



EVALUATION OF SEASONAL-COLD-WATER TEMPERATURE CRITERIA

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1.0 INTRODUCTION

In this report we evaluate the temperature requirements of cool and cold-water fishes that may occur in waters with temperatures that exceed 20°C. We begin by considering the physiological consequences of temperature to fish. This section is intended to give a general background on the effects of temperature on fish energetics and production. Second, we define several terms that are used to describe thermal regimes of fish. These definitions are needed to understand the various metrics used to describe thermal tolerance, resistance, and preference of fish. Third, we identify cool and cold-water species in Idaho that may reside in waters with temperatures that exceed 20°C and summarize available information on temperature ranges of these species. Fourth, we review relationships between stream temperatures and the distribution of fish in natural environments. In this section we draw upon field studies conducted in Idaho and Oregon. Finally, we offer conclusions based on our examination of the data and literature

Temperature is one of many factors that affect the spatial dynamics of fish both zoogeographically and locally (Fry 1971). Thus, one can describe temperature (or more formally, heat) as an ecological resource. For example, Magnuson et al. (1979) opined that fish respond to temperature in a manner similar to their response to other ecological resources such as food. Magnuson et al. (1979) noted that the thermal niche of fish can be defined by lethal limits, physiological or metabolic optima, by behavioral performance, or by behavioral preferences. Magnuson et al. (1979) showed that fish of temperate freshwater fall into three thermal groups along the temperature

resource axis—cold, cool, and warm-water fishes.

The idea of partitioning fish into thermal groups is not unique to the work of Magnuson et al. (1979). Fishery scientists have historically referred to fishes as warm-water fishes (sunfish and the like), cool-water fishes (yellow perch and the like), and cold-water fishes (rainbow trout and the like). Hokanson (1977) formally classified fish by their thermal requirements. He divided fish into temperate eurytherms, temperate mesotherms, and temperate stenotherms. He used “temperate” to acknowledge that each group in temperate climates is exposed to water temperatures less than 4°C during the winter, regardless of summer temperature needs. He did note that the groups could be real or only arbitrary divisions along a temperature continuum.

The work by Magnuson et al. (1979) demonstrates that fish species are not distributed uniformly along the temperature gradient based on laboratory estimates of temperature preference. Magnuson et al. (1979) showed that cold-water species are clearly separated from cool and warm-water species (Figure 1). Although there was considerable overlap between cool and warm-water species, the skewing of the distribution of species suggested interpretation of cool and warm-water groups with some overlap near 25° and 26°C (Magnuson et al. 1979). On the basis of temperature preferences, centrarchids, ictalurids, and percichthyids fell within the warm-water guild, percids and esocids were in the cool-water guild, and salmonids were in the cold-water guild. Both cyprinids and catostomids appeared in each of the three guilds, although few data were available for catostomids. Temperatures centered within each guild were 11.0°-14.9°C, 21.0°-24.9°C, and 27.0°-30.9°C (Magnuson et al. 1979). Armour (1991) reported highest average mean weekly temperatures for cold-water, cool-water, and warm-water species as 22°C, 29°C, and 30°C, respectively. Lyons et al. (1996) designated cold-water, cool-water, and warm-water stream communities as those with

maximum daily average temperatures of <22°C, 22-24°C, and >24°C, respectively.

The State of Idaho currently recognizes only two classes of aquatic life, cold and warm-water biota (salmonid spawning is a subclass of cold-water biota). Thus, Idaho has no temperature criteria or standards for protection of cool-water species. Most states have four or more aquatic life uses (Shumar, 1999). For example, Washington, Minnesota, New Mexico, and South Dakota each have five aquatic life uses, while Wyoming and Arizona each have four aquatic life uses. Oregon has seven aquatic life uses largely because Oregon targets life stages of both sea-run and resident salmonids, in addition to warm-water aquatic life. Montana has nine beneficial use classes.

The Idaho Division of Environmental Quality (IDEQ) recognizes that there are other aquatic communities within the state in addition to just cold-water and warm-water communities. Thus, IDEQ has proposed a “Seasonal Cold” aquatic life use, which is defined as “*water quality appropriate for the protection and maintenance of a viable aquatic life community of cool and cold water species, where cold water aquatic life may be absent during, or tolerant of, seasonally warm temperatures.*” The IDEQ has proposed a not-to-exceed temperature criteria of 27°C maximum daily maximum temperature (MDMT)¹ or 24°C maximum daily average temperature (MDAT)² for fish species occurring within Idaho waters classified as seasonal-cold-water uses (IDEQ 1999).

2.0 PHYSIOLOGICAL CONSEQUENCES OF TEMPERATURE

¹MDMT is the warmest daily maximum water temperature recorded during a given year or survey period.

²MDAT is the warmest daily average water temperature recorded during a given year or survey period.

In this section we provide a general overview of the physiological effects of temperature on fish, offering a general explanation of why temperature is important to fish. In addition, we provide a brief description of how fish cope with extreme temperatures.

Both biotic and abiotic factors affect fish physiology. Temperature is one of the most important (Fry 1971). The effects of temperature on biochemical and physiological processes of fish are well known (see Tytler and Calow 1985; Jobling 1994). These processes drive fish to select environmental temperatures at which they can function efficiently (Coutant 1987). Because different physiological processes (e.g., ingestion and metabolism) may have different optimal temperatures, the temperature selected by fish often represents a compromise, or integrated optimum. Fish appear to select temperatures that maximize the amount of energy available for activity and growth, or metabolic scope (the difference between standard³ and maximum⁴ metabolic rates) (Fry 1971; Hickman and Raleigh 1982; Jobling 1994). Certainly, habitat selection in the wild involves a compromise between temperature requirements and other important factors, such as food availability and avoidance of predators and competitors (Coutant 1987).

Physiological functions that are affected by temperature include growth, food consumption, metabolism, reproduction, activity, and survival. Typically, growth, food consumption, and activity increase with increasing temperature to some critical temperature, after which the rates rapidly decline. The most sensitive physiological function appears to be growth rate, which is an integrator of all physiological responses

³Standard metabolism is defined as the metabolic rate at zero swimming speed (i.e., organism is at complete rest) (Tytler and Calow 1985; Jobling 1994).

⁴Maximum metabolism is defined as the metabolic rate at maximum sustained swimming (a.k.a. active metabolic rate) (Tytler and Calow 1985; Jobling 1994).

(Brungs and Jones 1977). The rate of growth at various temperatures is a function of ingestion and metabolism (Jobling 1994). Under conditions of unlimited food, an increase in temperature will result in an increase in food intake, but at high temperature ingestion rates abruptly decline. Metabolic rate, on the other hand, increases with increasing temperature. The temperature at which the difference between ingestion rate and metabolic rate is maximum is called the optimum temperature for growth (Jobling 1994). These data can be used to estimate temperature criteria for fish in natural water bodies.

Extreme temperatures (both low and high) can lead to death. Proteins, including the enzymes that catalyze critical biochemical reactions, are temperature sensitive. High temperatures can cause structural degradation (denaturation), resulting in partial or complete loss of function. Death can occur quickly or may be delayed. The temperature at which a fish succumbs to thermal stress depends on the temperature to which it was acclimatized⁵ and on its developmental stage (e.g, embryo, fry, juvenile, adult). Fish that experience changing environmental temperatures, however, have cellular and subcellular mechanisms for adapting to the new conditions. Many physiological adjustments result from switching on or off genes that are responsible for the manufacture of particular proteins (Jobling 1994). For example, some fish (e.g., brown trout *Salmo trutta*, cutthroat trout *Oncorhynchus clarki*, rockbass *Ambloplites rupestris*, yellow bullhead *Ictalurus natalis*, fathead minnows *Pimephales promelas*) under heat stress initiate the synthesis of heat shock proteins (HSPs) (Fader et al. 1994). These reconfigured proteins that become denatured at higher temperatures, thereby allowing them to function biochemically. In addition, fish may produce alternate enzymes or isozymes to catalyze the same reaction more efficiently at different

⁵Acclimatization refers to adjustments made under natural environmental conditions, including seasonal changes in temperature, photoperiod, and associated hormones.

temperatures (Jobling 1994).

Although fish use both behavioral and physiological mechanisms to cope with high water temperatures, fish are increasingly susceptible to disease at high temperatures. Holt et al. (1975) investigated the effect of water temperature on mortality from experimental infection by *Flexibacter columnaris* and on mean time to death of three cold-water species, juvenile steelhead trout *O. mykiss*, coho salmon *O. kisutch*, and chinook salmon *O. tshawytscha*. With all three species, they found an inverse linear relationship between water temperature and the \log_{10} of the mean number of days from exposure to death. In other words, as the temperature increased above 12.2°C, the disease process progressively accelerated, resulting in a minimum time to death at 20.5° or 23.3°C and a maximum at 12.2°C. Hillman (1991) opined that temperature may have modified interactions between chinook salmon and redbreast shiners *Richardsonius balteatus* in laboratory channels by increasing their susceptibility to disease. He found that most migrants and a small fraction of resident chinook with shiners in warm water (18°-21°C) were infected with *F. columnaris*; the disease infected more sympatric shiners in cold water (12°-15°C) than shiners alone or shiners with chinook in warm water. In a similar study, Reeves et al. (1987) reported that most steelhead that migrated from lab channels were infected with *F. columnaris* in warm water (19°-22°C), and more than half of the migrant redbreast shiners were infected in cold water (12°-15°C). Not only does disease reduce competitive abilities (e.g., defense of territories), it probably makes fish more susceptible to predation and less able to perform essential functions such as feeding and swimming (McCullough 1999).

Temperature can also influence interactions among fish species. Competitive interactions among fluvial fish usually translates into attempts by individuals of the same or different species to secure adequate space and, therefore, food or cover or

both (Chapman 1966). Some studies have shown that competition among various fish species can be mediated or controlled by water temperature (Baltz et al. 1982; Reeves et al. 1987; Hillman 1991; De Staso and Rahel 1994). For example, in Deer Creek, California, Baltz et al. (1982) found that riffle sculpins *Cottus gulosus* successfully excluded speckled dace *Rhinichthys osculus* from riffle habitats at low temperatures, but not at high temperatures. Competition and thermal regimes were largely responsible for the zonation of fish in Rocky Mountain streams, with brook trout *Salvelinus fontinalis* at high elevation, brown trout at middle elevations, and creek chub *Semotilus atromaculatus* at low elevations (Taniguchi et al. 1998). In laboratory tests, creek chub were competitively dominant over brook trout at 24°C and brown trout at 26°C, but in the field, trout were typically replaced by chub in the range 22°-25°C.

In summary, temperature is important to fish because it affects their biochemical and physiological processes, which affect growth, health, behavior, reproduction, distribution, and ultimately survival. Temperature can also influence species interactions, such as predation and competition, and the occurrence of disease. Growth rate appears to be the most sensitive physiological function and is an integrator of all physiological responses. If given a choice, fish will select temperatures near their optimal growth temperature(s). Because physiological optima are affected by and interact with acclimation⁶ temperatures, as well as nutritional status, health, age, size, and genetics, temperature optima often are a “zone of efficient operation,” rather than a single temperature value (Crawshaw 1977). Thus, fish tend to have a range of optimal temperatures rather than a single optimum.

3.0 TERMINOLOGY

⁶Acclimation refers to the process of physiological adjustment, typically to a single parameter such as temperature, under artificial conditions.

In general, response of fish to temperature can be divided into tolerance, resistance, and preference (Jobling 1981). The incipient lethal temperatures (tolerance limits) define the boundaries for tolerance (Figure 2) (Jobling 1981). Outside the tolerance limits lie the zone of resistance, within which there is a strong interaction between temperature and exposure time. The upper boundary of the resistance zone is represented by the critical thermal maximum, where death is rapid (Figure 2). Survival times above critical thermal maximum are nearly zero. Both tolerance and resistance limits are dependent upon acclimation temperature and the previous thermal history. Within the thermal tolerance zone, fish, if given a choice, will spend most time within a certain temperature. If the fish are left exposed to a temperature gradient for a long period, they will gradually gravitate towards a final temperature preferendum (Figure 2). Thermal preference is also dependent upon previous thermal acclimation. Optimal temperatures are temperatures where physiological functions are maximized under conditions of excess food.

The literature is replete with terms that describe the temperature tolerance, resistance, and preferences of fishes. In this section, we define many of the terms used to describe the thermal regime of freshwater fish. We focus mostly on terms that describe optimum ranges and thermal maxima. Unless otherwise noted, these terms are described in Brungs and Jones (1977), Jobling (1981), Armour (1991), and McCullough (1999).

Observed Temperature Range – Temperatures under which a species has been observed in nature.

Optimum Temperature Range (OTR) – Range of temperatures that provide for feeding activity, normal physiological response, and normal behavior (i.e.,

without thermal stress symptoms). OTR is slightly wider than the optimal growth range.

Growth Optimum (GO) – Temperature under experimental conditions at which growth rates, expressed as weight gain per unit of time, are maximal for the life stage.

Zero Net Growth (ZNG) – Temperatures under experimental conditions at which instantaneous growth and mortality rates for populations are equal.

Physiological Optimum (PO) – Temperature under experimental conditions approximating that for optimum growth, stamina, heart performance, and other functions

Maximum Weekly Average Temperature (MWAT) – Average of daily maximum water temperatures measured over the warmest consecutive seven-day period.

Weekly Mean Temperature (95% WMT) – The 95th percentile of the weekly mean temperatures. Used by Eaton et al. (1995) to estimate the maximum temperature tolerated by a particular species in nature.

Short-Term Maximum (STM) – The maximum temperature, based on experimental data, that 50% of the fish could survive for a short time (1000 min - 7 days); it is the same as the incipient lethal temperature (ILT).

Critical Thermal Maximum (CTM) – Mean temperature at which individual fish lose equilibrium or die given a uniform rate of heating from an acclimation

temperature. CTM occurs at the upper boundary of the resistance zone.

Upper Lethal Temperature (ULT) – The temperature at which survival is 50% in a 10-minute exposure, given a prior acclimation to temperatures within the tolerance zone.

Upper Critical Range (UCR) – The temperature at which a significant disturbance in the normal behavior of a fish occurs, i.e., there are obvious signs of thermal stress. Also defined as the maximum temperature at which fish can survive for brief periods.

Upper Thermal Tolerance Limit (UTTL) – The upper temperature at which 50% of the population survives indefinitely. Jobling (1981) defines tolerance limit as incipient lethal temperature.

Upper Incipient Lethal Temperature (UILT) – The upper temperature that 50% mortality is observed for a given acclimation temperature. The UILT increases with acclimation temperatures to a point that higher acclimation temperatures have no effect.

Ultimate Upper Incipient Lethal Temperature (UUILT) – The highest temperature at which tolerance does not increase with increasing acclimation temperatures, i.e., it cannot be increased by raising the acclimation temperature.

Upper Avoidance Temperature (UAT) – Maximum temperature avoided by fish following acclimation to a given temperature.

Final Temperature Preferendum (FTP) – Eventual choice of temperature zone irrespective of acclimation history. Agrees closely with maximum growth temperature.

4.0 TEMPERATURE RANGES OF SEASONAL-COLD-WATER FISH

Before we identify the temperature ranges for cool and cold-water fishes, we first identify fish species in Idaho that would likely fall within the seasonal-cold-water classification. We recall that the seasonal-cold-water definition includes aquatic communities consisting of both cool and cold-water species, where cold-water species may be absent during, or tolerant of, seasonally warm temperatures. Thus, the list we provide includes both cool-water species and those cold-water species that may be tolerant of seasonally warm temperatures (water temperatures that exceed 20°C).

We identified fish species that would fall within the seasonal-cold-water classification by first compiling a list of all fish species occurring in Idaho, following the information in Simpson and Wallace (1982). We then identified each fish species in Idaho as cold-water, cool-water, or warm-water fish, following the classification in Magnuson et al. (1979), Armour (1991), and Zaroban et al. (1999). We removed from further analysis species that were classified as warm-water fish. We included all cool-water species and those cold-water species that we believed (based on professional judgement and experience) may occur in waters with temperatures that exceed 20°C. This resulted in thirty species in Idaho that would possibly fall within the seasonal-cold-water classification (Table 1). We identified six catostomids (suckers), ten cyprinids (minnows), two centrarchids (sunfish), two percids (perch), six salmonids (trout), one percopsid (trout-perch), one exocid (pike), one cottid (sculpin), and one acipenserid (sturgeon). We included no species of the petromyzontid (lamprey), ictalurid (catfish),

gadid (codfish), or poeciliid (livebearer) families because they included warm-water species or species that would generally not occur within waters classified as season-cold-water uses (e.g., Pacific lamprey *Entosphenus tridentatus* occur in waters supporting ESA-listed species).

Next, we searched the literature available to us to describe temperature tolerance, resistance, and preference for each species listed in Table 1. We focused our search on articles that summarized temperature requirements of freshwater fish (e.g., Black 1953; Calhoun 1966; Coutant 1977; Jobling 1981; Bell 1991; McCullough 1999). We did not attempt to verify the accuracy or validity of the temperature information presented in summary articles. Because temperature preference, tolerance, and resistance vary with acclimation history, nutritional status, health, age, size, genetics, etc., we reported the greatest range found in the literature for each temperature variable. To avoid cluttering the text and summary tables (Table 2) with citations and footnotes, we compiled all citations in Table 3. Citations in Table 3 are linked to the information in Table 2 by the temperature condition (e.g., OTR, GO, MWAT, CTM, UUILT, etc.). That is, references are listed for each temperature condition.

We found very little temperature information on catostomids occurring in Idaho (Table 2). Most information we reviewed suggests that catostomids are found in waters with temperatures less than 29°C, but preferred temperatures appear to be less than 22°C. We did find tolerance and resistance temperatures for white suckers⁷ *Catostomus commersoni*. Although they do not occur in Idaho (Simpson and Wallace 1982;

⁷The natural distribution of the white sucker extends from the Mackenzie River, Hudson Bay and the Labrador Peninsula south to Georgia and Oklahoma and from the Rocky Mountains to the Atlantic Coast (Brown 1971). The white sucker is found in most streams except for those with very cold temperatures and high velocities. Its habitat is varied, being present in both lakes and streams with high and low turbidities and fast or slow currents. Abundance is generally highest in impoundments.

Zaroban et al. 1999), their temperature preference, tolerance, and resistance may represent temperature ranges for catostomids that do occur within Idaho. White suckers have a growth optimum of 26°-27°C, MWAT for growth of 28°C, 95% weekly mean temperature of 27.3°C, and temperature preferendum of 18.3°-24°C (Brungs and Jones 1977; Coutant 1977; Jobling 1981; Eaton et al. 1995; Coutant 1977). The upper lethal and STM for white sucker are 31.2° and 31.6°C, respectively (Black 1953; Brungs and Jones 1977; Jobling 1981). The UILT for white sucker range from 26.3°-29.3°C (Wurtz and Renn 1964).

As with catostomids, we found little information on temperature ranges for cyprinids occurring in Idaho (Table 2). Most of the literature suggests that cyprinids are found in waters with temperatures less than 30°C, although leatherside chub *Gila copei* were observed in waters with temperatures less than 20°C. Redside shiners *Richardsonius balteatus* have a ULT of 25.0°-30.3°C, while peamouth *Mylocheilus caurinus* have a ULT of 27.0°C. We found the most information on northern pikeminnow *Ptychocheilus oregonensis*, which have an OTR of 16.1°-24.4°C, ULT of 29.4°-32.0°C, and a FTP of 16.1°-22.8°C. By comparison, longnose dace *Rhinichthys cataractae* have a FTP of 11.7°-21.1°C (Table 2). According to Elliott (1981), most cyprinids (except carp) have temperature optima ranging from 15°-32°C. McCullough (1999) reported that most cyprinids have an UUILT ranging from 29°-33°C.

We found numerous sources that describe the temperature ranges of centrarchids, percids, and esocids (Table 2). Centrarchids such as smallmouth bass *Micropterus dolomieu* and pumpkinseed sunfish *Lepomis gibbosus* are often found in waters with temperatures less than 31.0°C. They tend to have STMs between 35° and 36°C and upper tolerance limits between 28.0° and 37°C. McCullough (1999) reported that centrarchids have an UUILT that ranges from 33°-37°C. Both percids and esocids

generally occur in waters with temperatures less than 32°C. They tend to have optimal and preferred temperatures less than 27.0°C and thermal tolerances less than 35°C.

It is likely that both mottled sculpin *Cottus bairdi* and white sturgeon *Acipenser transmontanus* may occur in waters that could be classified as seasonal-cold-water uses. White sturgeon have optimal growth temperatures that range from 15.0°-25.0°C, depending on acclimation temperature (Table 2). Mottled sculpin, however, may be less tolerant of higher temperatures. What little information we found on mottled sculpin suggests that this species has a preferred temperature range of 12.8°-18.3°C (Table 2). Bond (1963), however, reported catching mottled sculpin at temperatures of 22°-24°C. We found no information on their tolerance or resistance temperatures.

Although salmonids are considered cold-water species, they may occur within waters classified as season-cold-water uses. Of the salmonids in Table 1, redband trout *O. mykiss gairdneri* and rainbow trout *O. mykiss* tend to have the highest temperature thresholds (Table 2). Both have been observed in waters with temperatures as high as 29.0°C. Behnke (1992) reported redband trout feeding at 28.3°C in Chino Creek, a tributary to the Owyhee River in northern Nevada. Zoellick (1999) reported temperatures at which redband trout were active in four Owyhee Mountain streams. During the three year study, he found redband trout in waters as warm as 29°C and daily average temperatures that reached 21°-23°C. Zoellick (1999) noted that in many cases the trout were limited by low flow or some other barrier rather than by temperature.

Other salmonids, such as brown trout, brook trout, Lahontan cutthroat *O. clarki henshawi*, and mountain whitefish *Prosopium williamsoni* may occur occasionally within streams classified as season-cold-water uses. These species tend to have optimal and

preferred temperatures less than 20°C and upper lethal temperatures approaching 28°C (Table 2). The upper critical range for brown trout has been reported to be as high as 30°C. Brook trout tend to be more sensitive to warmer temperatures than brown trout (Table 2). Barton et al. (1985) reported the upper temperature distributional limit for self-sustaining brook trout populations in southern Ontario streams as 25.6°C. Although temperature information on mountain whitefish is scarce, Eaton et al. (1995) reported a 95% WMT of 23.9°C for mountain whitefish. By comparison, they reported 95% WMT of 24°C for both rainbow and brown trout and 22.3°C for brook trout.

The above summary indicates that the cool and cold-water fish identified in Table 1 have a wide range of thermal tolerances, resistance, and preferences. The upper range of lethal temperatures and optimum or preferred temperatures generally ranged from 23°-36°C and 18°-33°C, respectively. As expected, cold-water species generally had lower thermal tolerances and preferences than cool-water species. Brook trout appeared to be less tolerant of warm temperatures than other salmonids. However, as we noted above, cold-water species may not be present in waters classified as seasonal-cold-water uses during the warmest time of the year. Redband trout and rainbow trout, which have a higher thermal resistance and tolerance than other salmonids, may occur in seasonal-cold waters during the warmest time of the year.

5.0 TEMPERATURES AND FISH COMMUNITIES: EXAMPLES FROM FIELD STUDIES

Information on observed distributions of fish in their natural habitat provides useful information to compare with laboratory data (i.e., thermal tolerance, preference, and resistance). Because laboratory studies generally assess fish response to one variable

(temperature) at a time, field observations provide insight on thermal requirements that integrate different effects, such as competition, predation, and disease. Other factors such as suitable habitat and water quality, stream flows, food availability, and angling pressure can also affect the distribution of fish in their natural environment. Because many of these factors operate cumulatively, a fish that is living at the margin of its tolerance range with respect to non-thermal factors will likely suffer higher mortality, lower growth rate, and lower reproductive success if subjected additionally to thermal stress (McCullough 1999). Therefore, our purpose in this section is to review relationships between temperatures and fish distribution in natural environments.

The Confederated Tribes of the Umatilla Indian Reservation (CTUIR) annually monitor habitat, water quality, and fish within the Umatilla Basin. As part of that study, they electronically record temperatures and assess status of fish populations with electrofishing techniques in various streams and reaches within the basin (CTUIR 1994; Contor et al. 1995; Contor et al. 1997). In the Umatilla River downstream from Pendleton (ca. River Mile (RM) 50), maximum water temperatures have exceeded 26°C (CTUIR 1994; Contor et al. 1995; Contor et al. 1997). Fish captured with electrofishing gear in this reach of river included smallmouth bass, chiselmouth *Acrocheilus alutaceus*, speckled dace *Rhinichthys osculus*, suckers, redbottom shiners, northern pikeminnow, and several warm-water species including carp *Cyprinus carpio*, white crappie *Pomoxis annularis*, black crappie *P. nigromaculatus*, and brown bullhead *Ictalurus nebulosus* (C. Contor, CTUIR, personal communication). Bluegill *Lepomis macrochirus* and pumpkinseed sunfish were captured near the mouth of the Umatilla River.

The Idaho Department of Fish and Game (IDFG) has conducted habitat and fish population surveys in streams in the Owyhee and Weiser basins, Idaho (K. Meyer,

IDFG, unpublished data). In four Owyhee tributary streams (Squawfish, Juniper, Corral, and South Fork Boulder creeks), MDATs ranged from 16.4°-19.3°C and MDMT ranged from 22.7°-24.8°C. Redband trout occurred in all sites, while redband shiners, speckled dace, largescale sucker, and Paiute sculpin⁸ *Cottus beldingi* occurred in one or more of the sites. In Beaver Creek, a tributary to the Weiser River, MDAT and MDMT were 20.6° and 28.6°C, respectively, and redband trout, brook trout, and sculpin (spp. unknown) occurred there (IDFG unpublished data).

In 1974, Gibson (1975) conducted a survey of fish populations and water quality in the Boise River from its mouth (confluence with the Snake River) upstream to Barber Dam (ca. 59 river miles). Thermographs recorded water temperatures at Barber (RM 58.9), Strawberry Glenn (RM 47.1), Middleton (RM 26.5), and Fort Boise (RM 0.1). Electrofishing equipment collected fish during the winter, summer, and fall. Gibson (1975) collected mountain whitefish, redband shiner, sucker, carp, chiselmouth, dace, and northern pikeminnow throughout the river from Barber Dam to the mouth. Largemouth bass *M. salmoides*, perch, pumpkinseed, black crappie, bluegill, smallmouth bass, channel catfish *I. punctatus*, brown bullhead, and Tui chubs *Gila bicolor* occurred only in the lower reaches of the river. Rainbow and brown trout and sculpin occurred in the middle and upper reaches of the river (Gibson 1975). These distributions appear to comport with the average weekly maximum temperatures recorded within each reach. Gibson (1975) found that average weekly maximum water temperatures at Fort Boise and Middleton (lower reaches) approached or exceeded 25°C (cool-water zone). Average weekly maximum temperatures at Barber Dam and Strawberry Glenn (upper reaches) were near 20°C (cold-water zone).

⁸Bond (1963) reported that the upper lethal temperature for the Paiute sculpin may be close to 30°C. He noted that a Paiute sculpin in his laboratory study survived until water temperature reached 31.2°C.

We examined IDEQ and EarthInfo electronic files for maximum temperatures and species compositions for waters that have temperatures that exceed 20°C (e.g., lower Boise, Owyhee, and Weiser rivers). Unfortunately, temperature and fish species data were not consistently collected at the same place and same time. Only on the Boise River near Parma (RM 5) did we find corresponding temperature and fish data. There, in 1996, MDAT and MDMT were 23.4° and 25.3°C, respectively, and mountain whitefish, rainbow trout, and smallmouth bass were present. During the period 1973-1997, MDMT for the Boise River near Parma ranged from 18.5° to 28.3°C.

Although temperature and fish data were not always matched in space and time, we did compare generally temperatures and fish presence in the Weiser and Owyhee rivers (IDEQ and EarthInfo data). On the Weiser River near the town of Weiser (RM 0.5), MDMTs have approached 27°C (MDMT of 27.8°C in 1960). Fish present in the lower Weiser River include rainbow trout, brown trout, mountain whitefish, smallmouth bass, yellow perch, and northern pikeminnow. Water temperatures have been monitored at several locations on the Owyhee River. At RM 1.6, MDAT and MDMT ranged from 22.3°-23.6°C and 23.6°-24.8°C, respectively. Fish species known to be present in this area include rainbow trout, smallmouth bass, yellow perch, mountain whitefish, and northern pikeminnow. Just upstream from Owyhee Reservoir (RM 71.5) MDMT ranged from 25.0°-27.2°, near Rome (RM 126) MDMT ranged from 24.5°-28.3°C, and just downstream from the confluence of the North Fork (RM 166) MDMT was 27.8°C. Fish present in this reach of the Owyhee River include mountain whitefish, northern pikeminnow, yellow perch, rainbow trout, and smallmouth bass.

These field studies suggest that several fish identified in Table 1 occur within natural waters with temperatures that occasionally exceed 25°C. Unfortunately, however, most fish population surveys were conducted at times when streams were not at MDMTs.

Thus, one cannot be certain that the same species would also be present at the time streams reach MDMTs. On the other hand, we would not expect cool-water species to be limited by temperatures exceeding 25°C because most have thermal tolerance limits greater than 25°C (see Table 2). Some cold-water species may avoid maximum temperatures greater than 25°C, but could use the streams at times when temperatures were cooler. Seasonal movements by salmonids (cold-water fish) between summer and winter habitat is common and trout frequently move throughout the summer in search of suitable habitat (see reviews in Gowan et al. 1994).

6.0 SUMMARY

Our purpose in this study was to review the temperature requirements of Idaho fishes that may occur in waters classified as “seasonal-cold-water uses.” We identified thirty species consisting of a mix of both cool and cold-water fishes. By definition, cold-water species need only be tolerant of or absent during periods of seasonally warm temperatures. The IDEQ has proposed a temperature criteria of 27°C maximum daily maximum temperature or 24°C maximum daily average temperature for fish occurring in waters classified as seasonal-cold-water uses. Based on our review of the information available to us, we believe that the proposed criteria should be lowered to better protect cold-water species. Cold-water species such as salmonids tend to have lower thermal limits than cool-water species, although species such as redband trout and rainbow trout have been found in waters with temperatures near 29°C. By lowering the temperature criteria 1°C, the maximum daily maximum temperature would be less than the upper lethal temperature for nearly all species identified in Table 1 (both the leopard dace and Lahontan cutthroat have a ULT of 23°C, but the thermal limits for these two species are mostly unknown). Although this reduction tends to be conservative on the side of cold-water species, which may or may not be present in

waters during the warmest season, it does not exclude any cool-water species. That is, a maximum daily maximum temperature of 26°C or a maximum daily average temperature of 23°C does not fall below the thermal optima or preferences of cool-water species.

CONCLUSION: We believe a not-to-exceed seasonal-cold-water temperature criteria of 26°C maximum daily maximum temperature or 23°C maximum daily average temperature will protect fish species occurring within waters classified as seasonal-cold-water uses.

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8.0 TABLES

Table 1. List of cool and cold-water fish in Idaho that may occur in waters with temperatures that exceed 20°C. Temperature classification follows Zaroban, et al. (1999).

Family	Common name	Species	Temperature classification
Catostomidae	Longnose sucker	<i>Catostomus catostomus</i>	Cold
	Utah sucker	<i>Catostomus ardens</i>	Cool
	Bridgelip sucker	<i>Catostomus columbianus</i>	Cool
	Bluehead sucker	<i>Catostomus discobolus</i>	Cool
	Largescale sucker	<i>Catostomus macrocheilus</i>	Cool
	Mountain sucker	<i>Catostomus platyrhynchus</i>	Cool
Cyprinidae	Utah chub	<i>Gila atraria</i>	Cool
	Tui chub	<i>Gila bicolor</i>	Cool
	Leatherside chub	<i>Gila copei</i>	Cool
	Longnose dace	<i>Rhinichthys cataractae</i>	Cool
	Leopard dace	<i>Rhinichthys falcatus</i>	Cool
	Speckled dace	<i>Rhinichthys osculus</i>	Cool
	Redside shiner	<i>Richardsonius balteatus</i>	Cool
	Chiselmouth	<i>Acrocheilus alutaceus</i>	Cool
	Peamouth	<i>Mylocheilus caurinus</i>	Cool
	Northern pikeminnow	<i>Ptychocheilus oregonensis</i>	Cool
Percopsidae	Sand roller	<i>Percopsis transmontana</i>	Cool
Centrarchidae	Pumpkinseed	<i>Lepomis gibbosus</i>	Cool
	Smallmouth bass	<i>Micropterus dolomieu</i>	Cool
Percidae	Yellow perch	<i>Perca flavescens</i>	Cool
	Walley	<i>Stizostedion vitreum</i>	Cool
Exocidae	Northern pike	<i>Esox lucius</i>	Cool
Cottidae	Mottled sculpin	<i>Cottus bairdi</i>	Cool
Acipenseridae	White sturgeon	<i>Acipenser transmontanus</i>	Cold

Salmonidae	Mountain whitefish	<i>Prosopium williamsoni</i>	Cold
	Lahontan cutthroat trout	<i>Oncorhynchus clarki henshawi</i>	Cold
	Redband trout	<i>Oncorhynchus mykiss gairdneri</i>	Cold
	Rainbow trout	<i>Oncorhynchus mykiss</i>	Cold
	Brown trout	<i>Salmo trutta</i>	Cold
	Brook trout	<i>Salvelinus fontinalis</i>	Cold

Table 2. Summary of temperature data for cool and cold-water fish in Idaho. Temperature conditions are described in Section 3.0. References for each temperature condition are given in Table 3.

Temperature condition (°C)	Life stage	Catostomidae (Suckers)				
		Longnose	Utah	Bluehead	Largescale	Mountain
Obs. range	Juvenile					
	Adult					
	Unknown		27.0	28.0		15.5-23.3
OTR	Juvenile					
	Adult					
	Unknown					
GO	Juvenile					
	Adult					
	Unknown					
ZNG	Juvenile					
	Adult					
	Unknown					
PO	Juvenile					
	Adult					
	Unknown					
MWAT	Juvenile					
	Adult					
	Unknown					
95% WMT	Juvenile					
	Adult					

	Unknown
STM	Juvenile
	Adult
	Unknown
CTM	Juvenile
	Adult
	Unknown

Table 2. Continued.

Temperature condition (°C)	Life stage	Catostomidae (Suckers)				
		Longnose	Utah	Bluehead	Largescale	Mountain
ULT	Juvenile					
	Adult					
	Unknown	26.5-27.0			29.4	
UCR	Juvenile					
	Adult					
	Unknown					
UTTL	Juvenile					
	Adult					
	Unknown					
UILT	Juvenile					
	Adult					
	Unknown					
UUILT	Juvenile					
	Adult					
	Unknown					
UAT	Juvenile					
	Adult					
	Unknown					
FTP	Juvenile					
	Adult					

OTR = optimum temperature range; GO = growth optimum; ZNG = zero net growth; PO = physiological optimum; MWAT = maximum weekly average temperature; 95% WMT = 95th percentile of the weekly mean temperature; STM = short-term maximum; CTM = critical thermal maximum; ULT = upper lethal temperature; UCR = upper critical range; UTTL = upper thermal tolerance limit; UILT = upper incipient lethal temperature; UUILT = ultimate upper incipient lethal temperature; UAT = upper avoidance temperature; FTP = final temperature preferendum.

Table 2. Continued.

Temperature condition (°C)	Life stage	Cyprinidae (Minnows)				
		Utah chub	Leatherside chub	Longnose dace	Leopard dace	Speckled dace
Obs. range	Juvenile					
	Adult			5.4-22.7		
	Unknown	15.6-31.1	10.0-20.0			10.0-32.0
OTR	Juvenile					
	Adult					
	Unknown					
GO	Juvenile					
	Adult					
	Unknown					
ZNG	Juvenile					
	Adult					
	Unknown					
PO	Juvenile					
	Adult					
	Unknown					
MWAT	Juvenile					
	Adult					
	Unknown					
95% WMT	Juvenile					
	Adult					

	Unknown
STM	Juvenile
	Adult
	Unknown
CTM	Juvenile
	Adult
	Unknown

Table 2. Continued.

Temperature condition (°C)	Life stage	Cyprinidae (Minnows)				
		Utah chub	Leatherside chub	Longnose dace	Leopard dace	Speckled dace
ULT	Juvenile					
	Adult					
	Unknown				23.1	
UCR	Juvenile					
	Adult					
	Unknown					
UTTL	Juvenile					
	Adult					
	Unknown					
UILT	Juvenile					
	Adult					
	Unknown					
UUILT	Juvenile					
	Adult					
	Unknown					
UAT	Juvenile					
	Adult					
	Unknown					
FTP	Juvenile					

Adult

Unknown

11.7-21.1

OTR = optimum temperature range; GO = growth optimum; ZNG = zero net growth; PO = physiological optimum; MWAT = maximum weekly average temperature; 95th WMT = 95th percentile of the weekly mean temperature; STM = short-term maximum; CTM = critical thermal maximum; ULT = upper lethal temperature; UCR = upper critical range; UTTL = upper thermal tolerance limit; UILT = upper incipient lethal temperature; UUILT = ultimate upper incipient lethal temperature; UAT = upper avoidance temperature; FTP = final temperature preferendum.

Table 2. Continued.

Temperature condition (°C)	Life stage	Cyprinidae (Minnows)			Centrarchidae	
		Redside shiner	Peamouth	Northern pikeminnow	Pumpkinseed	Smallmouth bass
Obs. range	Juvenile					20.3-31.0
	Adult					13.0-31.0
	Unknown	6.7-23.9			37.7	
OTR	Juvenile					
	Adult					
	Unknown			16.1-24.4		
GO	Juvenile					26.0-28.2
	Adult					26.0-29.0
	Unknown				15.0-30.0	26.0
ZNG	Juvenile					
	Adult					
	Unknown					
PO	Juvenile					
	Adult					
	Unknown					
MWAT	Juvenile					29.0-33.0
	Adult					29.0-33.0
	Unknown					29.0

95% WMT	Juvenile				
	Adult				
	Unknown				29.5
STM	Juvenile				35.0
	Adult				35.0
	Unknown			37.5	36.3
CTM	Juvenile				
	Adult				
	Unknown				

Table 2. Continued.

Temperature condition (°C)	Life stage	Cyprinidae (Minnows)			Centrarchidae	
		Redside shiner	Peamouth	Northern pikeminnow	Pumpkinseed	Smallmouth bass
ULT	Juvenile					35.0
	Adult					32.3
	Unknown	25.0-30.3	27.0	29.4-32.0	28.0-36.6	29.4-35.0
UCR	Juvenile					
	Adult					
	Unknown					
UTTTL	Juvenile					35.0
	Adult					
	Unknown					
UILT	Juvenile					
	Adult					
	Unknown			29.0		
UUILT	Juvenile					37.0
	Adult					
	Unknown					
UAT	Juvenile					35.0
	Adult				>31.0	

	Unknown			33.0
FTP	Juvenile		21.0-33.0	23.0-31.5
	Adult		26.0-32.0	21.0-31.0
	Unknown	16.1-22.8	26.0-31.5	20.0-31.3

OTR = optimum temperature range; GO = growth optimum; ZNG = zero net growth; PO = physiological optimum; MWAT = maximum weekly average temperature; 95% WMT = 95th percentile of the weekly mean temperature; STM = short-term maximum; CTM = critical thermal maximum; ULT = upper lethal temperature; UCR = upper critical range; UTTL = upper thermal tolerance limit; UILT = upper incipient lethal temperature; UUILT = ultimate upper incipient lethal temperature; UAT = upper avoidance temperature; FTP = final temperature preferendum.

Table 2. Continued.

Temperature condition (°C)	Life stage	Percidae		Esocidae	Cottidae	Acipenseridae
		Yellow perch	Walleye	Northern pike	Mottled sculpin	White sturgeon
Obs. range	Juvenile	11.0-31.0	15.0-34.0	5.8-33.0		
	Adult	10.0-26.0	0.0-35.0	1.0-29.4		0.0-25.0
	Unknown		32.2		<24.0	>25.0
OTR	Juvenile		20.0-26.0			
	Adult					
	Unknown	8.0-27.0	22.0-28.0	9.0-25.0		15.0-25.0
GO	Juvenile	26.0-30.0	22.0-28.0	21.0-26.0		15.0-25.0
	Adult	13.0-20.0	20.0-24.0	19.0-21.0		
	Unknown			19.0-26.0		
ZNG	Juvenile		29.0-30.0	28.0		
	Adult					
	Unknown	31.0	30.0			
PO	Juvenile					
	Adult					
	Unknown		24.6			
MWAT	Juvenile	29.0	25.0	28.0		

	Adult	29.0	25.0	28.0	
	Unknown	29.0			
95% WMT	Juvenile				
	Adult				
	Unknown	29.1	29.0	28.0	
STM	Juvenile			30.0	
	Adult			30.0	
	Unknown	35.0			
CTM	Juvenile				
	Adult				
	Unknown				

Table 2. Continued.

Temperature condition (°C)	Life stage	Percidae		Esocidae	Cottidae	Acipenseridae
		Yellow perch	Walleye	Northern pike	Mottled sculpin	White sturgeon
ULT	Juvenile		31.0-34.1			20.0-21.0 (embryo)
	Adult	21.0-32.3	29.0-35.0			
	Unknown	25.0-33.0	29.0	28.4-34.0		
UCR	Juvenile					
	Adult					
	Unknown	23.0-36.0		30.0-34.0		
UTTL	Juvenile	33.0	31.6			
	Adult					
	Unknown	30.0-33.3				
UILT	Juvenile			33.0		
	Adult			29.4		
	Unknown	25.0-29.7				
UUILT	Juvenile	29.2-35.0				
	Adult					
	Unknown		34.3			

UAT	Juvenile	25.0-26.5			
	Adult		24.0-30.0		
	Unknown		24.0		
FTP	Juvenile	12.2-27.0	22.0-25.0	24.0	
	Adult	17.6-27.0	20.0-25.0		
	Unknown	12.2-26.5	25.0	23.0-24.0	12.8-18.3

OTR = optimum temperature range; GO = growth optimum; ZNG = zero net growth; PO = physiological optimum; MWAT = maximum weekly average temperature; 95% WMT = 95th percentile of the weekly mean temperature; STM = short-term maximum; CTM = critical thermal maximum; ULT = upper lethal temperature; UCR = upper critical range; UTTL = upper thermal tolerance limit; UILT = upper incipient lethal temperature; UUILT = ultimate upper incipient lethal temperature; UAT = upper avoidance temperature; FTP = final temperature preferendum.

Table 2. Continued.

Temperature condition (°C)	Life stage	Salmonidae					
		Mountain whitefish	Lahontan cutthroat	Redband trout	Rainbow trout	Brown trout	Brook trout
Obs. range	Juvenile	0.0-20.6			0.0-24.0		0.0-24.0
	Adult	0.0-20.6			0.0-28.0		0.0-25.0
	Unknown		25.5	0.0-28.0	0.0-28.3	0.0-28.5	0.0-24.0
OTR	Juvenile						
	Adult						
	Unknown				10.0-22.0	4.0-23.9	7.0-20.3
GO	Juvenile	9.0-12.0			10.0-19.0	7.0-19.0	12.0-15.0
	Adult	9.0-12.0			10.0-14.0		10.0-19.0
	Unknown			20.0		10.0-15.6	
ZNG	Juvenile						
	Adult						
	Unknown					19.5-21.2	

PO	Juvenile				
	Adult				
	Unknown			17.0	
MWAT	Juvenile			19.0	17.0 19.0
	Adult			19.0	17.0 19.0
	Unknown			19.0	19.0
95% WMT	Juvenile				
	Adult				
	Unknown	23.9		24.0	24.1 22.3
STM	Juvenile			24.0	24.0 24.0
	Adult			24.0	24.0 24.0
	Unknown			24.0	24.0
CTM	Juvenile		19.4-22.6	26.3-29.4	24.8-29.9 27.2-29.8
	Adult				
	Unknown				

Table 2. Concluded.

Temperature condition (°C)	Life stage	Salmonidae					
		Mountain whitefish	Lahontan cutthroat	Redband trout	Rainbow trout	Brown trout	Brook trout
ULT	Juvenile				24.0-27.0	28.9	20.0-25.0
	Adult				21.0-27.0		25.0
	Unknown		23.0		29.4	23.0-26.4	20.1-28.5
UCR	Juvenile						
	Adult						
	Unknown				19.0-30.0	19.0-30.0	20.0-29.0
UTTLL	Juvenile				26.6	22.5-25.3	25.3
	Adult						

	Unknown			19.0-30.0	
UILT	Juvenile	26.2-27.2	24.0-26.7	23.0-26.3	24.0-25.5
	Adult				
	Unknown		26.5	21.5-26.7	23.5-25.5
UUILT	Juvenile				
	Adult			22.0-25.0	
	Unknown			25.0-30.0	
UAT	Juvenile		20.0-22.0	20.0-22.0	
	Adult				
	Unknown		19.0-25.0	20.0	20.0-25.0
FTP	Juvenile		7.0-19.0	17.6	12.0-19.0
	Adult		13.0-21.1	12.0-18.0	14.8-15.7
	Unknown	9.6-17.7	11.6-22.2	11.7-20.0	11.2-20.3

OTR = optimum temperature range; GO = growth optimum; ZNG = zero net growth; PO = physiological optimum; MWAT = maximum weekly average temperature; 95% WMT = 95th percentile of the weekly mean temperature; STM = short-term maximum; CTM = critical thermal maximum; ULT = upper lethal temperature; UCR = upper critical range; UTTL = upper thermal tolerance limit; UILT = upper incipient lethal temperature; UUILT = ultimate upper incipient lethal temperature; UAT = upper avoidance temperature; FTP = final temperature preferendum.

Table 3. List of references for temperature conditions described in Table 2.

Temperature condition (°C)	Reference
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Observed temperature range	Armour 1993a, 1993b; Baltz et al. 1982; Barans and Tubb 1973; Behnke 1981, 1992; Bond 1963; Calhoun 1966; Cech et al. 1984; Edwards et al. 1983; Ferguson 1958; Ford et al. 1995; Hosford 1986; McCullough 1999; Scott and Crossman 1973; Sigler and Sigler 1987; Wurtz and Renn 1964
Optimum temperature range (OTR)	Armour 1993a, 1993b; Coutant 1977; Elliott 1981; Jobling 1981; Pennell and Barton 1996; Piper et al. 1982; Scott and Crossman 1973
Growth optimum (GO)	Armour 1993a, 1993b, 1994; Brungs and Jones 1977; Doroshov 1988; Eaton et al. 1995; Edwards et al. 1983; Ford et al. 1995; Inskip 1982; Jobling 1981; McConnell 1989; McCullough 1999; McMahan et al. 1984
Zero net growth (ZNG)	Armour 1993a 1993b, 1994; Hokanson 1977; Inskip 1982; McCullough 1999
Physiological optimum (PO)	Armour 1993a, 1993b, 1994
Maximum weekly average temperature (MWAT)	Armour 1993a, 1993b; Brungs and Jones 1977; EPA 1986; Thurston et al. 1979
Weekly mean temperature (95% WMT)	Eaton et al. 1995
Short-term maximum (STM)	Armour 1993a, 1993b; Brungs and Jones 1977; Reutter and Herdendorf 1976; EPA 1986; Thurston et al. 1979
Critical thermal Maximum (CTM)	McCullough 1999
Upper lethal temperature (ULT)	Bell 1991; Black 1953; Behnke 1981; Brungs and Jones 1977; Calhoun 1966; Edwards et al. 1983; Ford et al. 1995; Jobling 1981; Krieger et al. 1983; McMahan et al. 1984; Scott and Crossman 1973; Thurston et al. 1979; Wang et al. 1985; Wang et al. 1987; Wurtz and Renn 1964
Upper critical range (UCR)	Armour 1994; Elliott 1981
Upper thermal tolerance limit (UTTL)	Eaton et al. 1995; Herman et al. 1964; Wurtz and Renn 1964
Upper incipient lethal temperature (UILT)	Elliott 1981; Ford et al. 1995; McCullough 1999; Mullan et al. 1986; Pennell and Barton 1996; Wurtz and Renn 1964
Ultimate upper incipient lethal temperature (UUILT)	Armour 1993a, 1993b, 1994; Brungs and Jones 1977; Krieger et al. 1983; McCullough 1999; Wurtz and Renn 1964
Upper avoidance temperature (UAT)	Armour 1993a, 1993b; Cherry et al. 1975; Coutant 1977; McCullough 1999
Final temperature preferendum (FTP)	Armour 1993a, 1993b, 1994; Bell 1991; Brungs and Jones 1977; Cherry et al. 1975; Cherry et al. 1977; Coutant 1977; Eaton et al. 1995; Edwards et al. 1983; Ferguson 1958; Ford et al. 1995; Herman et al. 1964; Ihnat and Bulkley 1984; Jobling 1981; Krieger et al. 1983; Mullan et al. 1986; Muller and Fry 1976; Reutter and Herdendorf 1976; Sigler and Sigler 1987; Wurtz and Renn 1964

9.0 FIGURES

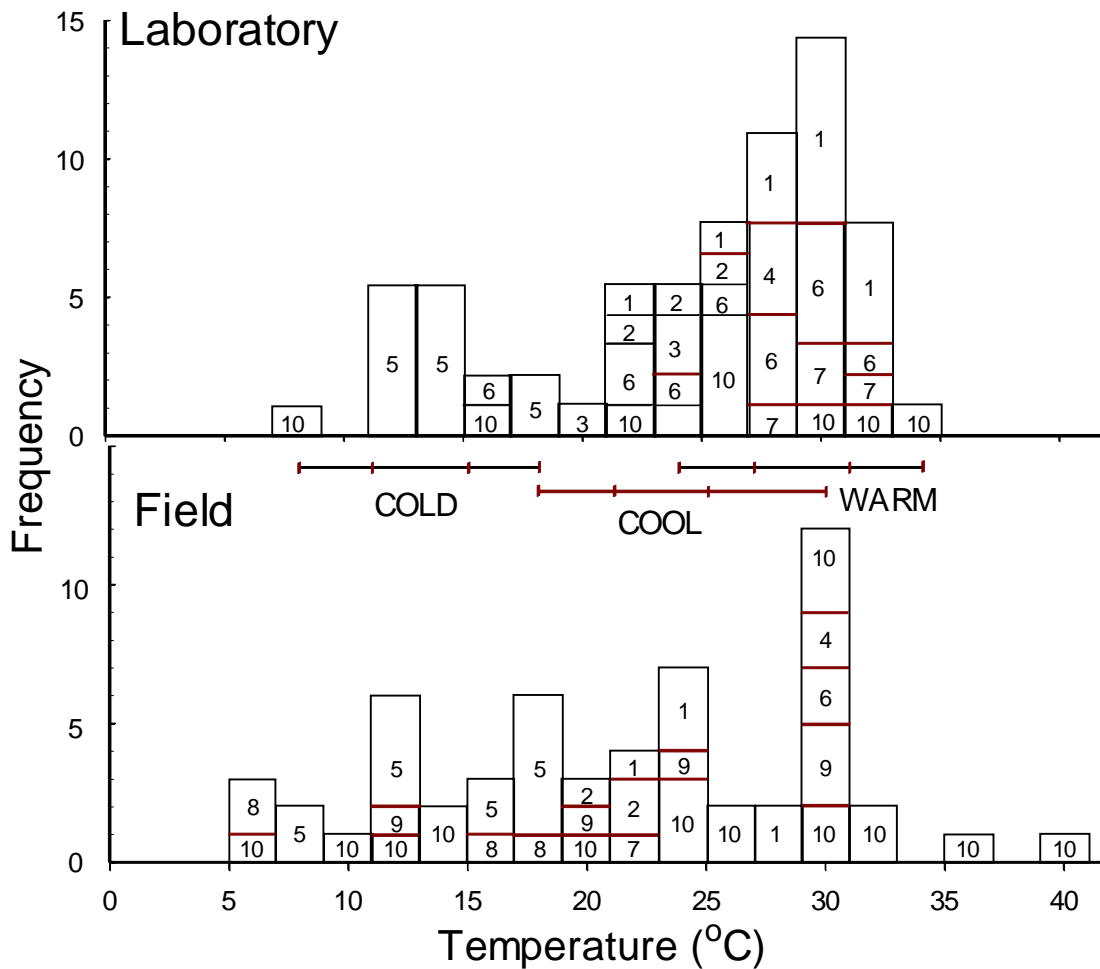


Figure 1. Frequency distribution of temperature preference (laboratory) and occupation (field) by freshwater fish at temperate latitudes (figure redrawn from information in Magnuson et al. 1979). An average temperature for each species was plotted separately for young and adults. Numbers in histograms represent families of fishes: 1 = Centrarchidae; 2 = Percidae; 3 = Esocidae; 4 = Ictaluridae; 5 = Salmonidae; 6 = Cyprinidae; 7 = Percichthyidae; 8 = Cottidae; 9 = Catostomidae; and 10 = other families. Brackets diagram thermal niches of a representative fish in the cold, cool, and warm-water guilds (Magnuson et al. 1979).

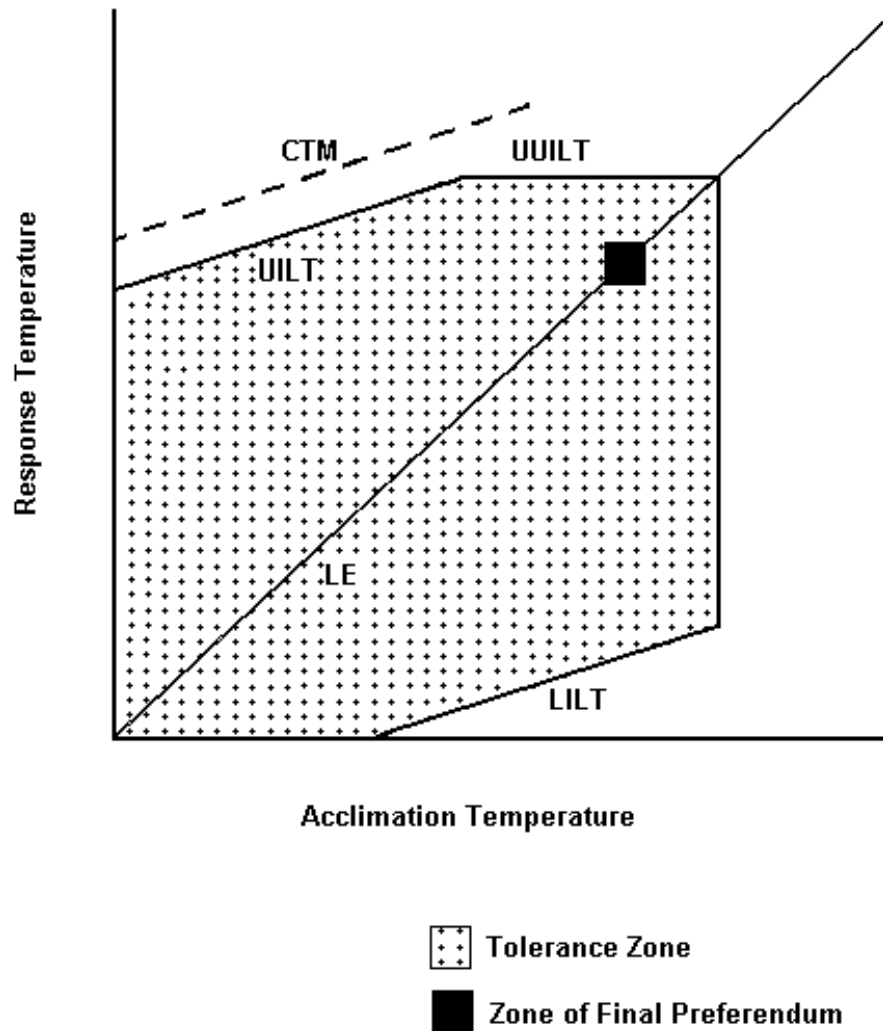


Figure 2. Diagram of temperature relations of fish (figure redrawn from information in Jobling 1981). CTM = critical thermal maximum; UILT = upper incipient lethal temperature; LILT = lower incipient lethal temperature; UUILT = ultimate upper

incipient lethal temperature; and LE = line of equality.