United States
Environmental Protection
Agency

EPA-910-D-01-001
May 2001

Issue Paper 1

Salmonid Behavior and Water Temperature

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

Sally T. Sauter, U.S. Geological Survey

John McMillan, Hoh Tribe

Jason Dunham, U.S. Forest Service

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Abstract

Animals react not only to immediate changes in their environment but also to cues that signal long-term changes to which they must adapt to survive. A proximate factor stimulates an animal's immediate behavioral response, whereas what is known as an ultimate factor causes an animal to adjust its behavior to evolving conditions, thereby increasing its fitness and chances of long-term survival. The Salmonid family are cold-blooded organisms that can respond to an uncomfortable water temperature by moving from one spot to another to maintain thermal comfort. If the reason they move is because of a discrepancy between the temperature of the surrounding water and a "set point" in their brains that registers thermal comfort, their response is known as behavioral thermoregulation. In this paper we discuss two kinds of behavioral thermoregulation: reactive and predictive. The reactive kind is in response to discomfort that is temporary and short term, and so it is a response to a proximate factor, as described above. Predictive thermoregulation occurs when the temperature of the water in which salmonids choose to swim reflects their adaptation over time to a changing environment and thus is a response to an ultimate factor, as described above. Sometimes water temperature stimulates behavior that has nothing to do with thermal comfort. What is known as orientation behavior occurs when water temperature cues fish to locate prey or, say, reduce competition with other fish.

In natural environments, the proximate and ultimate ecological factors driving thermal behavior are frequently complex and not easily separated. Understanding the underlying mechanisms and adaptive value of a behavioral response nonetheless is helpful when considering the influence of anthropogenic or human-caused changes in water temperature on salmonid populations.

When human activity alters water temperature, the impact may interfere with the successful adaptations that salmonids have made to local conditions and historical temperature patterns in the Pacific Northwest. Higher peak summer water temperatures caused by human activity, for example, may reduce or even eliminate salmonid feeding in some streams, increase harmful metabolic effects, and increase the feeding activity of fish that prey on juvenile salmonids. To counter these negative effects brought on by higher temperatures and to ensure the long-term survival of native salmonid populations, it may be necessary to protect and restore cold-water refuges, which human activities may be degrading. Activities such as irrigation and dam construction can harm cold-water refuges by reducing variation in water temperature and flow, reducing channel complexity, and disrupting seasonal recharge of groundwater, whose flow

not only protects resident salmonids from extreme seasonal temperature fluctuations but also may shelter migrating salmonids that travel long distances.

Introduction

Many species of native salmonids inhabit the freshwaters of the Pacific Northwest. A large number of these species are anadromous—they migrate from the ocean to spawn in streams. Many species have both anadromous and completely freshwater forms. As a group, the salmonids display broad genetic flexibility in their physiological, behavioral, morphological, and developmental capacity. This flexibility has fostered their rapid expansion and divergence in the highly diverse habitats of the Pacific Northwest. However, human activities have eliminated much of this diversity and pose a serious threat to the long-term survival of remaining populations. Much of the decline in salmonid populations is directly attributable to the effects of hydroelectric development and land use practices on water quality and quantity. Unfavorable natural cycles in climate and ocean conditions have exacerbated the human-induced decline in native salmonids.

Three largely human-caused water temperature problems represent a serious and continuing threat to remaining native salmonid populations in Pacific Northwest streams: (1) increasing stream temperatures, (2) shifts in annual temperature regimes (multiple external and internal factors affecting a stream's temperature), and (3) loss of cold-water refuges and connectivity. One reason for this threat is that much of salmonid behavior is influenced by water temperature.

Water temperature influences the behavior of fish more than any other nonliving variable (Beitinger and Fitzpatrick 1979). Because salmonids are cold-blooded organisms and live under temporally and spatially heterogeneous thermal conditions, water temperature can be thought of as a resource that fish utilize through behavioral means to control body temperature within narrow limits. Water temperature can serve as a proximate (immediate) or ultimate (evolutionary) cue in a behavioral response. Whenever the adaptive value of a behavioral response to water temperature is body temperature regulation, the behavioral response is known as behavioral thermoregulation (Reynolds 1977). Behavioral thermoregulation helps salmonids adapt through increased fitness and survival (Beitinger and Fitzpatrick 1979, Magnuson et al. 1979, Neill 1979, Reynolds and Casterlin 1979, Crawshaw et al. 1981).

Behavioral thermoregulation may be either predictive or reactive (Neill 1979). This delineation is based primarily on our ability to predict the environmental temperature. In response to predictable thermal characteristics of the environment, such as seasonal temperature changes, salmonids show inheritable local behavioral adaptation. Salmonids also sense and respond to their immediate thermal environment; this is reactive behavioral thermoregulation.

A salmonid's behavioral response to water temperature is not always behavioral thermoregulation, however (Reynolds 1977). Reynolds provides the following examples of evolutionarily adaptive nonthermal ecological factors that can be immediately cued by thermal stimuli: habitat selection, intraspecies size segregation, interspecies niche differentiation, isolating mechanisms, predator avoidance, prey location, escape reactions, and migrations (thermoperiodic, daily, seasonal, spawning) (see Table 1). In a natural environment, it is frequently difficult to determine whether the observed behavioral responses of salmonids are primarily to water temperature or to a combination of ecological cues, such as water temperature, daily exposure to light, and stream flow. However, water temperature is a controlling factor for all biochemical and physiological processes, and exerts strong influence on salmonid behavior.

Table 2 lists the behavioral thermoregulatory responses of salmonids to water temperature by species and life stage. The table summarizes the available scientific literature on salmonid preference and avoidance temperatures. Some of the literature provides clear examples of innate thermal preferences of different salmonids during their life cycle. These preferences are determined through evolutionary adaptation to predictable annual thermal regimes and are examples of predictive behavioral thermoregulation. In Table 2, the laboratory-derived preference temperatures of salmonids are listed under acute and final preference temperatures. Acute preference temperatures are influenced by acclimation temperature, which is discussed later in this paper.

The literature also discusses the avoidance temperatures of salmonids at specific life history stages. Avoidance of extreme water temperatures falls under reactive behavioral thermoregulation, and these data are presented when available. Like acute preference temperature, acute avoidance temperature is strongly influenced by the acclimation history of fish. The preferred and avoidance temperatures of native salmonids have not always been investigated for different life stages under controlled laboratory conditions. When available, we have included primary literature in Table 2 that suggests the preferred and avoidance temperatures of different salmonids based on observations in the field of fish distributions. However, water temperatures collected during field observations of salmonids reflect the influence of many ecological factors besides water temperature that act on fish in their natural habitat. Although laboratory studies are very different from conditions in the wild, a laboratory approach does allow the effects of temperature to be studied under controlled conditions. Even under controlled laboratory conditions, differences between studies in feeding protocol, temperature at which fish are acclimated, and whether fish are held under fluctuating or constant temperature cycles all influence the preference and avoidance temperatures of salmonids. In general, the acute preference temperature of salmonids increases with increasing acclimation temperature (Cherry et al. 1975), and salmonids on restricted rations tend to prefer lower water temperatures than their well-fed cohorts (Brett 1971).

Table 1. Summary of the three kinds of behavioral responses to water temperature

Behavioral Response	Proximate Factor	Ultimate Factor	Adaptive Value	Time Period
Predictive behavioral thermoregulation	Thermal or nonthermal cue	Water temperature	Body temperature regulation	Evolutionary
Reactive behavioral thermoregulation	Thermal cue	Water temperature	Body temperature regulation	Immediate
Orientation behavior	Thermal cue	Nonthermal ecological factor	Varies—see text for examples	Immediate

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids

Species: Bull trout (*Salvelinus confluentus*)

Life stage	Location; wild/hatchery	Aquatic system	Preferred field temp °F (°C)	Acclimation temp °F (°C)	Temp regime	Citation
juvenile	Throughout NW bull trout range; wild	stream	42.8-48.2 (6-9) AWAT ≤55.4-57.2 (≤13-14) MDMT	N/A	natural (see text on thermal regimes below)	Reiman and Chandler 1999
juvenile	Lake Pend Oreille, ID; wild	stream	46.04-57.02 (7 .8-13.9) MDMT	N/A	natural	Saffel and Scarnecchia 1995
juvenile	Lake Pend Oreille, ID; wild	stream	46.4-48.2 (8-9) instantaneous	N/A	natural	Bonneau and Scarnecchia 1996
juvenile	Flathead River, MT; wild	stream	≤60.62 (≤15.0) unknown	N/A	natural	Fraley and Shepard 1989
juvenile & adult	Columbia River, Kootenay, BC, Canada; wild	stream	53.6 (12.0) MDMT 51.26 (10.7) MDAT 52.88 (11.6) MWMT 50.36 (10.2) MWAT	N/A	natural	Haas, unpublished manuscript
adult-spawning	Flathead River, MT; wild	stream	≤50 (≤10.0) unknown	N/A	natural	Fraley and Shepard 1989
adult-upstream migration	Blackfoot River, MT; wild	stream	63.86 (17.7) DAT	N/A	natural	Swanberg 1997

Species: Cutthroat trout (*Oncorhynchus clarki*)

Life stage	Location; wild/hatchery	Aquatic system	Preferred field temp °F (°C)	Acclimation temp	Temp regime	Citation
juvenile & adult	Lake Pend Oreille drainage, ID; wild	stream	50-57.2 (10-14) instantaneous	N/A	natural	Bonneau and Scarnecchia 1996

Species: Steelhead trout (*Oncorhynchus mykiss*)

Life stage	Location; wild/hatchery	Aquatic system	Preferred field temp °F (°C)	Acclimation temp	Temp regime	Citation
juvenile-subyearling	South Umpqua River, OR; wild	river	59 (15.0) DMAT	N/A	natural	Roper and Scarnecchia 1994
juvenile-yearling	South Umpqua River, OR; wild	river	64.04 (17.8) DMAT	N/A	natural	Roper and Scarnecchia 1994
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Avoidance field temp °F (°C)**	**Acclimation temp**	**Temp regime**	**Citation**
juvenile	northern California; wild	stream	≥73.4 (≥23)	N/A	natural	Nielsen et al. 1994

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Rainbow trout (*Oncorhynchus mykiss*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Acute preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile	New and East Rivers, VA, USA; hatchery	tank; starved (see text above on feeding)	52.9°F [51.1-53.1] (11.6°C [10.6-11.7]) 54.7°F [54.5-56.1] (12.6°C [12.5-13.4]) 57.9°F [57.9-59.2] (14.4°C [14.4-15.1]) 62.4°F [61.2-62.4] (16.9°C [16.2-16.9]) 64.5°F [64.2-65.6] (18.1°C [17.9-18.7]) 68.2°F [67.5-69.1] (20.1°C [19.7-20.6]) 71.6°F [70.5-72.5] (22.0°C [21.4-22.5])	42.8 (6) 48.2 (9) 53.6 (12) 59 (15) 64.4 (18) 69.8 (21) 75.2 (24) (see text on acclimation below)	stable	Cherry et al. 1975
juvenile-1 month 6 months 10 months 12 months	Ontario, Canada; hatchery	tank; unknown	62.7 (17.08) 62.5 (16.92) 64.2 (17.88) 59.4 (15.21) 62.4 (16.91) 62.9 (17.20) 60.4 (15.75) 51.7 (10.95) 58.7 (14.82) 55.1 (12.85) 47.1 (8.40) 50.4 (10.20)	50 (10) 59 (15) 68 (20) 50 (10) 59 (15) 68 (20) 50 (10) 59 (15) 68 (20) 50 (10) 59 (15) 68 (20)	stable	Kwain and McCauley 1978
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Avoidance temp °F (°C)**	**Acclimation temp**	**Temp regime**	**Citation**
juvenile	New and East Rivers, VA, USA; hatchery	tank; starved	< 41>55.4 (<5 >13) < 46.4 >59 (<8 >15) < 51.8 >62.6 (<11>17) < 55.4 < 66.2 (<13 >19) < 55.4 < 66.2 (<13 >19) < 60.8 >73.4 (<16 >23) < 66.2 >77 (<19 >25)	42.8 (6) 48.2 (9) 53.6 (12) 59 (15) 64.4 (18) 69.8 (21) 75.2 (24)	stable	Cherry et al. 1975

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Rainbow trout (*Oncorhynchus mykiss*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp**	**Temp regime**	**Citation**
subyearling	Otterville, Ontario, Canada; hatchery	tank; fed	71.6 (22)	N/A	stable	Javaid and Anderson 1967
subyearling	Otterville, Ontario, Canada; hatchery	tank; starved	64.4 (18)	N/A	stable	Javaid and Anderson 1967
subyearling	Campbellville, Canada; hatchery	tank; fed	64.4-66.2 (18-19)	N/A	stable	McCauley and Pond 1971
juvenile	Waterloo County, Ontario, Canada; hatchery	tank; unknown	52.3 (11.3)	N/A	stable	McCauley et al. 1977
adult	unknown	tank; unknown	55.4 (13)	N/A	stable	Garside and Tait 1958
adult	New and East Rivers, VA, USA; hatchery	tank; starved	64.4 (18)	N/A	stable	Cherry et al. 1975
adult	New and East Rivers VA, USA; hatchery	tank, starved	66.6 (19.2)	N/A	stable	Cherry et al. 1977
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Final field preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile & adult	Columbia River, Kootenay, BC, Canada; wild	river	57.6 (14.2) MDMT	N/A	natural	Haas, unpublished manuscript
adult	Horsetooth Reservoir, Colorado; unknown	reservoir	66.0-69.9 (18.9-21.1) ATU	N/A	natural	Horak and Tanner 1964
adult	Lake Michigan; unknown	lake	61.7 (16.5) unknown	N/A	natural	Spigarelli 1975

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Spring chinook salmon (*Oncorhynchus tshawytscha*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Acute preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Dungeness, WA; hatchery	tank; unknown	53.6-55.4 (12-13) (all acclimation temps)	41, 50, 59, 68, and 73.4 (5, 10, 15, 20, and 23)	stable	Brett 1952
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Dungeness, WA; hatchery	tank; unknown	53.1 (11.7)	N/A	stable	Brett 1952
smolt	Little White Salmon N.F.H.; hatchery	tank; satiation	62.1 (16.7)	increasing temp acclimation, 3.6 (2) per month, range: 46.4-57.2 (8-14)	stable	Sauter 1996
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Preferred field temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
adult	Lake Michigan; hatchery	lake	63.1 (17.3)	N/A	natural	Spigarelli 1975

Species: Fall chinook salmon (*Oncorhynchus tshawytscha*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Preferred temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	upriver bright stock from Little White Salmon N.F.H.; hatchery	tank; satiation	63.1 (17.3)	increasing temp acclimation, 3.6 (2) per month, range: 53.6-57.2 (12-14)	stable	Sauter 1996
smolt	upriver bright stock from Little White Salmon N.F.H.; hatchery	tank; satiation	51.6 (10.9)	60.8 (16)	stable	Sauter 1996

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Coho salmon (*Oncorhynchus kisutch*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Acute preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Nile Creek, BC, Canada; hatchery	tank; unknown	53.6-57.2 (12-14)	41, 50, 59, 68 and 73.4 (5, 10, 15, 20 and 23)	stable	Brett 1952
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Bockman Creek, WA; wild	starved 24 hr prior to experiment	52.9 range: 44.6-69.8 (11.6 range: 7-21)	50 (10)	stable	Konecki et al. 1995
subyearling	Bingham Creek, WA; wild	starved 24 hr prior to experiment	69.8 range: 42.8-60.8 (9.9 range: 6-16)	50 (10)	stable	Konecki et al. 1995
adult	Lake Erie; hatchery	tank; unknown	52.5 (11.4)	unknown	stable	Reutter and Herdendorf 1974
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Preferred field temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
adult	Lake Michigan; hatchery	lake	63.1 (17.3)	N/A	natural	Spigarelli 1975

Species: Chum salmon (*Oncorhynchus keta*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Acute preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile-subyearling	Nile Creek, BC, Canada; hatchery	tank; unknown	53.6-57.2 (12-14) (all acclimation temps)	41, 50, 59, 68 and 73.4 (5, 10, 15, 20 and 23)	stable	Brett 1952
adult-migration	unknown	stream	44.6-51.8 (7-11) unknown	N/A	natural	Groot and Margolis 1991
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Nile Creek, BC, Canada; hatchery	tank; unknown	57.4 (14.1)	N/A	stable	Brett 1952

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Pink salmon (*Oncorhynchus gorbushka*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Dungeness, WA; hatchery	tank; unknown	53.1 (11.7)	N/A	stable	Brett 1952
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Preferred field temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile-subyearling	Dungeness, WA; hatchery	tank; unknown	53.6-56.3 (12-13.5)	41, 50, 59, 68 and 73.4 (5, 10, 15, 20 and 23)	stable	Brett 1952

Species: Sockeye salmon (*Oncorhynchus nerka*)

Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Acute preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile-subyearling	Issaquah, WA; hatchery	tank; unknown	53.6-57.2 (12-14)	5°, 10°, 15°, 20° and 23°C	stable	Brett 1952
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Acute avoidance temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
juvenile	Great Central Lake, BC, Canada; wild	lake	< 39.2 >64.4 (< 4 >18)	N/A	natural	LeBrasseur et al. 1978
Life stage	**Location; wild/hatchery**	**Aquatic system; feeding**	**Final preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Issaquah, WA; hatchery	tank; unknown	58.1 (14.5)	N/A	stable	Brett 1952
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Final field preference temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
subyearling	Babine Lake, BC; wild	lake	51.1 (15) ± 9 (5) DAT	N/A	natural	Brett 1971
smolts yearling & adult adult	Cultus Lake, BC; Wild Horsetooth Reservoir, CO; hatchery; Okanagan Reservoir, WA; hatchery	lake reservoir; Okanagan reservoir	51.1-55.0 (10.6-12.8) DAT	N/A	natural	Foerster 1937; Horak and Tanner 1964; Major and Mighel 1966

Table 2. Summary of scientific studies on preference and avoidance temperatures of salmonids (continued)

Species: Mountain whitefish (*Prosopium williamsoni*)

Life stage	**Location; wild/hatchery**	**Aquatic system**	**Preferred field temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
adult-spawning	Sheep River, Alberta, Canada; wild	river	32-46.4 (0-8) DAT	N/A	natural	Thompson and Davies 1976
adult-spawning	Montana; wild	river	<41.9 (<5.5) instantaneous	N/A	natural	Brown 1952
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Acute preferred field temp °F (°C)**	**Acclimation °F (°C) temp**	**Temp regime**	**Citation**
adult	Blacksmith Fork River, UT; wild	river	55.0 (12.8) DAT, prespawning 49.3 (9.6) DAT, postspawning 51.4 (10.8) DAT, winter 61.5 (16.4) DAT, spring	N/A	natural	Inhat and Bulkley 1984
Life stage	**Location; wild/hatchery**	**Aquatic system**	**Final preferred field temp °F (°C)**	**Acclimation temp °F (°C)**	**Temp regime**	**Citation**
adult	Blacksmith Fork River, UT; wild	river	63.9 (17.7) DAT, prespawning 53.4 (11.9) DAT, postspawning 49.8 (9.9) DAT, winter 61.3 (16.3) DAT, spring	N/A	natural	Inhat and Bulkley 1984

Temperature cycle also influences the preference temperature of fish. In the temperate climate of the Pacific Northwest, water temperature varies daily and seasonally, and salmonids in their natural environment are exposed to fluctuating water temperatures. In contrast, all of the laboratory experiments cited in Table 2 have acclimated salmonids to a stable temperature. Such a regime is less physiologically demanding than naturally fluctuating water temperatures (Reynolds and Casterlin 1979), and if feeding and acclimation remain constant, fish exposed to fluctuating thermal regimes may prefer slightly lower water temperatures than fish acclimated to a stable temperature. Because the experimental designs of thermal preference studies frequently vary in these important factors, Table 2 and the questions and answers below provide more information from primary literature sources on the feeding protocol, acclimation temperature, and temperature cycle.

The temperature metrics for field studies are given in Table 2 when available; frequently, they were not specified in the primary literature. For definition of temperature metric abbreviations and further information on temperature measurement and monitoring, see the Temperature Measurement and Monitoring issue paper.

Acute laboratory preference and avoidance temperatures usually represent an average temperature calculated from multiple temperature readings on fish location in a thermal gradient taken over a specific period of time. Final preference temperature also may be an average, or it may be derived from the intercept of a fish's acclimation and acute preference temperatures.

More information on the linkages among water temperature, life stage, and other ecological factors is provided in the questions and answers below.

What are final and acute preference temperature?

The final preference temperature is the innate, species-specific temperature preference of an organism dictated by a thermal set point in the brain (Hammel 1968 in Reynolds 1977). Fish placed in a laboratory temperature gradient will move toward the final preference temperature. This temperature is usually reached within 24 hours after an animal has been introduced to a laboratory temperature gradient (Reynolds and Casterlin 1979). Fry (1947) defined the final preference temperature as "a temperature around which all individuals [of a given species] will ultimately congregate, regardless of their thermal experience before being placed in the gradient" and that temperature "at which the preferred temperature is equal to the acclimation temperature." Using this definition, the final preference temperature of fish can be determined either by using a thermal gradient or by determining the acute preference temperature of fish held at different temperatures and using regression to find the intercept of acclimation temperature with acute preference temperature.

The ecological significance of a species' thermal preference is that it frequently coincides with the species' thermal optimum for physiological functioning. This optimum may shift with age and during various life history stages of an animal (Reynolds 1977, McCauley and Huggins 1979, Kelsch and Neill 1990). Innate thermal preferences displayed by salmonids with age and development reflect genetic adaptation of species or subspecies (stocks) to predictable annual thermal conditions in their environment (Magnuson et al. 1979).

The term *acute preference temperature* describes the immediate preference temperature of a fish placed in a laboratory gradient (Reynolds and Casterlin 1979). The acute preference temperatures of fish are measured within a short period (usually 2 h or less) after the fish have been introduced to a thermal gradient. Acute preference temperatures are strongly influenced by the fish's acclimation temperature.

What is acclimation temperature? How does it influence the acute preference temperature of salmonids?

Acclimation temperature or thermal acclimation refers to the physiological and biochemical restructuring of cellular and tissue components that occurs in response to temperature variations of 2-3 weeks or more under known or specified thermal conditions in the laboratory (Reynolds and Casterlin 1979, Withers 1992). In natural environments, both nonthermal factors and seasonal changes in water temperature shape the restructuring of cells and tissues. The term applied to this natural process is *acclimatization* (Reynolds and Casterlin 1979, Crawshaw et al. 1990, Withers 1992). A species-innate thermal preference can be altered over hours, days, and weeks by thermal acclimation or acclimatization (Reynolds and Casterlin 1979, Withers 1992). Thermal acclimation or acclimatization shifts the acute preferred temperature, avoidance temperatures, and thermal tolerance range of an animal as a result of physiological adjustment to current thermal conditions and involves "feedback to the genetic material, and subsequently to the protein synthetic system" (Hazel and Prosser 1974). Changes in enzyme structure and lipid membranes are perhaps the most notable alterations seen in response to variations in temperature (Withers 1992). The result of acclimation or acclimatization is an increase in the overall performance and survival of an animal in its environment. Wild salmonids acclimatized to daily average temperatures in the summer show slightly higher preference temperatures than fish acclimatized to daily average winter temperatures. The effect of acclimation temperature on the preference temperatures of rainbow trout under laboratory conditions can be seen in Table 2 (see Cherry et al. 1975).

Although salmonids tend to be adapted to a narrow temperature range (and thus are stenothermic), they show some capacity to acclimatize to higher daily and seasonal water temperatures (Javaid and Anderson 1967, Cherry et al. 1975). Notable differences exist in the degree of their stenothermy and capacity for thermal acclimation. For example, the literature suggests that rainbow trout may have a greater capacity for thermal acclimation than do Pacific salmon or char, and char are considerably more stenothermic than native trout or salmon (Brett 1952, Javaid and Anderson 1967).

It is important to remember that salmonids are physiologically adapted to live in cold-water environments, and their ability to acclimate to higher water temperatures is restricted to the cold-water range of temperatures in which they evolved. Under laboratory conditions, acclimation may extend the thermal limits of salmonids; however, in nature growth, survival, and successful reproduction are a much more rigorous test of thermal tolerances. Fish may be able to physiologically acclimate to some extreme thermal conditions in laboratory settings, but face "ecological death" under natural conditions where ecological factors such as food availability and vulnerability to predation are important components of survival (Magnuson et al. 1979, Dickerson and Vinyard 1999). Adaptation to higher environmental water temperatures and altered annual thermal regimes may require many generations (Nelhsen et al. 1991, Adkison 1995, Hendry et al. 1998); however, human-caused water temperature increases may be of such magnitude and occur so rapidly that they outpace the capacity of salmonid populations to genetically adapt (Quinn and Adams 1996).

What other ecological factors influence the acute preference temperature of salmonids?

Both laboratory and field experiments have shown that food availability affects the acute thermal preference of salmonids. Brett (1971) found strong evidence that restricted food conditions in Babine Lake, British Columbia, resulted in a daily pattern of vertical migration in sockeye salmon less than 1 year old (subyearlings). These vertical migrations likely represent a behavioral response to both thermal stratification of the lake and limited rations. By behaviorally thermoregulating at slightly lower water temperatures during the day, then migrating to the surface to feed at dusk and dawn, juvenile sockeye salmon maximize their growth potential by conserving energy when food is limited. In the laboratory, Javaid and Anderson (1967) starved juvenile rainbow trout acclimated at 68°F (20°C) and found that the selected temperature dropped from near 71.6-64.4°F (22-18°C) in a day once food was withheld. Selected temperature of starved juvenile rainbow trout remained at 64.4°F (18°C) for 2 weeks until feeding was resumed, when fish again began selecting 71.6°F (22°C) water temperatures within a day.

Another factor known to influence temperature selection is a salmonid's stock. Stock refers to populations of salmonids that originate from and have adapted to the environmental conditions characteristic of specific watersheds (Nehlsen et al. 1991). As mentioned earlier, one environmental characteristic that salmonids adapt to behaviorally is predictable annual temperature cycles. As a result, intraspecies adaptations may be seen in the temperature preferences of different stocks of salmonids. For example, Konecki et al. (1995) found slight differences in the temperature preferences of two populations of juvenile coho salmon. Coho salmon originating from a stream with lower and less variable water temperatures showed slightly lower preference temperatures and temperature range than fish originating from a more heterothermal stream (Table 2).

The age of salmonids also is important in determining their temperature preference. Kwain and McCauley (1978) found that the preferred temperature of rainbow trout decreased steadily with age (Table 2).

Very little information is available in the literature on the effect that daily temperature fluctuations have on salmonids' preference temperature. Field and laboratory studies such as Brett (1971) and Hokanson et al. (1977) have found that fluctuating water temperatures influence the thermoregulatory behavior of salmonids. Hokanson et al. (1977) investigated the growth and mortality rates of juvenile rainbow trout held at constant and daily fluctuating temperatures in the laboratory. Rainbow trout held at daily fluctuating temperatures did not acclimate to the average mean temperature, but to some temperature between the minimum and maximum daily temperature, and growth and mortality responses reflected water temperatures about 34.7°F (1.5°C) colder than fish held at a constant temperature. These physiological data suggest that salmonids acclimated to daily fluctuating temperature cycles may select lower preference temperatures than fish held at constant temperatures.

Why does food availability in the wild and under laboratory conditions affect water temperatures selected by salmonids?

The rates of all biochemical reactions, and therefore the metabolic rates of cold-blooded fishes, are controlled by temperature (Fry 1971, Elliot 1976, Beitinger and Fitzpatrick 1979). As metabolic rate increases with temperature, so does the need for food to keep pace with metabolic demand (Elliot 1976, Brett 1995, Higgs et al. 1995, Jobling 1981) (see Physiology issue paper for more information). Well-fed salmonids tend to behaviorally thermoregulate at slightly warmer water temperatures; the combination of abundant feeding opportunities and warmer water tends to maximize growth. When food is scarce, salmonids will select cooler water temperatures to lower their metabolic rate and conserve energy stores.

How does water temperature affect the feeding behavior of salmonids?

Increased water temperatures and a longer period of warmer water temperatures increase the feeding rate of salmonids provided that food is not limiting and water temperatures do not exceed the feeding temperature range (Elliott 1982, Linton et al. 1998). Linton et al. (1998) reported that a +3.6°F (2°C) increase in annual water temperature regime increased the feeding rate of rainbow trout in the winter and spring months, but significantly decreased feeding rate at peak summer temperatures 68°F (20°C), leading to an overall decline in growth rate. Appetite suppression occurred at lower temperatures in larger, older fish (Linton et al. 1998). At temperatures above a species preferred temperature range, feeding rate may continue to increase up to a point, but growth potential decreases (Linton et al. 1998). Appetite suppression, leading to a decrease in feeding rate also occurs in fish as temperature increases above a species' preferred range and may be a result of decreased activity in response to high metabolic demand (Jobling 1981, Linton et al. 1998). Elliott (1991) found that Atlantic salmon (*Salmo salar*) stopped feeding at elevated water temperatures, but quickly resumed feeding once water temperature was lowered. Research indicates that the appetite of juvenile sockeye salmon is completely inhibited at 75.2°F (24°C), and that the return of appetite is temperature-dependent (Brett and Higgs 1970, Brett 1971).

How does water temperature affect salmonid behavior at different life stages?

Larvae and juveniles. Juvenile salmonids require a variety of water temperatures. In general, larvae and young juveniles tend to be attracted to slightly warmer water temperatures for feeding and growth than are larger juveniles and adult fish. The innate thermal preference of some fish frequently decreases from the larvae through juvenile stages (Magnuson et al. 1979, McCauley and Huggins 1979), although research on age-related changes in the thermal preference of salmonids is scarce. Research by Kwain and McCauley (1978) (see Table 2) on juvenile rainbow trout found a steady decrease in the thermal preference of rainbow trout with age, with larvae preferring temperatures near 66.2°F (19°C), whereas yearlings selected water temperatures of about 55.4°F (13°C).

McCullough (1999) notes that the higher thermal preferences of young-of-year (YOY) salmonids may attract this age group to warmer downstream waters, improving growth opportunities early in the season. The study cautioned, however, that as seasonal water temperatures increase and the preferred temperature of the YOY age class decreases, this age group is least capable of reactive behavioral thermoregulation because of limited swimming capacity. YOY fish may be physically incapable of escaping unfavorably high stream temperatures by migrating to cooler upstream reaches.

Juvenile and adult salmonids frequently move downstream to warmer water temperatures in the fall and avoid extreme cold-water conditions in upstream reaches during the winter (Bjornn 1971, Pettit and Wallace 1975, Brown and MacKay 1995, Northcote 1997, Jakober et al. 1998). Cold winter temperatures are also known to prompt reactive behavioral thermoregulation in juvenile rainbow trout and coastal cutthroat trout. These juveniles will migrate downstream to overwinter in warmer main-stem areas following emergence (Behnke 1992, Trotter 1989). Cederholm and Scarlett (1981) report that juvenile winter steelhead leave their natal tributaries to overwinter in warmer downstream reaches.

For anadromous salmonids, such as spring and fall chinook salmon and steelhead, there is considerable variation in juvenile freshwater life history patterns. The temperature requirements for larvae and rearing juvenile trout and salmon are similar; however, the time of freshwater residence is quite variable. For example, spring chinook salmon rear for a year in headwater streams before juveniles emigrate during the spring freshet, whereas juvenile fall chinook salmon rear in mainstem rivers and emigrate as subyearlings during the summer after several months of freshwater rearing. Steelhead use headwater streams for rearing and emigrate in the spring, as do spring chinook salmon, but juveniles may occupy headwaters for 2 or 3 years before emigrating. Therefore, protective water temperature criteria must address the distribution and juvenile life history pattern of each anadromous species.

Smolts. Smoltification is a period of profound developmental change in juvenile salmonids. The physiological development that accompanies smolt migration contributes to the complex interaction between water temperature and emigration behavior of juvenile salmonids. By controlling biochemical and physiological reaction rates, water temperature affects the physiological development of smolts, as well as the timing and duration of smoltification. Of particular significance is the inhibition of the gill ATPase osmoregulatory enzyme at high water temperatures, which leads to a loss of migratory behavior in salmonids (see Physiology issue paper).

One area that has not been investigated is whether cold-water refuges have a role in supporting emigration and physiological smolt development in salmonid stocks that undergo long summer emigrations.

Adult potamodromous migrations. Potamodromous migration patterns are important life history variants for freshwater populations of native salmonids. These migrations support genetic diversity in the overall salmonid populations and direct fish to more spatially, seasonally, and developmentally suitable habitat (Northcote 1997). Water temperature generally increases longitudinally in streams from upstream to downstream reaches, and unfavorably high temperatures in downstream reaches may create thermal barriers that limit or halt migrations. Thermal barriers cause habitat fragmentation, disrupting migration patterns and isolating smaller populations from the overall population. The preferred temperatures for nonspawning adults during migration provide a useful temperature range from which seasonal thermal conditions in watersheds can be evaluated for migratory functionality. However, extreme water temperatures may pose a more serious migratory barrier than water temperatures ranging a few degrees above the cited preferred migratory temperature range of a species.

Spawning migrations. Water temperature is a critical environmental factor during the spawning migrations of salmonids because the fish fast during the migrations and must rely on stored energy reserves to complete the journey (Berman and Quinn 1991, Coutant 1999). Although salmonid spawning migrations occur throughout the year, high water temperatures are most likely to delay or be stressful to fish during summer and fall migrations (Table 3). In addition, salmonid stocks that make long-distance migrations to inland spawning grounds during the summer and fall may be more vulnerable to increased water temperatures and loss of cold-water refuges. Increased water temperatures are reported to create migrational blockages for several species of salmonids when water temperatures exceed 69.8°F (21°C) (Beschta et al. 1987, Major and Mighell 1967, cited in ODEQ 1995). For bull trout, water temperatures >55.4° (13°C) reportedly block migratory behavior (ODEQ 1995, Independent Scientific Group 1996, Spence et al. 1996). Higher water temperatures during spawning migrations also increase the harmful

Table 3. Seasonal spawning migration timing of Pacific Northwest salmonids

Species	**Spawning migration timing**	**Citations**
Steelhead (*O. mykiss*)	Winter stocks: November-April Summer stocks: May-October	Wydoski and Whitney 1979; Spence et al. 1996; Hicks 1999
Spring chinook salmon (*O. tshawytscha*)	May/June	Wydoski and Whitney 1979; Berman and Quinn 1991; Nehlsen et al. 1991; Spence et al. 1996; NMFS chinook status review
Fall/summer chinook salmon (*O. tshawytscha*)	Early fall	Nehlsen et al. 1991; NMFS chinook status review
Coho salmon (*O. kitsutch*)	Early fall into November; early July on Olympic Peninsula	Wydoski and Whitney 1979; Spence et al. 1996; NMFS coho status review
Pink salmon (*O. gorbuska*)	Late summer to early fall, every other year	Wydoski and Whitney 1979; Spence et al. 1996; Nehlsen et al. 1991
Chum salmon (*O. keta*)	Fall and winter; summer in Olympic Peninsula	Wydoski and Whitney 1979; Spence et al. 1996
Sockeye salmon (*O. nerka*)	Spring through fall	Wydoski and Whitney 1979; Quinn and Adams 1996
Anadromous coastal cutthroat trout (*O. clarkii*)	July through fall	Wydoski and Whitney 1979; Spence et al. 1996; Hicks 1999; Trotter 1989; NMFS 1998
Potamodromous coastal cutthroat trout (*O. clarkii*)	Very late winter to early spring	Trotter 1989
Westslope cutthroat trout (*O. clarkii*)	Very late winter to early spring	Trotter 1989
Rainbow/redband trout (*O. mykiss*)	Spring	Wydoski and Whitney 1979; Reiser and Bjornn 1979
Bull trout (*S. confluentus*)	Late summer through fall	Wydoski and Whitney 1979; Baxter and Hauer 2000
Mountain whitefish (*P. williamsoni*)	Fall	Wydoski and Whitney 1979; Spence et al. 1996

metabolic effects on adult fish. Prolonged exposure to elevated temperatures during migration is significantly related to prespawning mortality, and increased metabolic costs may deplete energy reserves before fish reach spawning grounds, reducing the size and number of viable eggs (Idler and Clemens 1959, Gilhousen 1980, Godfrey et al. 1954, Andrew and Geen 1960, CDE and IPSFC 1971, cited in ODEQ 1995).

Changes in the annual thermal regimes may also result in long-term behavioral changes to the timing of migratory patterns. Quinn and Adams (1996) observed that Columbia River basin sockeye salmon now migrate approximately 6 days earlier than historically. The migration of the sockeye salmon is cued by their exposure to light, but the earlier migration timing is a result of alterations to thermal and hydrological regimes in the river (Quinn and Adams 1996).

Adult holding/refugia. To reduce the energy costs of oversummering in fresh water before spawning, salmonids may select holding habitat based on nonthermal cues, such as groundwater flow, which later in the season provides critical cold-water refuge. This type of behavior falls under predictive behavioral thermoregulation. Examples of this are seen in adult spring chinook salmon, which migrate into the tributaries in the spring and oversummer in fresh water before spawning. Berman and Quinn (1991) found that adult spring chinook salmon in the Yakima River selected holding sites associated with islands, pools, and rock outcrops in the spring, and that these areas provided thermal refuges during the summer. A cooler holding habitat reduces basal metabolic demand during the summer and is critical to successful reproduction. Torgersen et al. (1999) reported that adult spring chinook salmon holding in the Middle Fork of the John Day River also select holding sites early in the season that provide cold-water refuge during the summer.

Spawning. Salmonid reproduction occurs within a variety of habitats ranging from streams and lakes to intertidal sloughs (Groot and Margolis 1991, Spence et al. 1996). The timing of spawning activity is genetically controlled, and many stocks have adapted to their locales, which likely enhances survival and reproductive success (Nehlsen et al. 1991, Sheridan 1962, Royce 1962, Burger et al. 1985, Brannon 1987, NMFS 1998). Most stocks of Pacific salmon, including summer/fall chinook, fall coho, pink, chum, and sockeye salmon, have evolved to spawn in the fall when stream flows are lowest and water temperatures decline. Other stocks, such as spring chinook and summer coho, typically spawn during late summer months. The trout indigenous to the Northwest evolved to spawn in the spring and are stimulated by rising water temperatures and high flows (Hicks 1999). Increased water temperatures on the spawning grounds can also lead to the cessation of spawning activity (Spence et al. 1996).

Literature reviews by Bjornn and Reiser (1991) and Spence et al. (1996) summarize salmonid spawning temperatures as ranging from 33.8°F (1°C) to 68°F (20°C) with most spawning occurring at temperatures between 39.2°F (4°C) and 57.2°F (14°C.) Table 4 lists water temperatures at which spawning of different salmonids has been observed (Reiser and Bjornn 1979, ODEQ 1995, Spence et al. 1996). The temperature metrics are not given with these studies but are assumed to be either instantaneous or daily average temperatures (DAT) at the time of spawning. Spawning temperatures likely reflect optimal physiological temperatures for incubation and development of eggs rather than preference temperatures of spawning adults.

Despite the variations in observed spawning temperatures, the Independent Scientific Group (1996) states that the optimal temperature for anadromous salmonid spawning is 50°F (10°C) and that stressful conditions for anadromous salmonids begin at temperatures greater than 60.08°F (15.6°C,) with lethal effects occurring at 69.8°F (21°C).

Do ecological interactions influence the behavior of salmon? What about observations of individual salmonids using habitat that lab studies suggest is too warm? Don't these observations suggest that the laboratory-based data are skewed?

The acute and innate final preference temperatures of fishes are often superseded by their more immediate nonthermal needs (Reynolds 1977, Reynolds and Casterlin 1979). Frequently, other environmental variables such as food availability or competitive interactions provide the adaptive value of a thermal response (Reynolds 1977). Under these circumstances, water temperature may influence fish behavior by serving as an orientation or direction cue. Nonthermal ecological factors such as stress, migrations, niche differentiation, escape reactions, photoperiod, intra- and interspecies interactions, prey location, disease, and chemicals can affect

Table 4. Selected water temperatures for spawning by Pacific Northwest salmonids. For the purpose of water temperature criteria protective of spawning salmonids, these references are assumed to be Daily Average Temperatures (DAT)

Species	**Selected Spawning Temperature Range °F (°C) (DAT)**	**Citation**
Steelhead (*O. mykiss*)	50-55 (10-12.8)	Bell 1991
Spring chinook salmon (*O. tshawytscha*)	39.9-64 (4.4-17.8)	Olson and Foster 1955, cited in ODEQ 1995
Fall/summer chinook salmon (*O. tshawytscha*)	41-56.1 (5-13.4)	Raleigh et al. 1986, cited in ODEQ 1995
Coho salmon (*O. kitsutch*)	50-55 (10-12.8)	Bell 1991
Pink salmon (*O. gorbuska*)	46.4-55.4 (8-13)	Independent Scientific Group, 1996
Chum salmon (*O. keta*)	46.4-55.4 (8-13)	Independent Scientific Group, 1996
Sockeye salmon (*O. nerka*)	36.1-46.4 (2.3-8)	Brannon 1987
Anadromous coastal cutthroat trout (*O. clarkii*)	42.9-62.9 (6.1-17.2) 39.9-48.9 (4.4-9.4)	Beschta et al. 1987; Trotter 1989
Potamodromous coastal cutthroat trout (*O. clarkii*)	≥41-42.8 (≥5-6)	Trotter 1989
Westslope cutthroat trout (*O. clarkii*)	44.9-55.0 (7.2-12.8)	Beschta et al. 1987; Trotter 1989
Rainbow/redband trout (*O. mykiss*)	up to 68 (20) 50-55 (10-12.8)	Hicks 1999 (literature review) Behnke 1992
Bull trout (*S. confluentus*)	peak: <44.6 (<7) cessation: >50 (>10)	Geotz 1989; Pratt 1992; Kraemer 1994; Fraley and Shepard 1989; James and Sexauer 1997; Wydoski and Whitney 1979
Mountain whitefish (*P. williamsoni*)	37.4-41 (3-5)	Brown 1952, 1972; Breder and Rosen 1966; Bruce and Starr 1985; Hildebrand and English 1991

the behavioral responses of fish to thermal stimuli (Reynolds 1977). Several examples are listed below:

1. Juvenile sockeye salmon make daily vertical migrations to feed in warmer surface waters, and return to colder, deeper waters to lower metabolic costs when food is limited (Brett 1971).

2. Some bacterial diseases alter the thermoregulatory behavior of fish by increasing their preference temperature (Reynolds et al. 1976a, Reynolds 1977c, Reynolds and Covert 1977). By increasing body temperature in response to bacterial invasion, fish may enhance their immune response to pathogens (Kluger 1978).

3. A study by Scrivener et al. (1994) found that juvenile ocean-type fall chinook salmon, rainbow trout, and mountain whitefish moved from the Fraser River into a small tributary

creek during the summer. The authors suggest that proximate cues of warmer water temperatures and clearer water attracted juvenile salmonids into the tributary, where feeding opportunities were enhanced.

4. Research by Fraser et al. (1993) found that juvenile Atlantic salmon (*Salmo salar*) switched between diurnal and nocturnal foraging in response to changes in water temperature. At warmer water temperatures characteristic of spring, summer, and fall months, the salmon fed mostly during the daylight hours. When water temperatures were decreased to reflect temperatures experienced by fish during winter months, nocturnal feeding increased and daylight feeding decreased. Feeding probably decreased when water temperatures were colder because fish digested food more slowly and because metabolic rates were lower at colder water temperatures. The authors concluded that the increase in nocturnal feeding at colder water temperatures may reflect increased avoidance of light in juvenile salmon at low water temperatures. At colder water temperatures, the escape responses of fish are decreased, and increased avoidance of light may provide adaptive value through predator avoidance.

The interactions between salmonid thermal behavior and predation and competition are important considerations and are discussed below. Additional information on multiple stressors and environmental interactions can be found in the Interactions issue paper.

Does water temperature affect the predator avoidance behavior of juvenile salmonids?

Higher water temperatures may affect predation on juvenile salmonids in several ways. Salmonids may be more vulnerable to predation when stressed by suboptimal elevated water temperatures. Mesa (1994) found that subyearling spring chinook salmon acutely stressed by handling or agitation were lethargic and more vulnerable to northern pikeminnow (*Ptychocheilus oregonensis*) predation than nonstressed fish. However, a study of subyearling fall chinook salmon with acute high water temperatures did not show increased predation vulnerability to smallmouth bass (M. Mesa, USGS Biological Resources Division, personal communication). If juvenile salmonids lose equilibrium due to acute thermal shock, their ability to avoid predators may be significantly reduced. Juvenile rainbow trout and chinook salmon were selectively preyed upon by larger fishes when thermally shocked (Coutant 1972a, as cited in Hicks 1999). The relative vulnerability to predation increased with duration of sublethal exposure to lethal temperatures through incapacitation. Coutant (1972b) found that the vulnerability of juvenile rainbow trout to predation depended on temperature and the duration of exposure to high water temperatures.

Temperature stress may also compromise the immune system of fish, making them more susceptible to disease (Becker and Fujihara 1978). The physiological stress of elevated water temperatures combined with other stressors such as disease in turn increases salmonid susceptibility to predation. When confronted by predatory fish, juvenile salmonids must have the scope for “burst” swimming to avoid predators. However, when challenged by either a low-to-moderate or a high infection level of *Renibacterium salmoninarum* (the infective bacterium for bacterial kidney disease), infected subyearling spring chinook salmon were twice as likely as noninfected fish to be consumed by either northern pikeminnow or smallmouth bass

(Mesa et al. 1998). Infection with the disease apparently reduced the chinooks' scope for activity, making the them more vulnerable. Many other physiological and environmental stressors may act in concert with suboptimal water temperatures to increase salmonid susceptibility to predation (see Interactions issue paper).

Does water temperature affect the predatory fish that feed on juvenile salmonids?

Higher water temperatures increase the feeding rate of predatory fish such as the native northern pikeminnow. This problem is magnified by the widespread occurrence of nonnative predatory fish in Pacific Northwest waters. Many of these introduced fishes function best in cool waters that serve as a transition between the cold water optimal for salmonids and warmer water optimal for warm-water fish.

Hydropower development of northwest rivers has raised seasonal water temperatures and the period of warm water in the fall, thus lengthening the seasonal feeding period of predatory fish. Impoundment has also changed the migratory behavior of juvenile salmonids by concentrating migrants in dam forebay and tailrace areas, creating unusually abundant feeding opportunities for predators, particularly northern pikeminnow, which feed heavily when prey is abundant (Poe et al. 1991, Vigg et al. 1991, Petersen and DeAngelis 1992). Impoundments also have slowed river flow, prolonging migration time and the length of time migrants are exposed to predators (Poe et al. 1991). In large northwest rivers, the most significant predator on juvenile salmonids is the northern pikeminnow, a native cyprinid species (Poe et al. 1991, Mesa 1994). Competition for food between the native northern pikeminnow and introduced predators, such as smallmouth bass and walleye, may increase northern pikeminnow predation pressure on juvenile salmonids (Li et al. 1987, Poe et al. 1994).

During the summer months, fish impoundment reduces river flow and seasonal water temperatures rise, providing optimal conditions for smallmouth bass that use the warmer, quieter nearshore areas where subyearling fall chinook salmon rear. This habitat overlap leads to high predation by the introduced bass (Gray and Rondorf 1986, Poe et al. 1991, Tabor et al. 1993, Giorgi et al. 1994, Poe et al. 1994, Zimmerman and Parker 1995, Petersen et al. 2000). Petersen et al. (2000) used bioenergetics modeling to estimate loss of emigrating salmonids to northern pikeminnow and smallmouth bass predation in the lower Snake River under current impounded conditions and simulated unimpounded conditions. The model's input temperature regime was manipulated to reflect the current impounded thermal regime and the predicted decrease in water temperatures if the four lower Snake River dams were removed (unimpounded) while holding all other model parameters and inputs (diet, population size, age structure) constant. Under these temperature simulations, Petersen et al. (2000) estimated a 7% decrease in predation loss of salmonids to smallmouth bass, and about a 9% decrease in loss to northern pikeminnow under the cooler, unimpounded thermal conditions simulated for the lower Snake River.

Warmer water temperatures also increase the abundance of predators that feed on juvenile salmonids. Maule and Horton (1985) studied growth and fecundity of walleye in the John Day Reservoir below McNary Dam on the Columbia River and found that the reservoir habitat provided low flow conditions and nearly ideal water temperatures for walleye growth. Water temperatures in the reservoir remained at or near the thermal optimum for walleye food consumption (71.6°F [22°C]) during the growing season, but did not increase to the maximum (80.6°F [27°C]) (Kitchell et al. 1977b, Maule and Horton 1985). Maule and Horton (1985) also reported walleye from the John Day Reservoir growing at close to the highest rate reported for the species.

What is competition and how does water temperature influence it?

Salmonids, like other animals and plants, compete with members of their own species (intraspecific competition) and with other species (interspecific competition) for limited resources. In natural environments, resources such as food and habitat often are limited. Water temperature is an aspect of habitat that can favor or exclude one fish species over another, influencing distribution.

Ecologists generally recognize two forms of competition: exploitative and interference. Exploitative competition occurs when individuals compete for access to a limited resource, which one species depletes so that it cannot be used by other species (Begon and Mortimer 1986). Interference competition occurs when individuals compete with each other for a limited resource. A common example in salmonids is territoriality (Grant et al. 1998). Salmonids often hold feeding territories and monopolize access to resources within the defended territory.

Temperature regime is key to the outcome of competitive interactions within a fish community. Fish competing within their optimum temperature range have an improved capability of performing compared with species operating outside their optimum temperature range. The ability of salmonids to compete for short- and long-term survival at the upper end of their thermal tolerance range involves multiple factors, including swimming performance; fecundity under a warm thermal regime; defending feeding stations; consuming food even in the absence of competition; sustaining maintenance requirements and growing; finding cold-water refuges and escape cover; avoiding cumulative mortification (Kilgour and McCauley 1986, as cited in McCullough 1999); and resisting disease, as well as avoiding direct short-term thermal death. Temperature regime operates directly on community composition through a species' thermal tolerance and preference. When thermal regimes exceed the optimum for salmonids, their suitable habitat area shrinks and warm-water tolerant species may fill these niches (McCullough 1999).

Does water temperature affect competition between nonnative salmonids, such as brook trout, and native salmonids?

Nonnative brook trout (*S. fontinalis*) have extensively colonized the inland western United States (Adams 1999) and may pose a serious threat to native salmonids, particularly cutthroat trout. Because brook trout do not hybridize with cutthroat trout, they are believed to affect the latter primarily through predation, disease transmission, or competition. Generally, competition is cited as the most important factor (Young 1995).

Temperature can have a dramatic effect on the coexistence of cutthroat and brook trout. DeStaso and Rahel (1994) studied interactions between brook and Colorado cutthroat trout (*O. c. pleuriticus*) in experimental stream tanks at different water temperatures. At temperatures of

50°F (10°C,) brook and cutthroat trout were nearly equal competitors, but at 68°F (20°C) brook trout were dominant. Schroeter (1998) studied competitive interactions between brook and Lahontan cutthroat trout in experimental field tanks with a natural water supply (~59°F [15°C]) and found brook and cutthroat trout to be equal competitors, unless density of the former was high (2 brook:1 cutthroat trout). Adams (1999) suggested that upstream limits to the distribution of brook trout could result from a growth disadvantage in higher elevation streams with shorter growing seasons.

Water temperature also influenced behavioral dominance and growth in a study of competition between brook trout and bull trout. McMahon et al. (1999) measured growth of subyearling bull trout and brook trout in sympatry (both species together) and allopatry (each species tested separately) at four temperatures (46.4°F, [8°C], 53.6°F, [12°C], 60.8°F, [16°C], and 68°F [20°C]). In allopatry, bull trout and brook trout growth was similar at lower temperature (46.4°F [8°C] and 53.6°F [12°C]), but brook trout grew significantly faster than bull trout at higher water temperatures (60.8°F [16°C] and 68°F [20°C])(see Physiology issue paper). The presence of brook trout had a significant negative effect on the growth of bull trout. Bull trout in sympatry with brook trout averaged 25% lower growth than in allopatry at all temperatures. In contrast, the presence of bull trout had a significant positive effect on brook trout growth, especially at temperatures (>53.6°F [12°C]), where brook trout growth in sympatry averaged 40% higher than in allopatry. The results of this study suggest that increases in water temperature tend to favor brook trout because of their higher temperature tolerance and preference range as well as their behavioral dominance (Nakano et al. 1998) when reared with bull trout. This competitive advantage would be most pronounce at water temperatures (>53.6°F [12°C]). In habitats where nonnative brook trout are present, cooler temperature criteria may be appropriate to protect native cutthroat trout and bull trout.

Does water temperature influence intraspecific competition between native salmonids?

The response of salmonids to temperature may depend on developmental stage, age, or body size. The effect of size on thermal response is poorly understood (Elliott 1981), but there is some evidence. For example, Meeuwig (2000) found the growth response of cutthroat trout to vary as a function of body size (range of mean body lengths among treatment groups = 29.5-121 mm). Larger cutthroat trout grew less at higher chronic temperatures (range of exposure = 53.6°F-75.2°F [12°C-24°C]). Potential competitive interactions within or among cohorts may therefore be affected by temperature. The exact nature of potential growth responses and implications for intraspecific competition has yet to be clearly defined in the literature, however.

The effect of temperature on the size and age of migrating fish may also affect intraspecific competition. For example, the effect of temperature on the age, size, and timing of emigration by Pacific salmon (e.g., Holtby 1988, Holtby et al. 1989) may affect the dynamics of competitive interactions among juveniles. A field study by Haas (unpublished manuscript) investigated the effect of small increases in water temperature on the competitive dominance of bull trout and rainbow trout in streams. This study found that bull trout density showed a decreasing trend whereas rainbow trout density showed an increasing trend with rising maximum stream temperatures above 55.4°F (13°C).

Another study by Northcote (1997) described a long-term program of research to understand competition between coastal cutthroat trout and Dolly varden char in lakes of British Columbia. One finding suggests that lower water temperatures in winter as well as summer influence the pattern of competitive interactions between native salmonids. In natural habitats, Northcote (1997) found that cutthroat trout used primarily epilimnetic habitats (shallower waters) while char used hypolimnetic (deeper) habitats. In lakes with experimentally introduced sympatric populations of trout and char, the same pattern was found. When only char were introduced into lakes, the fish showed a pronounced shift toward shallower water. Trout did not show a change in habitat use in the absence of char. This suggested that coastal cutthroat trout might exclude Dolly varden char from shallow habitats in lakes. Interestingly, the pattern of segregation was not observed in winter, when char frequently used shallow habitats. The seasonal pattern of segregation may reflect an influence of temperature. Temperatures are lower in winter, and char are known to have lower thermal optima than trout (e.g., McMahon et al. 1999). Alternatively, temperature may be indirectly affecting the distribution of char through an influence on preferred prey or another key resource. The specific influence of temperature has yet to be clearly demonstrated in this system, but it is clear that changes to thermal regimes may influence interspecific interactions.

Does water temperature influence interspecific competition between salmonids and other fishes?

In many streams of the Pacific Northwest, salmonids dominate in headwater fish assemblages but are replaced by other species in downstream areas. In particular, cyprinids tend to occupy similar habitats (e.g., midwater feeding) in warmer downstream habitats (see predation section above). This longitudinal variation in streams may be manifested as vertical stratification in lakes (e.g., salmonids in colder hypolimnion). Reeves et al. (1987) found water temperature influenced interactions between redside shiner (Cyprinidae: *Richardsonius balteatus*) and juvenile steelhead trout. In warmer (66.2°F -71.6°F [19°C-22°C]) water, redside shiners appeared to affect the growth of steelhead trout, and they used a wider variety of habitats in the presence of trout. Hillman (1991) found that water temperature influenced the interactions between redside shiner and juvenile chinook salmon. Shiners affected the distribution of juvenile chinook salmon in the laboratory when temperatures were warmer (66.2°F [18°C]-69.8°F [21°C]) but not at cold temperatures (53.6°F [12°C]-59°F [15°C]). Taniguchi et al. (1998) similarly studied competition between trout (brook trout and brown trout, Salmo trutta) and creek chub (Cyprinidae: *Semotilus atromaculatus*) and found the latter to be competitively dominant at higher (>68°F [20°C]) water temperatures. This pattern extended to longitudinal zonation of fish within streams. Less is known of the influence of temperature on behavioral interactions between nonnative, nonsalmonid fishes (e.g., many species of centrarchid fishes introduced for sport fisheries) and native salmonids. Because many of the introduced nonsalmonid fish are warm-water species, the capability of salmonids to compete or avoid predation should be reduced considerably as temperatures increase (see predation section above).

What is the role of cold-water refugia in salmonid habitat?

Cold-water refugia protect salmonids from extreme water temperatures and also permit them to behaviorally thermoregulate to conserve energy when water temperatures are suboptimal.

In stream reaches that have warmed above levels optimal for salmonids, fish persist by using cold-water refugia (Berman and Quinn 1991, Li et al. 1994, Neilson et al. 1994, McIntosh et al. 1995a, Torgersen et al. 1999, King 1937, Mantelman 1958, Gibson 1966, as cited in McCullough 1999). Extreme water temperatures are physiologically stressful to salmonids and can result in direct and indirect mortality of fish. Salmon behaviorally respond to stressfully high water temperatures by seeking cooler water. Suboptimal water temperatures may result in upstream migrations, or salmonids may explore local habitat for cold-water refugia. A study of steelhead in northern California streams found that age-1 steelhead moving into thermally stratified pools with cold groundwater input when temperatures in streams increased to 73.4°F (23°C) during the warmest part of the day (Nielsen et al. 1994). Snucins and Gunn (1995) reported a similar example of reactive behavioral thermoregulation by lake trout (*Salvelinus namaycush*). When water temperatures peaked during the summer in a warm isothermal lake, large lake trout began utilizing a cold-water seep. This behavior was unusual because the seep was located on the shoreline of the lake in shallow water, and lake trout prefer deep water.

During summer months, cold-water refugia likely contract streamflow and maximum stream temperatures. As cold-water refugia contract, competition between salmonids for this thermal resource may intensify, creating additional stress. Neilsen et al. (1994) found that age-0 and age-1 juvenile steelhead were less likely to use the cold-water refugia than older juveniles when oxygen levels were low. Low oxygen levels may have incurred high costs among younger steelhead, overshadowing the benefit of thermoregulatory behavior. This study also reports that fish using refugia were distinctly quiescent. A study of lake trout thermoregulatory behavior by Snucins and Gunn (1995) found that only the largest lake trout used the spatially limited refugia, raising the possibility that intraspecific competitive exclusion was limiting use of the refugia. Degradation or elimination of cold-water microhabitat from human activities may put some salmonid stocks at risk, because the fish can become marooned in pools or stream sections where the rising water temperatures result in either direct or indirect mortality.

How do salmonids use cold-water refugia?

Because salmonids, like most fish, take on the temperature of their surrounding environment, they control their body temperature behaviorally rather than physiologically. Behavioral thermoregulation requires a range of water temperatures from which fish can select those most appropriate to their immediate ecological and physiological needs. Research by Torgersen et al. (1999) and Berman and Quinn (1991) suggests that cold-water microhabitat is important to spring chinook salmon that oversummer in freshwater prior to spawning. The cold water protects the chinook from extreme summer water temperatures and reduces metabolic costs in freshwater prior to spawning, thereby improving spawner fitness. Brett's (1971) research on subyearling sockeye salmon in Babine Lake strongly suggests that juvenile sockeye used the vertical thermal variability of the lake to conserve energy for optimal growth.

Cold-water refugia may be particularly useful to salmonid populations that (1) reside at the southern end of their range, (2) inhabit marginally suitable habitat, and (3) undertake extensive migrations in the inland northwest. Research further suggests that the long-term persistence of some native salmonid populations in the Pacific Northwest may depend on the availability of cold-water refugia, especially during hot and dry climatic cycles.

Water temperatures affect the spatial distribution of salmonids along the stream course (Roper et al. 1994, Theurer et al. 1985), and, at finer spatial scales, salmonids use thermal refugia to avoid stressful temperatures (Gibson 1966, Kaya et al. 1977, Berman and Quinn 1991, Ebersol et al. 2000). Habitat and thermal diversity are especially high in alluvial floodplain river segments (Brown 1997, Cavallo 1997, Frissell et al. 1996), in part because in this geomorphic setting, hyporheic groundwater helps to create thermal refugia (Poole and Berman in press). Dams, however, often are built at constrictions in rivers just below large alluvial plains to maximize their reservoir storage capacity yet minimize their physical size. Dams therefore tend to inundate alluvial river segments (National Research Council 1996) where hyporheic buffering is prevalent (Coutant 1999, Poole and Berman in press), eliminating the cold-water refugia in these reaches. Other human land use activities such as logging, grazing, and farming can also reduce the abundance of thermal refugia in stream reaches (see Spatio-Temporal issue paper). Therefore, whether through inundation of alluvial river segments behind dams or simplification of in-stream habitat from land use activities, human activities have reduced the availability of thermal refugia within Pacific Northwest stream reaches. This loss of thermal refugia may create higher levels of thermal stress during the warmest months of the year (Ebersol et al. 2000) or during migration through warm river segments.

Conclusion

The family Salmonidae is a group of cold-water-adapted fish. Three genera of salmonid predominate in the Pacific Northwest: (1) *Salvelinus spp*.-(char), (2) *Oncorhynchus spp*.-(trout and salmon), and (3) *Prosopium spp*.-(whitefish). Native salmonids have dominated the freshwaters of the Pacific Northwest because historically water temperatures supported their ecological and physiological requirements. To protect and restore native Pacific Northwest salmonids will require protecting and restoring the natural thermal characteristics of their environment.

Human activities have altered the thermal characteristics of rivers and streams in the Pacific Northwest. Logging, farming, and hydropower development have (1) changed the natural annual thermograph of rivers and steams, disrupting adaptive life history strategies of salmonid populations; (2) increased summer maximum temperatures, which may interfere with migrations and result in feeding cessation, thermal stress, increased predation pressure, and competitive interaction that alter the distribution and abundance of native salmonids; and (3) reduced or eliminated cold-water refugia, which is an important source of thermal heterogeneity in aquatic systems, providing protection from thermally stressful maximum water temperatures and crucial habitat diversity for behavioral thermoregulation. From a behavioral perspective, the following considerations are important in developing water temperature criteria protective of native Pacific Northwest salmonids:

1. Anadromous Pacific salmon and steelhead display local adaptation to predictable annual thermal cycles.

2. The distribution and behavioral aspects of juvenile life history patterns such as rearing characteristics, length of freshwater rearing, and emigration timing of each anadromous species are affected by water temperature.

3. Migratory behavior of juvenile anadromous salmonids is influenced by water temperature. Gill ATPase, an enzyme that is crucial for seawater osmoregulation, is sensitive to elevated water temperatures. Decreasing gill ATPase activity is associated with loss of migratory behavior in anadromous juvenile salmonids. For successful smoltification in anadromous salmonids, research suggests spring water temperatures must not exceed 53.6°F (12°C) (Zaugg and Wagner 1973). Summer water temperatures for subyearling fall chinook salmon emigration suggest that fall emigrants may be more successful at higher water temperatures than spring emigrants.

4. Native char populations are the most stenothermic salmonids found in Pacific Northwest freshwaters. Char prefer water temperatures near 44.6°F + 9°F (7°C + 5°C) (Reiser and Bjornn 1979, Bonneau and Scarnecchia 1996, Spence et al. 1996).

5. Water temperatures of (>73.4°F [23°C]) for even short periods of time (hours) result in movement into cold water refugia by Pacific salmon and trout (Neilsen et al. 1991). Colder water temperatures are required for adult migration.

6. Mean daily water temperatures (>69.8°F [21°C]) decrease or eliminate feeding behavior by Pacific salmon and trout (Hokansen et al. 1977).

7. Larvae and juvenile salmonids require a variety of water temperatures for behavioral thermoregulation to optimize physiological functioning. A certain amount of thermal diversity is important and commonly available in undisturbed naturally occurring rearing habitat. Water temperature criteria can play a central role in the protection and rehabilitation of rearing habitat by protecting and promoting restoration of cold-water refugia, and by setting numeric criteria for water temperature based on the optimal temperatures that drive behavioral thermoregulation.

8. Potamodromous salmonids display a wide array of freshwater migratory strategies that support different life history stages and facilitate genetic exchange between isolated populations, thus forming a metapopulation. Fluvial–afluvial migration (from streams to rivers) is one migratory pattern seen in bull trout. Cold-water refugia contributes to habitat connectivity and may help support bull trout migrations.

9. Higher seasonal water temperatures and longer periods of warm water in aquatic systems increase the feeding rate of predatory fish species that prey on juvenile salmonids.

10. The preference temperatures of juvenile char, trout, and salmon suggest that interspecific competition plays a role in the distribution and phylogenetically derived thermal preferences of these fish.

11. Water temperature may play a crucial role in determining whether a native salmonid is displaced by an introduced salmonid. Native salmonids may be better able to compete at colder water temperatures with introduced salmonids such as the brook trout.

12. Many of the introduced fishes in the Pacific Northwest are cool- and warm-water fish, such as smallmouth bass and walleye, that do well in the impounded reservoirs characterized by reduced water flow, moderate winter temperatures, and warmer water temperatures during the summer and fall. These characteristics do not favor salmonid species. Native fish species, including salmonids, are no longer the dominant species in many high-order reaches of the lower Columbia River basin (Li et al. 1987). Increased water temperatures in reservoirs are an important determinant in this succession, although lack of reservoir flow and the resulting loss of the riverine ecosystem also contribute significantly to the problem.

13. Existing cold-water refugia may be important to salmonids migrating through main-stem rivers and large tributaries. Cold-water refugia are also important to spring migrants, such as chinook salmon, because refugia provide cold-water holding habitat over the warmest part of the summer prior to spawning.

14. Loss of thermal refugia from inundation of alluvial river segments behind dams may have important implications for migrating juvenile and adult salmonids, resulting in potentially higher levels of thermal stress during the warmest months of the year (Ebersol et al. 2000) or during migration through warm river segments.

Literature Cited

Adams SB. 1999. Peer review of bull trout temperature criteria. Report for U.S. Environmental Protection Agency, Seattle, WA.

Adkison MD. 1995. Populations differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? Can J Fish Aquat Sci 52:2762-2777.

Andrew FJ, Geen GH. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Int Pacif Salmon Fish Comm Bull XI. 259 pp.

Baxter CV, Hauer FR. 2000. Geomorphology, interaction of hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*): A multi-scale, hierarchical approach. Can J Fish Aquat Sci 57:1470-1481.

Becker CD, Fujihara MP. 1978. The bacterial pathogen *Flexibacter columnaris* and its epizootiology among Columbia River fish. A review and synthesis. Am Fish Soc Monogr 2: 92 pp.

Begon M, Mortimer M. 1986. Population ecology: A unified study of animals and plants. London: Blackwell Scientific Publications.

Behnke RJ. 1992. Native trout of western North America. Monograph 6. American Fisheries Society, Bethesda, MD.

Beitinger TL, Fitzpatrick LC. 1979. Physiological and ecological correlates of preferred temperature in fish. Am Zool 19:319-329.

Bell MC. 1991. Fisheries handbook of engineering requirements and biological criteria. U.S. Army Corps of Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, OR.

Berman CH, Quinn TP. 1991. Behavioral thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. J Fish Biol 39:301-312.

Beschta RL, Bilby RE, Brown GW, Holtby LB, Hofstra TD. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. In: Salo EO, Cundy TW, eds. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle. Contribution No. 57. Proceedings of a Symposium held at University of Washington, February 12-14, 1986, pp. 191-231.

Bjornn TC. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Trans Am Fish Soc 100:423-438.

Bjornn TC, Reiser DW. 1991. Habitat requirements of anadromous salmonids. Influence of forest and rangeland management on salmonid fishes and their habitats. Am Fish Soc Special Publ 19:83-138.

Bonneau JL, Scarnecchia DL. 1996. Distribution of juvenile bull trout in a thermal gradient of a plunge pool in Granite Creek, Idaho. Trans Am Fish Soc 125:628-630.

Brannon EL. 1987. Mechanisms stabilizing salmonid fry emergence timing. In: Smith HD, Margolis L, Wood CC, eds. Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can Spec Publ Fish Aquat Sci 96: 120-124.

Breder CM, Rosen DE. 1966. Modes of reproduction in fishes. Garden City, NY: Natural History Press.

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

Brett JR. 1995. Energetics. In: Groot C, Margolis L, Clarke WC, eds. Physiological ecology of Pacific salmon. Vancouver: UBC Press, pp. 1-68.

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

Brett JR, Higgs DA. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J Fish Res Bd Can 27:1767-1779.

Brown CJP. 1952. Spawning habit and early development of the mountain whitefish, *Prosopium williamsoni*, in Montana. Copeia 1952:109-113.

Brown AG. 1997. Biogeomorphology and diversity in multiple-channel river systems. Global Ecol Biogeogr Lett 6:179-185.

Brown LG. 1972. Early life history of the mountain whitefish, *Prosopium williamsoni* (Girard), in the Logan River, Utah. MS Thesis, Utah State University, Logan, UT. 40 pp.

Brown RS, MacKay WC. 1995. Spawning ecology of cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta. Can J Fish Aquat Sci 52:983-992.

Bruce PG, Starr PJ. 1985. Fisheries resources potential of Williston Reservoir and its tributary streams. Volume II. Fisheries resources potential of Williston Lake tributaries—a preliminary overview. BC Ministry of Environment, Fisheries Branch, Fisheries Technical Circular Number 69.

Burger CV, Wilmot RL, Wangaard DB. 1985. Comparison of spawning areas and times for two runs of chinook salmon (*Oncorhynchus tshawytscha*) in the Kenai River, Alaska. Can J Fish Aquat Sci 42:693-700.

Cavallo BJ. 1997. Floodplain habitat heterogeneity and the distribution, abundance and behavior of fishes and amphibians in the Middle Fork Flathead River Basin, Montana. Division of Biological Sciences, University of Montana, Missoula. 128 pp.

Cederholm CJ, Scarlett WJ. 1981. Seasonal immigrations of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977-1981. In: Brannon EL, Salo EO, eds. Proceedings of the Salmon and Trout Migratory Behavior Symposium. School of Fisheries, University of Washington, Seattle. pp. 98-110.

Cherry DS, Dickson, KL, Cairns J. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J Fish Res Bd Can 34:239-246.

Cherry, DS, Dickson KL, Cairns J. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. J Fish Res Bd Can 32(4):485-491.

Coutant CC. 1972a. Effect of thermal shock on vulnerability to predation in juvenile salmonids. I. Single shock temperature. AEC Research and Development Report. Battelle Pacific Northwest Laboratories. BNWL-1521.

Coutant CC. 1972b. Effect of thermal shock on vulnerability to predation in juvenile salmonids. II. A dose response by rainbow trout to three shock temperatures. AEC Research and Development Report. Battelle Pacific Northwest Laboratories. BNWL-1519.

Coutant CC. 1999. Perspectives on temperature in the Pacific Northwest's fresh waters. Environmental Sciences Division Publication #4849 (ORNL/TM-1999/44). Oak Ridge National Laboratory, Oak Ridge, TN.

Crawshaw LI, Wollmuth LP, O'Connor CS, Rausch RN, Simpson L. 1990. Body temperature regulation in vertebrates: Comparative aspects and neuronal elements. Schonbaum E, Lomax P, eds. Thermoregulation: Physiology and biochemistry. New York: Pergamon Press.

De Staso JD, Rahel FJ. 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 BR, Vineyard GL. 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.

Ebersol JL, Liss WJ, Frissell CA. In Press. Relationship between stream temperature, thermal refugia, and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecol Freshwater Fish.

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

Elliot JM. 1981. Some aspects of thermal stress on freshwater teleosts. In: Pickering AD, ed. Stress and fish. San Diego, CA: Academic Press, pp. 209-245.

Fry FEJ. 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser., No. 55. Pub Ont Fish Res Lab, No. 68. 62 pp.

Fry FEJ. 1971. The effect of environmental factors on the physiology of fish. In: Hoar WS, Randell DJ, eds. Fish physiology. Vol. VI: Environmental relations and behavior. San Diego, CA: Academic Press, pp. 1-98.

Foerster RE. 1937. The relation of temperature to the seaward migration of young sockeye salmon (*Oncorhynchus nerka*). J Fish Biol Bd Can 3:421-438.

Fraley J, Shepard B. 1989. Life history, ecology, and population status of migratory bull trout (*Salvelinus confluentus*) in the Flathead Lake and River system, Montana. Northwest Sci 63:133-143.

Fraser NHC, Metcalfe NE, Thorpe JE. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proc R Soc Lond B:135-139.

Frissell CA, Ebersol JL, Liss WJ, Cavallo BJ, Poole GC, Stanford JA. 1996. Potential effects of climate change on thermal complexity and biotic integrity of streams: Seasonal intrusion of non-native fishes. U.S. Environmental Protection Agency, Duluth, MN. #CR-822019-01-0.

Garside ET, Tait JS. 1958. Preferred temperature of rainbow trout (*Salmo gairdneri*, Richardson) and its unusual relationship to acclimation temperature. Can J Zool 36:563-567.

Geotz FA. 1989. Biology of the bull trout *Salvelinus confluentus*: A literature review. U.S. Forest Service, Willamette National Forest, Eugene, OR.

Gibson RJ. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. J Fish Res Bd Can 23:1977-1980.

Gilhousen P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. Int Pac Salmon Fish Comm Bull XXII: 51 pp.

Giorgi AE, Miller DR, Sandford BP. 1994. Migratory characteristics of juvenile ocean-type chinook salmon, *Oncorhynchus tshawytscha*, in John Day Reservoir on the Columbia River. US Nat Mar Fish Serv Fish Bull 92:872-879.

Godfrey H, Hourston WR, Stokes JW, Withler FC. 1954. Effects of a rockslide on Babine River salmon. Bull Fish Res Bd Can No. 101.

Grant JWA, Steingrímsson SÓ, Keeley ER, Cunjak RA. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. Can J Fish Aquat Sci 55 (Suppl 1):181-190.

Gray GA, Rondorf DW. 1986. Predation on juvenile salmonids in Columbia River reservoirs. In: Hall GE, Van Den Avyle MJ, eds. Reservoir fisheries management: Strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, MD.

Groot C, Margolis L, eds. 1991. Pacific salmon life histories. Vancouver: University of British Columbia Press, 564 pp.

Haas GR. 2000. Unpublished manuscript. Maximum temperature and habitat mediated interactions and preferences of bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*).

Hammel HT. 1968. Regulation of internal body temperature. Ann Rev Physiol 30:641-710.

Hazel JR, Prosser CL. 1974. Molecular mechanisms of temperature compensation in poikilotherms. Physiol Rev 54:620-677.

Hendry AP, Hensleigh JE, Reisenbichler RR. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. Can J Fish Aquat Sci 55:1387-1394.

Hicks M. 1999. Evaluating standards for protecting aquatic life in Washington's surface water quality standards. Preliminary draft of draft discussion paper (vol. 1) and draft supplementary appendix (vol. 2). WA Dept of Ecology, Water Quality Program, Olympia, WA.

Higgs DA, MacDonald JS, Levings CD, Dosanjh BS. 1995. Nutrition and feeding habits in relation to life history stage. In: Groot C, Margolis L, Clarke WC, eds. Physiological ecology of Pacific salmon. Vancouver: University of British Columbia Press, pp. 159-316.

Hildebrand L, English K. 1991. Lower Columbia River fisheries inventory. 1990 Studies. Volume I Main report. Submitted to B.C. Hydro Environmental Resources by R.L. & L. Environmental Services, Ltd., Edmonton, Alberta and LGL Ltd., Sydney, BC.

Hillman TW. 1991. The effect of temperature on the spatial interaction of juvenile chinook salmon and the redside shiner and their morphological differences. PhD dissertation. Idaho State University, Pocatello, ID. 90 pp.

Hokanson KEF, Kleiner CF, Thorslund TW. 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 BL. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 45:502-515.

Holtby LB, McMahon TE, Scrivener JC. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon (*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Can J Fish Aquat Sci 46:1396-1405.

Horak OL, Tanner HA. 1964. The use of vertical gill nets in studying fish depth distribution, Horsetooth Reservoir, Colorado. Trans Am Fish Soc 93:137-145.

Idler DR, Clemens WA. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Progress Report, Int. Pac. Salmon Comm. 80 pp.

Independent Scientific Group. 1996. Return to the river: Restoration of salmonid fishes in the Columbia River ecosystem. Prepublication copy.

Inhat JM, Bulkley RV. 1984. Influence of acclimation temperature and season on acute temperature preference of adult mountain whitefish, *Prosopium williamsoni*. Environ Biol Fish 11(1):29-40.

Jakober MJ, McMahon TE, Thurow RF, Clancy CG. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Trans Am Fish Soc 127:223-235.

James PW, Sexauer HM. 1997. Spawning behavior, spawning habitat and alternative mating strategies in an adfluvial population of Bull trout. In: Mackay WC, Brewin MK, Monita M, eds. Friends of the bull trout conference proceedings. Bull Trout Task Force (Alberta), c/o Trout Unlimited Canada, Calgary.

Javaid MY, Anderson JM. 1967. Thermal acclimation and temperature selection in Atlantic salmon, *Salmo salar*, and rainbow trout, *S. gairdneri*. J Fish Res Bd Can 24:1507-1513.

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

Kaya CM, Kaeding LR, Burkhalter DE. 1977. Use of a cold water refuge by rainbow and brown trout in a geothermally heated stream. Progressive Fish-Culturist 39:37-39.

Kelsch SW, Neill WH. 1990. Temperature preference versus acclimation in fishes: Selection for changing metabolic optima. Trans Am Fish Soc 119:601-610.

Kilgour DM, McCauley RW. 1986. Reconciling the two methods of measuring upper lethal temperature in fishes. Environ Biol Fish 17(4):281-290.

King W. 1937. Notes on the distribution of native speckled and rainbow trout in the streams of the Great Smoky Mountains National Park. J Tenn Acad Sci 12:351-361.

Kitchell JF, Stewart DJ, Weininger D. 1977. Applications of bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J Fish Res Bd Can 34:1922-1935.

Kluger MJ. 1978. The evolution and adaptive value of fever. Am Sci 66:38-43.

Konecki JT, Woody CA, Quinn TP. 1995. Critical thermal maxima of coho salmon (*Oncorhynchus kisutch*) fry under field and laboratory acclimation regimes. Can J Zool 73:993-996.

Konecki JT, Woody CA, Quinn TP. 1995. Temperature preference in two populations of juvenile coho salmon, *Oncorhynchus kisutch*. Environ Biol Fish 44:417-421.

Kraemer C. 1994. Some observations on the life history and behavior of the native char, Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) of the north Puget Sound region. Draft report. Washington State Department of Fish and Wildlife, Mill Creek, WA.

Kwain W, McCauley RW. 1978. Effects of age and overhead illumination on temperatures preferred by underyearling rainbow trout, *Salmo gairdneri*, in a vertical temperature gradient. J Fish Res Bd Can 35:1430-1433.

LeBrasseur RJ, McAllister CD, Barraclough WE, Kennedy OD, Manzer J, Robinson D, Stephens K. 1978. Enhancement of sockeye salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: Summary report. J Fish Res Bd Can 35:1580-1596.

Li HW, Lamberti GA, Pearsons TN, Tait CK, Li JL, Buckhouse JC. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Trans Am Fish Soc 123:627-640.

Li HW, Shreck CB, Bond CE, Rexstad E. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. In: Matthews WJ, Heins DC, eds. Community and evolutionary ecology of North American stream fishes. Norman, OK: University of Oklahoma Press, pp.193-202.

Magnuson JJ, Crowder LB, Medvick PA. 1979. Temperature as an ecological resource. Am Zool 19:331-343.

Major RL, Mighel JL. 1967. Influence of Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of sockeye salmon. Fish Bull 66(1):131-147.

Mantelman II. 1958. Distribution of the young of certain species of fish in temperature gradients. Izv Vses Nauchno-Issled Inst Ozern Rechn Rybn Khoz 47:3-61. (Translated from the Russian by Fish Res Board Can Transl Ser 257, 1960.)

Maule AG, Horton HF. 1985. Probable causes of the rapid growth and high fecundity of walleye, *Stizostedion vitreum vitreum*, in the mid-Columbia River. Fish Bull 83(4):701-706.

McCauley RW, Elliot JR, Read ALA. 1977. Influence of acclimation temperature on preferred temperature of rainbow trout, *Salmo gairdneri*. Trans Am Fish Soc 106:362-365.

McCauley RW, Huggins NW. 1979. Ontogenetic and non-thermal seasonal effects on thermal preferenda of fish. Am Zool 19:267-271.

McCauley RW, Pond WL. 1971. Temperature selection of rainbow trout (*Salmo gairdneri*) fingerlings in vertical and horizontal gradients. J Fish Res Bd Can 28:1801-1804.

McCullough DA. 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. Report to the U.S. Environmental Protection Agency, Region 10, Seattle, WA.

McIntosh BA, Price DM, Torgersen CE, Li HW. 1995. Distribution, habitat utilization, movement patterns, and the use of thermal refugia by spring chinook in the Grande Ronde, Imnaha, and John Day Basins. Progress report to the Bonneville Power Administration, Project No. 88-108, FY 1995.

McMahon T, Zale A, Selong J, Barrows R. 1999. Growth and survival temperature criteria for bull trout. Annual report to National Council for Air and Stream Improvement. Bozeman, MT.

Meeuwig MH. 2000. Effects of constant and cyclical thermal regimes on growth, feeding, and swimming performance of cutthroat trout of variable sizes. MS thesis, University of Nevada, Reno.

Mesa MG. 1994. Effects of multiple acute stressors on the predation avoidance ability and physiology of juvenile chinook salmon. Trans Am Fish Soc 123:786-793.

Mesa MG, Poe TP, Maule AG, Shreck CB. 1998. Vulnerability to predation and physiological stress responses in juvenile salmon (*Oncorhynchus tshawytscha*) experimentally infected with *Renibacterium salmoninarum*. Can J Fish Aquat Sci 55:1599-1606.

Nakano S, Fausch KD, Furukawa-Tanaka T, Maekawa K, Kawanabe H. 1998. Resource utilization by bull char and cutthroat trout in a Montana stream in Montana, USA. Jap J Ichtyol 39:211-217.

National Research Council. 1996. Upstream: Salmon and society in the Pacific Northwest. Washington, DC: National Academy Press. 452 pp.

Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4-21.

Neill WH. 1979. Mechanisms of fish distribution in heterothermal environments. Am Zool 19:305-317.

Neilsen JL, Lisle TE, Ozaki V. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Trans Am Fish Soc 23:613-626.

NMFS (National Marine Fisheries Service). 1998. Progress of species status reviews in NMFS Northwest Region. File 1 pg 898.pfd at NOAA website http://www.noaa.gov.

NMFS Chinook Status Review: Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, Grant WS, Waknitz FW, Neely K, Lindley ST, Waples RS. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, NOAA Tech Memo. NMFS-NWFSC-35. 443 pp.

NMFS Coho Status Review: Weitkamp LA, Wainwright TC, Bryant GJ, Milner GB, Teel DJ, Kope RG, Waples RS. Status review of coho salmon from Washington, Oregon, and California. U.S. Department of Commerce, NOAA Tech.

Northcote TG. 1997. Potamodromy in Salmonidae—Living and moving in the fast lane. N Am J Fish Manage 17:1029-1045.

ODEQ (Oregon Department of Environmental Quality). 1995. 1992-1994 Water quality standards review. Department of Environmental Quality, Standards and Assessment Section. Final issues papers. Portland, OR.

Olson PA, Foster RF. 1955. Temperature tolerance of eggs and young of Columbia River chinook salmon. Trans Am Fish Soc 85:203-207.

Petersen J, Barfoot C, Sauter S, Gadomski D, Connolly P, Poe T. 2000. Predicting the effects of dam breaching in the lower Snake River on predators of juvenile salmon. Report prepared for U.S. Army Corps of Engineers, Walla Walla District, Walla Walla, WA.

Petersen JH, DeAngelis DL. 1992. Functional response and capture timing in an individual-based model: Predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. Can J Fish Aquat Sci 49:2551-2565.

Pettit SW, Wallace RL. 1975. Age, growth, and movement of mountain whitefish *Prosopium williamsoni* (Girard), in the North Fork Clearwater River, Idaho. Trans Am Fish Soc 1:68-76.

Pianka ER. 1994. Evolutionary ecology. New York: Harper Collins College Publishers, pp. 82-120.

Poe TP, Hansel HC, Vigg S, Palmer DE, Prendergast LA. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Trans Am Fish Soc 120(4):405-419.

Poe TP, Shively RS, Tabor RA. 1994. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake Rivers. In: Stouder D, Fresh K, Feller R, eds. Theory and application in fish feeding ecology. Columbia, SC: University of SC Press, pp. 347-360.

Poole GC, Berman CH. In Press. An ecological perspective on in-stream temperature: Natural heat dynamics and mechanisms of human-caused thermal degradation. Ecol Manage.

Pratt KL. 1992. A review of bull trout life history. In: Howell P, Buchanan D, eds. Proceedings of the Gearhart Mountain Bull Trout Workshop. Oregon Chapter of the American Fisheries Society.

Quinn TP, Adams DJ. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77(4):1151-1162.

Raleigh RF, Miller WF, Nelson PC. 1986. Habitat suitability index models and instream flow suitability curves: Chinook salmon. US Fish Wildlife Serv Biol Rep 82(10.122). 64 pp.

Reeves GH, Everest JD, Hall JD. 1987. Interaction between 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.

Reiman BE, Chandler GL. 1999. Empirical evaluation of temperature effects on bull trout distribution in the Northwest. Final Report, Contract No. 12957242-01-0, U.S. Environmental Protection Agency, Boise, ID.

Reiser DW, Bjornn TC. 1979. Habitat requirements of anadromous salmonids. Gen Tech Rep PNW96. USDA Forest Service. Pacific Northwest Forest and Range Experiment Station. Portland, OR. 54 pp.

Reutter JM, Herdendorf CE. 1974. Laboratory estimates of the seasonal final temperature preferenda of some Lake Erie fish. Proc 17th Conf Great Lakes Res 1974:59-67.

Reynolds WW. 1977a. Temperature as a proximate factor in orientation behavior. J Fish Res Bd Can 34:734-739.

Reynolds WW. 1977b. Fever and antipyresis in the bluegill sunfish, *Lepomis macrochirus.* Comp Biochem Physiol 57C (2):165-167.

Reynolds WW, Casterlin ME. 1979. Behavioral thermoregulation and the “final preferendum” paradigm. Am Zool 19:211-224.

Reynolds WW, Casterlin ME, Covert JB. 1976. Behavioral fever in teleost fishes. Nature 259:41-42.

Reynolds WW, Covert JB. 1977. Behavioral fever in aquatic ectothermic vertebrates. In: Drugs, biogenic amines and body temperature. Proceedings of the 3rd International Symposium on Pharmacological Thermoregulation, Banff, Alberta, 14-17 Sept 1976 (Karger, Basel).

Roper BB, Scarnecchia DL, Marr TJL. 1994. Summer distribution of and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Trans Am Fish Soc 123:298-308.

Royce WF. 1962. Pink salmon fluctuations in Alaska. In: Wilimovsky NJ, ed. Symposium on Pink Salmon. H.R. MacMillan Lectures in Fisheries. Institute of Fisheries, University of British Columbia, Vancouver, BC. pp. 15-23.

Saffel PD, Scarnecchia DL. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. Northwest Sci 69:304-317.

Sauter ST. 1996. Thermal preference of spring and fall chinook salmon during smoltification. MS thesis. Portland State University, Portland, OR.

Schroeter RE. 1998. Segregation of stream-dwelling Lahontan cutthroat trout and brook trout: Patterns of occurrence and mechanisms for displacement. MS thesis, University of Nevada, Reno.

Scrivener JC, Brown TG, Andersen BC. 1994. Juvenile chinook salmon (*Oncorhynchus tshawytscha*) utilization of Hawks Creek, a small and nonnatal tributary of the upper Fraser River. Can J Fish Aquat Sci 51:1139-1146.

Sheridan WL. 1962. Relation of stream temperatures to timing of pink salmon escapements in southeast Alaska. pp. 87-102. In: Wilimovsky NJ, ed. Symposium on pink salmon. H.R. Macmillan Lectures in Fisheries, University of British Columbia. Vancouver, British Columbia, Canada.

Snucins EJ, Gunn JM. 1995. Coping with a warm environment: Behavioral thermoregulation by lake trout. Trans Am Fish Soc 124:118-123.

Spence BC, Lomnicky GA, Hughes RM, Novitzki RP. 1996. An ecosystem approach to salmonid conservation. ManTech Environ Res Serv Corp, Corvallis, OR. TR-4501-96-6057.

Spigarelli SA. 1975. Behavioral responses of Lake Michigan fishes to a nuclear power plant discharge. In: Environmental effects of cooling systems at nuclear power plants. International Atomic Energy Agency (IAEA), Vienna. pp. 479-498.

Swanberg TR. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Trans Am Fish Soc 126:735-746.

Tabor RA, Shively RS, Poe TP. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. N Am J Fish Manage 13:831-838.

Taniguchi R, Rahel FJ, Novinger DC, Gerow KG. 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 FD, Lines I, Nelson T. 1985. Interaction between riparian vegetation, water temperature, and salmonid habitat in the Tucannon River. Water Res Bull 21:53-64.

Thompson GE, Davies RW. 1976. Observations on the age, growth, reproduction, and feeding of mountain whitefish (*Prosopium williamsoni*) in the Sheep River, Alberta. Trans Am Fish Soc 105:208-219.

Torgersen CE, Price DM, Li HW, McIntosh BA. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecol Appl 9:301-309.

Trotter P. 1989. Coastal cutthroat trout: A life history compendium. Trans Am Fish Soc 118:463-473.

Vigg S, Poe TP, Prendergast LA, Hansel H. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Trans Am Fish Soc 120:421-438.

Withers PC. 1992. Comparative animal physiology. New York: Saunders College Publishing, pp. 122-191.

Wydoski RS, Whitney RR. 1979. Inland fishes of Washington. Seattle: University of Washington Press.

Young MK. 1995. Colorado River cutthroat trout. In: Young MK, ed. Conservation assessment for inland cutthroat trout. USDA Forest Service, Gen. Tech. Report RM-GTR-256. pp. 16-23.

Zaugg WS, Wagner HH. 1973. Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmo gairdneri*): Influence of photoperiod and temperature. Comp Biochem Physiol 45B:955-965.

Zimmerman MP, Parker RM. 1995. Relative density and distribution of smallmouth bass, channel catfish, and walleye in the lower Columbia and Snake rivers. Northwest Sci 69:19-28.