22.9065	-0.7611	--	(v) Brett 1952	21.03		v,x
chinook salmon	20	24.7	21.3981	-0.7253	--	(w) Blaham and McConnel, unpublished in: NAS/NAE 1973	20.90		w,x
	--	--	--	--	19	(x) Brett et al. 1982		23.95	v
								23.15	w

a Data represent the ultimate upper incipient lethal temperature where available or the upper incipient lethal temperature when an estimate of the ultimate level was not available.

Differences between maximum and minimum MWAT and acute criteria are 3.3° and 3.5° C, respectively (Table 6.1). This exercise demonstrates that the EPA method is highly objective and reproducible; there were no difficulties in updating the analysis with results of more recent studies. Brungs and Jones also provide criteria for other life history stages.

Field Observation Methods

Observation of temperature at which fish occurrence is verified is another method used for estimating fish temperature requirements. Bovee (1978) recommended the use of fish observations where temperature is simultaneously collected to determine a "probability of use" curve based on the distribution of observations. This technique of characterizing physical environmental conditions in conjunction with fish observations forms the basis for the U.S. Fish and Wildlife Service Instream Flow Incremental Methodologies (IFIM) Habitat Suitability Index model (HSI) (McMahon 1983). This method has been used to evaluate population effects from physical habitat alterations. Presumably, this method would reflect preference temperatures of the fish, but their quantitative relationship to optimal temperature, growth, or lethal temperatures cannot be known since results would also strongly reflect the ambient temperature occurring when observations were made and may not indicate true preference or long-term exposure.

Eaton et al. (1995) proposed a technique for deriving the maximum thermal tolerance of fish matching stream temperature records with fish presence data. Their fish and temperature data matching system (FTDMS) provides a direct measure of the temperatures that are utilized by fish populations in nature. In this protocol, fish presence data are matched with weekly mean temperatures taken from the same location and time period to derive a fish presence by temperature frequency distribution. An estimate of the maximum temperature tolerance for a species is assumed to be equivalent to the temperature at which 95% of the fish observations occur for a large (n = 1000 matches) database that represents the geographic range limits of the species. The 95th percentile observation is proposed as a safe estimate of thermal tolerance to protect against inaccuracies in temperature records and biased observations of fish presence that may be contained in the database.

The FTDMS is recommended as an approach for determining the maximum temperatures that limit the distribution of salmonids. With regard to temperature criteria, this method seems to relate best to the acute temperatures rather than the chronic temperatures. Table 7.2 lists the mean weekly temperature derived from over 1000 field observations (Eaton et. al 1995). The field observation method of establishing upper lethal limits suggested by Eaton et al. (1995) produced very similar results to those of Brungs and Jones

Table 7.2 Water temperature criteria for salmonids based on the fish and temperature data matching system (FTDMS). Taken from Table 1 in Eaton et al. (1995).

Species	Mean weekly temperature (°C) for the 95th percentile observation
Oncorhynchus clarki (Cutthroat trout)	23.2
O. gorbushcha (pink salmon)	21.0
O. keta (chum salmon)	16.8
O. kisutch (coho salmon)	23.4
O. mykiss (steelhead/rainbow trout)	24.0
O. tschawytscha (chinook salmon)	24.0

(1977) which were based on laboratory tests (Table 7.1): field observation estimates were within 1°C of EPA's acute temperature criteria for all salmonids except chum salmon. These observations suggest that laboratory derived criteria can predict the thermal tolerance limits in nature reasonably well.

RISK ASSESSMENT APPROACH

The temperature assessment methods described in Sections 5 and 6 followed a risk assessment approach and provided a time-integrated and quantitative estimate of the influence of the temperature regime on the potential growth of salmon within selected stream reaches where temperature was known. This approach could be used to develop site-specific or regional temperature criteria for both acute and chronic effects on summer rearing. Here we use the results of the acute and growth analyses to evaluate generally applied temperature indices used as temperature criteria. The assessment of acute temperatures suggested that 26°C is threshold temperature for salmonid species (Section 4).

The reduction from maximum potential growth due to temperature regime was calculated for a number of stream segments with widely varying temperature regimes in Section 6, based on a growth model developed in Section 5. The range of temperatures where growth was within 10% and 20% of optimum based on those analyses is shown in Figure 7.1. For each temperature indices, coho and steelhead reduction from maximum growth (RMG) are
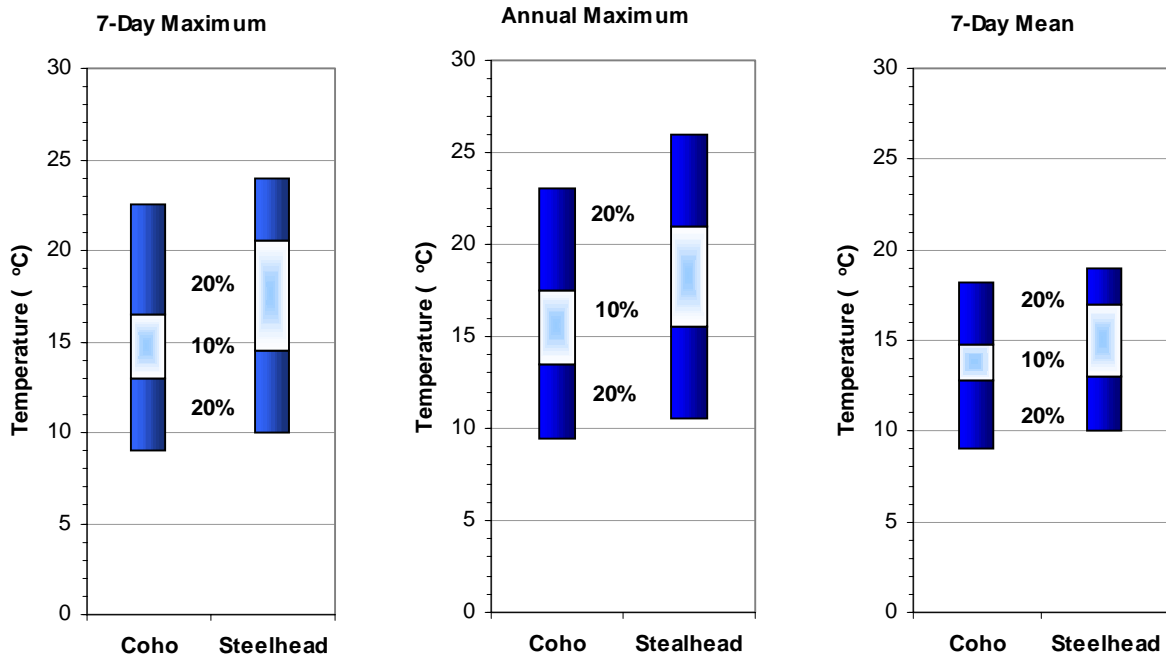
Figure 7.1 Range of temperature where reduction from maximum potential growth (RMG, %) was 10 and 20% during the summer months for coho and steelhead, using three temperature indices.   (See Section 6 for methods and Table 6.2 for results by site. RMG is greater than 20% at temperatures outside of the temperature ranges indicated. RMG is minimized near the optimal temperature for each species and increases at temperatures warmer or cooler than the optimal.

plotted together to facilitate comparison among species. Growth is highest within the range of optimal temperatures, and declines at temperature higher and lower than optimal.

There is a narrow range of temperature where growth is optimized for each species. Growth rate is highest at sites with 7-day maximum temperatures between 9°C to 17°C. Patterns are similar for other temperature indices (7-day mean and annual maximum temperature), although the temperature range enveloping various levels of growth reduction vary with each temperature index.

Steelhead and coho often occur together in stream environments, and their growth responses are similar, although there are important differences in threshold values. Selecting the criteria based on the 10% RMG for the more thermally sensitive coho would suggest an upper threshold of 16.5°C for the 7-day maximum temperature and 14.8°C for the 7-day mean temperature. Selecting the criteria based on the 10% RMG for the steelhead would suggest an upper threshold of 20.5°C for the 7-day maximum temperature and 17.0°C for the 7-day mean temperature. The upper end of the temperature range is well below temperatures where behavioral avoidance has been observed (e.g. Bisson et al. 1988, Nielsen et al. 1994), and interspecies competitive interactions have been noted (e.g., Reeves et al. 1987; Taniguchi et al. 1998).

Table 7.3   Temperature criteria (°C) for growth of juvenile salmonids derived from temperature analysis at values of reduction from maximum growth (RMG) of 10% and 20%.

Temperature Index	Coho		Steelhead		MWAT (Updated EPA method (Table 6.1)
	10% RMG	20% RMG	10% RMG	20% RMG	
7-day Maximum[a] (°C)	13.0-16.5	9.0-20.5	14.5-20.5	10.0-24	
7-day Mean[b] (°C)	12.8-14.8	9.0-19.0	13.0-17.0	10.0-19.0	19.7 coho 19.6 steelhead
Annual Maximum[c] (°C)	13.5-17.5	9.5-23.0	15.5-21.0	10.5-26.0	

[a]maximum value of the 7-day moving average of the daily maximum temperature;

[b]maximum value of the 7-day moving average of the daily mean temperature;

[c] instantaneous maximum observed during the summer;

The growth effects predicted by the criteria will be the same wherever the fish live. Even though streams for resident trout may be naturally colder due to proximity to headwaters, the growth/food/and temperature effects should be the same. It should also be noted that these criteria are only appropriate for streams with normal seasonal and daily temperature fluctuations. Streams or other aquatic environments (e.g., thermal plumes at discharge sites) with significantly different temperature patterns would require site specific analysis, i.e., characterization of their temperature regimes to determine exposure.

Review Approach

Temperature criteria derived by the review approach are based on the professional interpretation of temperature requirement information organized by life stages and time periods for each species of interest. These temperature requirements are derived primarily from key review articles (e.g., Bjornn and Reiser 1991, Bell 1973, 1986). Measurements of performance optima from laboratory studies and field observations of temperature during different life stages may also be used.

Criteria, for example, are derived by selecting a temperature regime low enough to protect the most sensitive life stage for the summer juvenile rearing period. Protection of this life stage is assumed to protect all other life stages that may occur at the same time (e.g., adult holding). The review method is not a defined protocol, but rather is a general approach for evaluating temperature information. Review-based approaches are inherently more subjective as analysts attempt to explicitly synthesize a number of factors and species into one recommended criteria.

Table 7.4. Examples of four water temperature envelopes by life stage summaries for spring chinook salmon. (Temperature in °C.)

Life stage	Bell (1973)	Bjornn and Reiser (1991)	Armour (1991)[a]	ODEQ (1995)
Adult migration	3.3-13.3	3.3-13.3	3.3-13.3	3.3-13.3
Spawning	5.6-13.9	5.6-13.9	5.6-13.9	5.6-12.8
Incubation	5.0-14.4	5.0-14.4	5.0-14.4	4.5-12.8
Juvenile rearing	Optimum 7.2-14.4	Preferred 12-14	7.9-13.8	Positive growth 4.5-19.1 Optimum production 10.0-15.6

[a]All data are for the recommended temperature range

Data linking fish performance and temperature are evaluated by a professional, or group of professionals, who identify the temperature range that provides some level of protection. While the analysis may include laboratory or field derived data, the manner in which such data are used is not explicitly defined, as it is in the EPA and FTDMS methods (e.g. ODEQ 1995, WDOE 1998a). Also, the level of protection[1] generally is not explicitly defined and appears to vary depending on policy objectives and the amount of available information.

Bell (1973) conducted one of the first reviews of temperature to establish criteria, compiling most of the information known at the time, and presented the data in the form of temperature ranges or envelopes by species and life stage. Bell (1973) synthesized a temperature range from the available information to provide a recommendation. However, he did not describe the method by which the recommendations were derived, including consideration of safety factors, and he did not attribute the recommendations with specific citations (i.e., only a list of references is given). Thus the scientific source for each recommendation cannot be verified and the primary data sources that may have been used are not directly tied to the final recommendations.

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[1] Level of protection refers to what percentage of the individuals representing a race, subspecies or species are protected (e.g., 90, 95 99, 100%). Similarly, it refers to the percentage of streams that would be protected, and what percentage of the time. For example, a goal may be to protect 95% of the salmonid races and streams 95% of the time.

A series of subsequent reviews have relied heavily on the work of Bell (1973) to develop and revise temperature criteria. For example both Armour (1991) and ODEQ (1995) cite Bjornn and Reiser (1991) as the source for some of their temperature recommendations. Bjornn and Reiser (op cit) reference Bell (1986), which is the second edition of Bell (1973), as source for their temperature information. The Bell (1973) report is also the basis for U.S. Fish and Wildlife Service recommended temperature criteria for coho salmon (Laufle et al. 1986), chinook salmon (Allen and Hassler 1986), and steelhead trout (Pauley et al. 1986). These references are also cited for temperature criteria in the "ManTech Report" sponsored by the National Marine Fisheries Service (Spence et al. 1996). The interdependence of these review reports results in recommended temperature criteria that are remarkably similar. For example, chinook criteria shown in Table 7.4 are the same in each of four different papers.

This review approach has formed the basis for temperature criteria in the Pacific Northwest in recent years, despite the lack of firmly documented primary data (ODEQ 1995, WDOE 1999). Criteria developed in Oregon (ODEQ 1995) and proposed in Washington (WDOE 1999a) appear to be based on less quantitative approaches than advocated by Hokanson (1977), Brungs and Jones (1977), Armour (1991) and Eaton et al. (1995), although experimental biological effects data are available for this purpose. The primary weaknesses of review approaches are the absence of a clearly defined decision process for selecting and evaluating temperature information, synthesizing factors of safety and uncertainty into the criteria, and lack of clear linkages to field and laboratory data. In some cases, the numbers for juvenile rearing derived from literature reviews are consistent with those produced from risk analysis and other quantitative methods (e.g., Bjornn and Reiser 1991). However, in most cases, the recommended ranges assume greater growth at lower temperatures than is likely to occur and less growth at warmer temperatures.

Temperature Criteria

Existing and proposed temperature criteria, including objective criteria and those that were derived primarily by the review method described above, are presented in Tables 7.5 and 7.6. Only criteria relevant to the growth period of juvenile salmon and trout, exclusive of bull trout, are shown for this example. The Oregon temperature criteria combine trout and salmon species together, with a different standard for bull trout. The proposed Washington criteria group salmon species and steelhead with one criteria, and cutthroat trout for another. Washington's proposed criteria also vary the maximum temperature by specified periods during the summer months, a detail we will not address during subsequent analyses.

Table 7.5 Existing and proposed temperature criteria for anadromous salmon species and steelhead derived from various methodologies relevant to the summer growth period. Numbers are maximum allowable values.

Method	ACUTE Temperature (°C)	ACUTE Metric	SUB-LETHAL Temperature (°C)	SUB-LETHAL Metric
EPA (Brungs and Jones 1977)	24.0	Annual instantaneous maximum [a]	18.0	Maximum 7-day moving average of the daily mean
Eaton et. al. (1995)	23.5	Maximum 7-day moving average of the daily mean	--	--
Risk Assessment (this report)	25.5	Annual instantaneous maximum [a]	16.5	Maximum 7-day moving average of the daily maximum
ODEQ (1995)	None specified	--	17.8 (64°F)	Maximum 7-day moving average of the daily maximum
WDOE proposed (1999)	21.0 (June-Sept)	Annual instantaneous maximum	16.5	Maximum 7-day moving average of the daily maximum
WDOE (current)	None specified	--	16.0 (AA)[b] 18.0 (A) 21.0 (B)	Annual instantaneous maximum

[a] assumed at least a 1-hour interval
[b] streams are classified as AA, B and C according to WAC 173-201-080

Each criterion/standard in Tables 7.5 and 7.6 typically is assumed to represent the no-effect level for the most sensitive life stage of the most sensitive species, plus a safety factor. The EPA's goal is to protect 95% of the species 95% of the time. This level of protection is extended to include economically important species, ecological keystone species, and threatened and endangered species (Stephan et al. 1985). Other groups of scientists have suggested that protecting 90% of the species will protect aquatic communities (SETAC 1994). It is not always necessary to protect 95% of the individuals in a population when it is desired to protect the species, based on rationales presented by Ricker (1975). However, in the case of the ODEQ and WDOE criteria, the actual level of protection embodied in the criteria has not been defined.

Temperature criteria from the various methods have the following similarities and differences (Tables 7.5 and 7.6):

- Most index the juvenile growth phase, which lasts several months, with the warmest 7-day period occurring during that interval.

- No criteria use an averaging period longer than a week. One specifies the annual instantaneous maximum (e.g., Washington's existing temperature criteria).

- Criteria vary in whether the daily maximum or mean is used to calculate temperature during the averaging period.

- No criteria state an acceptable level of variation in the threshold temperature, indicating that are likely to result from natural factors and uncertainty.

- Some criteria do not specify upper acute temperature levels, relying instead on the temperature criteria derived for chronic effects to control maximum temperature.

- For most of the criteria, the temperature range of 16° to 18^oC is used as the upper maximum.

- No criteria establish a minimum threshold temperature.

The temperature criteria derived from the review approach are more variable, although much of the data used are similar among the evaluations (ODEQ, 1995 WDOE, 1999). The Oregon and proposed Washington criteria are reasonably similar to the EPA criteria for salmonids (Tables 7.5 and 7.6).

The differences in the temperature indices used by different sources makes it difficult to compare them. In Table 7.7 we translate each recommended threshold to each of the short-term indices, using the relationships between indices shown in Figure 3.7 (Section 3). When placed on a common footing, it is evident that there are differences among the recommended criteria.

Table 7.6 Existing and proposed temperature criteria cutthroat trout derived from various methodologies relevant to the summer growth period. Numbers are maximum allowable values.

	ACUTE		SUB-LETHAL	
Method	Temperature (^oC)	Metric	Temperature (^oC)	Metric
EPA (Brungs and Jones 1977)	24.2	Annual instantaneous maximum [a]	18.5	Maximum 7-day moving average of the daily mean
Eaton et. al. (1995)	23.2	Maximum 7-day moving average of the daily Mean	--	--
Risk Assessment (this report)	26.3	Annual instantaneous maximum [a]	16.5	Maximum 7-day moving average of the daily maximum
ODEQ (1995)	None specified	--	17.8 (64^oF)	Maximum 7-day moving average of the daily maximum
WDOE proposed (1999)	14.5	Annual instantaneous maximum[a]	13.0	Maximum 7-day moving average of the daily maximum
WDOE (current)	None specified	--	16.0 (AA)[b] 18.0 (A) 21.0 (B)	Annual instantaneous maximum

[a] assumed at least a 1-hour interval
[b] streams are classified as AA, B and C according to WAC 173-201-080

Table 7.7 Threshold temperatures for short-term duration indices from various sources. Temperatures have been translated to common values using relationships among temperature indices developed in Section 3 (see Figure 3.7). Values in bold type are original reported numbers. Authors report recommendations in a variety of metrics. Each recommended value is also translated to the other metrics using the regression relationships presented in Section 3 to facilitate their comparison.

Species	Reference	Sub-Lethal Thresholds			Acute Threshold--
		Annual Maximum Temperature (°C)	7-Day Maximum (°C)	7-Day Mean (MWAT) (°C)	Annual Maximum Temperature (°C)
Coho salmon	EPA 1977	21.5	21.2	**18.0**	**24.9**
	Risk assessment (this report)	**17.5**	**16.5**	**14.8**	**25.5**
	ODEQ (1995)	19.0	**17.8**	16.0	--
	WDOE (existing)	**16.0**	15.5	14.3	--
	WDOE (proposed)	17.0	**16.5**	15.0	21.0
	Eaton (1995)	--	--	**23.4**	30.5
Steelhead trout	EPA 1977	24.0	23.0	**19.0**	**26.0**
	Risk assessment (this report)	**21.0**	**20.5**	**17.0**	**26.0**
	ODEQ (1995)	19.0	**17.8**	16.0	--
	WDOE (existing)	**16.0**	15.5	14.3	--
	WDOE (proposed)	17.0	**16.5**	15.0	21.0
	Eaton (1995)	--	--	**24.0**	31.0

The temperature analysis developed in this report produced similar though not identical criteria to those developed using a variety of other methods.   The thresholds derived from the risk assessment methods are somewhat lower than the EPA recommendations (Brungs and Jones 1977), largely because of the restriction to 10% growth loss and the realistic accounting of food consumption. Brungs and Jones (1977) used the **7-day mean temperature** (MWAT) of 18°C for coho and 19°C for steelhead. The growth analysis suggests that an upper threshold for the 7-day mean temperature of 14.8°C for coho and 17.0°C for steelhead will maintain growth within 10% of optimum, and 19°C will maintain growth within 20% of optimum.

Eaton et al. (1995) primarily studied the upper temperature limiting salmonid distribution but not growth. Their numbers are several degrees higher than our recommendation for acute thresholds. Indeed, their thresholds are so high that it would suggest that coho and steelhead still live in natural streams until maximum temperatures reach upper critical lethal levels for a significant period of time (at least 1 week). This appears to confirm that the thresholds we have identified are conservative and not likely to result in population loss. No site included in the risk assessment had 7-day mean temperature anywhere close to the upper threshold that limits distribution, although this was not true for some rivers in the region found in U.S.G.S. water resources records (see Appendix B). Coho, steelhead

and/or cutthroat trout were present in all of these streams. We estimate that growth loss due to temperature for Eaton's (1995) upper limits for coho and steelhead would be approximately 50%.

Temperature criteria derived with the risk-based methods have only moderate agreement with criteria derived through various reviews. It appears that the review approach tends to recommend similar temperatures for the lower end of the range but lower temperatures for the upper end of the range, than was found by risk analysis and other methods. While the example ranges we cite are for chinook salmon, the temperature response curves for coho (this report) are very similar to those of chinook (Brett et al. 1982). It is difficult to directly compare with recommendations from these reviews since no indexing temperature measure is provided.

ODEQ (1995) criteria appear to match results of the growth assessment reasonably well, despite its reliance on reviews rather than laboratory data. ODEQ (1995) specifies the maximum 7-day temperature at 17.8^{o}C. The **7-day maximum** criteria derived for coho are 16.5^{o}C for 10% growth reduction and approximately 19°C for 20%. However, if just steelhead were considered, the threshold would be 20.5^{o}C for 10% growth reduction.

Current WDOE criteria specifying an **annual maximum** of 16°C for Class AA streams are lower than that derived from the risk assessment approach. Risk assessment suggests the annual maximum should be between 13.5^{o}C and 17.5^{o}C for coho, or between 15.5 ^{o}C and 21.0^{o}C for steelhead, to maintain no more than 10% growth loss. The current criteria for Class A (<18°C) and Class B (21°C) streams is more comparable to risk assessment results. The proposed temperature criteria published as a discussion draft by WDOE (1999) are very similar to those derived with the growth assessment for 10% growth loss for coho; 16.5^{o}C 7-day maximum for all anadromous salmon rearing. This criteria is lower than needed for steelhead.

Discussion

The quantitative analysis confirmed that biologically meaningful temperature thresholds could be identified with and of the indices (annual maximum, 7-day maximum or 7-day mean). There is no consensus on what index to use for temperature criteria, introducing additional confusion in comparing among them. This study found that all of the most typical indices are closely related to one another, and that any could be used with satisfactory results. The 7-day mean temperature was most closely correlated with growth loss estimates and therefore may be the best indexing measure for this purpose. However, other measure are quite suitable. It is important that the selected temperature match the time-averaging period appropriately. It should be noted that the longer the averaging period, the lower the threshold value.

The growth analysis developed in this paper can form a basis for selecting temperature criteria, but some other methods also were reproducible and produced similar though not identical results. The risk assessment results described in this report rely on similar laboratory data as used by Brungs and Jones in developing EPA recommendations (1977). Our results suggest lower criteria by a few degrees, primarily because we use observed temperature regimes to estimate the growth of fish over the long-term, and because we account for realistic estimates of food consumption. Analyzing temperature relative to duration did affect the choice of thresholds. In the case of coho, temperature thresholds

were lowered, while in the case of steelhead the thresholds were similar, and could possibly be raised.

CONCLUSIONS

❑ Risk assessment-based approaches allows the effects of magnitude, duration and frequency of temperature on fish growth and survival to be quantified in an objective and repeatable manner.

❑ Moderate temperatures are likely to be more biologically productive for salmonid species than very warm or cold temperatures at the level of food availability that appears to exist in streams.

❑ The U.S. EPA (1977) temperature criteria were found to be the most objectively defined and consistent with risk assessment results. They generally appear to allow up to 18% reduction in coho growth due to temperature.

SECTION 8 A DISCUSSION OF THE SCIENTIFIC AND MANAGEMENT IMPLICATIONS OF FINDINGS

Introduction

In this section we review the information presented in the report and identify the scientific and management implications of the results. This section serves as both a summary of key findings and a synthesis of information for scientists and policy-makers.

For ease of reading, we conduct this discussion without extensive referencing from within the report or from external documents or the scientific literature. Although these sources of information are critical for the context of this discussion, they have been described and referenced in detail in the main body of the report. We have included several key figures found in previous chapters.

The Regulatory Context of Temperature Criteria

The Clean Water Act requires states to protect the public's values for water bodies. To administer the CWA, the state water quality agencies must:

- assign beneficial uses to each water body (e.g., fishable, swimmable, aquatic life),
- specify water quality criteria that are sufficient to protect the designated beneficial uses,
- assess and report on the condition of water bodies relative to those criteria (305b),
- identify the sources of pollutants,
- develop various management steps to protect or restore water body conditions to meet criteria,
- monitor the water quality on an ongoing basis.

The type of regulatory activities and management restrictions that may be imposed depends on the current and projected condition of the water body relative to the criteria. Therefore, the water quality criteria have enormous legal and economic meaning, and their appropriateness is of great concern to the public, scientists, and regulators.

States have specified fish species in the cold water guild (salmon and char) as the designated beneficial uses in many streams and rivers of the Pacific Northwest region. Water temperature plays a role in virtually every aspect of fish life, and adverse levels of temperature can affect behavior (e.g. feeding patterns or the timing of migration), growth, and vitality. Fish have ranges of temperature wherein all of these functions operate normally contributing to their health and reproductive success. Outside of the range, these functions may be partially or fully impaired, manifesting in a variety of internal and externally visible symptoms. Fish have a number of physiologic and behavioral mechanisms that enable them to resist adverse effects of temporary excursions into temperatures that are outside of their preferred or optimal range. However, high or low temperatures of sufficient magnitude, if exceeded for sufficient duration, can exceed their ability to physiologically adapt and can cause growth or weight loss, disease, competitive

displacement by species better adapted to the prevailing temperature, or even death. Fish are adapted over some evolutionary time frame to the prevailing water temperatures, and climatic gradient is among the primary factors that determine the extent of a species' geographic distribution.

States in the Pacific Northwest have authorized numeric temperature criteria to protect fish for nearly three decades. Many are currently reviewing their criteria in the triennial review process specified in the Clean Water Act, with the help of the U.S. EPA, who must also approve them. Many streams and rivers in the Pacific Northwest region have been identified by the states as exceeding their current water quality criteria according to their 305b reports to Congress, with a large number of them listed for temperature impairment (303d lists). To further add to public concern, specific species or stocks within the salmon and char genera have also been listed as threatened or endangered under the Endangered Species Act in a number of geographic locations. The ESA does not require identification of a specific "pollutant" causing population decline, but high levels of stream temperature during the summer months are widely viewed as one of the primary habitat conditions that contributes to the decline of cold water fish species in freshwater habitats.

Effects of Temperature on Salmonids

Figure 8.1 The general biological effects of temperature on salmonids. Effects depend on the level of temperature and its duration. Two important elements of temperature affect the growth and survival of fish: 1) the relationship between temperature, metabolism and food conversion efficiency as it controls growth over relatively long periods, and 2) the thermal tolerance of fish to lethal temperatures over relatively short periods. Fish have various physiological and behavioral mechanisms that enable them to resist adverse effects of temporary excursions into temperatures outside of their preferred or optimal growth range but within the upper critical lethal limit.

The Characteristics of Temperature Criteria

Temperature criteria typically have two key elements—a threshold temperature that signals when adverse biological response is likely to occur, and an averaging period that indexes the duration of exposure likely to trigger that response. The combination of the threshold temperature and the duration of exposure to that temperature are an expression of the risk imposed by the environmental temperature to the targeted fish species. Because of the ability of fish to acclimate and adapt to temperatures outside of their optimal conditions, both exposure duration and magnitude of temperature are necessary to determine the degree of risk that this fluctuation may pose to each species. Environmental temperature can annually range over the entire spectrum from optimal to adverse in response to the cyclic movement of the sun. Exposure to temperature is mediated by

stream, geographic, and riparian forest characteristics. A factor of safety is typically added when selecting numeric criteria to account for the uncertainties in knowledge associated with each of these elements and any factors that are not unaccounted for.

The averaging period has typically been either the annual maximum temperature (observed for a period as short as an hour, but more probably occurring for several hours on sequential days), or a weekly average (generally focused on the warmest seven consecutive days) observed for the year. For example, Washington's current criteria specify the annual maximum temperature, expressed as the maximum hourly temperature that occurs each year. Oregon specifies the average of the daily <u>maximum</u> temperature of the 7 warmest consecutive days. The U.S. EPA (1977) recommends the average of the daily <u>mean</u> temperature of the 7 warmest consecutive days (MWAT). Some have also argued that the daily temperature fluctuation should also be accounted for, but this characteristic has not been widely specified in states' criteria.

The Basis for Derivation of Temperature Criteria

A number of different approaches have been used to develop and justify the temperature criteria that are currently widely used in the Pacific Northwest region. All draw upon a large body of scientific research focused on the thermal tolerance of fish. There has been considerable laboratory testing for many fish species, including salmonids, beginning early in the 1900's and continuing today. Much of the available research on temperature tolerances was performed prior to 1980 and was stimulated principally by the need to assess the impact of heated effluent from power plants, dams and other facilities. Since that time, the research focus has been to add species and refine the understanding of contributing factors such as the effect of acclimation temperatures, daily diurnal temperature fluctuations, and food rations, and to enhance understanding of the interaction of temperature with other pollutants. A considerable amount of the available research has been performed in the laboratory setting. Ecological field studies have lagged behind laboratory work, although their application has increased in recent years.

Various methods have been used to analyze temperature effects on fish to develop criteria. The methods vary in terms of degree of objectivity or subjectivity by which the information is synthesized into recommended criteria, the degree to which data forms the basis for the criteria, and the extent to which population effects can be probabilistically determined. The temperature criteria in use in Pacific Northwest states have largely been drawn from professionals' review and interpretation of available scientific literature (e.g. ODEQ 1995). There also has been some effort to use the more well-established scientific relationships to synthesize objective analyses of threshold temperatures and the duration of exposure (e.g., U.S. EPA 1977). This approach has not been widely integrated into regulatory activity.

In recent years, the EPA and the National Academies of Science and Engineering have promoted risk assessment techniques to develop water quality criteria, including protocols that have been peer-reviewed nationally. Risk assessment is designed to enhance understanding of the potential adverse effects of a pollutant on a species by combining the information from biological studies with an analysis of each population's potential exposure to those effects. These methods are formal, objective, and analytical. They have been primarily applied to contaminant pollutants; guidance for other pollutants is still under development. Risk assessment can lead to site or season-specific criteria.

To date, naturally occurring "pollutants", such as water temperature, have not been addressed with risk assessment techniques to determine criteria. Instead, temperature criteria generally are simple indices that summarize the seasonal and diurnal range of temperature observed in natural streams into the averaging period, and that address the complex array of biological responses of all of the life functions with the temperature threshold value. Although there is a general interest in tailoring criteria to specific life functions at specific times of year, this has not been widely accomplished to date. In most states, simple numeric indices are applied over broad regions to primarily address the high temperatures that may occur during the warm summer months, targeting the most sensitive species that are likely to occur in the water body. The methods described earlier fall short of the objectively rigorous expectations of formal risk assessment.

Criteria selection teams are faced with a challenge. It is difficult to match simple criteria to multi-species communities dwelling in streams and rivers whose temperatures naturally vary with position in watershed and climate. Specifying the wrong criteria could have negative, possibly catastrophic, biological consequences. At the same time, the need for management solutions that may accompany even small changes in criteria can have large economic and legal consequences. In addition, all approaches to developing biologically meaningful temperature criteria face significant technical challenges. Some of these stem from the selection process itself. Subjective reviews often lack a clearly defined decision process for selecting and evaluating temperature information, and they fail to establish a clear linkage between field and laboratory data. Furthermore, subjective evaluations often use unquantified safety and uncertainty factors.

The more that scientific research can be used to quantitatively assess the extent that risk to fish is minimized, such as those promoted as risk assessment techniques, the more confident the public and regulators can be that temperature criteria are protective. Such confidence does not currently exist. Over the past 25 years since temperature criteria were first adopted, there has been considerable debate over them but little scientific experimentation to validate or improve them. While the subjective analyses that form the basis of current temperature criteria are apparently consistent with the scientific literature, they have failed to generate measurable hypotheses that can be scientifically tested and rejected.

The objective of this report was to synthesize relevant temperature research and to develop quantitative risk assessment techniques that could be objectively applied to natural streams 1) to identify the risks posed by ambient temperature and to suggest temperature criteria, and 2) to formulate experimentally testable hypotheses. Analysis focused on the summer rearing phase of juvenile salmonids because most existing temperature criteria target annual maximum temperatures, salmonids are of primary interest in much of the Pacific Northwest region, and there is a rich history of laboratory experimentation available to draw from.

Quantitative Analyses to Assess the Effects of Temperature on Fish in Natural Environments

The conceptual approach that frames this report is that temperature is a fundamental component of fish habitat. Water temperature is the thermostat that controls energy intake and expenditure. The overall success of individual fish is partially a result of the cumulative effect of its environmental temperature on its ability to grow and survive over

time. If energy intake is adequate to fuel the physiological energy consumption, mediated in large part by the environmental temperature, then the organism can live in a healthy state. The individual is not likely to be healthy if the water temperatures force energy consumption at a pace that cannot be sustained by food intake, dictated in part by appetite and in part by food supply, for long periods of time. If the duration of moderately negative temperatures is fairly short, cessation of feeding or refuge seeking by the individual fish may be sufficient to withstand short-term excursions into higher temperatures. If this continues for long, the fish loses growth opportunity, and may be displaced by competitors in the population. If temperatures reach a more severe level of impairment, it creates physiological stress, loss of appetite, and can leave the fish open to disease and competitive pressures from other species. Stress is exacerbated at high temperature because dissolved oxygen content of the water is inversely related to its temperature. If temperatures reach very high levels, it invokes significant stress that causes immediate death. For salmonids, this temperature occurs at approximately 30°C. Low temperatures can also induce cessation of feeding, but unless water freezes, the fish also can withstand excursions into cold water temperature by limiting activity. Temperature is not the only ecological factor of importance to biologic productivity, but if its central effect on the individual can be accounted for, then the influence of other environmental factors, such as food supply and population dynamics, may become more apparent in the complex ecology of natural environments.

We work from the assumption that there is a continuum of biologic response to temperature that ranges from healthy, as indicated by maximum growth, to unhealthy, culminating in direct mortality. Along this spectrum there are a variety of ways that temperature effects manifest in the organism's physiologic condition or its behavior. Some of these characteristics can be readily observed in natural environments and are simultaneously amenable to quantification and prediction based on measured temperature. These include the growth (weight change), direct mortality, and embryo development (not addressed in this report). These functions lend themselves to mathematical expressions, many of which have already been established for many species, including salmonids. Laboratory studies have shown that activity rates are closely correlated with temperature and that they can be predicted with some precision with linear or non-linear equations.

We were able to develop models for direct mortality and growth as a function of temperature for several species of salmonids using laboratory data and bioenergetic principles available in the scientific literature (Figure 8.2). An extensive portion of this report describes and corroborates these models. The relationships were formulated in a way that they can be applied in natural ecological settings. The growth model simulates weight gain over time in relation to daily temperature and food supply. Its formulation constitutes a new contribution to modeling fish biological response to habitat factors.

Importantly, the models predict qualities that allow them to be corroborated against measurable population characteristics, and therefore they produce hypotheses that can be rejected by direct observation. The methods are objective and repeatable. Our comparisons of simulated growth (or more specifically weight gain) of 21 populations living in natural streams showed consistent and close agreement with observed weight characteristics (Figure 8.3).

We were not able to fully corroborate the acute temperature model because, when temperature records available to us were scanned for occurrence of combinations of temperature and duration sufficient to cause mortality, none were found. The data

represented a wide variety of streams, including many with high annual maximum temperature. Therefore, although no mortality was reported in the field studies, model predictions cannot be considered fully corroborated until direct mortality is observed at predicted exposures. Failure to detect mortality is consistent with the general perception that direct mortality from temperature rarely occurs within the natural range of a species distribution. Nevertheless, lethal temperatures can and have occurred in the region, and there are situations where further analysis for risk of direct mortality to salmonids is warranted.

Some concern has been expressed that the use of information from laboratory studies to define temperature criteria for fish living in natural streams is inappropriate. Such concerns confuse the synthesis of scientific information into temperature criteria since so much of the most relevant information comes from laboratory experiments. Laboratory and field studies each have unique limitations. Laboratory studies are conducted in highly artificial environments that create stresses from the experimental procedures. Field studies are labor intensive, and discerning the effect of temperature by empirical observation in streams is problematic given the multivariate and dynamic nature of the interaction, and the difficulty of measuring some of the key fundamental relationships in natural

Figure 8.2 The acute and chronic effects of temperature species have been quantified for a number of salmonid species. Direct mortality in relation to exposure time for 4 species is shown in A. If the combination of temperature and continuous duration depicted by the regression lines occurs, 10% of the population is likely to die in each incidence of exceedence. In natural stream environments, stream temperatures must generally exceed the highest short duration temperatures (e.g. 26°C or higher) for there to be a risk of direct mortality because temperatures rarely remain at these temperatures continuously due to natural daily temperature fluctuation.

A.
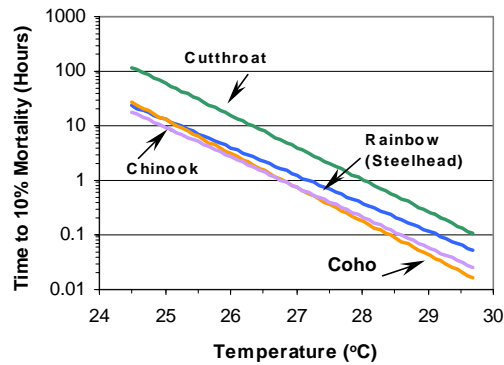
The relationship between daily temperature, food consumption, and growth rate for coho salmon is shown in B. Growth rate is strongly influenced by temperature, with optimal growth occurring when fish feed at satiation ration and temperature is approximately 17°C (optimal temperature for growth). Growth rate declines with temperatures either warmer or colder than the optimal. Growth effects are significant at temperatures greater than 22°C and less than 9°C. Each line represents a level of food consumption. This relationship and one for steelhead (not shown) were used with daily temperature measured in a number of streams and rivers to assess the long-term effect of temperature on weight gain during the summer months. During this period, temperature in many of the study streams ranged over much of the spectrum of positive growth shown by the curves.

B.
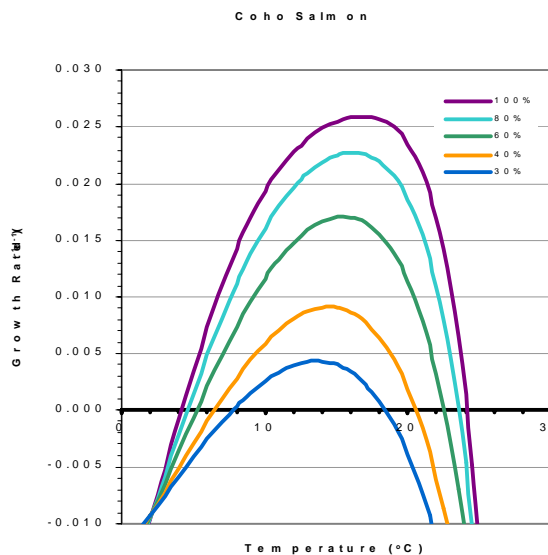
environments. Many scientists have argued that best way to investigate ecological problems involves a combination of laboratory and field experiments.

Our results suggest that laboratory results are of fundamental value in explaining observed fish growth in natural streams. We could not reject the hypotheses regarding growth in relation to environmental temperature using simulations based on the laboratory research. In fact, the simulations were remarkably representative of the observed weight gain of naturally spawned and hatchery-raised populations in streams. We also believe that the direct mortality from the lethal temperature model would predict mortality consistent with the temperatures where death has been observed, but we do not know if the proportion of population experiencing mortality would be as we predict. Confirming this may be important for assessing the environmental factors controlling species distribution, but less important to establishing criteria. Temperature criteria should primarily target sublethal effects to protect fish health.

Some biological responses to temperature can be observed, but they are not amenable to mathematical expression or prediction. These include behavioral responses such as cessation of feeding and seeking refuge, and competitive interactions. There are internal physiological stress effects that stimulate such externally visible symptoms, and additional study associating stress measures with temperature characterization would be a useful augmentation of the analyses of growth. Although associated with environmental temperature, the occurrence of some responses depends on the presence of specific factors such as cold water refuges or disease organisms that respond consistently with the prevailing temperature. (The role of temperature in increasing incidence of disease is particularly problematic since some disease organisms are more virulent in cold temperatures while others are more virulent in warm temperatures.) There are also factors that interact directly, indirectly or independently of temperature, to affect the organism's condition. These include, but are not limited to, ecological constraints on food supply, population interactions, and genetic adaptability. Increased understanding of these in the context of environmental temperature would enhance understanding of the effects of environmental temperature.
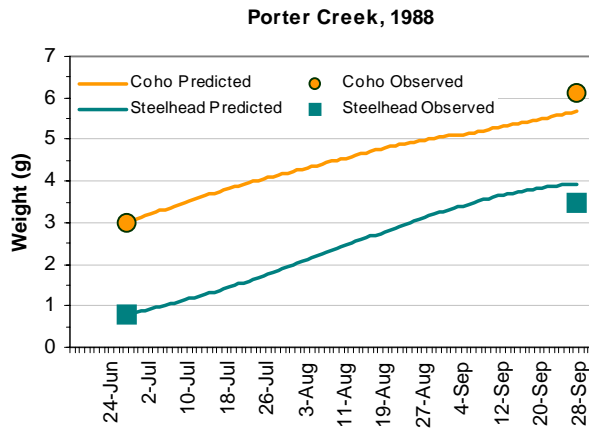
Figure 8.3 Simulation of weight gain for coho and steelhead in relation to temperature and food supply using the growth model developed in this report in relation to observed weight of populations living in natural streams. Model simulations computed daily weight gain using the measured daily temperature and estimates of food consumption derived from observing population growth rates and back calculating how much food had to have been consumed to account for the weight gain between two sampling intervals. Results shown for Porter Creek for both species are similar to those observed at most sites. Overall, predicted weight deviated only 8% from observed on average for both species in 21 population simulations. Such good modeling results establish confidence in use of the model to estimate the effects of temperature on growth for determining temperature criteria. It also confirms the strong signature of prevailing temperature on the size of fish in natural streams.

The Scientific Basis for Translating Quantitative Biological Analyses to Temperature Criteria

A synthesis of the scientific literature supports the premise that the temperatures associated with the spectrum of biologic responses fall between low level growth loss and direct mortality, escalating as temperatures move towards the extremes of the tolerance range. The criteria suggested by our analyses for growth and direct mortality envelop these responses. For coho (one of the more comprehensively studied species), the approximate temperatures associated with various biological effects that we could broadly interpret from our modeling and the scientific literature are listed in Table 8.1.

On one end of the spectrum is direct mortality from short-term exposure to high temperature. Clearly, direct mortality is an unacceptable endpoint condition, and would not fully protect fish. However, it is important to be on the alert for these conditions, because there are some geographic, watershed, and climatic conditions where acute lethal temperatures have been documented in natural conditions or due to management activities. On the other end of the temperature spectrum, positive growth for juveniles, or weight maintenance for adults, is a measurable quality that is very responsive to temperature (among other factors). Therefore, it can be a sensitive and early indicator of the general health of individual fish. While a variety of ecological factors are known to influence population characteristics, the growth simulations showed that there is a very strong temperature signature in the size and condition of fish observed in natural streams.

Table 8.1 The spectrum of coho salmon response at temperature thresholds synthesized from this report and the scientific literature. Threshold values are approximations, due to lack of consistency in reporting results among studies. Results were standardized to 7-day maximum temperature using regression relationships between various temperature indices described in Section 3. Assumptions regarding the relationship between reported measures and 7-day maximum temperatures were assigned to standardize results.

Biologic Response	Approximate Temperature Threshold °C (Average of the 7-day daily maximum temperature)
Upper Critical Lethal Limit (death within minutes)	31
Geographic limit of species (Eaton 1995)	30
Growth loss 40% (simulated at average food supply)	30
Acute threshold (this report)	26
Acute threshold selected by U.S. EPA 1977	25
Complete cessation of feeding (laboratory studies)	24
Growth loss of 20% (simulated at average food supply)	22.5
Increased incidence of disease (under specific situations)	22
Temporary movements to thermal refuges	22
Growth loss of 10% (simulated at average food supply)	16.5
Optimal growth at range of food satiation (laboratory)	14-17
Growth loss of 10% (simulated at average food supply)	9.5
Cessation of feeding and movement to refuge	4

There is no consensus among physical or biological scientists as to how to report temperature regimes represented in their studies. Therefore, we had to translate these reported temperature measures to a common standard (7-day average of the daily maximum temperature) using relationships between temperature indices developed in the report. The values in Table 8.1 should therefore be viewed as approximate[1]. One can see that simulated growth loss values identify biologic effects closest to what appears to be the healthiest conditions. At the temperatures where avoidance behavior or competitive exclusion can be observed, the growth simulation would have predicted measurable and possibly significant growth loss.

Importantly, the analysis leads to the conclusion that the cumulative effects on potential weight gain due to the temperature regime for the summer rearing period can be a bell weather of more visible, and possibly more serious, effects observed at higher temperatures. It appears that temperature criteria selected on the basis of growth can be protective without explicitly accounting for all biologic responses or causal mechanisms. Concentrating on those that can be quantified and simulated (growth, direct mortality, incubation) allows the interactions between biologic response to environmental characteristics to be quantified. Thus, it may be the most sensitive indicator of effects that can also be measured in populations in natural streams without sacrificing fish. This also allows multiple species living in a common stream to be assessed and compared on the same objective basis, and in relation to observed and potential stream temperature regimens.

Temperature Thresholds Based on Risk Assessment

The growth simulation method was very sensitive to temperature, predicting a range of average population weights that varied with temperature regime. The method is capable of assessing a specific biological response on a continuous temperature scale. However, the results also support the concept that useful thresholds can be assigned, experimentally tested, and justified with probabilistic risk assessment. When this approach is applied at a site, with interpretation assisted by the mathematical model, it appears that rather small changes in average population weight could be detected. According to typical size distributions in populations of juvenile salmon populations, a minimum detectable weight loss or gain due to any factor would be approximately 20%. The growth simulation can associate such small changes with a temperature threshold. Without an assist in hypothesis formulation by the growth simulation techniques, it would probably be difficult to have confidence in interpreting the influence of temperature on population weight differences as small as 20% .

Risk level for establishing thresholds. A quantitative expression of the consequence of size completes the formal appraisal of risk. There is ample evidence to suggest that larger size conveys many competitive and survival benefits. We attempted to associate risk with growth loss to guide selection of threshold values. We did so for coho salmon based on scientific literature that suggests that size at the end of the juvenile growth phase contributes to the individual's success at later life history stages. We found that weight loss as small as 20% of the average population weight at the end of the juvenile summer rearing phase may be important in this context. However, the research results supporting this conclusion are neither abundant nor sufficiently consistent to have full confidence in using them to select risk criteria. For example, later success in the marine environment

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[1] The 7-day maximum and annual maximum temperature are closely related and are often within 1° to 2°C of each other.

also depends on timing and location factors. Nevertheless, within the juvenile rearing phase, studies have consistently reported that larger size generally conveys a number of advantages such as better feeding position and lower mortality. Such observations indicate that working with growth or weight maintenance is a useful approach. The threshold level of growth loss is an important policy choice if it is used to determine the thresholds in numeric temperature criteria. Knowledge of the implications of growth and size to organism success is not as well quantified as desired to guide that important decision. Establishing the effect of size on organism success merits greater research attention.
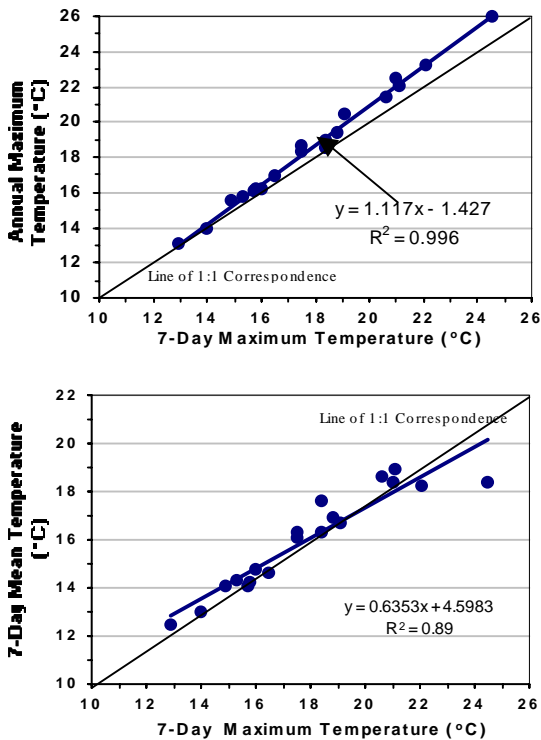
Figure 8.4 The relationship between various temperature indices currently used as the averaging period for temperature criteria. The averaging period has typically been either the annual maximum temperature (observed for a period as short as an hour, but more probably occurring for several hours on sequential days), or a weekly average (generally focused on the warmest seven consecutive days) observed for the year. For example, Washington's current criteria specify the annual maximum temperature, expressed as the maximum hourly temperature that occurs each year. Oregon specifies the average of the daily <u>maximum</u> temperature of the 7 warmest consecutive days. The U.S. EPA (1977) recommends the average of the daily <u>mean</u> temperature of the 7 warmest consecutive days (MWAT). All of these indices represent the upper tail of the distribution of temperatures observed during the summer months, and are closely related to one another. We conclude that any of the indices can be used for the purpose of temperature criteria because they are closely related. Furthermore, the short-term measures appear to adequately represent chronic exposure and long-term effects.

Nevertheless, several lines of evidence, as well as precedent in the scientific literature, suggest growth loss values between 10 and 20% as an appropriate, risk-guided threshold. We selected a growth loss of 10% as a threshold in our discussions and to compare temperature criteria with other existing criteria derived from other approaches. This level should prevent a statistically observable change in average population weight, assuming that population numbers remain consistent for the period. It is possible that somewhat higher growth loss would be acceptable, although we suspect that growth loss can't be much higher since temperatures associated with higher growth loss begin to coincide with the outward manifestation of other adverse effects such as avoidance behavior (Table 8.1). We do not attempt to quantify the response of resident adult fish to growth loss as an indicator of adverse temperature effects, although the same physiologic mechanisms manifest as weight loss in resident adults and undoubtedly have ecological ramifications.

Averaging periods for criteria. Temperature criteria use short-term averaging periods as indices of the long-term response. Results provided in this report confirm that these indices can be used reliably to represent the long-term temperature regime. All of the indices (annual maximum temperature, 7 day averages of the daily maximum or

daily mean temperature) characterize the upper tail of the sampled temperature distribution, and they are closely correlated with each other. This makes selection among them a matter of procedural and logistical concerns, rather than a biological question. Some standardization of reporting measures would be most helpful. We urge scientists to provide at least one of these indexing measures with their study results, thus enabling comparisons among them as well as their use in supporting the development of temperature criteria for regulatory purposes. We found that the average of the maximum 7 consecutive days of the daily mean temperature (MWAT, U.S. EPA 1977) was best correlated with growth simulations, but the annual maximum and 7-day maximum were also quite suitable. Appropriate temperature thresholds vary with each index.

Temperature Criteria Derived From Risk Assessment

Thresholds generated from risk assessment are reasonably consistent with criteria developed previously, including those derived from subjective review methods and objective analysis, and those currently authorized by states. The upper temperature thresholds associated with 10% weight reduction are 16.5^{o} and 20.5^{o}C for coho and steelhead respectively (Figure 8.4). Sub-lethal thresholds suggested by the risk assessment method tend to be slightly lower than those derived from objective methods (e.g. EPA 1977), probably because we directly accounted for realistic estimates of food
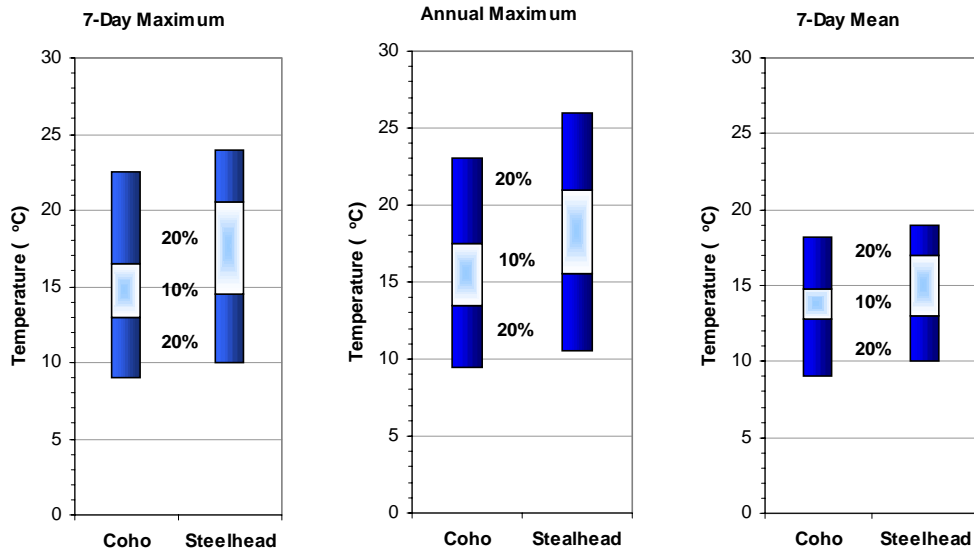
Figure 8.4 Temperature range for increments of growth loss associated with long-term temperature regime as expressed for 3 temperature indices and 2 species of salmonids. The inner range represents up to 10% growth loss and the outer range represents up to 20% growth loss. Above and below the ranges shown the growth loss exceeds 20% and was as high as 50% near the extremes of the temperature range. Risk assessment associated with growth loss suggests that a 10% limit would prevent any measurable effect on average coho population weight. A loss of 20% would be detectable and the temperature associated with this level of growth loss coincides with temperatures associated with avoidance behavior. Therefore, thresholds selected at 10% may be most appropriate for establishing temperature criteria. The threshold temperature varies with each index.

availability in the simulations. The risk-derived thresholds tend to be somewhat higher than those emerging from subjective evaluations (e.g. WDOE 1999), possibly because we did not add arbitrary safety factors (Figure 8.5). We believe that the choice of low thresholds of growth loss (e.g. 10%) provides an adequate margin of safety. Using the growth loss to set the risk level also prevents any unintended consequences of selecting values that are too low for a particular species. Our results demonstrated that temperatures that are low relative to a species' optimum have growth loss effects that are comparable to those associated with those that are high relative to the optimum.

When two or more species coexist, as is often the case, it may be appropriate to select the threshold for the more sensitive species. In the case of coho and steelhead, there would be no negative effect on steelhead by targeting lower temperatures appropriate for coho, the more sensitive species. If the margin between species is wider, the tradeoffs for species could be evaluated in selecting the temperature threshold if growth models for all species were available.

The fundamental relationship quantifying growth and mortality were similar, though not identical, for the two salmon species we modeled. However threshold temperatures
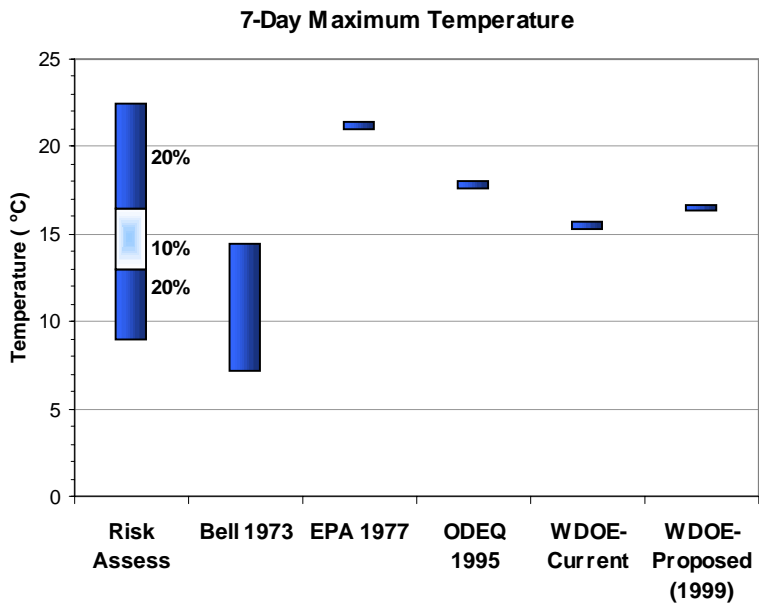
Figure 8.5 A comparison of temperature criteria for coho and recommended ranges from a variety of sources standardized to the 7-day maximum temperature. The risk assessment is the range of values developed in this report. Bell (1973) is the original source of temperature range recommendations that have been widely used as the basis for subjective analyses. These were used in part to form criteria used by Oregon (ODEQ 1995) and the current and proposed criteria for Washington (WDOE). The U.S. EPA used an objective approach based on the growth curves to determine threshold criteria. The various methods vary in terms of degree of objectivity or subjectivity by which the information is synthesized into recommended criteria, the degree to which data forms the basis for the criteria, and the extent to which population effects can be probabilistically determined. The temperature criteria in use in Pacific Northwest states have largely been drawn from professionals' review and interpretation of available scientific literature (e.g. ODEQ 1995). There has been some previous effort to use the more well-established scientific relationships to develop objective analyses of threshold temperatures and the duration of exposure (e.g., U.S. EPA 1977). This approach has not been widely integrated into regulatory activity.

generated through growth simulation varied between them, reflecting the differences in food consumption estimated by observing population growth in natural streams that was used in the modeling. This result highlights the importance of food availability as an important factor determining fish growth, a conclusion consistent with observations from field ecological studies. The simulation results suggest that coho populations ate at approximately 50% of satiation rations and steelhead, using a different feeding strategy, ate at 100% satiation. Importantly, food availability influences the temperature threshold for adverse effects. There is very little documentation of how much food is available for fish dwelling in streams and rivers, and how management activities may alter it. Greater understanding of how site and watershed conditions determine how much food is available and how it is allocated within populations would allow understanding of how temperature affects total productivity in addition to its effect on weight gain of the individuals in the population.

The analyses documented in this report addressed the juvenile rearing phase of coho salmon and steelhead trout. These species are widely distributed within the region, they are listed as threatened and endangered in a number of locations, and there was sufficient laboratory and population data to build models and corroborate them in natural streams. Nevertheless, this is a limited representation of the fish species that occur in the Pacific Northwest. Similar techniques could be applied to all fish species if the fundamental laboratory relationships used in the growth simulation method were available. Currently, there are a number of gaps in information for key functions used in modeling species of interest such as cutthroat trout and bull trout.

Analysis of lethal temperatures suggested that a threshold of 26°C for annual maximum temperature is a signal of imminent risk of direct mortality to salmonids. Although the occurrence of water temperature this high is rare, it has occasionally been observed in natural streams as well as in those impacted by anthropogenic activities in some situations. We also recommend site-specific analysis of duration of exposure when annual maximum temperature is between 24° and 26°C in order to assure that duration/magnitude thresholds are not exceeded. The relationship between thresholds for growth and mortality suggests that, if growth thresholds are met, lethal temperatures will not occur. However, there are situations where rivers and streams cannot be expected to meet these criteria, even under natural conditions. Acute criteria may be most helpful for triggering additional study in certain situations, and for prioritizing restoration activities.

It may be useful to vary temperature criteria on a seasonal basis matching fish requirements, although differing criteria for too fine a resolution of time may be difficult to administer and may offer relatively little additional benefit if ambient temperatures are generally within exposure duration limits. The risk-based approach could be used to investigate the need for more finely tuned seasonal criteria. or to develop site-specific criteria. The concept of selecting criteria for particular species appears valid, and the risk assessment method can be employed to help guide the selection of appropriate criteria for target species or it can be used to address multiple species living in the same location. There was no indication in our analysis that criteria for daily fluctuating temperature would improve biological characterization. Also, some states have a maximum allowable increase in temperature as well as an upper threshold. The value of this provision is not immediately apparent in the context of either acute or chronic effects analysis discussed in this report.

Uncertainties in Applying Criteria in Natural Environments

There are natural factors contributing to uncertainty and variability when it comes to administering temperature criteria. There are systematic patterns in temperature dictated by watershed and geographic conditions. It is important to recognize that the attainment of biologically based criteria will vary with watershed characteristics. Temperature regime also varies annually by as much as several degrees due to climatic factors, so it may be appropriate to establish confidence limits around threshold values to determine whether water quality standards are attained.

Conclusion

In conclusion, the analytical approaches to assessing risk to salmon associated with ambient environmental temperature presented in this report appear to be promising techniques for objectively defining temperature criteria. They could also assist ecological field studies to segregate the effects of temperature from other habitat and population factors that influence productivity. The risk-based analyses support the approach and general range of numeric threshold values currently used as temperature criteria by Pacific Northwest states. However, the specific numbers generated by quantitative risk analysis techniques vary slightly from existing authorized criteria. Assuming the most sensitive salmon species is used to select the threshold, and a growth loss threshold of 10%, the levels suggested by risk assessment are slightly higher than used by Washington and slightly lower than used by Oregon. Additional research is needed to develop the biological basis for other species of interest.

SECTION 9   LITERATURE CITED

Adams, S.M. and J.E. Breck. 1990. Bioenergetics. In: Shreck, C.B. and P.B. Moyle, eds. Methods for fish biology. American Fisheries Society. Bethesda, MD.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington D.C. 493 pp.

Alabaster, J. S. and A. L. Downing. 1966. A field and laboratory investigation of the effect of heated effluents on fish. Fish. Min. Arg. Fish Food (Great Britian) Ser. I Sea Fish 6(4): 1-42.

Alabaster, J. S. and Welcomme. 1962. Effect of concentration of dissolved oxygen on survival of trout and roach in lethal temperatures. Nature 194: 107.

Allen, M.A. and T.J. Hassler. 1986. Species profiles and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—chinook salmon. U.S. Fish and Wildlife Service Biological Report 82 (11.62).26 pp.

Anderson, D.R. 1986. Proceedings: risk assessment in aquatic ecology. Electric Power Research Institute, Palo Alto, CA. Report No. EPRI EA-4438.

Armour, C.L. 1991. Guidance for evaluating and recommending temperature regimes to protect fish. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. Instream Flow Information Paper 28. Biological Report 90(22). 13 pages.

Averett, C. L. 1968. Influence of temperature on energy and material utilization by juvenile coho salmon. PhD Thesis. Oregon State University, Corvallis, OR.

ASTM. 1997. Annual Book of Standards. American Society for Testing and Materials, Philadelphia, Pennsylvania.

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

Baltz, D.M., P.B. Moyle, and N.J. Knight 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichys osculu*s. Can. J. Fish. Aquat. Sci.. 39:1502-1511.

Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. Aquat. Sci. 43:160-168.

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Trans. Am. Fish. Soc. 118: 597-607.

Bell, M.C. 1973, 1986, and 1990. Fisheries handbook of engineering requirements and biological criteria. US Army Corps of Engineers, North Pacific Division, Portland, OR.

Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby, and T.D. Hofstra. 1987. Stream temperatures and aquatic habitat: fisheries and forestry interactions. In: Salo, E.O. and T.W. Cundy, eds., Proc. Symposium Streamside management: forestry and fishery interactions. Held. Feb 12-14, 1986. University of Washington, Seattle, WA.: 191-232.

Bilby, R.E. and P.A. Bisson. 1992. Allochthonous and autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aq. Sci. 49:540-551.

Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic systems of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. 53:164-173.

Bilby, R.E., B.R. Fransen, P.A. Bisson, and J.K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. 55:1909-1929.

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

Bisson, P.A. and G.E. Davis. 1976. Production on juvenile chinook salmon, *Oncorhynchus tshawytscha*, in a heated model steam. Fishery Bulletin 74(4): 763-774.

Bisson, P.A., J.L. Nielsen, and J.W. Ward. 1988a. Summer production of coho salmon stocked in Mount St. Helens streams 3-6 years after the 1980 eruption. Trans. Am. Fish. Soc. 117: 322-355.

Bisson, P.A. K. Sullivan, and J.L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. 117:262-273.

Bisson, P.A. and R.E. Bilby. 1998. Organic matter and trophic dynamics. In: Naiman, R.J. and R.E. Bilby, eds. River ecology and management: lessons from the Pacific coastal region. Springer, New York: 373:398.

Bjornn, T.C. and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19:83-138.

Black, J. 2000. Summer temperatures in small stream sources on managed Olympic Peninsula timberlands. M.S. Thesis, U. Washington, Seattle, WA.

Blahm and McConnell 1970. Unpublished data cited in National Academy of Sciences and National Academy of Engineering (NAS/NAE). 1973.

Blahm and Parente 1970. Unpublished data cited in National Academy of Sciences and National Academy of Engineering (NAS/NAE). 1973.

Boisclair, D. and W.C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. 46:1859-1867.

Boisclair, P. and W.C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). Can. J. Fish. Aq. Sci. 48: 1337-1344.

Bovee, K.D. 1978. Probability of use criteria for the family Salmonidae. U.S. Fish and Wildlife Service, Coop. Instream Flow Service Group. Instream Flow Information Paper No. 4. FWS/OBS-78/07.

Brett, J.R. 1952. Temperature tolerance in young Pacific salmon, Genus *Oncorhynchu*s. Journal of the Fisheries Research Board of Canada 9(6):265-323.

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

Brett, J.R. 1958. Implications and assessments of environmental stress. In P.A. Larkin, editor. The Investigation of Fish-Power Problems. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver: 60-83.

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*). Amer. Zool. 11(1):99-113.

Brett, J.R. 1995. Energetics. pp. 3-68. *In*: C. Groot, L. Margolis, and W.C. Clarke [Editors]. Physiological Ecology of Pacific Salmon. UBC Press, Vancouver, B.C.

Brett, R.J., 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. Canada 26:2363-2394.

Brett, R.J., W.C. Clarke, and J.E. Shelbourn. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon *Oncorhynchus tshawytsch*a. Can. Tech. Rep. Fish. Aquat. Sci. No. 1127.

Brown, G.W. 1969. Predicting temperatures of small streams. Wat. Resources Res. 5: 68-75.

Brungs and Jones. 1977. Temperature criteria for freshwater fish: protocol and procedures. Ecological Research Series., U.S. Environmental Protection Agency, EPA-600/3-77-061. 130 pp. [Also cited as U.S. EPA 1977.]

Bustard, D.R. and D.W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Onchorynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Research Bd. Can. 32: 667-680.

Cairns, J.,Jr., A.L. Buikema, Jr., A.G. Heath, and B.C. Parker. 1978. Effects of temperature on aquatic organism sensitivity to selected chemicals. Virginia Water Resources Research Center, Bulletin 106. 88 pages.

Cederholm, C.J., R.E. Bilby, P.A. Bisson, T.W. Bumstead, B.R. Fransen, W.J. Scarlett, and J.W. Ward. 1997. Response of juvenile coho salmon and steelhead to placement of large woody debris in a coastal Washington stream. N. Am. J. Fish. Manage. 17(4):947-963.

Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Midland Nat. 100:345-357.

Chapman, D.W. and T.C. Bjornn 1969. Distribution of salmonids in streams with special reference to food and feeding. Proc. Symposium on Trout in Streams. In: T.G. Northcote [ed]. Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries. Univ. Brit. Col, Vancouver, B.C. : 153-176.

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

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

Coutant, C.C. and S. S. Talmage. 1977. Thermal effects. J. Water Pollution Control Federation 49:1369-1425.

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

De Staso, J. III., and F.J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Trans. Am. Fish. Soc. 123:289-297.

Dickerson, B.R. and G.L. Vinyard. 1999. Effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan cutthroat trout. Trans. Am. Fish. Soc. 128: 516-521.

Dill, L., R. Ydenberg, and A. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 59: 1801-1809.

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 clark*i. Trans. Am. Fish. Soc. 104(3):552-554.

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.

Elliott, J.M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. J. Animal Ecol. 44:806-821.

Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta*) in relation to body weight , water temperature and ration size. J. Animal Ecology 45:923-948.

Elliott, J.M. 1981. Some aspects of thermal stress on freshwater teleosts. Pages 209-245 *In* A. D. Pickering editor, Stress and Fish. Academic Press, London.

Everson, L.B. 1973. Growth and food consumption of juvenile coho salmon exposed to natural and elevated fluctuating temperatures. M.S. Thesis, Oregon State University, Corvallis, OR. 68 pp.

Fagerlund, U.H.M, J.R. McBride, and I.V. Williams. 1995. Stress and tolerance. pp. 461-503. *In*: C. Groot, L. Margolis, and W.C. Clarke [Editors]. Physiological Ecology of Pacific Salmon. UBC Press, Vancouver, B.C.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. 62: 441-451.

Filbert, R.B. and C.P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. Trans. Am. Fish. Soc. 124:824-835.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Biol. Ser. 55,Publs. Ont. Fish. Res. Lab 68: 5-62.

Fry, F.E. J. 1967. Responses of vertebrate poikilotherms to temperature. Pages 375-409 *in* A.H. Rose editor. Thermobiology. Academic Press, London.

Fransen, B.R., P.A. Bisson, J.W. Ward, and R.E. Bilby. 1993. Physical and biological constraints on summer rearing of juvenile coho salmon (*Oncorhynchus kisutch*) in small western Washington streams. In: Berg, L. and P.W. Delaney, eds., Proceedings of the Coho Workshop. Nanaimo, B.C. May 26-28, 1992: 271-288.

Giannico, G.R. and M.C. Healey. 1998. Effects of flow and food on winter movements of juvenile coho salmon. Trans. Am. Fish. Soc. 127: 645-651.

Golden, J. T. 1978. The effects of fluctuating temperatures on the lethal tolerance of coastal cutthroat trout (*Salmo clarki* clarki). MS. Thesis. Oregon State University, Corvallis, OR.

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. Bd. Canada 29: 251-264.

Hall, J.D., and R.L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. In: T.G. Northcote [ed.]. Proc. Symposium on slamon and trout in streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver: 355-375.

Hansen, D.J. 1989. Status of the development of water quality criteria and advisories. Water Quality Standards for 21st Century, 1989. Pp. 163-169. U.S. Environmental Protection Agency, Env. Res. Lab., Narragansett, Rhode Island.

Hansen, M.J., D. Boisclair, S.B. Brandt, S.W. Hewett, J.F. Kitchell, J.C. Lucas, and J.J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Trans. Am. Fish. Soc. 122:1019-1030.

Hanson, P.C., T.B. Johnson, D.E. Schindler and J.F. Kitchell. 1997. Fish Bioenergetics 3.0 Users manual. University of Wisconsin-Madison Center for Limnology, U. Wisconsin, Madison.

Hartman, G.F. and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences 223.

Hawkins, C. P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Riparian canopy and substrate composition interact to influence the abundance of salmonids, sculpins, and salamanders in streams. Can. J. of Fish. and Aquat. Sci. 40:1173-1185.

Hetrick, N.J., M.A. Brusven, T.C. Bjornn, R.M. Keith, and W.R. Meehan. 1998a. Effects of canopy removal on invertebrates and diet of juvenile coho salmon in a small stream in southeast Alaska. Trans. Am. Fish. Soc. 127: 876-888.

Hetrick, N.J., M.A. Brusven, W.R. Meehan, and T.C. Bjornn. 1998. Changes in solar input, water temperature, periphyton accumulation, and allochthonous input and storage after canopy removal along two small salmon streams in southeast Alaska. Trans. Am. Fish. Soc. 127: 859-875.

Hewett, S.W. and B.L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea grant Institute. Tech. Rept WIS-SG-92-250, Madison.

Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptions to the seasonal temperature cycle. J. Fish. Res. Bd. Can. 34:1524-1550.

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. Bd. Can. 34:639-648.

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 *(O. kisutch*) returning to Carnation Creek, British Columbia. In: C.D. Levings, L.B. Holtby, and M.A. Henderson, eds. Proceedings of the Natioanl Workshop on effects of habitat alternation on slamonid stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105: 62-81.

Hynes, H.B.N. 1970. The ecology of running waters. University of Toronto Press, Waterloo. 555 pp.

Iverson, R.A. 1972. Effects of elevated temperature on juvenile coho salmon and benthic invertebrates in model stream communities. Ph.D. thesis, Oregon State University, Corvallis, OR. 98 pp.

Jobling, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. 19:439-455.

Keith, R.M., T.C. Bjornn, W.R. Meehan, N.J. Hetrick, and M.A. Brusven. 1998. Response of juvenile salmonids to riparian and insteam cover modifications in small streams flowing through second-growth forests of S.E. Alaska. Trans. Am. Fish. Soc. 127: 889-907.

Kitchell, J.F., J.F. Koonce, R.V. O'Neill, H.J. Shugart Jr., J.J. Magnuson, R.S. Booth. 1974. Trans. Am. Fish. Soc. 4:786-798.

Laufle, J.C., G.B. Pauley, and M.F. Shepard. 1986. Species profiles and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—coho salmon. U.S. Fish and Wildlife Service Biological Report 82 (11.62). 18 pp.

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: 632-635.

Linton, T. K., S.D. Reid and C.M. Wood. 1997. The metabolic costs and physiological consequences to juvenile rainbow trout of a simulated summer warming scenario in the presence and absence of sublethal ammonia. Trans. Am. Fish. Soc. 126:259-272.

Magnuson, J.J., L.B. Crowder and P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19: 331-343.

Mallet, J.P., S. Charles, J. Persat, and P. Auger. 1999. Growth modelling in accordance with daily water temperature in European grayling (*Thymallus thymallus* L.) Can. J. Fish. Aquat. Sci. 56: 994-1000.

Martel, G. 1996. Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Can J. Fish. Aq. Sci. 53: 660-669.

Martin, D.J. 1985. Production of cutthroat trout (*Salmo clarki*) in relation to riparian vegetation in Bear Creek, Washington. Ph.D. Thesis, University of Washington, Seattle, WA.

Martin, D.J., L.J. Wasserman, and V.H. Dale. 1986. Influence of riparian vegetation on post-eruption survival of coho salmon fingerlings on the westside streams of Mount St. Helens, Washington. N. Am. J. Fish. Manage. 6:1-8.

Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. 40(4):775-788.

Matthews, K.R., N.H. Berg, D.L. Azuma and T.R. Lambert. 1994. Cool water formation and trout habitat use in a deep pool in the Sierra Nevada, California. Trans. Am. Fish. Soc. 123: 549-564.

McCullough, D.A. 1999. 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. U.S. EPA Report # EPA 910-R-010. 279 pp.

McLean, W.E., J.O. T. Jensen, and D.F. Alderdice. 1993. Oxygen consumption rates and water flow requirements of salmon (*Oncorhynchus* spp.) in the fish culture environment. Aquaculture 109:281-313.

McConnell and Blahm 1970. Unpublished data cited in National Academy of Sciences and National Academy of Engineering (NAS/NAE). 1973.

McMahon, T.E. 1983. Habitat suitability index models: Coho salmon. U.S. Dept. Int., Fish Wildl. Serv. FWS/OBS-82/10.49. 29 pp.

Mount, D.I., N.A. Thomas, T.J. Norbert, M.T. Barbour, T.H. Roush, W.F. Brades. 1984. Effluent and ambient toxicity testing and instream community and response on the Ottawa River, Lima, Ohio. EPA, Office of Water Enforcement and Permits, Washington, D.C. EPA-600/3-84-0890.

Murphy, M.L., C.P. Hawkins, and N.H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. of the Am. Fish. Soc. 110:469-478.

Murphy, M.L. 1998. Primary production. In: Naiman, R.J. and R.E. Bilby, eds. River ecology and management: lessons from the Pacific coastal region. Springer, New York: 144-168.

National Academy of Sciences and National Academy of Engineering (NAS/NAE). 1973. Water quality criteria 1972. A report fo the Committee on Water Quality Criteria. US Environmental protection Agency Pub. No. EPA-R3-73-033. Wasington, D.C. 553p.

National Academy of Sciences Committee on Protection and Management of Pacific Northwest Anadromous Salmonids. 1996. Upstream-salmon and society in the Pacific Northwest. National Academy Press, Washington D.C. 452 pp.

Ney, J.T. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122: 736-748.

Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile salmon. Trans. Am. Fish. Soc. 121:617-634.

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.

Oregon Department of Environmental Quality (ODEQ). 1995. Water quality standards review. Department of Environmental Quality Standards & Assessment Section. Portland, OR.

Oregon Department of Environmental Quality (ODEQ). 1997. Clean Version. Proposed revisions to Division 122: Hazardous substance remedial action rules. Section 340-122-084 covers risk assessment.

Parkhurst, B.R., W. Warren-Hicks, R. D. Cardwell, J. Volosin, T. Etchison, J.B. Butcher, and S. M. Covington. 1996. Methodology for aquatic ecological risk assessment: A multi-tiered approach. Project 91-AER-1. Prepared for Water Environment Research Foundation, Alexandria, Virginia.

Pauley, G.B., B.M. Bortz, and M.F. Shepard. 1986. Species profiles and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Steelhead Trout. U.S. Fish and Wildlife Service Biological Report 82 (11.62). 24 pp.

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.

Puckett, K.J. and L.M. Dill. 1985. The energetics of feeding territoriality in juvenile coho samon (*Oncorhynchus kisutch*). Behavior 42: 97-111.

Quinn, T. and N. Peterson. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aq. Sci. 53: 1555-1564.

Railsback, S.F. 1997. Guidance for using a bioenergetics model to assess effects of stream temperature. Tech. Report 001.8-97-8. Pacific Gas and Electric Company, San Ramon CA.

Railsback, S.F. and K.A. Rose. 1997. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Tech. Report 001.8-97-8. Pacific Gas and Electric Company, San Ramon CA: C1-C25.

Railsback, S.F. and K.A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Am. Fish. Soc. 128:241-256.

Rand, P.S., D.J. Stewart, P.W. Seelbach, M.L. Jones, and L.R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. 122:415-438.

Reeves, G.H., F.H. Everest, and J.D. Hall. 1987. Interactions between the redside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Can.J. Fish. Aquat. Sci. 44:1603-1613.

Reiser, D.W., and T.C. Bjornn. 1979. Habitat requirements of anadramous salmonids. U.S.D.A. For. Serv. Pac. NW For. And Range Exp. Station. Gen. Tech. Rep PNW-96.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada. No. 91. 382 pp.

Sandercock, F.K. 1995. Life history of coho salmon. *In*: C. Groot and L. Margolis (eds.). Pacific Salmon Life Histories. UBC Press, Vancouver, B.C: 395-446.

SAS Institute Inc. (1989) *SAS/STAT User's Guide, Version 6, Fourth Edition*. Cary, NC: SAS Institute Inc.

SETAC [Society for Environmental Chemistry and Toxicology]. 1994. Aquatic risk assessment and mitigation dialogue group. Final report. SETAC Foundation for Environmental Education, Inc., Pensacola, Florida. USA.

Shelbourn, J. E. , J. R. Brett, and S. Shirahata. 1973. Effect of temperature and feeding regime on the specific growth rate of sockeye salmon fry (*Oncorhynchus nerka*) with a consideration of size effect. J. Fish. Res. Bd. Canada. 30:1191-1194.

Shuter, B.J. , J.A. MacLean, F.E.J. Fry and H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. 109: 1-34.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. Second Edition. W.H. Freeman and Company, New York. 859 pp.

Solomon, K.R., D.B. Baker, R. P. Richards, K.R. Dixon, S.J. Klaine, T.W. La Point, R. J. Kendall, C.P. Weisskopf, J.M. Giddings, J.P. Giesy, L.W. Hall, Jr., and W.M. Williams. 1996. Ecological risk assessment of atrazine in North American surface waters. Environmental Toxicology and Chemistry. 15:31-76.

Spehar, R. and W. Adams. 1998. Person communications with Robert Spehar, U.S. EPA, Duluth, Minnesota, and D. William Adams, U.S. EPA Science Advisory Board, November 1998 telephone conversations.

Spence, B.C., G.A. Lomnicky, R.M. Hughes, and R.P. Novitzki. 1996. An ecosystem approach to salmonid conservation. TR-4501-96-6057. ManTech Environmental Research Services Corp. Corallis OR. (Available from the National Marine Fisheries Service, Portland, Oregon.)

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. 111:199-209.

Sprague, J.B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Research 3:793-821.

Stephan, C.E., D.I. Mount, D.J. Hansen, J.H. Gentile, G.A. Chapman, and W.A. Brungs. 1985. Guidelines for deriving numerical national water quality criteria for the protection of aquatic organisms and their uses. U.S. Environmental Protection Agency, Washington, D.C. NTIS No. PB85-227049. 98 pages.

Stewart, D.J., and M. Ibarra. 1991. Predation and production of salmonine fishes in Lake Michigan, 1978-88. Can. J. Fish. Aq. Sci. 48:909-922.

Sullivan, K., S.H. Duncan, P.A. Bisson, J.T. Heffner, J.W. Ward, R.E. Bilby, and J.L. Nielsen. 1987. A summary report of the Deschutes River basin: sediment, flow, temperature, and fish habitat. Technical Report 044-5002/87/1, Weyerhaeuser Company, Tacoma, WA 129 pp.

Sullivan, K. and T.A. Adams. 1990. The physics of stream heating: An analysis of temperature patterns in streams environments based on physical principles and stream data. Weyerhaeuser Technical Report. 044-5002.90/2. Technology Center, Tacoma, WA 98477.

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 Report No. TFW-WQ3-90-006. Washington Dept. Nat. Resources, Olympia, WA. 224 pp.

Suter, G.W. II, L.W. Barnthouse, S.M. Bartell, T. Mill, D. Mackay, and S. Paterson. 1993. Ecological risk assessment. Lewis Publishers, Boca Raton, Florida, 538 pp.

Suter, G.W. and J.B. Mabrey. 1994. Toxicological benchmarks for screening potential contaminants of concern for effects on aquatic biota: 1994 revision. Oak Ridge National Laboratory, NTIS No. DE95oo5996/WEP. 106 pp.

Sweeney, Bernard W. and Robin L. Vannote. 1986. Growth and production of a stream stonefly: influences of diet and temperature. Ecology 67(5): 1396-1410.

Symons, P. 1971. Behavioral adjustment of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. 40:569-587.

Tang, M. and D. Boisclair. 1995. Relationship between respiration rate of juvenile brook trout (*Salvilinus fontinalis*), water temperature, and swimming characteristics. Can. J. Fish. Aquat. Sci. 52:2138-2145.

Taniguchi, Y., 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.

Theurer, F.D. , K.A. Voos, and W.J. Miller. 1984. Instream water temperature model. Instream Flow Info. Paper No. 16. U.S.D.I. Fish and Wildlife Service FWS/OBS-84/15.

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. 115:52-59.

Thornton, K.W. and A.S. Lessem. 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. Soc.. 107: 284-287.

U.S. EPA. 1977. Temperature criteria for freshwater fish: protocol and procedures. Ecological Research Series. U.S. Environmental Protection Agency Office of Research and Development, Environmental Research Laboratory, Duluth, Minnesota. EPA-600/3-77-061. 130p. [Also cited as Brungs and Jones, 1977].

U.S. EPA. 1980. Ambient water quality criteria for polynuclear aromatic hydrocarbons. EPA-440/5-80/069. Available from National Technical Information Service, Springfield, Virginia. 186 pp.

U.S. EPA. 1990. Guidance for data useability in risk assessment. Office of Emergency and Remedial Response. EPA/540/G-90/008. 261 pp.

U.S. EPA. 1992. Framework for ecological risk assessment. Risk Assessment Forum, U.S. Environmental Protection Agency, Washington, D.C. EPA/630/R-92/001. 41 pp.

U.S. EPA. 1993. Interim report on data and methods for assessment of 2,3,7,8-tetrachlorodibenzo-p-dioxin risks to aquatic life and associated wildlife. U.S. Environmental Protection Agency, Environmental Res. Lab., Duluth, MN. EPA/600/R-93-055.

U.S. EPA. 1994. Water quality standards handbook. Second edition. EPA, Office of Water, Washington, D.C. EPA-823-B-94-005a.

U.S. EPA. 1995. Draft proposed guidelines for ecological risk assessment. U.S. Environmental Protection Agency, Risk Assessment Forum, Washington, D.C. EPA/630/R-95/002. 144 pp.

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. 109:336-339.

Walters, C.J., and J.R. Post. Density-dependent growth and competitive asymmetries in size-structured fish populations: a theoretical model and recommendations for field experiments. Trans. Am. Fish. Soc. 122:34-35.

Warren, C.E. 1971. Biology and water pollution control. W.B. Saunders Company, Philadelphia. 434 pp.

Washington Departement of Ecology (WDOE). 1999a. Draft: Evaluating standards for protecting aquatic life in Washington's surface water quality standards. Temperature criteria. Preliminary Review Draft Discussion Paper. Appendix. 54 pages., Washington Department of Ecology, Olympia, WA.

Washington Departement of Ecology (WDOE). 1999b. Draft: Evaluating standards for protecting aquatic life in Washington's surface water quality standards. Temperature criteria. Preliminary Review Draft Discussion Paper. Supplementary Appendix. 122 pages. , Washington Department of Ecology, Olympia, WA.

Weatherly, A.H. 1972. Growth and ecology of fish populations. Academic Press, London.285 pp.

Weatherly, A.H. and H.S. Gill. 1995. Growth. Pages 101-158 *In*: [ed] C. Groot, L. Margolis, and W.C. Clarke. Physiological ecology of Pacific Salmon. UBC Press, Vancouver, B.C. Canada.

Weatherly, N.S. and S. J. Ormerod. 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. Freshwater Biology 24:109-122.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Can. J. Fish. and Aquat. Sci. 42:1668-1672.

Winberg, G.G. 1971. Symbols, units, and conversion factors in studies o freshwater productivity. International Biological Program, London.

Wurtsbaugh, W.A. 1973. Effects of temperature, ration, and size on the growth of juvenile steelhead trout, *Salmo gairdneri*. M.S. Thesis, Oregon State University, Corvallis, OR. 69. pp.

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, W.D. and D. S. Robson. 1978. Estimation of population number and mortality rates. Pages 137-164 *In:* T. Bagenal (ed) Methods for assessment of fish production in fresh waters. IBP Handbook No 3. Blackwell Scientific, Oxford London.

SECTION 10   APPENDICES

APPENDIX A

DATA USED TO DEVELOP RELATIONSHIPS BETWEEN GROWTH RATE, TEMPERATURE AND RATION AND CONSUMPTION DETERMINED FROM LABORATORY STUDIES

Coho salmon

Steelhead trout

DESCRIPTION OF METHODOLOGY

The temperature risk assessment relies on growth/ration/temperature relationships developed in laboratory experiments. In these experiments, the growth of individual or populations of fish are tracked over intervals of time under known temperature and food ration. Previously published studies were used to either obtain growth curves already developed by the authors (sockeye and chinook salmon), or to develop curves from original data provided by researchers (coho salmon and steelhead trout). In the studies used in this analysis, temperatures were maintained at constant levels for the duration of each trial, and various levels of food were provided as treatments. Trials were repeated at several levels of temperature.

Data used for growth of coho salmon was taken from Everson (1973). Growth of juvenile coho was studied in 60 trials where temperature was varied from 11.1^o to 22.4^oC and food ration was varied from satiation to near starvation. Experiments were replicated in 1969 and 1970. Everson reported growth rates of individual fish. Table A.1 shows the trial averages. The average for each trial at each temperature/treatment replication were used in to develop specific growth curves in the main body of the report.

Data used for growth of steelhead analysis taken from Wurtsbaugh and Davis (1977). Growth of juvenile steelhead was studied in the laboratory. A total of 44 trials were completed over the course of a year, varying temperature from 6.9^o to 22.5^oC and ration over the range from satiation to near starvation. Table A.2 shows data for each trial.

Both studies were conducted at Oregon State University, and local stocks were used. In both experiments, the fish were acclimated for approximated 14-16 days before trials, and fasted for 48 hours before tests began. The fish were fed for 23 days, and their weights were measured after 25 days.

Abbreviations used in the tables for coho:

Variable	Information
Season	Trials were run during 5 intervals of time over a 1 year time span (1969-70)
Temperature	Temperature was daily mean temperature averaged for the 30 day interval of the trial
Food Level	At each temperature, 4 food trials ranging from near starvation to satiation were run.. Each trial had 3-4 fish.
Rep	Rep appears on the Everson all sheet. It is the data for each of the 3-4 fish in the trial.
Initial Wet Weight (g)	Starting weight of the fish, measured.
Final Wet Weight (g)	Ending weight of the fish, measured.
Initial Dry Weight (g)	Starting dry weight of the fish, estimated based on dry to weight weight factor, Table 1
Final Dry Weight (g)	Ending dry weight of the fish, measured after sacrificing the fish.
Dry Food (mg)	Measured dry weight of the food fed to the fish during the trial.
Wet Food (mg)	Estimated wet weight of the food, based on factors in Table 1
Init Weight Wet Weight Consumption (g/g/day)	Estimated consumption per day for wet weight of fish relative to the initial wet weight at beginning of trial.
MidWeight Wet Weight Consumption (g/g/day)	Estimated consumption per day for wet weight of fish relative to the midpoint between start and end wet weight.
Init Weight Dry Consumption g/g/day	Estimated consumption per day for dry weight of fish relative to the initial dry weight at beginning of trial.
Mid Weight Dry Consumption g/g/day	Estimated consumption per day for dry weight of fish relative to the midpoint between start and end dry weight.
% Fish Moisture Dry/Wet	Fish moisture factor, from Table 1
Daily Growth Rate—Wet (g/g/d)	Growth rate calculated as (end weight-start weight)(.5*(start weight+endweight)/30 using wet weights
Daily Growth Rate—Dry (g/g/d)	Growth rate calculated as (end weight-start weight)(.5*(start weight+endweight)/30 using dry weights

Note that rations and growth rates can be expressed as grams of body weight per day, referenced as g/g/d, g g^{-1} d^{-1}, or g/g/day. These are also sometimes referenced as % body

Table A.1 Experimental data for growth of coho salmon in relation to temperature and food consumption. Data is from Everson, 1973.

Trial	Fish Size	Temperature	Food Level	Initial Wet Weight (g)	Final Wet Weight (g)	Initial Dry Weight (g)	Final Dry Weight (g)	Dry Food (mg)	Wet Food (mg)	Init Weight Wet Weight Consumption (g/g/day)	Mid Weight Wet Weight Consumption (g/g/day)	Init Weight Dry Consumption g/g/day	Mid Weight Dry Consumption g/g/day	% Fish Moisture Dry/Wet	Wet Daily Growth Rate (g/g/d)	Dry Daily Growth Rate (g/g/d)
Trial 1	Med	14.5	1	1.68	1.78	0.30	0.36	344	480	0.0098	0.0095	0.0395	0.035	0.1780	0.0019	0.0066
Trial 2	Med	14.5	2	1.88	2.82	0.34	0.60	924	1289	0.0235	0.0185	0.0946	0.067	0.1780	0.0135	0.0187
Trial 3	Med	14.5	3	1.69	2.91	0.30	0.63	1297	1809	0.0457	0.0310	0.1841	0.111	0.1780	0.0197	0.0251
Trial 4	Med	14.5	4	1.43	2.64	0.25	0.57	1344	1875	0.0443	0.0309	0.1783	0.109	0.1780	0.0200	0.0256
Trial 5	Med	18.6	1	1.58	1.60	0.28	0.30	345	481	0.0103	0.0102	0.0414	0.040	0.1780	0.0003	0.0020
Trial 6	Med	18.6	2	1.82	2.22	0.32	0.49	1023	1426	0.0269	0.0241	0.1083	0.086	0.1780	0.0068	0.0139
Trial 7	Med	18.6	3	3.09	3.91	0.55	0.91	1657	2311	0.0253	0.0222	0.1018	0.077	0.1780	0.0079	0.0165
Trial 8	Med	18.6	4	2.64	3.37	0.47	0.79	1912	2666	0.0350	0.0302	0.1410	0.103	0.1780	0.0084	0.0172
Trial 9	Med	20.8	1	1.33	1.21	0.24	0.23	342	477	0.0122	0.0128	0.0491	0.050	0.1780	-0.0032	-0.0016
Trial 10	Med	20.8	2	1.62	2.21	0.29	0.47	957	1334	0.0278	0.0234	0.1121	0.084	0.1780	0.0105	0.0164
Trial 11	Med	20.8	3	1.68	2.66	0.30	0.62	1392	1942	0.0397	0.0307	0.1597	0.106	0.1780	0.0147	0.0223
Trial 12	Med	20.8	4	2.23	3.75	0.40	0.87	2008	2801	0.0433	0.0315	0.1745	0.107	0.1780	0.0174	0.0252
Trial 13	Med	11.1	1	1.77	2.29	0.34	0.45	439	608	0.0116	0.0101	0.0434	0.037	0.1940	0.0086	0.0093
Trial 14	Med	11.1	2	1.92	2.94	0.37	0.62	793	1096	0.0195	0.0153	0.0728	0.054	0.1940	0.0142	0.0169
Trial 15	Med	11.1	3	1.67	2.62	0.32	0.56	949	1312	0.0274	0.0208	0.1022	0.073	0.1940	0.0151	0.0183
Trial 16	Med	11.1	4	1.81	3.38	0.35	0.73	1262	1745	0.0329	0.0227	0.1226	0.078	0.1940	0.0201	0.0233
Trial 17	Med	15.2	1	2.03	2.35	0.39	0.47	445	615	0.0106	0.0098	0.0396	0.075	0.1940	0.0051	0.0063
Trial 18	Med	15.2	2	1.77	2.44	0.34	0.53	764	1057	0.0202	0.0168	0.0751	0.075	0.1940	0.0108	0.0144
Trial 19	Med	15.2	3	1.49	2.86	0.29	0.61	1088	1504	0.0339	0.0232	0.1262	0.075	0.1940	0.0209	0.0237
Trial 20	Med	15.2	4	1.71	3.04	0.33	0.66	1256	1737	0.0345	0.0247	0.1288	0.075	0.1940	0.0186	0.0217
Trial 21	Med	17.8	1	1.59	1.82	0.31	0.36	443	612	0.0132	0.0122	0.0491	0.075	0.1940	0.0048	0.0054
Trial 22	Med	17.8	2	1.85	2.52	0.36	0.53	796	1101	0.0218	0.0181	0.0811	0.075	0.1940	0.0108	0.0133
Trial 23	Med	17.8	3	1.74	2.88	0.34	0.63	1071	1481	0.0286	0.0216	0.1067	0.075	0.1940	0.0160	0.0196
Trial 24	Med	17.8	4	2.42	3.96	0.47	0.89	1413	1954	0.0283	0.0212	0.1054	0.075	0.1940	0.0164	0.0210

Trial	Fish Size	Temperature	Food Level	Initial Wet Weight (g)	Final Wet Weight (g)	Initial Dry Weight (g)	Final Dry Weight (g)	Dry Food (mg)	Wet Food (mg)	Init Weight Wet Weight Consumption (g/g/day)	Mid Weight Wet Weight Consumption (g/g/day)	Init Weight Dry Consumption g/g/day	Mid Weight Dry Consumption g/g/day	% Fish Moisture Dry/Wet	Wet Daily Growth Rate (g/g/d)	Dry Daily Growth Rate (g/g/d)
Trial 25	Large	9.4	1	4.11	4.46	0.86	0.95	472	633	0.0051	0.0049	0.0182	0.075	0.2100	0.0027	0.0031
Trial 26	Large	9.4	2	4.08	4.67	0.86	1.00	711	955	0.0078	0.0073	0.0277	0.075	0.2100	0.0045	0.0051
Trial 27	Large	9.4	3	3.70	4.59	0.78	0.99	873	1172	0.0106	0.0094	0.0374	0.075	0.2100	0.0072	0.0078
Trial 28	Large	9.4	4	3.80	4.99	0.80	1.09	1122	1505	0.0132	0.0114	0.0469	0.075	0.2100	0.0091	0.0103
Trial 29	Large	13.1	1	2.85	2.81	0.60	0.56	313	419	0.0049	0.0049	0.0174	0.075	0.2100	-0.0004	-0.0024
Trial 30	Large	13.1	2	3.30	3.67	0.69	0.76	569	764	0.0077	0.0073	0.0273	0.075	0.2100	0.0034	0.0031
Trial 31	Large	13.1	3	3.83	4.69	0.80	0.99	902	1211	0.0105	0.0095	0.0374	0.075	0.2100	0.0067	0.0068
Trial 32	Large	13.1	4	3.57	4.55	0.75	0.97	1066	1430	0.0133	0.0117	0.0473	0.075	0.2100	0.0079	0.0085
Trial 33	Large	15.8	1	2.96	2.87	0.62	0.56	330	443	0.0050	0.0051	0.0177	0.075	0.2100	-0.0012	-0.0036
Trial 34	Large	15.8	2	3.10	3.20	0.65	0.64	467	627	0.0069	0.0068	0.0246	0.075	0.2100	0.0011	-0.0003
Trial 35	Large	15.8	3	3.29	3.79	0.69	0.79	761	1022	0.0104	0.0096	0.0368	0.075	0.2100	0.0048	0.0047
Trial 36	Large	15.8	4	3.59	4.65	0.75	1.00	1099	1475	0.0137	0.0119	0.0487	0.075	0.2100	0.0086	0.0094
Trial 37	Small	11.4	1	0.70	0.73	0.12	0.12	142	208	0.0098	0.0098	0.0396	0.075	0.1700	0.0002	-0.0011
Trial 38	Small	11.4	2	0.76	0.90	0.13	0.16	202	295	0.0130	0.0119	0.0524	0.075	0.1700	0.0057	0.0065
Trial 39	Small	11.4	3	0.72	0.93	0.12	0.16	235	343	0.0158	0.0139	0.0636	0.075	0.1700	0.0081	0.0085
Trial 40	Small	11.4	4	0.69	1.01	0.12	0.18	321	469	0.0228	0.0185	0.0916	0.075	0.1700	0.0126	0.0141
Trial 41	Small	14.8	1	0.77	0.66	0.13	0.11	144	211	0.0091	0.0099	0.0366	0.075	0.1700	-0.0056	-0.0083
Trial 42	Small	14.8	2	0.58	0.55	0.10	0.09	145	212	0.0121	0.0125	0.0487	0.075	0.1700	-0.0024	-0.0034
Trial 43	Small	14.8	3	0.56	0.60	0.09	0.10	170	249	0.0149	0.0143	0.0598	0.075	0.1700	0.0023	0.0011
Trial 44	Small	14.8	4	0.63	0.75	0.11	0.13	267	390	0.0206	0.0188	0.0827	0.075	0.1700	0.0056	0.0061
Trial 45	Small	17.2	1	0.82	0.75	0.14	0.13	161	235	0.0096	0.0100	0.0385	0.075	0.1700	-0.0029	-0.0029
Trial 46	Small	17.2	2	0.65	0.54	0.11	0.08	139	203	0.0104	0.0114	0.0419	0.075	0.1700	-0.0059	-0.0094
Trial 47	Small	17.2	3	0.69	0.76	0.12	0.13	210	307	0.0149	0.0142	0.0599	0.075	0.1700	0.0030	0.0040
Trial 48	Small	17.2	4	0.74	0.89	0.13	0.16	277	405	0.0181	0.0165	0.0729	0.075	0.1700	0.0057	0.0068
Trial 49	Med	15.8	1	1.65	1.86	0.31	0.37	352	452	0.0091	0.0086	0.0376	0.075	0.1890	0.0037	0.0049
Trial 50	Med	15.8	2	1.83	2.38	0.35	0.53	643	825	0.0150	0.0131	0.0618	0.075	0.1890	0.0084	0.0131

Table A.1 Continued. Experimental data for growth of coho salmon in relation to temperature and food consumption. Data is from Everson, 1973.

Trial	Fish Size	Temperature	Food Level	Initial Wet Weight (g)	Final Wet Weight (g)	Initial Dry Weight (g)	Final Dry Weight (g)	Dry Food (mg)	Wet Food (mg)	Init Weight Wet Weight Consumption (g/g/day	Mid Weight Wet Weight Consumption (g/g/day)	Init Weight Dry Consumption g/g/day	Mid Weight Dry Consumption g/g/day	% Fish Moisture Dry/Wet	Wet Daily Growth Rate (g/g/d)	Dry Daily Growth Rate (g/g/d)
Trial 51	Med	15.8	3	1.70	2.49	0.32	0.55	823	1056	0.0207	0.0168	0.0854	0.075	0.1890	0.0126	0.0174
Trial 52	Med	15.8	4	1.93	3.14	0.36	0.73	1202	1543	0.0267	0.0203	0.1101	0.075	0.1890	0.0160	0.0221
Trial 53	Med	19.2	1	1.53	1.56	0.29	0.30	316	406	0.0088	0.0088	0.0364	0.075	0.1890	0.0005	0.0012
Trial 54	Med	19.2	2	1.84	2.22	0.35	0.48	626	804	0.0145	0.0132	0.0600	0.075	0.1890	0.0062	0.0102
Trial 55	Med	19.2	3	1.60	2.22	0.30	0.49	759	975	0.0203	0.0170	0.0838	0.075	0.1890	0.0108	0.0153
Trial 56	Med	19.2	4	1.64	2.62	0.31	0.65	1029	1320	0.0268	0.0207	0.1106	0.075	0.1890	0.0152	0.0226
Trial 57	Med	22.4	1	1.97	1.93	0.37	0.38	404	518	0.0087	0.0088	0.0361	0.075	0.1890	-0.0007	0.0007
Trial 58	Med	22.4	2	1.54	1.69	0.29	0.33	395	507	0.0109	0.0104	0.0451	0.075	0.1890	0.0032	0.0037
Trial 59	Med	22.4	3	1.62	2.03	0.31	0.45	742	952	0.0196	0.0174	0.0808	0.075	0.1890	0.0075	0.0124
Trial 60	Med	22.4	4	1.84	2.36	0.35	0.51	844	1084	0.0201	0.0173	0.0830	0.075	0.1890	0.0084	0.0126

Table A.2 Experimental data for growth of steelhead trout in relation to temperature and food consumption. Data is from Wurtsbaugh and Davis, 1977.

Trial	Temperature °C	Season	Initial Wet Weight (g)	Final Wet Weight (g)	Initial Dry Weight (g)	Final Dry Weight (g)	Dry Weight Consumption (g/g/d)	Mid Weight Dry Consumption (g/g/d)	% Fish Moisture Dry/Wet	Final Dry Weight %	Dry Daily Growth Rate (g/g/d)	Wet Daily Growth Rate (g/g/d)
Trial 1	6.9	Winter	2.03	1.82	0.443	0.337	0.5	0.04870	0.218	0.185	-0.011	**-0.436**
Trial 2	6.9	Winter	2.01	1.96	0.438	0.380	1.5	0.15345	0.218	0.194	-0.006	**-0.101**
Trial 3	6.9	Winter	1.95	2.1	0.425	0.456	2.5	0.27525	0.218	0.217	0.003	**0.296**
Trial 4	6.9	Winter	1.91	2.3	0.416	0.534	4.2	0.49874	0.218	0.232	0.010	**0.741**
Trial 5	9.4	Spring	2.35	2.35	0.470	0.430	2.5	0.28127	0.2	0.183	-0.004	**0.000**
Trial 6	9.4	Spring	2.25	2.71	0.450	0.526	4.9	0.59764	0.2	0.194	0.006	**0.742**
Trial 7	9.4	Spring	2.36	3.19	0.472	0.657	7	0.98800	0.2	0.206	0.013	**1.196**
Trial 8	9.4	Spring	2.23	3.38	0.446	0.690	10.2	1.44779	0.2	0.204	0.017	**1.640**
Trial 9	10	Autumn	0.98	0.96	0.190	0.177	2.2	0.10086	0.194	0.184	-0.003	**-0.082**
Trial 10	10	Autumn	1.04	1.31	0.202	0.261	4.3	0.24857	0.194	0.199	0.010	**0.919**
Trial 11	10	Autumn	1.02	1.64	0.198	0.341	7.9	0.53226	0.194	0.208	0.021	**1.865**
Trial 12	10	Autumn	1	1.89	0.194	0.412	14	1.06054	0.194	0.218	0.029	**2.464**
Trial 13	10.1	Winter	1.96	1.66	0.414	0.300	0.6	0.05355	0.211	0.181	-0.013	**-0.663**
Trial 14	10.1	Winter	1.96	1.82	0.414	0.351	1.5	0.14340	0.211	0.193	-0.007	**-0.296**
Trial 15	10.1	Winter	1.97	2.02	0.416	0.396	2.7	0.27391	0.211	0.196	-0.002	**0.100**
Trial 16	10.1	Winter	1.94	2.35	0.409	0.496	4.9	0.55443	0.211	0.211	0.008	**0.765**
Trial 17	12.6	Spring	2.29	2.29	0.463	0.428	3.8	0.42313	0.202	0.187	-0.003	**0.000**
Trial 18	12.6	Spring	2.33	2.82	0.471	0.541	6.1	0.77173	0.202	0.192	0.006	**0.761**
Trial 19	12.6	Spring	2.24	3.17	0.452	0.650	9.1	1.25390	0.202	0.205	0.014	**1.375**
Trial 20	12.6	Spring	2.28	3.75	0.461	0.810	12.7	2.01701	0.202	0.216	0.022	**1.950**
Trial 21	13	Winter	1.92	1.7	0.394	0.296	2	0.17235	0.205	0.174	-0.011	**-0.486**
Trial 22	13	Winter	1.84	1.72	0.377	0.316	3	0.26013	0.205	0.184	-0.007	**-0.270**
Trial 23	13	Winter	1.86	2.21	0.381	0.477	5.7	0.61180	0.205	0.216	0.009	**0.688**
Trial 24	13.3	Autumn	1	0.93	0.199	0.169	2.2	0.10127	0.199	0.182	-0.006	**-0.290**

Table A.2 Continued. Experimental data for growth of steelhead trout in relation to temperature and food consumption. Data is from Wurtsbaugh and Davis, 1977.

Trial	Temperature °C	Season	Initial Wet Weight (g)	Final Wet Weight (g)	Initial Dry Weight (g)	Final Dry Weight (g)	Dry Weight Consumption (g/g/d)	Mid Weight Dry Consumption (g/g/d)	% Fish Moisture Dry/Wet	Final Dry Weight %	Dry Daily Growth Rate (g/g/d)	Wet Daily Growth Rate (g/g/d)
Trial 25	13.3	Autumn	0.98	1.17	0.195	0.227	4.6	0.24265	0.199	0.194	0.006	**0.707**
Trial 26	13.3	Autumn	1.02	1.55	0.203	0.315	7.7	0.49822	0.199	0.203	0.017	**1.650**
Trial 27	13.3	Autumn	0.97	2.11	0.193	0.473	16.5	1.37294	0.199	0.224	0.034	**2.961**
Trial 28	15.2	Spring	2.28	2.33	0.456	0.419	5.5	0.60184	0.2	0.18	-0.003	**0.087**
Trial 29	15.2	Spring	2.25	3.17	0.450	0.669	10.2	1.42656	0.2	0.211	0.016	**1.358**
Trial 30	15.2	Spring	2.25	3.73	0.450	0.791	15.4	2.38846	0.2	0.212	0.022	**1.980**
Trial 31	16.2	Summer	1.14	1.21	0.239	0.241	4.9	0.29412	0.21	0.199	0.000	**0.238**
Trial 32	16.2	Summer	1.23	1.57	0.258	0.345	6.8	0.51315	0.21	0.22	0.012	**0.971**
Trial 33	16.2	Summer	1.18	1.64	0.248	0.364	9.5	0.72661	0.21	0.222	0.015	**1.305**
Trial 34	16.2	Summer	1.2	2.13	0.252	0.494	14.3	1.33376	0.21	0.232	0.026	**2.234**
Trial 35	16.4	Autumn	0.94	1.29	0.185	0.258	8.3	0.45980	0.197	0.2	0.013	**1.256**
Trial 36	16.4	Autumn	0.92	2.04	0.181	0.469	20.1	1.63423	0.197	0.23	0.035	**3.027**
Trial 37	19.5	Summer	1.19	1.28	0.258	0.274	6	0.39911	0.217	0.214	0.002	**0.291**
Trial 38	19.5	Summer	1.21	1.53	0.263	0.341	7.9	0.59621	0.217	0.223	0.010	**0.934**
Trial 39	19.5	Summer	1.16	1.63	0.252	0.380	10.3	0.81307	0.217	0.233	0.016	**1.348**
Trial 40	19.5	Summer	1.18	2.02	0.256	0.475	15.7	1.43412	0.217	0.235	0.024	**2.100**
Trial 41	22.5	Summer	1.1	1.21	0.243	0.258	7.4	0.46327	0.221	0.213	0.002	**0.381**
Trial 42	22.5	Summer	1.1	1.25	0.243	0.273	9.2	0.59294	0.221	0.218	0.005	**0.511**
Trial 43	22.5	Summer	1.11	1.41	0.245	0.326	11	0.78515	0.221	0.231	0.011	**0.952**
Trial 44	22.5	Summer	1.16	1.61	0.256	0.390	13.4	1.08202	0.221	0.242	0.017	**1.300**

LITERATURE CITED

Brett, R.J., 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. Canada 26:2363-2394.

Brett, R.J., 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. No. 1127.

Everson, L.B. 1973. Growth and food consumption of juvenile coho salmon exposed to natural and elevated fluctuating temperatures. M.S. Thesis, Oregon State University, Corvallis, OR. 68 pp.

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.

APPENDIX B

**REGIONAL TEMPERATURE DATA FOR THE PACIFIC NORTHWEST
REGION, FROM U.S. GEOLOGICAL SURVEY WATER RESOURCES
DATA**

Washington

Oregon

Idaho

From 1978-79 Water Resources Data
U.S. Geological Survey

Table B.1 Annual maximum temperature for 1978-79 and most extreme temperature measured at all stream and river sites listed in the U.S.G.S. water resources inventory for Washington.

State	River	USGS Station Number	Basin Area (km^2)	1979 Annual Maximum Temperature (°C)	Extreme Maximum (°C)
Washington	Wynoochee River	12037400	401	22.5	24
	N.F. Skokomish River	12056500	148	14	15
	Skokomish River	12056500	588	16	20.5
	Nisqually River near National	12082500	344	18	18.5
	Nisqually River near LaGrande	12086500	756	18	18.5
	Green River	12113000	1,033	22.5	24
	Cedar River near Landsburg	12117500	313	15.5	19.5
	Cedar River near Renton	12119000	477	23	24
	M.F. Snoqualmie River	12141300	399	18.5	
	N. F. Snoqualmie River	1214200	166	21	
	S. F. Snoqualmie River		108	19	
	Skagit River	12179000	3,300	13	
	Tank Creek	12197040	6	17.5	
	Minkler Creek	12197110	13	21	21
	Black Creek	12197680	1	16.5	17.5
	Wiseman Creek	12197700	8	16	16.5
	Skagit River near Sedro Woolley	12199000	7,809	18	18
	Skagit River near Mount Vernon	12200500	8,011	17.5	17.8
	Kalama River	14223600	325	20.5	21.5
	Cowlitz River near Randall	14233400	2,668	18.5	19
	Cowlitz River below Mossyrock Dam	14234810	2,989	11	15
	Cowlitz River below Mayfield Dam	14238000	3,626	12.5	21
	Tilton River	14236200	365	21.5	24.5
	Columbia River at Warrendale	14128910	621,600	22	22.5
	Columbia River at Bradwood, OR	14247400	665,900	21.5	22.5
	Columbia River at Northport, WA	12433000	154,600	20	21
	Columbia River at Grand Coulee Dam	12472900	193,500	19	19
	Columbia River at Richland	12473520	251,000	21	21.5
	Columbia River at Umatilla	14019250	554,300	22	22.5
	Pend Oreille River	12398600	65,300	23	24.5
	Spokane River	12433000	15,590	20.5	24.5
	Yakima River at Kiona	12510500	14,543	28	29
	Snake River at Anatone	13334300	241,000	23.5	25
	Snake River at Burbank	13353200	281,800	23.5	24

Table B.2 Annual maximum temperature for 1978-79 and most extreme temperature measured at all stream and river sites listed in the U.S.G.S. water resources inventory for Oregon.

State	River	USGS Station Number	Basin Area (km^2)	1979 Annual Maximum Temperature (ºC)	Extreme Maximum (ºC)
Oregon	Columbia River at Rainier	14245295	664,900	21.5	23.5
	Columbia River at Wama	14247295	665,000	21.5	22.5
	Columbia River at Vancouver	14144700	624,200	22	23.5
	Owyhee River	13184000	29,300	25	25
	Meadow Creek near Starkey	13318050	86	25	25
	Meadow Creek above Bear Cr.	133`8060	125	26	26.5
	Minam River	13331500	622	24.5	27
	Umatilla River	14020000	339	24.5	25
	John Day River	14048000	19,600	31	33
	Deschutes River near Bend	14064500	4,556	17	17
	Deschutes River near Madras	14092500	20,250	14	18
	Deschutes River near Moody	14103000	27,200	23	23
	DonnerundBlitzen River	10396000	518	25.5	28.5
	Willamette at Portland	14211720	28,700	24	27.5
	Bull Run River	14138850	124	17	17
	Fir Creek	14138870	14	14.5	15
	N. F. Bull Run River	14138900	22	14	
	S.F. Bull Run River	14139800		17	
	M. F. Willamette near Oak Ridge	14144800	668	20	23
	Hills Creek	14144900	136	19	22.5
	M.F. Willamette above Salt Cr.	14145500	1,015	17	25
	M. F. Willamette below N. Fork	14148000	2,393	19	23.5
	M.F. Willamette near Dexter	14150000	2,593	17.5	18.5
	Fall Creek	14150300	306	25	25
	Wineberry Creek	14150800	114	24	26.5
	Fall Creek below Wineberry Cr.	14151000	482	20.5	26
	M.F. Willamette at Jasper	14152000	3,471	17.5	21
	Coast Fork Willamette River	14152500	187	24.5	25.5
	McKenzie River below Trail Cr. Dam	14158850	477	11	12
	McKenzie River at McKenzie Bridge	14159000	901	13	13.5
	S. Fork McKenzie	14159200	414	17	17
	S. Fork McKenzie near Rainbow	14159500	539	14	20
	Blue River	14161100	119	23	23
	McKenzie River near Vida	14162500	2,409	15	16
	Willamette River at Harrisburg	14166000	8,860	20	24
	Mary's River	14171000	412	22.5	23.5
	Calapooia River at Holley	14172000	272	29	29.5
	Calapooia River at Albany	14173500	963	28	28.5
	N. Santiam River below Boulder	14178000	559	17.5	19.5
	Breitenbush River	14179000	275	16.5	18
	N. Santiam River at Niagara	14181500	1,173	13.5	16.5
	S. Santiam River below Cascadia	14185000	451	24	25
	M. Santiam River near Cascadia	14185800	269	22	22.5
	Quartzville Creek	14185900	257	24	25.5
	S. Santiam River near Foster	14187200	1,443	14.5	15.5
	S. Santiam River near Waterloo	14187500	1,658	18	26
	Santiam River	14189000	4,640	23	23.5
	Willamette River at Salem	14191000	18,900	24	25.5
	Tualatin River near Gaston	14202500	126	24	
	Tualatin River at West Linn	14207500	1,829	23.5	27.5

Table B.2 Continued Annual maximum temperature for 1978-79 and most extreme temperature measured at all stream and river sites listed in the U.S.G.S. water resources inventory for Oregon.

State	River	USGS Station Number	Basin Area (km^2)	1979 Annual Maximum Temperature (^{o}C)	Extreme Maximum (^{o}C)
Oregon	Nehalem River	14301000	1,728	24.5	24.5
	Nestucca River	14303600	466	23.5	24
	Big Rock Creek	14304850	18	19.5	
	Siletz River	14305500	523	24.5	
	Siuslaw River	14307620	1,523	31	31
	S. Umpqua River at Days Cr.	14308600	1,660	29	30
	S. Umpqua River near Roseburg	14312260	4,657	25	29
	N. Umpqua River at Winchester	14319500	3,481	26	26.5
	Umpqua River	14321000	9,539	27	30
	Rogue River below Prospect	14330000	982	20.5	20.5
	S. Fork Rogue River	14335075	637	20	20
	Rogue River at McLeod	14335075	1.787	14.5	14.5
	Big Bull Creek	14337500	635	24	24
	Rogue River near McLeod	14337600	2,429	14.5	18
	Elk Creek	14337800	204	27.5	28.5
	W. Branch Elk Creek	14337870	37	24	25.5
	Elk Creek near Trail	14338000	344	31.5	31.5
	Rogue River at Dodge Bridge	14339000	3,147	18.5	20
	Rogue River at Raygold	1435900	5,317	19	22
	Rogue River at Grants Pass	14361500	6,369	17	23.5
	Rogue River near Merlin	14370400	8,472	22.5	25.5
	Rogue River at Marial	14372250	9,873	24.5	27.5
	Rogue River near Agnes	14372300	10,202	24.5	26.5
	Elliot Creek	14361600	134	22.5	23
	Carberry Creek	14361700	178	23.5	23.5
	Applegate River near Copper	14362000	583	25.5	26.5
	Applegate River near Applegate	14366000	1,251	26	28
	Applegate River near Wilderville	14369500	1,808	28	28

Table B.3 Annual maximum temperature for 1978-79 and most extreme temperature measured at all stream and river sites listed in the U.S.G.S. water resources inventory for Idaho.

State	River	USGS Station Number	Basin Area (km^2)	1979 Annual Maximum Temperature (^{o}C)	Extreme Maximum (^{o}C)
Idaho	Kootenai River at Leonia	12305000	30,407	14	
	Kootenai River near Copeland	12318500	34,710	19	24
	Kootenai River at Porthill	12322000	35	20	23.5
	Salmon River at Whitebird	13269000	35,090	25	28
	Yankee Fork Salmon River	13296000	505	16	17.5
	N. Fork Clearwater near Canyon	13340600	3,520	21.5	23
	Clearwater River near Peck	13341050	6,320	21	25
	Clearwater River at Spalding	13342500	24,790	22	28
	Bear River at Border, WY	10039500	6,439	23	23
	Salt River above reservoir, Alpin WY	13023000	1,160	16.5	21
	Snake River at Weiser	13269000	565	28.5	
	Snake River at Hells Canyon Dam	13269000	190,000	19.5	20
	Snake River near Irwin	13032500	13,533	15.5	18.5
	Snake River at Neeley	13077000	35,200	23.5	23.5
	Snake River at Minidoka	13081500	40,700	23	23.5
	Snake River at King Hill	13081500	92,700	20.5	23.5
	Willow Creek near Ririe	13058000	1,620	25	

APPENDIX C

**ACUTE EFFECTS OF TEMPERATURE ON SALMON AND TROUT: DATA USED,
ANALYSES AND ASSUMPTIONS**

Chinook salmon
Chum salmon
Coho salmon
Cutthroat trout
Pink salmon
Rainbow trout
Sockeye salmon

DESCRIPTION OF METHODOLOGY

This memorandum summarizes how estimated acute thermal effects curves were generated for selected species of salmon and trout: pink salmon, chum salmon, coho salmon, sockeye salmon, chinook salmon, rainbow trout (steelhead), and cutthroat trout. Effects of elevated temperatures on these fish species were of interest; thus, curves were generated from available data for acclimation temperatures of 15°C and higher.

Most of the available thermal effects information is based on 50% survival; however, curves for 90% survival (10% mortality) were desired. The process by which 10% mortality curves were estimated from the 50% mortality information is detailed here. Three attachments are provided to illustrate the data used and analyses:

Attachment 1: Acute Effects of Temperature on Salmonids: Median Lethal Times (LT50) in Relation to Temperature

Attachment 2: LT50 to LT10 Conversion Factors for Pacific Salmon: Sockeye and Chinook.

Attachment 3: Acute Effects of Temperature on Salmonids: Times to 10% Mortality (LT10) In Relation to Temperature.

ACUTE THERMAL EFFECTS CURVES ASSOCIATED WITH 50% MORTALITY

Data from several sources were used to generate curves showing the relationship between temperature and duration to 50% mortality (EPA 1977, Brett 1952, and Golden 1978). Each curve estimates the length of time 50% of a species population can survive at some temperature above its upper incipient lethal temperature. For the remainder of this memorandum, this temperature will be referred to as the LT50, the temperature causing 50% mortality in a population of fish within a specified length of time.

EPA (1977, page 11 of text and page 38 of Appendix A) provides a regression equation relating exposure time (in minutes) to the LT50 (in EC):

$$\log[\text{exposure time}] = a + b*\text{LT50},$$

which can also be written as

$$\text{LT50} = (\log[\text{exposure time}] - a)/b.$$

The regression coefficients, a and b, are provided in EPA (1977) for many fish species, including all those identified above, except cutthroat trout (pages 55-58 of Appendix B). Golden (1978, Figure 4 on page 14) provides regression coefficients for cutthroat trout. The coefficients in EPA (1977) were gathered from many different sources, including Brett's 1952 paper summarizing his study of lethal temperatures for the five salmon species. In the attachments, the specific studies are cited rather than the EPA (1977) document.

The acute thermal effects curves provided in Attachment 1 were generated in Excel using regression coefficients provided in EPA (1977) and Golden (1978) and the second form of the regression equation presented above for a range of times (durations). For the five salmon species, Brett (1952) provided ultimate upper incipient lethal temperatures, and the acute curves were discontinued at these values. For rainbow trout and cutthroat trout, the curves were discontinued at 25 °C.

Although it was assumed that the regression coefficients in Appendix B of EPA (1977) were correct, one appeared to be in error. The value for a was given as 16.2444 for pink salmon at an acclimation temperature of 20 °C from Brett's study (1952). The resulting curve did not match the one presented in Figure 5 of Brett (1952). To generate a curve more representative of Brett's (1952) figure, a value of 13.2444 was used for a instead.

A few of the studies included in EPA (1977) were excluded from Attachment 1. These were studies in which the fish being tested showed signs of gas bubble disease or other effects of gas supersaturation.

COMPARISON OF LT50 AND LT10 CURVES

In the EPA (1977) document, two unpublished studies provided regression coefficients for both 50% and 10% (LT10) mortality curves at acclimation temperatures of 15EC or higher. McConnell and Blahm (1970) calculated regression coefficients for sockeye salmon; and Blahm and McConnell (1970) calculated regression coefficients for both spring and fall runs of chinook salmon. Using the regression coefficients generated from these studies, LT50 and LT10 values were calculated for a range of durations.

Attachment 2 contains two tables (one each for sockeye and chinook salmon) of the calculated values and their ratios (i.e, LT10/LT50). For the range of durations calculated, the LT10 values were 98.0 to 99.7% of the LT50 values. This is consistent with Brett (1958, page 76 and Figure 4), who indicated that differences between temperatures for 50% mortality and those for <50% mortality are relatively small, "implying that temperatures of this order have only to increase slightly to cause a large difference in mortality."

ACUTE THERMAL EFFECTS CURVES @ 10% MORTALITY

Based on the comparison of LT50 and LT10 curves generated from the McConnell and Blahm (1970) and Blahm and McConnell (1970) studies, and to be somewhat conservative, LT10 curves were estimated for the other studies by applying a factor of 0.98 to each curve. That is, each LT10 value was estimated to be 98% of the LT50 value calculated from the regression equation. The estimated LT10 curves are presented in Attachment 3.

Based on visual inspection of the LT50 and LT10 curves included in Attachment 1 from these two studies, the slopes were similar. That is, on the log-time scale, the differences between the LT50 and LT10 curves were approximately constant. (There was insufficient information presented in Appendix B of the EPA (1977) document to statistically compare the slopes.) Had the differences not appeared constant, the application of a singe adjustment factor would not have been appropriate.

KEY ASSUMPTIONS/ISSUES

The following text summarizes key assumptions used when evaluating the available data and estimating the LT10 curves. Other issues relevant to the use of these data are also identified. The information is presented in bullet form and can be expanded upon at a later date if desired.

- The most important assumption is that the data provided in EPA (1977) were representative of the same species from different locations (i.e., different stocks). There are many factors to consider with such an assumption: different environmental influences (water quality, temperature fluctuations), genetic differences, size, life stage, etc.

- As stated above, the regression coefficients reported in EPA (1977) were assumed to be correct.

- The adjustment factor estimated from the McConnell and Blahm (1970) and Blahm and McConnell (1970) data for sockeye and chinook salmon was assumed to be appropriate to use in estimating LT10 curves for the other salmon and trout species.

- Effects curves appear to differ for fish tested using a constant acclimation temperature versus a fluctuating one (see Attachment 1 for cutthroat trout). Can results based on constant acclimation temperatures be applied to fish living in streams with temperatures fluctuating on a daily and seasonal basis?

- For many of the studies, the test fish were obtained from a hatchery, and sometimes from a limited number of females. While this limited variability in the biological responses to temperature because of the genetics, it also may have limited the representativeness of the results for a wider population of fish of same species.

APPENDIX C REFERENCES

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

Brett, J.R. 1958. Implications and assessments of environmental stress. Pages 60-83 in P.A. Larkin, editor. The Investigation of Fish-Power Problems. H.R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver.

EPA. 1977. Temperature criteria for freshwater fish: protocol and procedures. U.S. Environmental Protection Agency Office of Research and Development, Environmental Research Laboratory, Duluth, Minnesota. EPA-600/3-77-061. 130p.

Golden, J.T. 1978. The effects of fluctuating temperatures on the lethal tolerance limits of coastal cutthroat trout (*Salmo clarki clarki*). Thesis, Oregon State University, Corvallis, Oregon. 29p.

APPENDIX C
ATTACHMENT 1

Acute Effects of Temperature on Salmonids:
Median Lethal Times (LT50) in Relation to Temperature

CHINOOK SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Brett(1952)	juv. frshwtr fry	16.4454	-0.5364	4	-0.9906	0.1	29.2
							0.25	28.5
							0.5	27.9
							1	27.3
							2	26.8
							4	26.2
							6	25.9
							8	25.7
							10	25.5
							12	25.3
							13	25.3
							14	25.2
							16	25.1
20C	Brett(1952)	juv. frshwtr fry	22.9065	-0.7611	7	-0.9850	0.1	29.1
							0.25	28.6
							0.5	28.2
							2	27.4
							4	27.0
							6	26.7
							8	26.6
							10	26.4
							16	26.2
							24	25.9
							40	25.7
							60	25.4
							80	25.3
							100	25.1
24C	Brett(1952)	juv. frshwtr fry	18.9940	-0.5992	9	-0.9923	0.1	30.4
							0.25	29.7
							0.5	29.2
							1	28.7
							2	28.2
							4	27.7
							6	27.4
							8	27.2
							10	27.1
							16	26.7
							24	26.4
							40	26.1
							56	25.8
							72	25.6
							96	25.4
							120	25.3
							140	25.1
17C	Coutant (1970)	"Jacks" (1-2 yrs)	13.2502	-0.4121	4	-0.8206	0.1	30.3
							0.25	29.3
							0.5	28.6
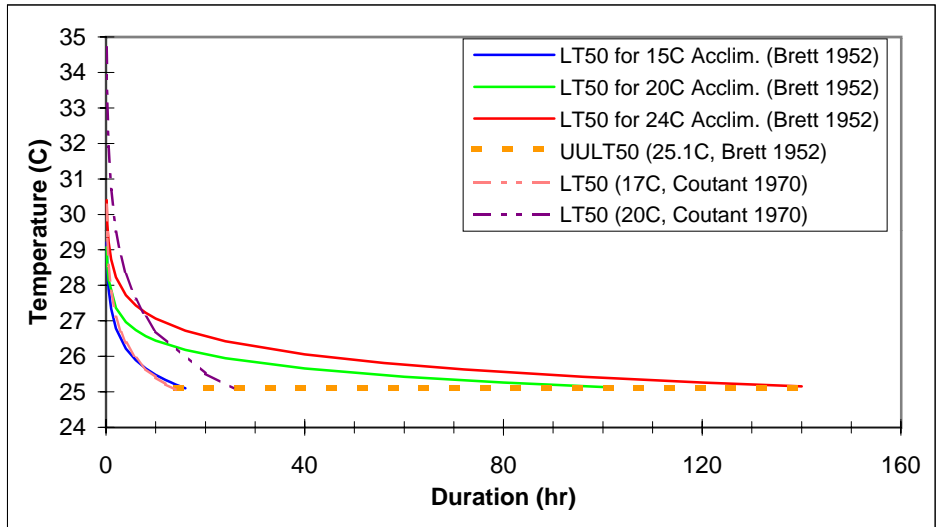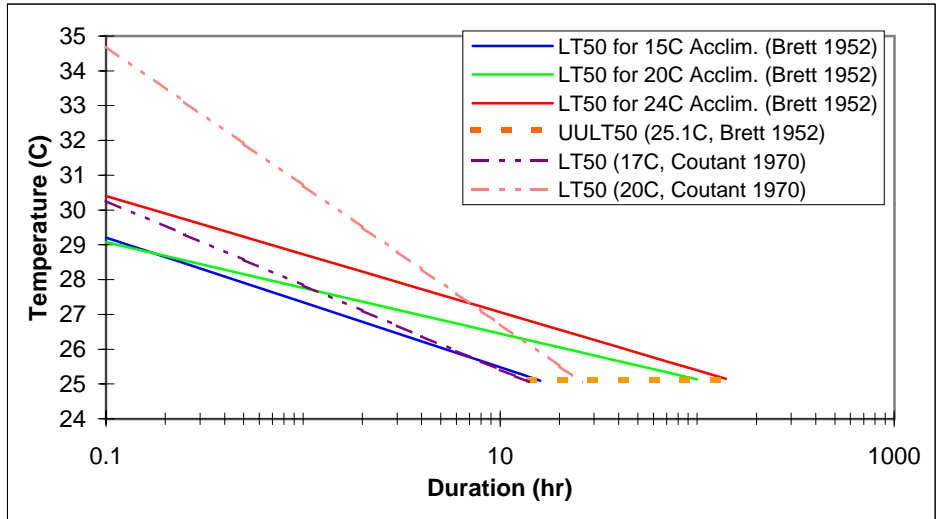
CHINOOK SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
							1	27.8
							2	27.1
	The 17C and 19C temperatures were Columbia River						3	26.7
	temperatures (at Grand Rapids Dam) during fall						4	26.4
	migrations two different years.						6	25.9
							8	25.6
							10	25.4
							12	25.2
							14	25.1
19C	Coutant (1970)	"Jacks" (1-2 yrs)	9.4683	-0.2504	4	-0.9952	0.1	34.7
							0.25	33.1
							0.5	31.9
							1	30.7
							2	29.5
							3	28.8
							4	28.3
							6	27.6
							8	27.1
							10	26.7
							20	25.5
							26	25.1

CHINOOK SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
20C	Blahm & McConnell (1970) unpublished data	juv. (spring run)	21.3981	-0.7253	3	-0.9579	0.1	28.4
							0.25	27.9
							0.5	27.5
							1	27.1
							2	26.6
							4	26.2
							8	25.8
							10	25.7
							16	25.4
							20	25.3
							24	25.1
							26	25.1
20C	Blahm & McConnell (1970) unpublished data 10% mortality	juv. (spring run)	22.6664	-0.7797	4	-0.9747	0.1	28.1
							0.25	27.6
							0.5	27.2
							1	26.8
							2	26.4
							4	26.0
							6	25.8
							8	25.6
							10	25.5
							12	25.4
							16	25.2
							20	25.1
20C	Blahm & McConnell (1970) unpublished data 90% mortality	juv. (spring run)	20.9294	-0.7024	3	-0.9463	0.1	28.7
							0.25	28.1
							0.5	27.7
							2	26.8
							4	26.4
							6	26.2
							8	26.0
							10	25.8
							16	25.6
							20	25.4
							24	25.3
							32	25.1

CHINOOK SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
20C	Blahm & McConnell (1970) unpublished data	juv. (fall run)	22.2124	-0.7526	4	-0.9738	0.1	28.5
							0.25	28.0
							0.5	27.6
							1	27.2
							2	26.8
							4	26.4
							8	26.0
							10	25.8
							16	25.6
							20	25.4
							24	25.3
							34	25.1
20C	Blahm & McConnell (1970) unpublished data 10% mortality	juv. (fall run)	21.6756	-0.7438	4	-0.9550	0.1	28.1
							0.25	27.6
							0.5	27.2
							1	26.8
							2	26.3
							4	25.9
							6	25.7
							8	25.5
							10	25.4
							12	25.3
							14	25.2
							16	25.1
20C	Blahm & McConnell (1970) unpublished data 90% mortality	juv. (fall run)	20.5162	-0.6860	3	-0.9475	0.1	28.8
							0.25	28.2
							0.5	27.8
							2	26.9
							4	26.4
							6	26.2
							8	26.0
							10	25.9
							16	25.6
							20	25.4
							24	25.3
							32	25.1

COHO SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Brett(1952)	juv. frshwtr fry	20.4066	-0.6858	6	-0.9681	0.1	28.6
							0.25	28.0
							0.5	27.6
							1	27.2
							2	26.7
							4	26.3
							6	26.0
							8	25.8
							10	25.7
							12	25.6
							16	25.4
							20	25.3
							32	25.0
20C	Brett(1952)	juv. frshwtr fry	20.4022	-0.6713	4	-0.9985	0.1	29.2
							0.25	28.6
							0.5	28.2
							2	27.3
							4	26.8
							6	26.6
							8	26.4
							10	26.3
							16	25.9
							24	25.7
							40	25.4
							48	25.2
							56	25.1
							70	25.0
23C	Brett(1952)	juv. frshwtr fry	18.9736	-0.6013	5	-0.9956	0.1	30.3
							0.25	29.6
							0.5	29.1
							1	28.6
							2	28.1
							4	27.6
							6	27.3
							8	27.1
							10	26.9
							16	26.6
							24	26.3
							40	25.9
							56	25.7
							72	25.5
							96	25.3
							120	25.1
							140	25.0
17C	Coutant (1970)	adult	5.9068	-0.1630	5	-0.9767	0.1	31.5
	Reported acclimation temp. was the Columbia River						0.2	29.6
	temp. (at Priest Rapids Dam) during fall migration.						0.3	28.5

COHO SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
							0.4	27.8
							0.5	27.2
							0.6	26.7
							0.7	26.3
							0.8	25.9
							0.9	25.6
							1	25.3
							1.1	25.1
							1.15	25.0
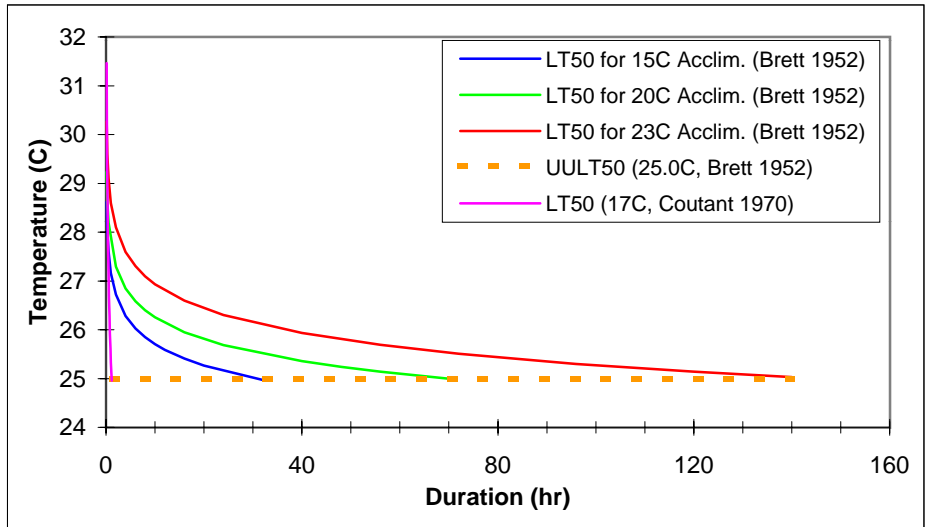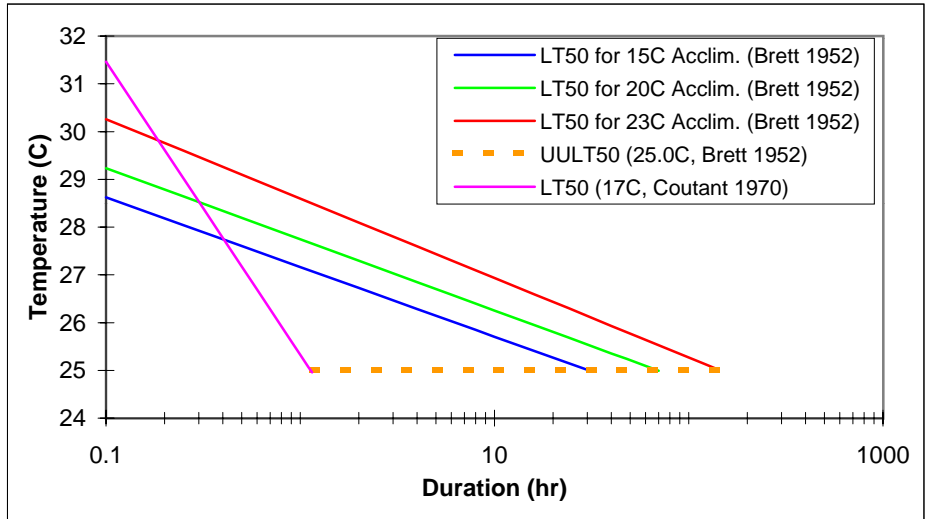
RAINBOW TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Alabaster & Downing (1966)	juvenile	15.6500	-0.5000	2	---	0.1	29.7
							0.25	28.9
							0.5	28.3
							1	27.7
							2	27.1
							4	26.5
							6	26.2
							8	25.9
							10	25.7
							12	25.6
							16	25.3
							20	25.1
							24	25.0
18C	Alabaster & Welcomme (1962) Dissolved Oxygen at 7.4 mg/L	juvenile	18.4654	-0.5801	5	-0.9787	0.1	30.5
							0.25	29.8
							0.5	29.3
							2	28.2
							4	27.7
							6	27.4
							8	27.2
							10	27.0
							16	26.7
							24	26.4
							40	26.0
							80	25.5
							120	25.2
							160	25.0
18C	Alabaster & Welcomme (1962) Dissolved Oxygen at 3.8 mg/L	juvenile	13.6531	-0.4264	5	-0.9742	0.1	30.2
							0.25	29.3
							0.5	28.6
							1	27.8
							2	27.1
							4	26.4
							6	26.0
							7	25.9
							8	25.7
							9	25.6
							10	25.5
							12	25.3
							14	25.2
							16	25.0

RAINBOW TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
20C	Alabaster & Downing (1966)	juvenile	19.6250	-0.6250	2	---	0.1	30.2
							0.25	29.5
							0.5	29.0
							1	28.6
							2	28.1
							4	27.6
							6	27.3
							8	27.1
							12	26.8
							20	26.5
							32	26.1
							40	26.0
							80	25.5
							120	25.2
							160	25.0
20C	Craigie (1963) Raised in soft water, tested in soft water (SS)	yearling	14.6405	-0.4470	3	-0.9787	0.1	31.0
							0.25	30.1
							0.5	29.4
							1	28.8
							2	28.1
							4	27.4
							6	27.0
							8	26.8
							10	26.5
							16	26.1
							20	25.9
							24	25.7
							32	25.4
							40	25.2
							48	25.0
20C	Craigie (1963) Raised in soft water, tested in hard water (SH)	yearling	15.0392	-0.4561	3	-0.9917	0.1	31.3
							0.25	30.4
							0.5	29.7
							1	29.1
							2	28.4
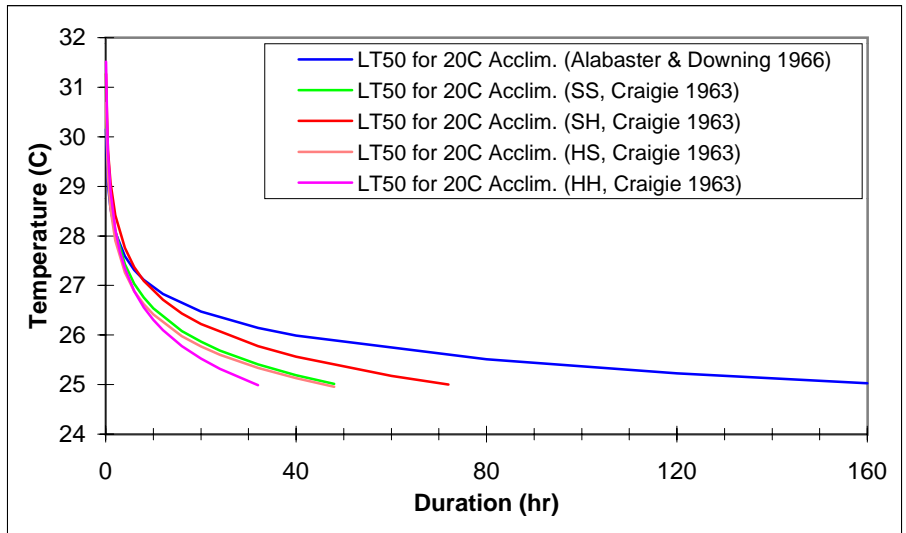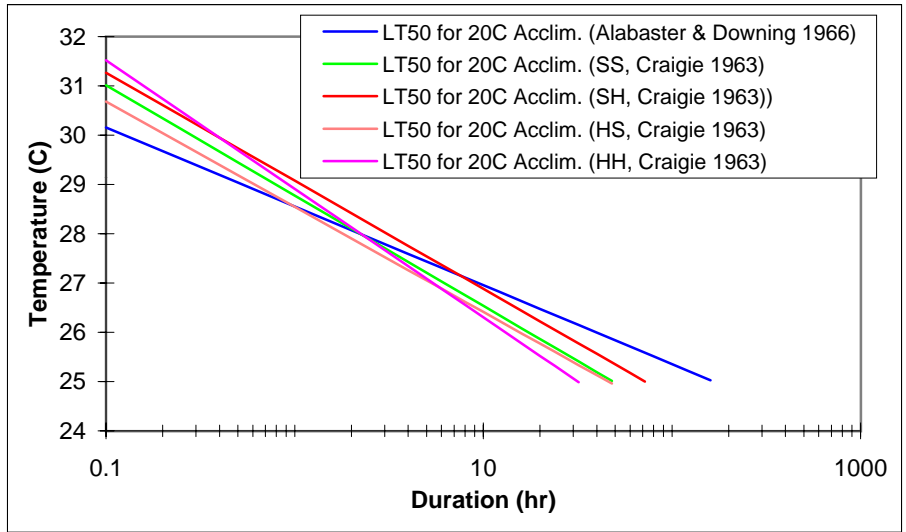
RAINBOW TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
							4	27.8
							6	27.4
							8	27.1
							12	26.7
							16	26.4
							20	26.2
							32	25.8
							40	25.6
							60	25.2
							72	25.0
20C	Craigie (1963)	yearling	15.1473	-0.4683	3	-0.9781	0.1	30.7
	Raised in hard water, tested in soft water (HS)						0.25	29.8
							0.5	29.2
							1	28.5
							2	27.9
							4	27.3
							6	26.9
							8	26.6
							10	26.4
							16	26.0
							20	25.8
							24	25.6
							32	25.3
							40	25.1
							48	25.0
20C	Craigie (1963)	yearling	12.8718	-0.3837	3	-0.9841	0.1	31.5
	Raised in hard water, tested in hard water (HH)						0.25	30.5
							0.5	29.7
							1	28.9
							2	28.1
							3	27.7
							4	27.3
							6	26.9
							8	26.6
							10	26.3
							12	26.1

RAINBOW TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
							16	25.8
							20	25.5
							24	25.3
							32	25.0

CUTTHROAT TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
23C	Golden (1978)	juvenile	18.092	-0.56523	?	-0.996	0.1	30.6
	1975 tests, hatchery only						0.25	29.9
							0.5	29.4
							1	28.9
							8	27.3
							16	26.7
							24	26.4
							32	26.2
							40	26.0
							60	25.7
							80	25.5
							120	25.2
							160	25.0
13-25C	Golden (1978)	juvenile	22.543	-0.71999	?	-0.999	0.1	30.2
	1975 tests, hatchery only						0.25	29.7
							0.5	29.3
							2	28.4
							4	28.0
							8	27.6
							16	27.2
							24	26.9
							40	26.6
							80	26.2
							160	25.8
							240	25.5
							300	25.4
							560	25.0
23C	Golden (1978)	juvenile	18.3166	-0.5723	?	-0.990	0.1	30.6
	1976 tests, hatchery and wild trout data pooled						0.25	30.0
							0.5	29.4
							1	28.9
							2	28.4
							4	27.8
							8	27.3
							12	27.0
							16	26.8
							24	26.5
							40	26.1
							80	25.6
							120	25.3
							160	25.0
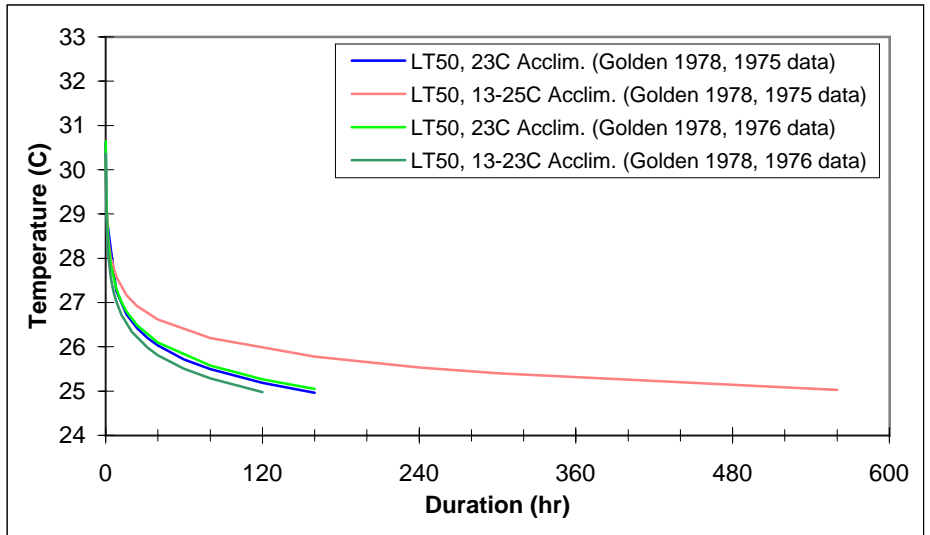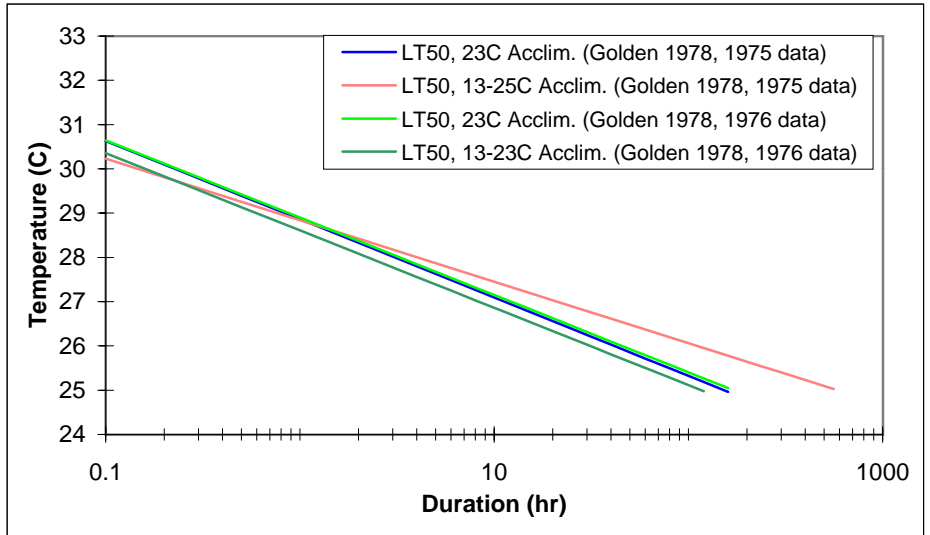
CUTTHROAT TROUT

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
13-23C	Golden (1978)	juvenile	18.1515	-0.5723	?	-0.992	0.1	30.4
	1976 tests, hatchery and wild trout data pooled						0.25	29.7
							0.5	29.1
							1	28.6
							2	28.1
							4	27.6
							6	27.3
							8	27.0
							12	26.7
							20	26.3
							32	26.0
							40	25.8
							60	25.5
							80	25.3
							120	25.0

SOCKEYE SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Brett(1952)	juv. frshwtr fry	15.8799	-0.5210	7	-0.9126	0.1	29.0
							0.25	28.2
							0.5	27.6
							1	27.1
							2	26.5
							4	25.9
							6	25.6
							8	25.3
							10	25.1
							12	25.0
							13	24.9
							14	24.9
							24	24.4
20C	Brett(1952)	juv. frshwtr fry	19.3821	-0.6378	5	-0.9602	0.1	29.2
							0.25	28.5
							0.5	28.1
							2	27.1
							4	26.7
							6	26.4
							8	26.2
							10	26.0
							16	25.7
							24	25.4
							40	25.1
							48	25.0
							56	24.9
							116	24.4
23C	Brett(1952)	juv. frshwtr fry	20.0020	-0.6496	4	-0.9981	0.1	29.6
							0.25	29.0
							0.5	28.5
							1	28.1
							2	27.6
							4	27.1
							6	26.9
							8	26.7
							10	26.5
							16	26.2
							24	25.9
							40	25.6
							56	25.4
							72	25.2
							96	25.0
							120	24.9
							220	24.4
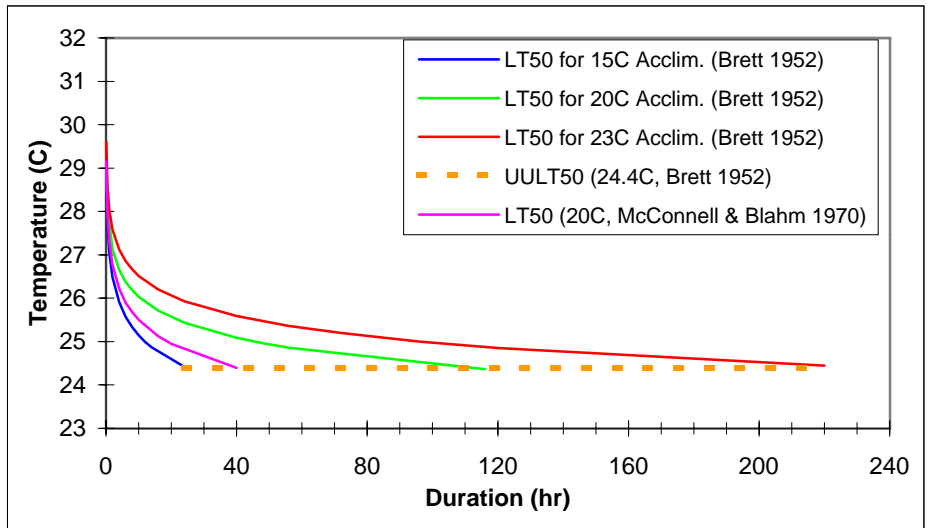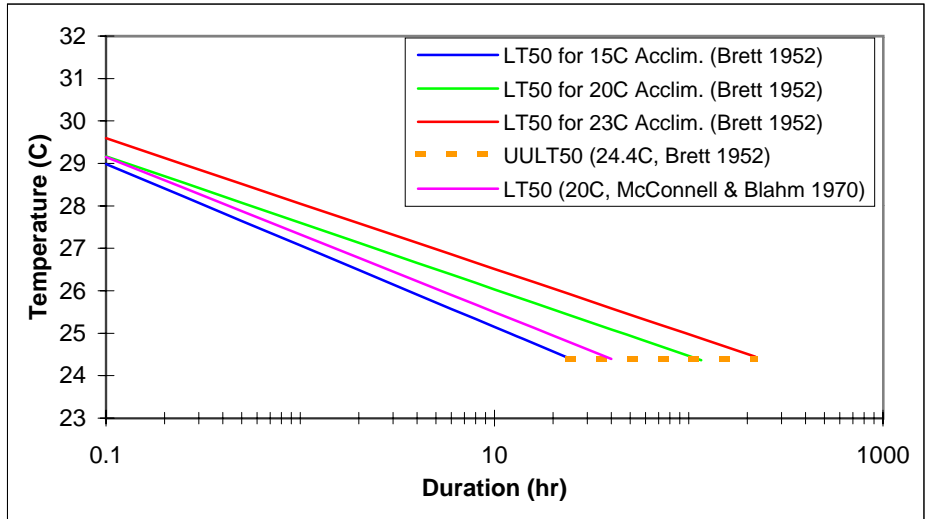
SOCKEYE SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
20C	McConnell & Blahm (1970) unpublished data	juvenile (under yearling)	16.7328	-0.5473	6	-0.9552	0.1	29.2
							0.25	28.4
							0.5	27.9
							1	27.3
							2	26.8
							4	26.2
							6	25.9
							8	25.7
							10	25.5
							16	25.1
							20	24.9
							40	24.4
20C	McConnell & Blahm (1970) unpublished data 10% mortality	juvenile (under yearling)	17.5227	-0.5861	6	-0.9739	0.1	28.6
							0.25	27.9
							0.5	27.4
							1	26.9
							2	26.3
							3	26.0
							4	25.8
							6	25.5
							8	25.3
							10	25.2
							12	25.0
							28	24.4
20C	McConnell & Blahm (1970) unpublished data 90% mortality	juvenile (under yearling)	15.7823	-0.5061	6	-0.9539	0.1	29.6
							0.25	28.9
							0.5	28.3
							2	27.1
							4	26.5
							6	26.1
							8	25.9
							10	25.7
							16	25.3
							20	25.1
							24	24.9
							44	24.4
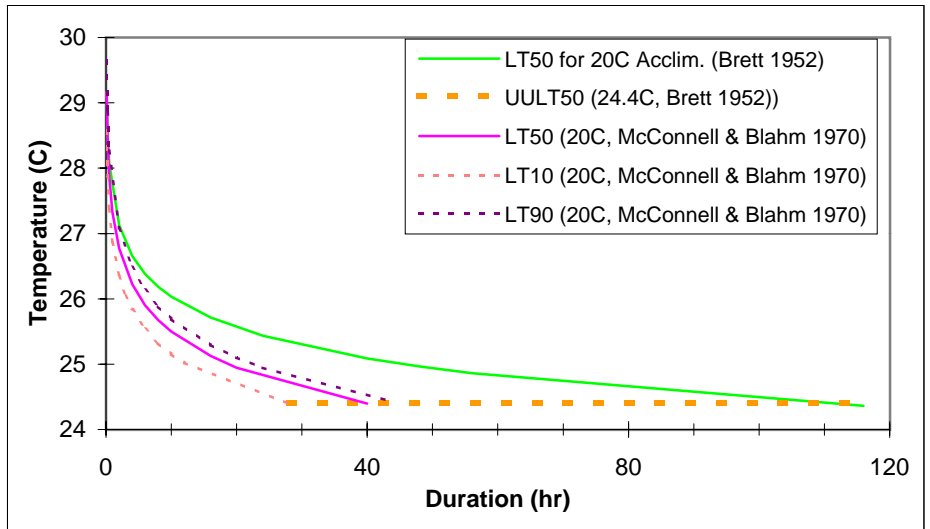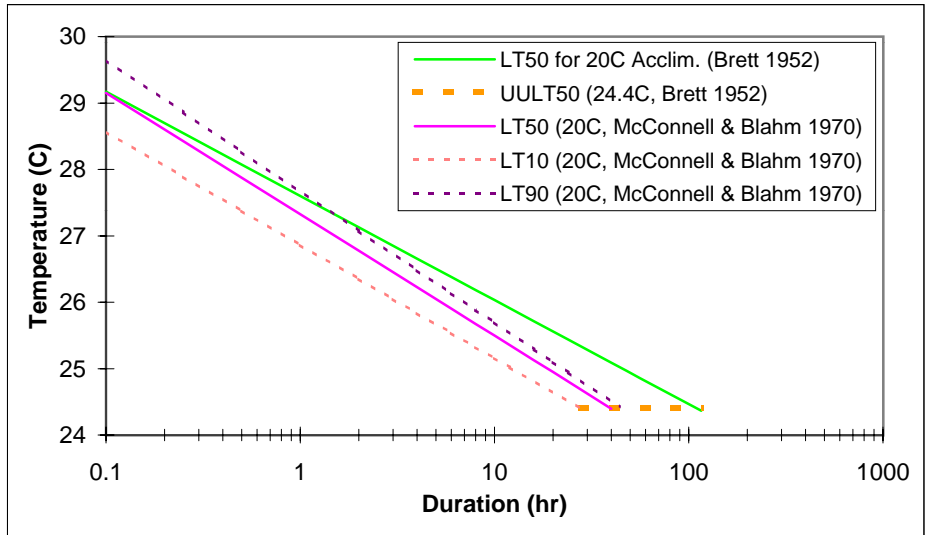
CHUM SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Brett(1952)	juv. frshwtr fry	15.8911	-0.5252	8	-0.9070	0.1	28.8
							0.25	28.0
							0.5	27.4
							1	26.9
							2	26.3
							4	25.7
							6	25.4
							8	25.2
							10	25.0
							12	24.8
							16	24.6
							20	24.4
							40	23.8
20C	Brett(1952)	juv. frshwtr fry	16.1894	-0.5168	9	-0.9750	0.1	29.8
							0.25	29.1
							0.5	28.5
							2	27.3
							4	26.7
							6	26.4
							8	26.1
							10	26.0
							16	25.6
							24	25.2
							40	24.8
							60	24.4
							80	24.2
							132	23.8
23C	Brett(1952)	juv. frshwtr fry	15.3825	-0.4721	4	-0.9652	0.1	30.9
							0.25	30.1
							0.5	29.5
							1	28.8
							2	28.2
							4	27.5
							6	27.2
							8	26.9
							10	26.7
							16	26.3
							24	25.9
							40	25.4
							56	25.1
							72	24.9
							96	24.6
							120	24.4
							240	23.8
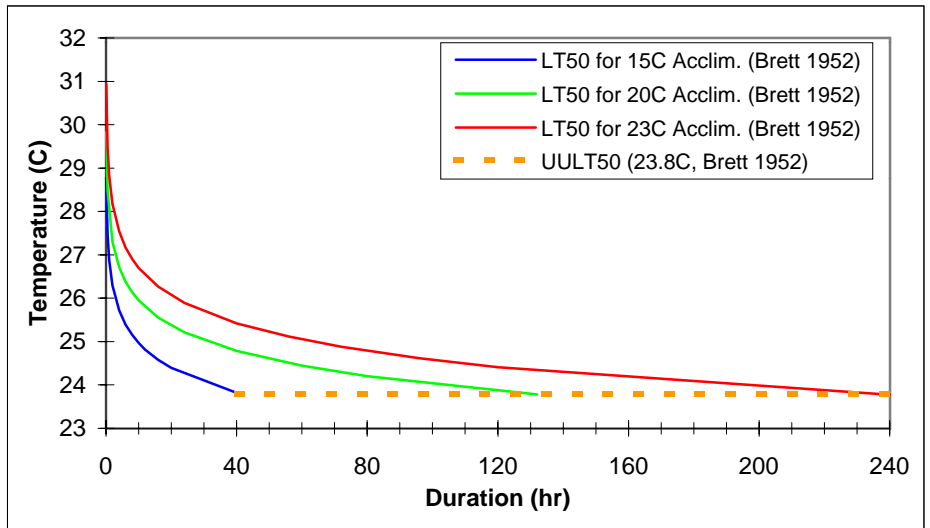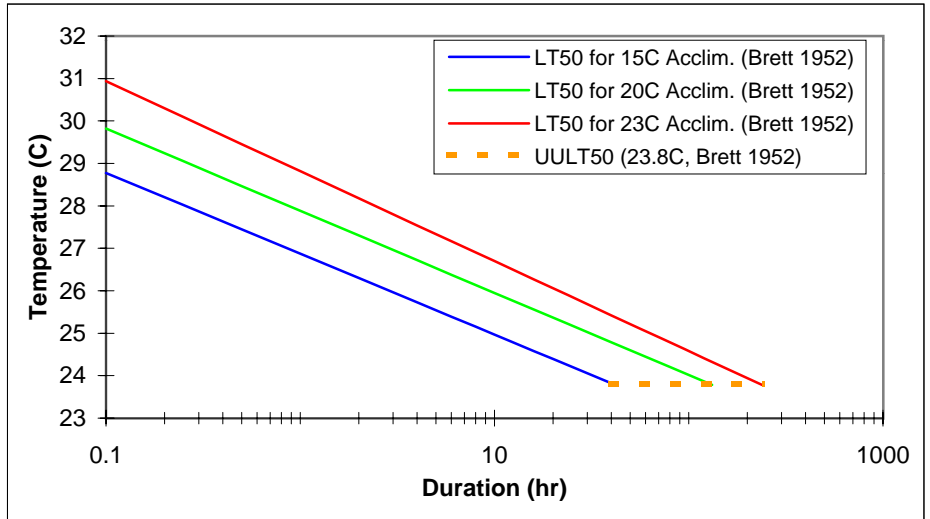
PINK SALMON

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT50(C)
15C	Brett(1952)	juv. frshwtr fry	12.8937	-0.4074	8	-0.9884	0.1	29.7
							0.25	28.8
							0.5	28.0
							1	27.3
							2	26.5
							4	25.8
							6	25.4
							8	25.1
							10	24.8
							12	24.6
							16	24.3
							20	24.1
							24	23.9
20C	Brett(1952)	juv. frshwtr fry	*13.2444*	-0.4074	7	-0.9681	0.1	30.6
			16.2444 in EPA (1977), but				0.25	29.6
			the resulting curve does not				0.5	28.9
			match the information				1	28.1
			presented in Brett (1952)				2	27.4
			<Fig. 5>				4	26.7
							6	26.2
							8	25.9
							10	25.7
							16	25.2
							24	24.8
							32	24.5
							40	24.2
							56	23.9
24C	Brett(1952)	juv. frshwtr fry	14.7111	-0.4459	6	-0.9690	0.1	31.2
							0.25	30.4
							0.5	29.7
							1	29.0
							2	28.3
							4	27.7
							6	27.3
							8	27.0
							10	26.8
							16	26.3
							24	25.9
							40	25.4
							56	25.1
							72	24.8
							96	24.6
							120	24.3
							192	23.9
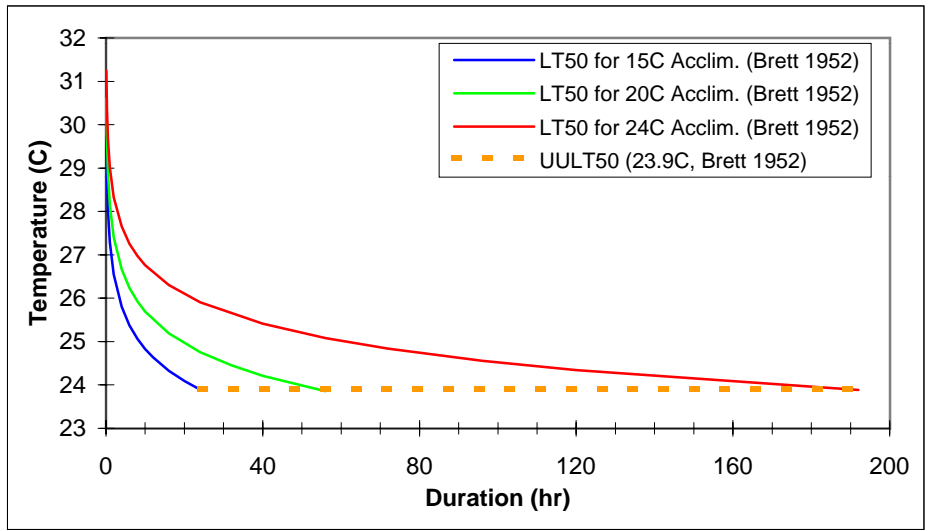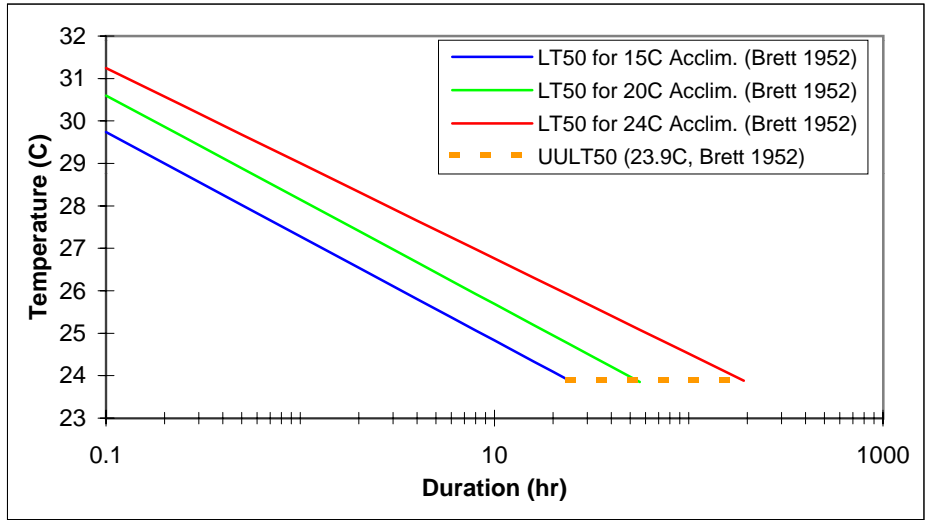
APPENDIX C
ATTACHMENT 2

LT50 to LT10 Conversion Factors for Pacific Salmon: Sockeye and Chinook.

Attacment 2: Sockeye Salmon (20C Acclimation Temperature)
From McConnell & Blahm (1970) unpublished data

16.7328	-0.5473	17.5227	-0.5861	LT10/LT50	Delta T
Time(hr)	LT50(C)	Time(hr)	LT10(C)	Ratio	(C)
0.1	29.2	0.1	28.6	98.00%	0.6
0.25	28.4	0.25	27.9	98.12%	0.5
0.5	27.9	0.5	27.4	98.21%	0.5
1	27.3	1	26.9	98.31%	0.5
2	26.8	2	26.3	98.41%	0.4
3	26.5	3	26.0	98.47%	0.4
4	26.2	4	25.8	98.52%	0.4
6	25.9	6	25.5	98.58%	0.4
8	25.7	8	25.3	98.63%	0.4
12	25.4	12	25.0	98.70%	0.3
16	25.1	16	24.8	98.74%	0.3
20	24.9	20	24.6	98.78%	0.3
24	24.8	24	24.5	98.81%	0.3
32	24.6	32	24.3	98.86%	0.3
40	24.4	40	24.1	98.90%	0.3
60	24.1	60	23.8	98.98%	0.2
80	23.8	80	23.6	99.03%	0.2

Attachment 2: Chinook Salmon (20C Acclimation Temperature)
From Blahm & McConnell (1970) unpublished data

Spring Run					
21.3981	-0.7253	22.6664	-0.7797	LT10/LT50	Delta T
Time(hr)	LT50(C)	Time(hr)	LT10(C)	Ratio	(C)
0.1	28.4	0.1	28.1	98.74%	0.4
0.25	27.9	0.25	27.6	98.86%	0.3
0.5	27.5	0.5	27.2	98.95%	0.3
2	26.6	2	26.4	99.13%	0.2
4	26.2	4	26.0	99.23%	0.2
6	26.0	6	25.8	99.28%	0.2
8	25.8	8	25.6	99.33%	0.2
10	25.7	10	25.5	99.36%	0.2
16	25.4	16	25.2	99.43%	0.1
24	25.1	24	25.0	99.49%	0.1
40	24.8	40	24.7	99.57%	0.1
60	24.6	60	24.5	99.64%	0.1
80	24.4	80	24.3	99.68%	0.1
100	24.3	100	24.2	99.72%	0.1

Fall Run						
22.2124	21.6756	-0.7526	21.6756	-0.7438	LT10/LT50	Delta T
Time(hr)	Time(hr)	LT50(C)	Time(hr)	LT10(C)	Ratio	(C)
0.1	0.1	28.5	0.1	28.1	98.65%	0.4
0.25	0.25	28.0	0.25	27.6	98.60%	0.4
0.5	0.5	27.6	0.5	27.2	98.56%	0.4
2	2	26.8	2	26.3	98.49%	0.4
4	4	26.4	4	25.9	98.44%	0.4
6	6	26.1	6	25.7	98.42%	0.4
8	8	26.0	8	25.5	98.40%	0.4
10	10	25.8	10	25.4	98.39%	0.4
16	16	25.6	16	25.1	98.36%	0.4
24	24	25.3	24	24.9	98.33%	0.4
40	40	25.0	40	24.6	98.30%	0.4
60	60	24.8	60	24.4	98.27%	0.4
80	80	24.6	80	24.2	98.25%	0.4
100	100	24.5	100	24.1	98.24%	0.4

APPENDIX C
ATTACHMENT 3

Acute Effects of Temperature on Salmonids: Times to 10% Mortality (LT10)
In Relation to Temperature.

CHINOOK SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Brett(1952)	juv. frshwtr fry	16.4454	-0.5364	4	-0.9906	0.1	28.6
							0.25	27.9
							0.5	27.3
							1	26.8
							2	26.2
							4	25.7
							6	25.4
							8	25.1
							10	25.0
							12	24.8
							13	24.8
							14	24.7
							16	24.6
20C	Brett(1952)	juv. frshwtr fry	22.9065	-0.7611	7	-0.9850	0.1	28.5
							0.25	28.0
							0.5	27.6
							2	26.8
							4	26.4
							6	26.2
							8	26.0
							10	25.9
							16	25.7
							24	25.4
							40	25.1
							60	24.9
							80	24.8
							100	24.6
24C	Brett(1952)	juv. frshwtr fry	18.9940	-0.5992	9	-0.9923	0.1	29.8
							0.25	29.1
							0.5	28.6
							1	28.2
							2	27.7
							4	27.2
							6	26.9
							8	26.7
							10	26.5
							16	26.2
							24	25.9
							40	25.5
							56	25.3
							72	25.1
							96	24.9
							120	24.8
							140	24.6

CHINOOK SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
17C	Coutant (1970)	"Jacks" (1-2 yrs)	13.2502	-0.4121	4	-0.8206	0.1	29.7
							0.25	28.7
							0.5	28.0
							1	27.3
							2	26.6
	The 17C and 19C temperatures were Columbia River						3	26.1
	temperatures (at Grand Rapids Dam) during fall						4	25.8
	migrations two different years.						6	25.4
							8	25.1
							10	24.9
							12	24.7
							14	24.6
19C	Coutant (1970)	"Jacks" (1-2 yrs)	9.4683	-0.2504	4	-0.9952	0.1	34.0
							0.25	32.5
							0.5	31.3
							1	30.1
							2	28.9
							3	28.2
							4	27.7
							6	27.1
							8	26.6
							10	26.2
							20	25.0
							26	24.6
20C	Blahm & McConnell (1970) unpublished data	juv. (spring run)	21.3981	-0.7253	3	-0.9579	0.1	27.9
							0.25	27.3
							0.5	26.9
							1	26.5
							2	26.1
							4	25.7
							8	25.3
							10	25.2
							16	24.9
							20	24.8
							24	24.6
							26	24.6

CHINOOK SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
20C	Blahm &	juv. (spring run)	22.6664	-0.7797	4	-0.9747	0.1	28.1
	McConnell (1970)						0.25	27.6
	unpublished data						0.5	27.2
	10% mortality	NOT ADJUSTED					1	26.8
							2	26.4
							4	26.0
							6	25.8
							8	25.6
							10	25.5
							12	25.4
							16	25.2
							20	25.1
							32	24.9
							48	24.6
20C	Blahm &	juv. (fall run)	22.2124	-0.7526	4	-0.9738	0.1	27.9
	McConnell (1970)						0.25	27.4
	unpublished data						0.5	27.0
							1	26.6
							2	26.2
							4	25.8
							8	25.4
							10	25.3
							16	25.0
							20	24.9
							24	24.8
							34	24.6
20C	Blahm &	juv. (fall run)	21.6756	-0.7438	4	-0.9550	0.1	28.1
	McConnell (1970)						0.25	27.6
	unpublished data						0.5	27.2
	10% mortality	NOT ADJUSTED					1	26.8
							2	26.3
							4	25.9
							6	25.7
							8	25.5
							10	25.4
							16	25.1
							20	25.0
							24	24.9
							32	24.7
							40	24.6

COHO SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Brett(1952)	juv. frshwtr fry	20.4066	-0.6858	6	-0.9681	0.1	28.0
							0.25	27.5
							0.5	27.0
							1	26.6
							2	26.2
							4	25.8
							6	25.5
							8	25.3
							10	25.2
							12	25.1
							16	24.9
							20	24.8
							32	24.5
20C	Brett(1952)	juv. frshwtr fry	20.4022	-0.6713	4	-0.9985	0.1	28.6
							0.25	28.1
							0.5	27.6
							2	26.7
							4	26.3
							6	26.1
							8	25.9
							10	25.7
							16	25.4
							24	25.2
							40	24.8
							48	24.7
							56	24.6
							70	24.5
23C	Brett(1952)	juv. frshwtr fry	18.9736	-0.6013	5	-0.9956	0.1	29.7
							0.25	29.0
							0.5	28.5
							1	28.0
							2	27.5
							4	27.0
							6	26.8
							8	26.6
							10	26.4
							16	26.1
							24	25.8
							40	25.4
							56	25.2
							72	25.0
							96	24.8
							120	24.6
							140	24.5
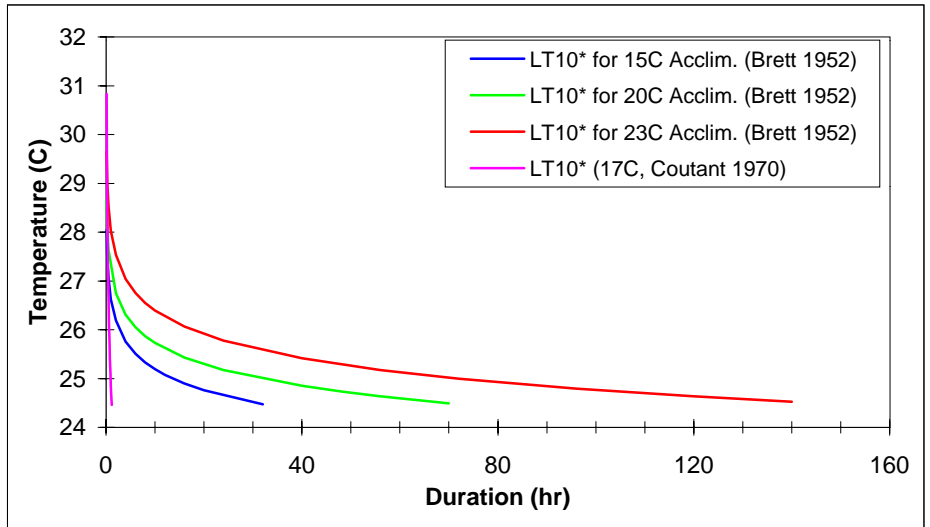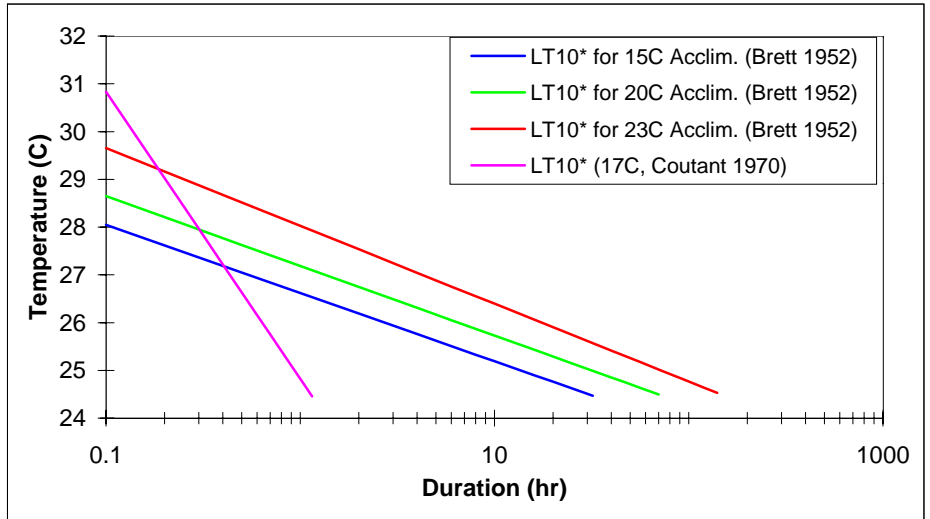
COHO SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
17C	Coutant (1970)	adult	5.9068	-0.1630	5	-0.9767	0.1	30.8
	Reported acclimation temp. was the Columbia River						0.2	29.0
	temp. (at Priest Rapids Dam) during fall migration.						0.3	28.0
							0.4	27.2
							0.5	26.6
							0.6	26.2
							0.7	25.8
							0.8	25.4
							0.9	25.1
							1	24.8
							1.1	24.6
							1.15	24.5

RAINBOW TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Alabaster & Downing (1966)	juvenile	15.6500	-0.5000	2	---	0.1	29.1
							0.25	28.4
							0.5	27.8
							1	27.2
							2	26.6
							4	26.0
							6	25.7
							8	25.4
							10	25.2
							12	25.1
							16	24.8
							20	24.6
							24	24.5
18C	Alabaster & Welcomme (1962) Dissolved Oxygen at 7.4 mg/L	juvenile	18.4654	-0.5801	5	-0.9787	0.1	29.9
							0.25	29.2
							0.5	28.7
							2	27.7
							4	27.2
							6	26.9
							8	26.7
							10	26.5
							16	26.2
							24	25.9
							40	25.5
							80	25.0
							120	24.7
							160	24.5
18C	Alabaster & Welcomme (1962) Dissolved Oxygen at 3.8 mg/L	juvenile	13.6531	-0.4264	5	-0.9742	0.1	29.6
							0.25	28.7
							0.5	28.0
							1	27.3
							2	26.6
							4	25.9
							6	25.5
							7	25.4
							8	25.2
							9	25.1
							10	25.0
							12	24.8
							14	24.7
							16	24.5

RAINBOW TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
20C	Alabaster & Downing (1966)	juvenile	19.6250	-0.6250	2	---	0.1	29.6
							0.25	28.9
							0.5	28.5
							1	28.0
							2	27.5
							4	27.0
							6	26.8
							8	26.6
							12	26.3
							20	25.9
							32	25.6
							40	25.5
							80	25.0
							120	24.7
							160	24.5
20C	Craigie (1963) Raised in soft water, tested in soft water (SS)	yearling	14.6405	-0.4470	3	-0.9787	0.1	30.4
							0.25	29.5
							0.5	28.9
							1	28.2
							2	27.5
							4	26.9
							6	26.5
							8	26.2
							10	26.0
							16	25.6
							20	25.3
							24	25.2
							32	24.9
							40	24.7
							48	24.5

RAINBOW TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
20C	Craigie (1963)	yearling	15.0392	-0.4561	3	-0.9917	0.1	30.6
	Raised in soft water, tested in hard water (SH)						0.25	29.8
							0.5	29.1
							1	28.5
							2	27.8
							4	27.2
							6	26.8
							8	26.6
							12	26.2
							16	25.9
							20	25.7
							32	25.3
							40	25.1
							60	24.7
							72	24.5
20C	Craigie (1963)	yearling	15.1473	-0.4683	3	-0.9781	0.1	30.1
	Raised in hard water, tested in soft water (HS)						0.25	29.2
							0.5	28.6
							1	28.0
							2	27.3
							4	26.7
							6	26.3
							8	26.1
							10	25.9
							16	25.5
							20	25.3
							24	25.1
							32	24.8
							40	24.6
							48	24.5

RAINBOW TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
20C	Craigie (1963)	yearling	12.8718	-0.3837	3	-0.9841	0.1	30.9
	Raised in hard water, tested in hard water (HH)						0.25	29.9
							0.5	29.1
							1	28.3
							2	27.6
							3	27.1
							4	26.8
							6	26.3
							8	26.0
							10	25.8
							12	25.6
							16	25.3
							20	25.0
							24	24.8
							32	24.5

CUTTHROAT TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
23C	Golden (1978)	juvenile	18.092	-0.56523	?	-0.996	0.1	30.0
	1975 tests, hatchery only						0.25	29.3
							0.5	28.8
							1	28.3
							8	26.7
							16	26.2
							24	25.9
							32	25.7
							40	25.5
							60	25.2
							80	25.0
							120	24.7
							160	24.5
13-25C	Golden (1978)	juvenile	22.543	-0.71999	?	-0.999	0.1	29.6
	1975 tests, hatchery only						0.25	29.1
							0.5	28.7
							2	27.9
							4	27.4
							8	27.0
							16	26.6
							24	26.4
							40	26.1
							80	25.7
							160	25.3
							240	25.0
							300	24.9
							560	24.5
23C	Golden (1978)	juvenile	18.3166	-0.5723	?	-0.990	0.1	30.0
	1976 tests, hatchery and wild trout data pooled						0.25	29.4
							0.5	28.8
							1	28.3
							2	27.8
							4	27.3
							8	26.8
							12	26.5
							16	26.3
							24	26.0
							40	25.6
							80	25.1
							120	24.8
							160	24.5
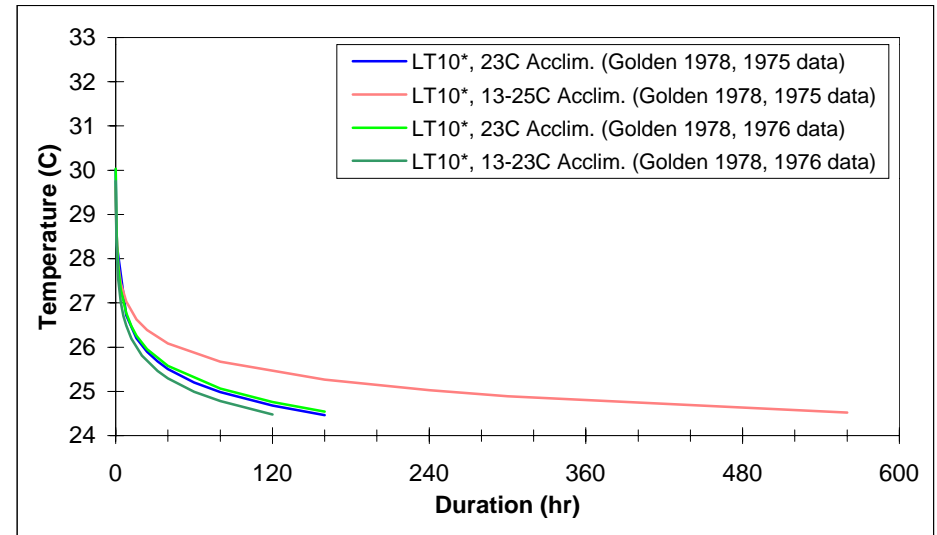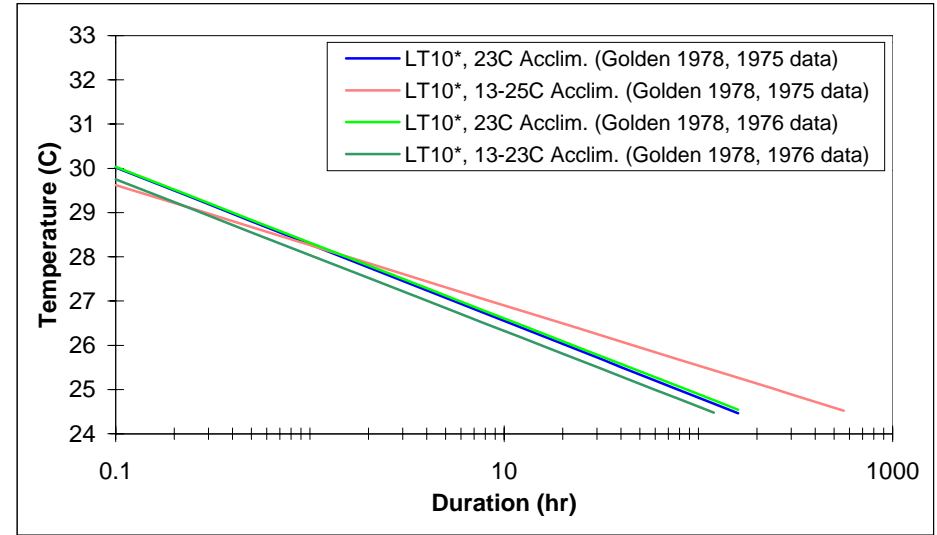
CUTTHROAT TROUT -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
13-23C	Golden (1978)	juvenile	18.1515	-0.5723	?	-0.992	0.1	29.7
	1976 tests, hatchery and wild trout data pooled						0.25	29.1
							0.5	28.6
							1	28.0
							2	27.5
							4	27.0
							6	26.7
							8	26.5
							12	26.2
							20	25.8
							32	25.5
							40	25.3
							60	25.0
							80	24.8
							120	24.5

SOCKEYE SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Brett(1952)	juv. frshwtr fry	15.8799	-0.5210	7	-0.9126	0.1	28.4
							0.25	27.7
							0.5	27.1
							1	26.5
							2	26.0
							4	25.4
							6	25.1
							8	24.8
							10	24.6
							12	24.5
							13	24.4
							14	24.4
							24	23.9
20C	Brett(1952)	juv. frshwtr fry	19.3821	-0.6378	5	-0.9602	0.1	28.6
							0.25	28.0
							0.5	27.5
							2	26.6
							4	26.1
							6	25.9
							8	25.7
							10	25.5
							16	25.2
							24	24.9
							40	24.6
							48	24.5
							56	24.4
							116	23.9
23C	Brett(1952)	juv. frshwtr fry	20.0020	-0.6496	4	-0.9981	0.1	29.0
							0.25	28.4
							0.5	27.9
							1	27.5
							2	27.0
							4	26.6
							6	26.3
							8	26.1
							10	26.0
							16	25.7
							24	25.4
							40	25.1
							56	24.9
							72	24.7
							96	24.5
							120	24.4
							220	24.0

SOCKEYE SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
20C	McConnell &	juvenile	16.7328	-0.5473	6	-0.9552	0.1	28.6
	Blahm (1970)	(under yearling)					0.25	27.9
	unpublished data						0.5	27.3
							1	26.8
							2	26.2
							4	25.7
							6	25.4
							8	25.2
							10	25.0
							16	24.6
							20	24.4
							40	23.9
20C	McConnell &	juvenile	17.5227	-0.5861	6	-0.9739	0.1	28.6
	Blahm (1970)	(under yearling)					0.25	27.9
	unpublished data						0.5	27.4
	10% mortality NOT ADJUSTED						1	26.9
							2	26.3
							3	26.0
							4	25.8
							6	25.5
							8	25.3
							10	25.2
							12	25.0
							20	24.6
							32	24.3
							52	23.9

CHUM SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Brett(1952)	juv. frshwtr fry	15.8911	-0.5252	8	-0.9070	0.1	28.2
							0.25	27.5
							0.5	26.9
							1	26.3
							2	25.8
							4	25.2
							6	24.9
							8	24.6
							10	24.5
							12	24.3
							16	24.1
							20	23.9
							40	23.3
20C	Brett(1952)	juv. frshwtr fry	16.1894	-0.5168	9	-0.9750	0.1	29.2
							0.25	28.5
							0.5	27.9
							2	26.8
							4	26.2
							6	25.9
							8	25.6
							10	25.4
							16	25.0
							24	24.7
							40	24.3
							60	24.0
							80	23.7
							132	23.3
23C	Brett(1952)	juv. frshwtr fry	15.3825	-0.4721	4	-0.9652	0.1	30.3
							0.25	29.5
							0.5	28.9
							1	28.2
							2	27.6
							4	27.0
							6	26.6
							8	26.4
							10	26.2
							16	25.7
							24	25.4
							40	24.9
							56	24.6
							72	24.4
							96	24.1
							120	23.9
							240	23.3
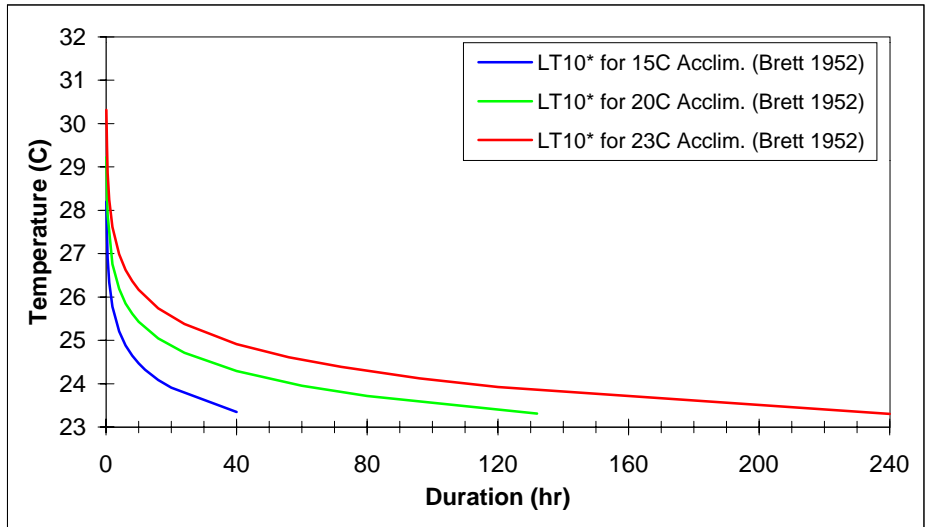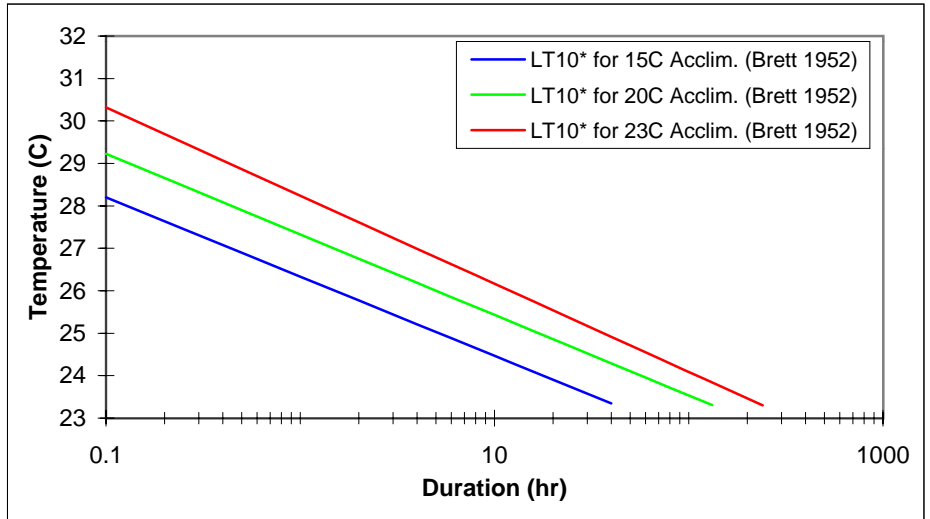
PINK SALMON -- Estimated LT10s

Acclim.	Source	Age/Size	a	b	N	r	Time(hr)	LT10*(C)
15C	Brett(1952)	juv. frshwtr fry	12.8937	-0.4074	8	-0.9884	0.1	29.1
							0.25	28.2
							0.5	27.5
							1	26.7
							2	26.0
							4	25.3
							6	24.9
							8	24.6
							10	24.3
							12	24.1
							16	23.8
							20	23.6
							24	23.4
20C	Brett(1952)	juv. frshwtr fry	*13.2444*	-0.4074	7	-0.9681	0.1	30.0
			16.2444 in EPA (1977), but				0.25	29.0
			the resulting curve does not				0.5	28.3
			match the information				1	27.6
			presented in Brett (1952)				2	26.9
			<Fig. 5>				4	26.1
							6	25.7
							8	25.4
							10	25.2
							16	24.7
							24	24.3
							32	24.0
							40	23.7
							56	23.4
24C	Brett(1952)	juv. frshwtr fry	14.7111	-0.4459	6	-0.9690	0.1	30.6
							0.25	29.7
							0.5	29.1
							1	28.4
							2	27.8
							4	27.1
							6	26.7
							8	26.4
							10	26.2
							16	25.8
							24	25.4
							40	24.9
							56	24.6
							72	24.3
							96	24.1
							120	23.9
							192	23.4