



# Technical Synthesis

## Scientific Issues Relating to Temperature Criteria for Salmon, Trout, and Char Native to the Pacific Northwest

**A summary report submitted to the Policy  
Workgroup of the EPA Region 10 Water  
Temperature Criteria Guidance Project**

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## Preface

This document is a product of a Technical Workgroup established by the U.S. Environmental Protection Agency (EPA) to assist them in developing temperature criteria guidance for EPA Region 10. The purpose of the EPA guidance is to help Pacific Northwest states and tribes adopt water temperature standards that:

- Meet the biological requirements of native salmonids (Pacific salmon, trout, and char) species for survival and recovery pursuant to the Endangered Species Act (ESA).
- Provide for the protection and propagation of salmonids under the Clean Water Act (CWA).
- Meet the salmonid rebuilding needs of federal trust responsibilities with treaty tribes.

The project focuses on salmonids because the ESA, CWA, and tribal treaties all address the protection and/or restoration of salmonids. Additionally, this approach is scientifically sound since salmonids can also be viewed as “umbrella species” that are indicators of the biological integrity of aquatic ecosystems in the Pacific Northwest. Where salmonid populations are healthy, habitat conditions are apt to be suitable for other native aquatic species as well.

To provide a scientific foundation for the project, the Technical Workgroup developed five technical summaries on the major physical and biological considerations for developing water temperature standards:

1. thermal effects on salmonid physiology,
2. thermal effects on salmonid behavior,
3. interactions between multiple stressors – thermal and other – affecting salmonids,
4. thermal influences on salmonid distribution, and
5. spatial and temporal variation in patterns of stream temperature.

Each of these summary papers is available on the internet under the “Water” link at the EPA’s Region 10 website (<http://www.epa.gov/region10/>) or by contacting EPA Regional Office in Seattle, WA.

This document has two purposes. First, it attempts to concisely synthesize the findings of the technical summaries. Second, it outlines several conclusions drawn by the Technical Workgroup based on the literature review included in the technical summaries. Therefore, this document takes the first step beyond the technical summaries and begins to discuss the implications of the technical findings for water quality criteria for temperature. The conclusions outlined toward the end of this document represent the collective *interpretation* of the scientific literature by the Technical Workgroup rather than “facts” established by experimentation. Further, a panel of experts on salmonid biology and stream temperature provided external, independent peer review of the technical summaries, this synthesis, and its conclusions. Thus, this synthesis and its conclusions are important in that they represent broad consensus of the members of the Technical Workgroup and concurrence of the majority of the scientific review panel.

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## Introduction

Water temperature affects the distribution, health, and survival of native salmonids (salmon, trout, and char) and other aquatic organisms by influencing their physiology and behavior. Since salmonids are ectothermic (cold-blooded), temporally and spatially heterogeneous thermal conditions are a resource that fish utilize through behavioral means to control body temperature within narrow limits (see Behavioral technical summary). Water temperatures, along with adequate flow, food, oxygen, shelter, and other resources, determine habitat suitability for each species. While community composition is shaped by numerous habitat components, each of which can provide optimal or suboptimal conditions, temperature is an important aspect of habitat quality. Further, temperature acts synergistically with other environmental stressors, thereby affecting the ability of individual fish to survive and reproduce, and affecting salmonid population viability.

Water that is too warm can cause direct mortality of salmonids. In addition, temperature influences the abundance and well-being of organisms by controlling their metabolic processes. While lethal temperatures occur in nature and can be locally problematic, temperatures in the range where sublethal effects occur are widespread and may have the greatest effect on the overall well-being and patterns of occurrence of our native fish populations. As stream temperatures and patterns of heating and cooling (the “thermal regime”) change due to land management or other impacts, salmonid fishes may be exposed to temperatures outside their physiologic optimum, and fish communities may be altered accordingly (see Distribution technical summary).

Salmonids have physiological (see Physiology technical summary) and behavioral (see Behavior technical summary) adaptations to temperature dynamics that once allowed them to thrive in the ecologically-diverse rivers and streams of the Pacific Northwest, even though stream temperatures have never been optimal in all places and at all times (see Spatio-temporal technical summary). However, where human-caused changes to stream thermal

regimes have occurred, they have contributed to degradation of habitat conditions that prevent salmonids from continuing to flourish. While many factors contribute to the decline in native salmonid populations, alteration of temperature regimes has played an important role where it has occurred, both directly and through synergistic interaction with other factors such as habitat loss and disease.

## Project Background

Many laws and regulations govern the use of water in the United States. In the Pacific Northwest, two federal statutes play key roles: the Clean Water Act (CWA) and the Endangered Species Act (ESA). The CWA provides the statutory basis for water quality standards programs and defines broad water quality goals. The ESA provides a means whereby the ecosystems upon which threatened and endangered species depend may be conserved, and to provide a program for the conservation of such species. Under the ESA, all federal departments are required to conserve threatened and endangered species. Further, under federal treaties with the Columbia River tribes, the federal trust responsibility imposes an obligation on all federal agencies to protect and restore fish and their habitats as necessary to fulfill the intent of the treaties.

The ESA is an important statute in the regulation of water quality, because threatened and endangered salmonids depend on cold, clean water, and because federal agencies are required to cooperate with state and local agencies to resolve water resource issues in concert with conservation of endangered species. The issues of clean water (CWA) and species recovery (ESA) are widespread. Many major watersheds in the region contain streams listed as “water quality limited” due to temperature, and most are important to the recovery of at least one listed salmonid species. Both the CWA and ESA should therefore play complementary roles in the recovery of salmonids in the Pacific Northwest.

### *Clean Water Act*

A water quality standard defines the water quality goals for a water body by designating the use or uses

to be made of the water, by setting “criteria” necessary to protect the uses, and by preventing or limiting degradation of water quality through antidegradation provisions. Under section 304(a) of the CWA, EPA publishes water quality criteria that reflect available scientific information on the levels of specific chemicals or parameters for the protection of aquatic life or human health. These criteria are intended to provide protection for all surface waters on a national basis, and may be used by states as a basis for developing enforceable water quality criteria as part of their standards. The criteria are provided as guidance, to assist states and tribes in setting water quality standards.

The foundation for EPA’s national criteria for temperature was established by the National Academies of Sciences and Engineering in a review for EPA, *Water Quality Criteria 1972: Report to the U.S. Environmental Protection Agency*. The report focuses on preferred methods and procedures for judging thermal requirements rather than on providing specific numerical values for various species of concern. The report suggested that species and life stages be protected from several levels of negative effects of increased temperature: lethal effects, sublethal effects, habitat exclusion, and reproductive continuity. The report also focused on the importance of establishing upper limits for a maximum weekly average temperature, and on establishing a time-dependent maximum temperature for short exposures. The work was based on the physiological requirements of species and did not take into account the physical aspects of stream or lake systems. EPA later augmented this work and established numeric temperature criteria for certain species including coho and sockeye salmon (EPA 1976).

EPA’s 1986 *Quality Criteria for Water* report, as updated in *National Recommended Water Quality Criteria* (EPA 1999), contains summaries of all contaminants and conditions for which EPA has developed criteria recommendations. The criteria serve as guidance to assist states and tribes in adopting water quality standards, as required by

section 303(c) of the CWA. Once adopted, states and tribes are to submit the standards to EPA for review and approval or disapproval. EPA reviews the standards to determine compliance with the CWA and implementing regulations and to ensure the criteria associated with the standard are protective of the designated beneficial uses.

#### *Endangered Species Act*

When a state proposes a water quality standard that may affect species listed as threatened or endangered populations under the ESA, EPA must consult with the U.S. Fish and Wildlife Service (USFWS) and/or the National Marine Fisheries Service (NMFS) prior to approving the standard, in order to ensure that the proposed standard will not jeopardize the continued existence of a listed species. In order to streamline the process of review and consultation for future water temperature standards in the Pacific Northwest, EPA Region 10 developed a program that allows Oregon, Washington, Idaho, Native American tribal governments, EPA, NMFS, and USFWS to develop guidance jointly for the development of water temperature criteria. All of the participating agencies and tribes hope to use the final product to harmonize the ESA and CWA with respect to water temperature standards, and to help remove water temperature as an impediment to the recovery of imperiled native salmonids.

#### *Treaty Rights and the Trust Responsibility*

Through their treaties, tribes reserved the right to fish at all usual and accustomed fishing places and to take a "fair share" of the fish destined to pass to such areas. The Supreme Court has determined that the tribes' fair share is 50 percent of the harvestable fish, unless a moderate living standard can be met with less. Guaranteed by treaty, these tribal fishing rights may only be abrogated by specific congressional legislation – no one may use any method to otherwise deprive treaty fishermen of their right to a fair share of the anadromous fish (those that migrate from streams to the ocean and back).

As trustee of the tribes, the federal government also has the affirmative obligation to safeguard the subject matter of the treaty fishing right – the fish. Thus, federal agencies must use their authorities in a manner that will protect and prevent degradation of the habitat needed to support anadromous fish species. At a minimum, agencies have the duty to refrain from activities that will interfere with the fulfillment of treaty fishing rights. Anything less would amount to a de facto abrogation of Native American treaty rights. Thus, unless federal agencies can demonstrate that treaty fishing rights are presently being fulfilled, they cannot justify approving activities that will cause further degradation of anadromous fish habitat. Similarly, they cannot "balance" their treaty obligations against competing impacts to non-Native Americans or "delay" such obligations in order to minimize those impacts.

The federal trust obligation also mandates that Federal agencies enhance salmonid habitat where necessary to safeguard the fish that underlie the treaty fishing right. Arguably, this Federal trust obligation does not cease once a fish run becomes viable, but must continue to allow for harvestable populations of fish and meaningful fulfillment of the treaty right to take fish.

## **Project Structure**

EPA initiated development of guidance for regional temperature criteria through a multi-agency effort intended to develop guidance for regional temperature criteria that would be protective of native salmonids, would recognize the natural temperature potential and limitations of streams, could be effectively incorporated by states and tribes in water quality standards programs, and would be endorsed by EPA, USFWS, NMFS, states, and tribes in the Pacific Northwest. Additionally, it is intended that EPA use the new criteria guidance to evaluate revisions to state and tribal temperature standards, and that states and tribes will use the new criteria guidance to revise their temperature standards. The Technical Workgroup developed a technical

interpretation of the project goals (see Appendix A) that articulates the goals in terms of viable salmonid populations, distribution of coldwater habitat to support viable populations, and coldwater habitat support of all life history stages of salmonids.

The individuals involved in the project are employees of tribes and state and federal agencies, and are divided into a technical and a policy workgroup. The Policy Workgroup is comprised of agency/tribal managers and has the ultimate decision-making authority regarding the final form of the guidance. The Technical Workgroup, comprised of agency and tribal scientists, is responsible for developing draft guidance and providing technical review of the Policy Workgroup's final decision.

Water temperature improvement alone can not restore native fish populations; however, temperature improvements are necessary to restore requisite freshwater habitat for both resident salmonids (those that fulfill their entire life cycle in streams, rivers, and/or lakes) and anadromous salmonids. Relatively high freshwater survival is necessary to produce sufficient numbers of spawning adults. For example, since mortality is high during the egg to smolt periods in the freshwater and estuarine phases of anadromous salmonid development, reducing mortality during these stages offers significant opportunities for restoration of anadromous fish (Federal Caucus 2000). For anadromous fish, freshwater survival is particularly important during periods of poor ocean productivity.

## **How cold must water temperatures be to support salmonids?**

Viable populations of native salmonids in the Pacific Northwest need abundant cold water that is well-distributed over space and time to meet their freshwater habitat needs (see Physiology, Behavior, Multiple stressors, and Distribution technical summaries). The importance of cold water habitat to salmonids is documented by scientific research (summarized in the Physiology, Behavior, and Multiple stressors technical summaries). The

thermal tolerances expressed by salmonids are lower than those expressed by other groups of fishes, such as centrarchids (e.g., smallmouth bass, perch) and cyprinids (e.g., carp, northern pikeminnow).

Salmonid feeding, growth, resistance to disease, competitive ability, and predator avoidance are impaired by unsuitable temperatures (see Physiology, Behavior, and Multiple stressors technical summaries). For instance, adult fish holding in warm water experience bioenergetic stress and consume their stored energy more rapidly, which may result in reduced spawning success. Prolonged holding in sub-optimal temperatures can result in multiple stresses, such as concurrent thermal stress, disease, and energy depletion. Additionally, thermal stress experienced while fish are holding can decrease gamete viability. Warm temperatures can alter growth and development rates for juveniles and salmonids that feed in fresh water. In addition, warm water can present thermal barriers to adult and juvenile migrations. If enough fish are affected, salmonid population viability may be reduced.

Temperature-dependent life stages for salmonids include spawning, egg incubation, emergence, rearing, smoltification, migration, and pre-spawn holding. Any of these salmonid life stages can be present (depending on species and location) during summer months when streams in Pacific Northwest are warmest. Scientific evidence suggests that small increases in temperatures (e.g., 2-3°C) above biologically optimal ranges can begin to reduce salmonid fitness in some of these life stages.

While individual salmonids may be observed in streams where temperatures exceed laboratory-determined thermal tolerances, these observations alone are not grounds for concluding that warmer streams and rivers can support healthy salmonid populations. Individual fish may stray or be trapped in waters where temperatures are stressful or ultimately lethal. Further, if coldwater pockets (micro-refugia) are available in warm streams, small number of salmonids may be able to survive by exploiting these cold areas for short periods to avoid heat stress (see Behavioral technical summary), even

though the majority of habitat in the stream is too warm to support salmonids

Thermal conditions supporting and/or impairing various life stages and biological functions of some salmonids have been identified, primarily in laboratory settings (Table 1). These numbers are based on documenting the response of *individual fish* to various water temperatures. Therefore, there is some uncertainty regarding whether many of the temperatures listed are appropriate targets for supporting viable salmonid *populations* in rivers and streams. This uncertainty is compounded because most laboratory studies address single stressors while providing optimal conditions for other environmental factors, even though temperature does not act independently from other factors (Table 2, see also Multiple stressors technical summary). For example, when salmonids are fed to satiation, temperatures associated with maximum growth-rates are higher than under conditions of more natural (limited) food supply. Similarly, allowing salmonids to slowly acclimate to warm temperatures in the laboratory will extend their thermal tolerance, yet migrating salmonids pass rapidly through thermally diverse environments and may not have time to acclimate in the field. It is difficult to mimic field conditions in the laboratory, or to disentangle the effects of the multiple, interacting factors in complex natural systems. Because field conditions are more ecologically complex than laboratory settings, the uppermost laboratory-derived thermal limits are not likely to prevent adverse effects in a natural setting. Thus, where studies have attempted to derive the uppermost thermal limits for salmonids, they have measured responses of *individual fish* to water temperature in a *laboratory setting*. Stream temperatures may have to be somewhat cooler than measured uppermost thermal tolerances in order to support viable salmonid *populations* in *natural settings*.

Because various salmonid species and life stages show high fitness in a range of laboratory-derived optimal water temperatures, these temperatures (e.g., optimal temperatures shown on Table 1) can provide

**Table 1.** Estimates of thermal conditions known to support various life stages and biological functions of bull trout (a species extremely intolerant of warm water) and anadromous (ocean-reared) salmon. These numbers do not represent rigid thresholds, but rather represent temperatures above which adverse effects are more likely to occur. In the interest of simplicity, important differences between various species of anadromous salmon are not reflected in this table and requirements for other salmonids are not listed. Likewise, important differences in how temperatures are expressed are not included (e.g., instantaneous maximums, daily averages, etc.). These numbers are taken from the Physiology technical summary; that summary should be consulted for more detailed discussions and for references to scientific literature that support these numbers.

Consideration	Anadromous Salmon	Bull Trout
Temperature of common summer habitat use	10-17°C	6-12°C
Lethal temperatures (one week exposure)	Adults: >21-22°C Juveniles: >23-24°C	Juveniles: >22-23°C
Adult migration	Blocked: >21-22°C	Cued: 10-13°C
Swimming speed	Reduced: >20°C Optimal: 15-19°C	
Gamete viability during holding	Reduced: >13-16°C	
Disease rates	Severe: >18-20°C Elevated: 14-17°C Minimized: <12-13°C	
Spawning	Initiated: 7-14°C	Initiated: <9°C
Egg incubation	Optimal: 6-10°C	Optimal: 2-6°C
Optimal growth	Unlimited food: 13-19°C Limited food: 10-16°C	Unlimited food: 12-16°C Limited food: 8-12°C
Smoltification	Suppressed: >11-15°C	

conservative guidance for identifying instream temperatures most likely to protect salmonids. We do not intend to imply, therefore, that all streams must provide these optimal conditions at all times or in all places. We simply intend to focus our attention on identifying temperatures that are very likely to support viable salmonid populations.

The scientific research reviewed in the Physiology, Behavior and Multiple-stressor technical summaries shows that salmonids require a diversity of cold water temperatures in streams (Table 1) and that these temperatures must exist at appropriate locations and at appropriate times of the year. While laboratory evidence suggests adult salmon can generally survive a week or more at constant temperatures of 21°C and can often tolerate

temperatures as warm as 18°C for prolonged periods under controlled experimental settings, constant temperatures above 16°C have been shown to be intolerable for species such as bull trout. Not only do different species have unique temperature requirements, but individual species have unique temperature requirements for different life stages (spawning, incubation, juvenile growth, seawater adaptation, and adult migration) (see Physiology technical summary). The times at which those life stages occur are highly variable among streams of our region. In consideration of the available scientific information, we conclude that viable salmonid populations will require a variety of cold water temperatures (Table 1) that are well-distributed over space and time.

**Table 2.** Examples of considerations for interpreting laboratory observations of thermal tolerances and preferences for salmonids.

Consideration	Effect	Implication
Acclimation	When salmonids are acclimated to warmer temperatures in the lab, incipient lethal and other threshold temperatures rise to a limited extent	Results from laboratory studies are not directly comparable unless acclimation conditions are the same. Further, direct comparisons between lab and field conditions may be precluded because temperatures may vary considerably in the field. To make comparisons between lab and field studies, some researchers assume that fish are acclimated to a temperature between the mean and the maximum daily temperature.
Feeding	Feeding to satiation increases optimal growth temperatures relative to when food is limited. Food quality and cost of foraging may also be important	In the field, food availability is usually limited. Thus, lab tests where feeding levels are at satiation can overestimate suitable temperatures for growth and certain other performances. Also, food quality in the laboratory may differ from foods available in the field, and fish in the field must expend more energy to locate, and capture prey. Foraging costs (energy expenditure) may be reduced considerably under laboratory conditions than under field conditions, thereby reducing stress.
Social interactions	Can mitigate or exacerbate various thermal stresses	Social conditions in the field, especially territoriality, are key components of salmonid population regulation and behavior. Experimental studies seldom consider the role of social factors, which could mitigate or exacerbate responses to stressful temperatures. Unnatural social circumstances in the laboratory include, but are not limited to: possible high fish densities, wild vs. hatchery fish behavior, and altered community age structure. In the field, high fish density or low food availability can result in fish being forced to inhabit marginal thermal habitat. Mixtures of species and age classes can intensify social interactions in the field, whereas lab studies typically use single species and age classes per test.
Physiochemical conditions	Can alter stress response in a number of ways	Artificial lighting, photoperiod, thermal regulation, water chemistry, habitat structure (lab apparatus), cover, etc., may not reflect field conditions and are tied to physiological and behavioral responses to stress. Response may be partially determined by physical features of the experimental apparatus (e.g., horizontal vs. vertical thermal gradient in preference tests).
Handling	Causes additional stress	Repeated handling of fish, invasive procedures, and interaction with apparatus (e.g., tank maintenance), can alter both physiological and behavioral responses to stress.
Fish size/stage	Response may be size, age, or stage-dependent	Most laboratory studies focus on early life stages (e.g., eggs, fry, juveniles). This may not reflect the total life cycle in the wild. For example, adults and emergent fry can be more sensitive to elevated temperature than juveniles.
Exposure	Exposure in lab and field settings may differ	Natural streams have a diurnal range of temperatures and may have cooler areas in pools, tributaries, or where ground water upwells where fish can take refuge from warm temperatures. Fish in a laboratory aquarium cannot escape their test conditions, which may be constant.

**How much cold water is necessary to support salmonids? When and where must it exist?**

Temperature criteria to protect salmonids have traditionally attempted to identify the warmest water temperatures that can support salmonids. However, identifying water temperature thresholds is not

sufficient to ensure support for viable salmonid populations.<sup>1</sup> It is also important to determine how much cold water is needed, and here and when it be available.

Native Pacific salmon, trout, and char have complex life histories (Figure 1) that evolved in the spatially and temporally dynamic landscapes of the

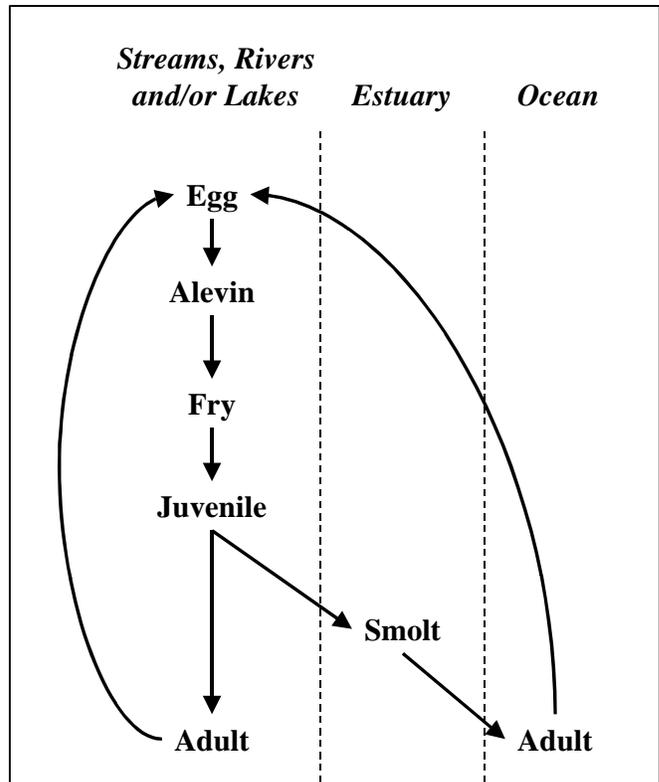
<sup>1</sup> Viable populations are defined in Appendix A

Pacific Northwest (see Distribution technical summary). Accordingly, providing enough cold water at the right places and times to support the recovery of native salmonids will require restoration and protection of natural ecosystem processes and patterns, including thermal regimes and spatial patterns of thermal habitat (see Spatial-temporal technical summary). Thus, our understanding of the biological and physical diversity of natural processes should provide guidance for developing temperature criteria. Maintaining biological diversity and natural system dynamics are important goals when considering how much cold water is necessary, when it is necessary, and where it is necessary.

*Biological diversity*

The spatial and temporal dynamics of natural thermal regimes lead to variations in life history characteristics (e.g., growth, timing of migration, age at reproduction). These characteristics interact in complex ways to determine individual fitness, and patterns of life history variability, viability, and productivity among populations and species. Within a species, individuals and populations with different life cycles and life histories may fare differently under changing environmental conditions. Variability in life history strategies may therefore confer stability and increased productivity to salmonid populations in naturally variable environments. Alteration of natural thermal regimes may cause populations to decline or important life history variability to be lost (see Spatio-temporal technical summary).

Criteria for temperature standards sometimes use specific characteristics of individuals and/or populations (e.g., density of fish, growth, fecundity, or survival) to simplify the task of managing or tracking population response. However, there is risk associated with using a small set of population indices (e.g., Sullivan 2000) or attempting system-wide maximization of any of these measures because of interaction or feedback among multiple factors. For instance, Holtby (1988) found that logging increased winter water temperature and subsequently the growth of juvenile coho salmon. While this



**Figure 1.** A simplified general sequence of events in the life cycle of salmonid fishes. All salmonids deposit eggs in freshwater (stream or lake) habitats. Depending on temperature and other factors, eggs hatch into alevins (sac fry). Alevins typically remain in or near spawning substrates until the yolk sac is absorbed. Following absorption of the yolk sac, the young are referred to as “fry.” This stage signifies the initiation of active feeding and development into fully formed juveniles. Juveniles may remain in their natal tributary or lake and mature as adults. This is referred to as a “resident” life history. Known migratory life histories include migrations to non-natal lakes and streams (potadromy) and marine habitats (anadromy). The transition to the marine environment involves complex physiological changes, referred to as “smoltification” in juvenile salmonids. Adults of some species may make repeated transitions between freshwater and marine habitats, however. Migratory behavior varies substantially among species, and within and among local populations, in many cases.

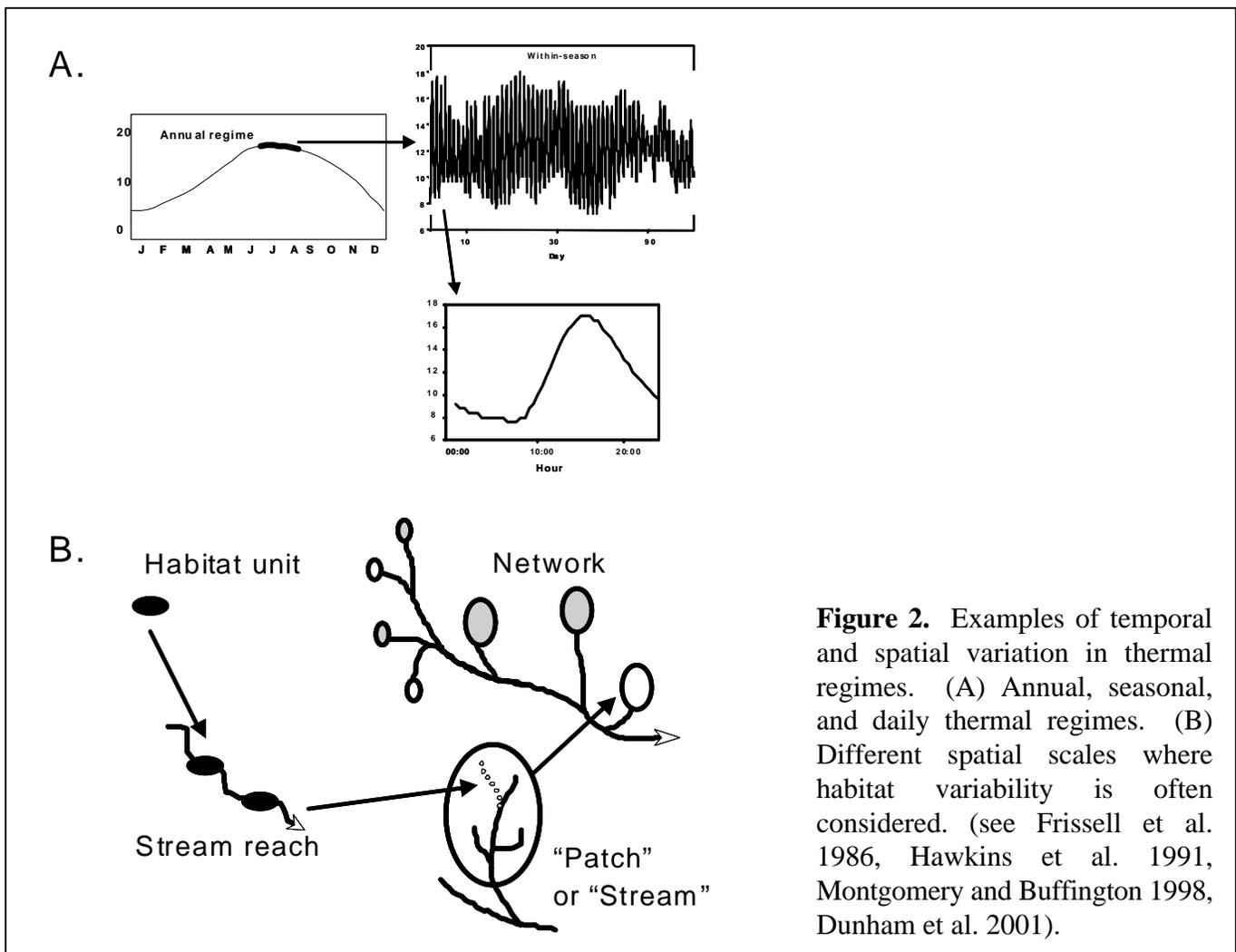
might be expected to be beneficial, the increased growth accompanied earlier migration, reduced marine survival, and an overall reduction in the number of returning fish. This illustrates how attempting to maximize a single metric (in this case, growth) might have unintended negative consequences for the population as a whole. This is not to say that growth should be ignored as an important factor for monitoring salmonid populations. It simply underscores that *single* measures are not effective indicators of population status and that attempts to maximize such measures are associated with biological risks. In fact, these simplified approaches may reduce rather than preserve natural biological diversity and viability of salmonid populations by focusing attention on specific performance measures at the expense of

other important aspects of biological diversity (Lichatowich 1997).

### Natural temperature dynamics

Natural landscapes represent a complex mosaic of physical and biological diversity. Ecosystem processes that shape these physical and biological patterns can operate on a number of scales in time or space. A natural thermal regime can be considered in terms of magnitude, frequency, duration, and timing of events (e.g., summer maximum temperatures) and rates of change (i.e., how fast temperatures heat or cool) at different temporal and spatial scales.

Temporal scale. Temporal variation of a thermal regime can be considered in terms of variability



**Figure 2.** Examples of temporal and spatial variation in thermal regimes. (A) Annual, seasonal, and daily thermal regimes. (B) Different spatial scales where habitat variability is often considered. (see Frissell et al. 1986, Hawkins et al. 1991, Montgomery and Buffington 1998, Dunham et al. 2001).

among years, within a year (among seasons), within seasons (among days or weeks), and within a single day (among hours) (Figure 2). Thermal regimes affect salmonids at all of these scales (see Spatio-temporal technical summary). Decadal-scale variation in climate and temperature (e.g., El Niño events, Pacific decadal oscillations) may affect long-term patterns of productivity in salmon populations. Within years, the timing and locations of various parts of the salmonid life cycle are linked to seasonal patterns of stream temperature and habitat availability. Smaller-scale weekly or daily variability in temperature also may be important as they affect chronic or acute thermal stress (see Physiology technical summary) and individual behaviors, such as migration, habitat selection, predator avoidance, competition, and behavioral thermoregulation (see Behavior technical summary).

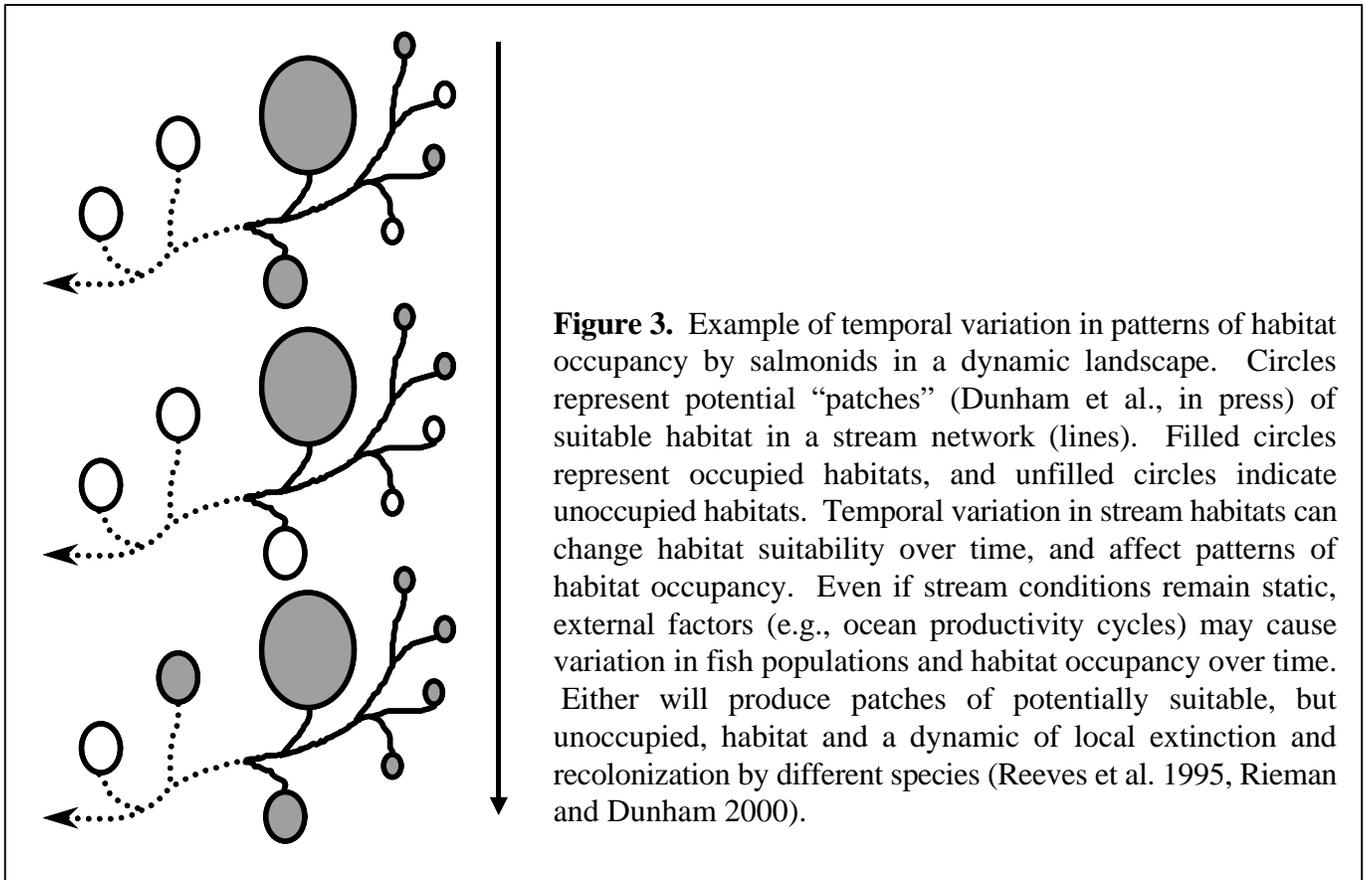
Spatial scale. Spatial pattern is an important part of a thermal regime. Spatial variation can occur within a few meters, such as with pools and riffles, within a larger habitat scale including stream reaches, individual streams, and stream networks (Figure 2). Two important aspects of the spatial distribution of thermal habitat are the size and locations of thermal refuges. For coldwater fish, thermal refuges can be defined as patches of cold water that allow individuals or populations to persist in a thermal regime that ranges (in time or space) outside of the zone of tolerance or preference for a given species. Thermal refuges may range in size from fine scale (e.g., pockets of cold water provided by thermal stratification and localized ground water upwelling to cold side channels and backwaters in alluvial systems) to coarse scale (e.g., thermal variation between headwater creeks to larger main-stem rivers; see Spatio-temporal technical summary).

Landscape context. Protection of fish at specific sites is not sufficient to guarantee the health of a local population. Emerging evidence (see Distribution technical summary) suggests the health of local populations may depend on the landscape context – specifically, the size, number,

connectivity, location, and quality of occupied and unoccupied habitats within which the population lives. The landscape context refers to the spatial as well as temporal dynamics of habitat change and occupation. Where habitat is degraded, fish populations that decline will not recover until the habitat has recovered. In some cases, however, habitat is not just degraded, but a disturbance renders the habitat temporarily unsuitable (e.g. local temperature increases in a portion of a stream network) for salmonid survival. In these cases, although that habitat may ultimately recover, the loss of certain species from the disturbed area can be either temporary or permanent. Species loss is likely to be temporary if other suitable habitats (refuges from disturbance) are: 1) large enough to maintain viable populations of affected fish, and 2) interconnected to allow emigration from the refuge(s) to the disturbed site when (or if) it recovers from the disturbance. This underscores the fact that not all suitable habitat is necessarily occupied at all times in a dynamic natural landscape. Therefore, protection of some amount of currently occupied and unoccupied habitat may be needed to provide a sufficiently large network of well-connected habitat distributed across the landscape (Figure 3). Specific answers to the questions of precisely “how large?” or “how connected?” are only beginning to be addressed as principles of conservation biology are integrated into salmonid ecology (see Distribution technical summary), but those efforts suggest that habitat must be widespread and well-connected in order to meet a goal of maintaining viable salmonid populations.

#### *Incorporating thermal regimes*

While we do not fully understand how natural ecosystems function, natural conditions serve as models of stream temperature dynamics known to have supported viable salmonid populations. It is difficult to prescribe “appropriate” thermal regimes from inferences about biological conditions or physical conditions alone. Our biological understanding of salmonids has provided important insights into the effects of temperature, but it does



not directly address the causes of thermal degradation. If one accepts that salmonids are adapted to survive in the historic conditions of the Pacific Northwest, it follows that temperature standards that encourage attempts to restore an ecosystem’s thermal dynamics (e.g., address the causes of thermal degradation) will provide a very high likelihood of supporting viable salmonid populations.

In an ideal world, we might eliminate thermal degradation by restoring stream temperatures to pre-settlement thermal regimes that historically supported viable salmonid populations. However, restoration of historical conditions can be an unreasonable goal given that restoration opportunities may be limited to varying degrees by certain “irreversible” human-caused or natural landscape changes, such as development of major urban centers and volcanic eruptions. Yet, the continuing collapse of salmonid populations

suggests that the existing amount and distribution of suitable habitat in the Pacific Northwest is inadequate to maintain viable salmonid populations. Therefore, based on the scientific review contained in the technical summaries, the Technical Workgroup concludes water temperature criteria should ideally address thermal regimes, and that four actions relevant to thermal regimes may be necessary and should be strongly considered in order to ensure adequate amounts and distributions of cold water to support salmonid populations.

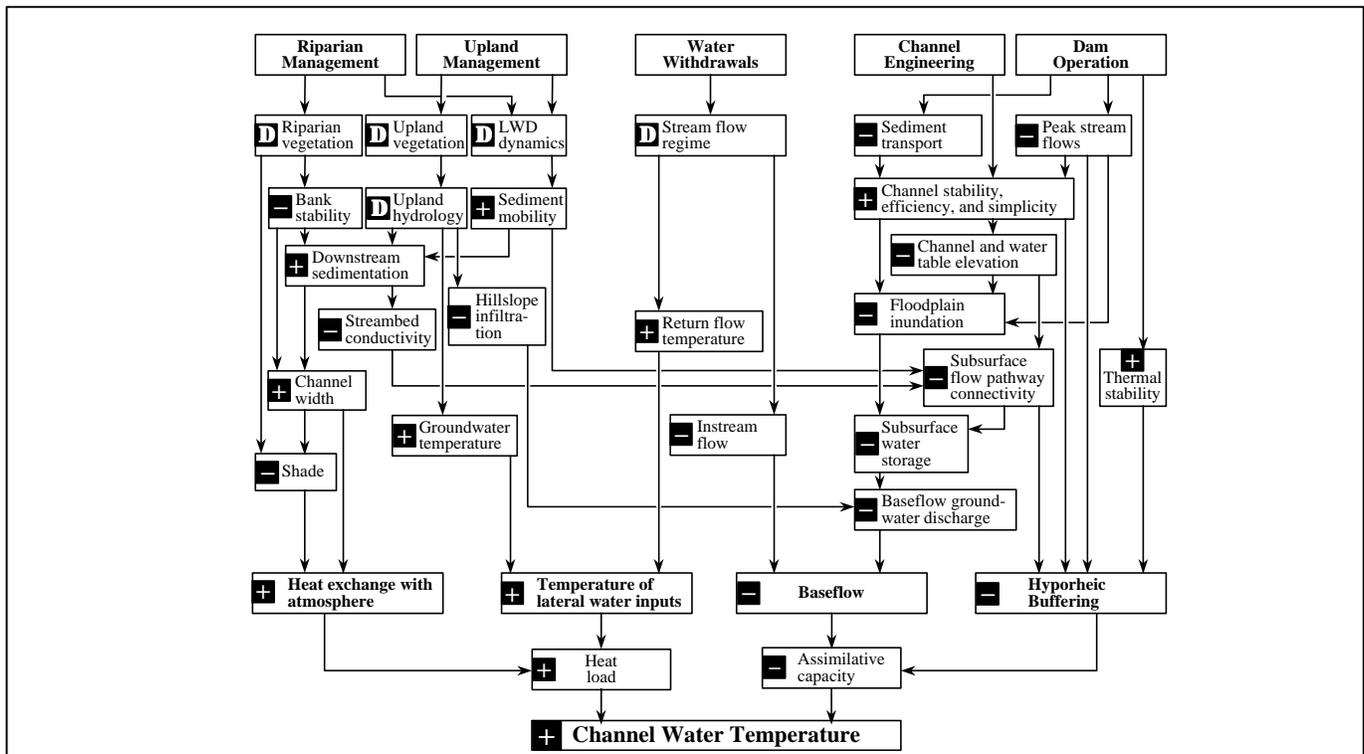
- 1) Immediate protection of remaining suitable habitat from thermal degradation.
- 2) Restoration of some amount of thermally degraded habitat. Given that thermal degradation in many streams may not be reversible due to policy considerations or social and economic realities, it is likely that much or even all habitat that can be restored will need to

be restored in order to support viable populations.

- 3) Implementation of restoration across a broad spectrum of habitats from headwaters to ocean because the life histories of salmonids span entire watersheds.
- 4) Protection and restoration targets based on consideration of a wide array of evidence with an emphasis on natural temperature dynamics. Engineering artificial thermal regimes may entail greater uncertainty and risk than attempting to mimic natural processes and patterns (see Poff et al. 1997 for a discussion of the importance of maintaining or restoring natural regimes).

## How do human activities affect stream temperatures?

Water temperature is determined by interactions between the amount of water flowing in the stream, the structural configuration of the stream and riparian zone, and various factors external to the stream/riparian zone (see Spatio-temporal technical summary). In many river basins of the Pacific Northwest, land management activities have (1) reduced connectivity (i.e., the flow of energy, organisms, and materials) between streams, riparian areas, floodplains, ground water, and uplands; (2) altered floodplain function, wetlands, water tables, and base flows; (3) elevated fine sediment yields, making streams wider and shallower, with fewer



**Figure 4.** Some pathways of human-caused warming of stream channels (From Poole and Berman 2001.). The symbol “+” indicates an expected (but not certain) increase, “-” an expected (but not certain) decrease, and “Δ” either an expected increase or decrease depending on the specific circumstance or measurement used. This graphic is designed to illustrate the complexity associated with stream temperature dynamics. It is not intended to be a comprehensive summary. Additional arrows and boxes are possible under various conditions.

pools; (4) reduced instream and riparian large woody debris that traps sediment, stabilizes stream banks, and helps form pools; (5) reduced or eliminated riparian vegetation; and (6) altered peak flow volumes and timing (FEMAT 1993, Henjum et al. 1994, Rhodes et al. 1994, Wissmar et al. 1994, National Research Council 1996, Spence et al. 1996, Oregon Coastal Salmon Restoration Initiative 1997, Quigley and Arbelbide 1997, McIntosh et al. 2000). Thus, human activities can alter stream temperature through a variety of complex and interactive pathways (Figure 4). In developing guidance for water quality criteria, we believe it is important to consider a wide array of pathways by which human actions alter temperature and the ways in which different approaches to temperature standards might be effective or ineffective at addressing the influence of each pathways.

Human-caused changes to stream temperature are often hard to quantify, often because of difficulty determining what the “natural” water temperature would have been in the absence of human-caused degradation. However, scientific research has shown that human activities have the potential to alter thermal regimes (see Spatio-temporal technical summary). Along with changes in mean temperature, more subtle changes in stream temperature may be manifested as changes in temperature extremes, in temperature variation, or in the timing of temperature extremes (see Spatio-temporal technical summary). Although some human impacts (e.g., dams) can reduce diurnal temperature variation, human-caused degradation often simplifies stream structure, which eliminates the coldest water habitats and reduces *spatial* temperature variation within stream reaches. At the same time, human-caused degradation often increases the *daily* and *seasonal* temperature variation in stream reaches by interrupting natural processes that buffer stream temperature such as riparian shade, in-stream flow, and ground water influx. (see Spatio-temporal technical summary). While these effects might seem to offset one another, they instead have a synergistic negative effect on salmonid populations. Increases in daily

and seasonal variation expose fish to higher summertime maximum temperatures. At the same time, loss of coldwater habitat that reduces spatial variation within stream reaches precludes salmonids’ ability to escape high temperatures or avoid other detrimental physiological and ecological conditions (see Behavior technical summary).

Human influences on stream temperature are inherently cumulative; as the amount and intensity of land-use and river flow regulation increase in a basin, so too does the magnitude of in-stream temperature changes (see Spatio-temporal technical summary). Thus, problematic water temperatures are most apt to occur in basins where urbanization and intensive land-use activities (such as logging and agriculture) are widespread and/or where dams or water withdrawals have substantially altered natural flow regimes. In these basins, stream warming will occur if human actions cause more heat to be added to stream, and some of that heat will remain in the stream as water moves downstream. Any accumulated additional heat will remain in the stream until downstream conditions (e.g., riparian vegetation, geomorphology, etc.) create the opportunity for heat to dissipate back out of the stream channel (see Spatio-temporal technical summary). Some streams dissipate added heat effectively and may eventually return to pre-disturbance conditions, while others will retain at least some of the added heat for long distances. The distance over which the additional heat can persist in a stream may range from a few meters to many kilometers. Thus, in some circumstances, heat added to cold headwater streams might not create thermally unsuitable salmonid habitat in the headwaters themselves, but may instead contribute to unacceptably warm temperatures at some distance downstream.

In areas where human activities have warmed streams, those same activities often eliminate naturally-occurring thermal refugia (from pockets of cold water in warmer streams to entire watersheds that contain thermally optimal temperature regimes) or isolate such refugia from other suitable thermal

habitat. Loss of these important landscape features reduces the ability of salmonids to avoid thermal stress and therefore is apt to decrease survivorship through periods of temperature extremes (see Spatio-temporal and Distribution technical summaries).

### How can we contend with scientific uncertainty when establishing temperature criteria?

Developing temperature criteria to protect salmonids is challenging in part because scientific understanding of stream temperature dynamics, salmonid biology/ecology, and their interactions is imperfect. To maximize the potential for success,

the process of developing criteria must be founded on scientific information yet be flexible to accommodate scientific uncertainty. Clearly, there are limits to our knowledge. For instance, our knowledge regarding historical distributions of salmonids is extensive, but the details regarding population sizes and habitat utilization within each individual basin is often limited. Data describing historical thermal regimes is scarce and our knowledge of natural distributions of coldwater habitat is imperfect. In addition, we lack the ability to precisely measure or predict the interactions between thermal stress and other biophysical stressors in the freshwater environment. Although salmonid distributions can be correlated with

Table 3. Examples of uncertainties and certainties associated with determining criteria for water temperature standards based on protecting viable populations of salmonids in the Pacific Northwest.

	<b>Uncertainty</b>	<b>Certainty</b>
How Cold	Relationships between lab-derived temperature thresholds and requisite temperatures in the field Maximum allowable temperatures that will support viable populations Precise thresholds of harmful temperatures (e.g., see Table 2) Effects of multiple stressors	Salmonids can experience physiological stresses where water temperatures are not optimal General ranges of water temperatures necessary for survival and reproduction. Both lethal and sub-lethal effects affect salmonid survival Thermal tolerance in salmonids is affected by other stresses and vice versa.
How Much, When and Where?	Mechanisms and dynamics of cumulative effects on stream temperature dynamics Patterns of environmental variability required to support populations Historical thermal regimes in streams Measures of historical fish distribution and trends in fish populations	Cumulative effects occur and can result in synergistic temperature changes within in streams subject to multiple disturbances. Complex physical habitat structure creates spatially and temporally diverse coldwater habitats that salmonids have evolved to exploit Salmonid survival requires a variety of cold water temperatures that are well-distributed over space and time. Salmonid populations have declined precipitously and their distributions have been reduced throughout the region
Human Influence	Data on the alteration of thermal regimes Exactly what management actions are necessary to protect salmonids Maximum levels of degradation that will allow salmon to persist	Thermal regimes have been altered substantially over time; where altered, streams are generally warmer in the summer and more spatially homogeneous The types of activities affecting stream temperature Salmonid populations require a safety buffer in the face of a variable environment

thermal regimes (see Distribution and Behavioral technical summaries), the population responses to changes in thermal regime cannot be precisely specified because a multitude of factors influences salmonid population dynamics. Further, we are uncertain about the precise number and distribution of specific coldwater habitat features (e.g., thermal refugia) needed to restore thermal regimes and support viable populations.

Yet, in spite of these shortcomings, our scientific knowledge is extensive and can provide substantial guidance to the development of temperature criteria. We know salmonids need cold water. We know that much larger salmonid populations occupied a much greater network of northwest streams and rivers only 150 years ago. We know that salmonids evolved to exploit and rely upon the natural thermal regimes of Northwest rivers. We have extensive research showing how the physical structure of streams and rivers influences thermal regimes. We know that many human activities have altered (e.g., typically warmed) natural thermal regimes. Some major sources of uncertainty and certainty are contrasted in Table 3.

While uncertainty constrains our ability to precisely qualify and quantify the risks associated with different management actions, scientific knowledge has defined many causal relations that exist between the thermal environment, biotic community, and human activities. This certainty affords confidence in the desired outcome of management actions (Tickner et al. 2000). Given uncertainty, we are challenged to make decisions based on what we know, while taking adequate precautions to avoid irretrievable or irreversible mistakes. Thus, in moving forward scientists have recommended a cautious and conservative approach, especially when actions may affect threatened or endangered species. For instance, when managing natural resources in the face of uncertainty, Ludwig et al. (1993) offered some guiding principles: consider a range of alternatives and favor actions that accommodate uncertainties; favor actions that are informative; probe and experiment; monitor

results; update assessments and modify policies accordingly; and favor actions that are reversible. Others have recommended that sources of certainty, uncertainty, and related assumptions that underlie temperature criteria development be clearly and completely documented (see Tickner et al. 2000, for examples).

Participants in this project are charged with developing new temperature criteria guidance that will provide sufficient cold water to restore and sustain viable salmonid populations, yet there is no way to determine with certainty *exactly* how cold streams must be, how much coldwater habitat is needed, and what spatial and temporal configurations will be requisite. However, from the certainties listed in Table 3, we can infer several tenets from which criteria robust to uncertainty can be designed.

- 1) Human actions have caused thermal degradation of aquatic habitats. Although it is only one of many factors, it is an important factor that has contributed to declines in salmonid populations.
- 2) Existing amounts and/or spatial and temporal distributions of essential habitat, including thermal dynamics thereof, may not be sufficient to support viable salmonid populations.
- 3) Restoration and protection of thermal regimes will need to address the amount and distribution of thermally suitable water and its spatial and temporal association with other characteristics of salmonid habitat.

While restoration of stream temperature will not be the only action necessary to restore salmonid populations, we conclude that widespread restoration of temperature regimes will favor recovery of salmonids. We further conclude that restoration will require modification of human actions shown to cause thermal degradation and that temperature criteria will need to define “coldwater habitat” and provide guidance for determining the amount and distribution thereof. Thus, to meet the goals of this project (Appendix A), we conclude that the available science suggests that salmonid

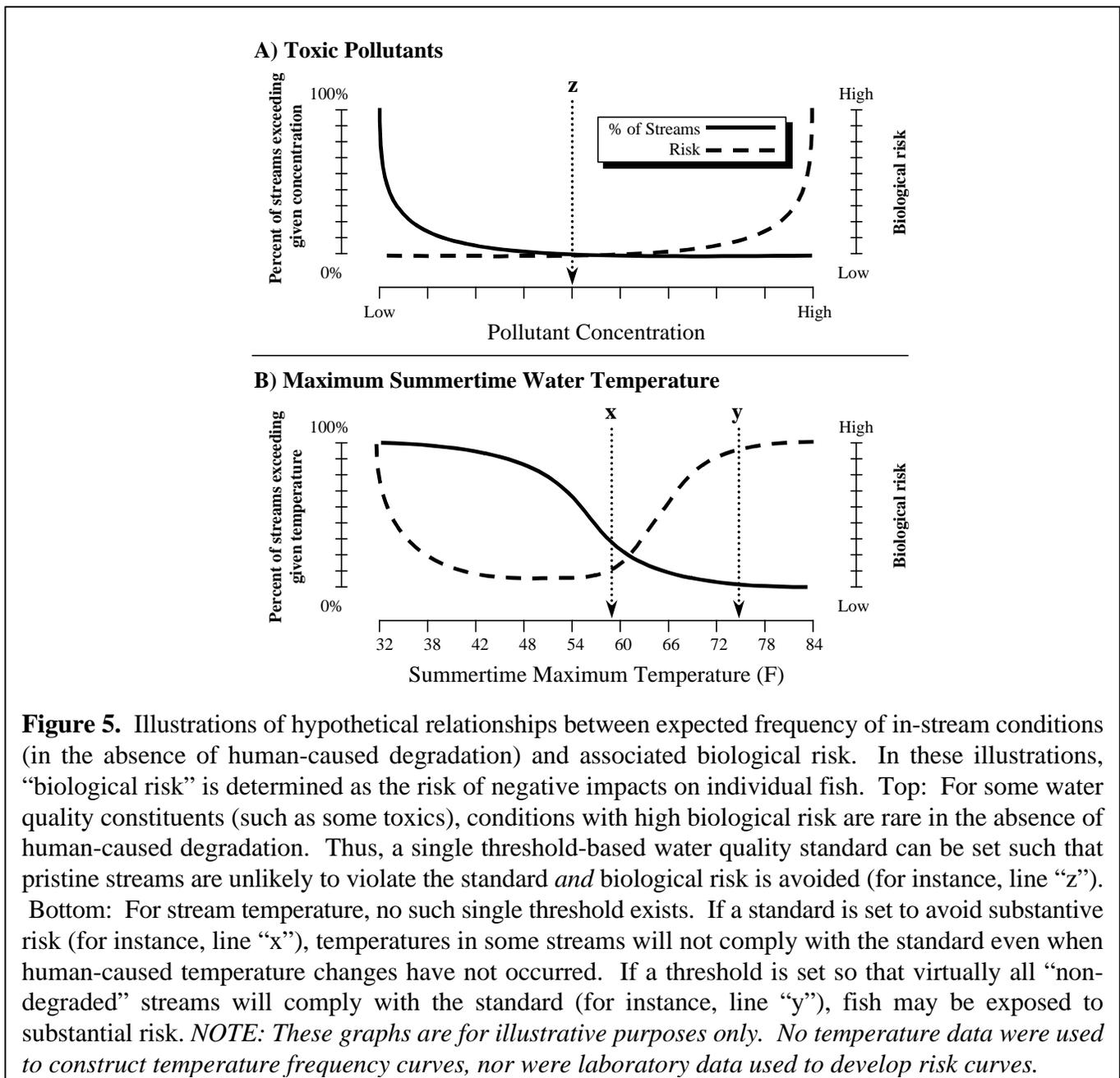
recovery will require more cold water than is currently available, and that the cold water must be well distributed and connected.

As the results of efforts and progress to provide cold, well-connected, and well-distributed aquatic habitat are compiled, and as salmonid populations change in response to those efforts, criteria may be revisited and refined. Yet, in light of scientific uncertainties, the threatened and endangered status of salmonids in the Pacific Northwest, and the extent

of human alterations to their habitat, and conclusions of other scientists (e.g., Ludwig et al. 1993, Tickner et al. 2000) we believe it is important to avoid initially underestimating the thermal requirements of salmonids.

## Implications for Water Temperature Standards

In concept, a conventional approach to developing water quality standards (such as often



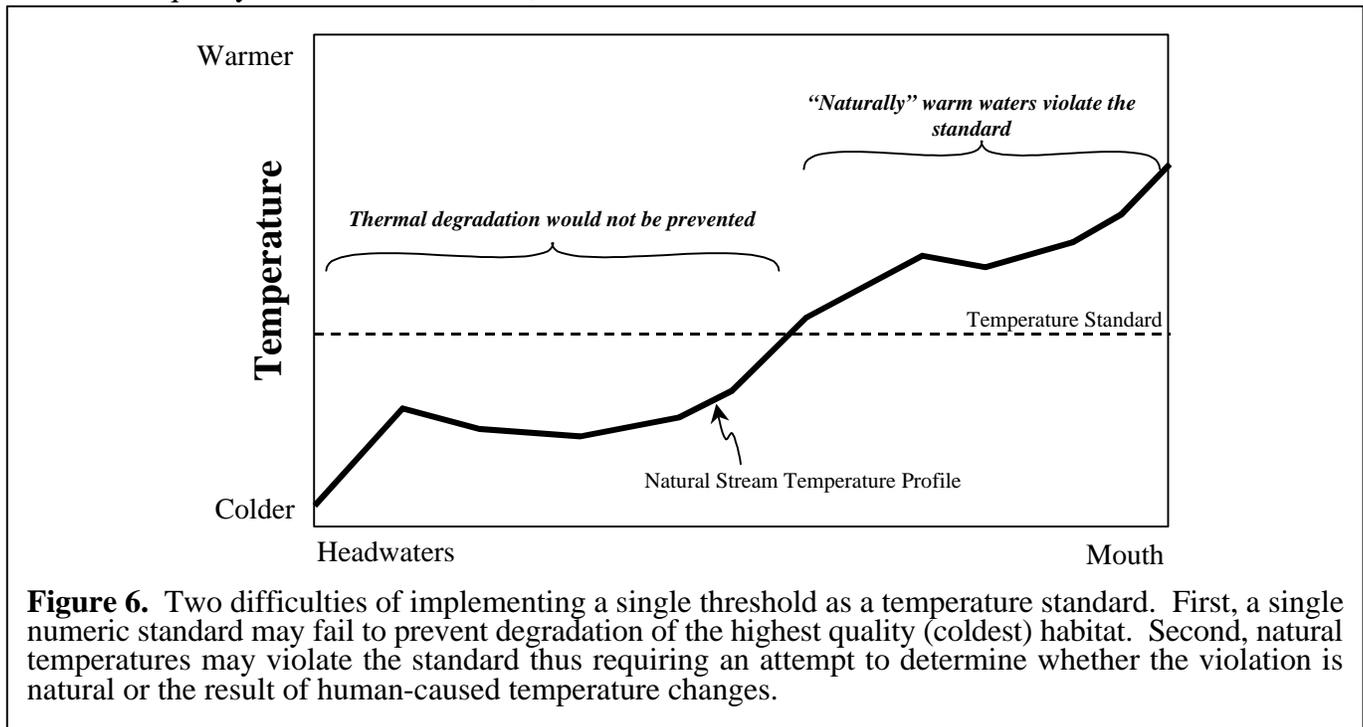
**Figure 5.** Illustrations of hypothetical relationships between expected frequency of in-stream conditions (in the absence of human-caused degradation) and associated biological risk. In these illustrations, “biological risk” is determined as the risk of negative impacts on individual fish. Top: For some water quality constituents (such as some toxics), conditions with high biological risk are rare in the absence of human-caused degradation. Thus, a single threshold-based water quality standard can be set such that pristine streams are unlikely to violate the standard *and* biological risk is avoided (for instance, line “z”). Bottom: For stream temperature, no such single threshold exists. If a standard is set to avoid substantive risk (for instance, line “x”), temperatures in some streams will not comply with the standard even when human-caused temperature changes have not occurred. If a threshold is set so that virtually all “non-degraded” streams will comply with the standard (for instance, line “y”), fish may be exposed to substantial risk. *NOTE: These graphs are for illustrative purposes only. No temperature data were used to construct temperature frequency curves, nor were laboratory data used to develop risk curves.*

used for toxic pollutants) attempts to identify a threshold value that is low enough to minimize risks to aquatic biota. For many parameters, the threshold level is above the range of naturally-occurring conditions in streams. Where this occurs (Figure 5, top), a conventional threshold standard is effective, scientifically defensible, and relatively easy to determine. For water temperature, however, there are several reasons why a single threshold approach to determining water quality criteria can be problematic.

Stream temperatures associated with increased biological risk might occur relatively frequently in some stream reaches under natural conditions (Figure 5, bottom). Natural stream conditions would violate temperature thresholds that were predicated on eliminating biological risk to individual fish. Natural stream temperatures vary across space and time, particularly in large, dynamic landscapes such as the Pacific Northwest. Applying a conventional standard may result in two undesirable consequences illustrated by Figure 6. First, human-caused warming of the best thermal habitat may be allowed where local stream temperatures are naturally below the water quality criterion. Second, streams

naturally warmer than the criterion will be identified as candidates for remediation. Salmonids require a variety of cold water temperatures, but a single threshold standard does not recognize the diversity of water temperatures needed by various species and over space and time.

Temperature standards are developed primarily to protect aquatic biota as the beneficial use most sensitive to water temperature. Yet, water temperature is the expression of a set of heat transfer processes that are in turn influenced by the physiographic, climatic, and hydrologic variables acting on a particular stream segment. Some of these variables can be altered by human activity and some cannot. Therefore, in setting water temperature standards to protect aquatic biota both the biological and physical processes must be considered. A good standard will protect high-quality habitat and guide restoration of degraded habitat, while recognizing that some naturally warm reaches are also part of the aquatic landscape. It will limit the extent to which the standard may be under-protective in some locations and overly stringent in others.



The next task of the Technical Workgroup is to develop conceptual models or frameworks for a temperature standard. In order to avoid the limitations and achieve the objectives described above, the workgroup is analyzing the characteristics of conventionally derived standards and thinking about alternate ways to structure a standard. Described below are possible alternative factors to new standards that the workgroup will consider and evaluate.

Standard development. By convention, water quality standards are designed to remove unacceptable stresses on individual fish. Alternatively, a standard could attempt to describe conditions that would be necessary to maintain viable populations.

Comparison used. The type of comparison used to determine compliance may range from single temperature thresholds to multiple thresholds or even thermal regimes. Single thresholds are individual numbers that are compared to measures of water temperature. Multiple thresholds are groups of thresholds that can be compared across space and/or time to measures of water temperatures. Regimes are compared using metrics that describe the spatial or temporal distribution of temperatures such as mean, range, variance, and timing.

Scientific foundation of numeric values. Numeric values for standards can be determined based on salmonid biology (e.g., lethal or optimal temperatures for salmonids), temperature dynamics of streams (e.g., patterns of heating and cooling), or a combination of both.

Spatial scale of a management unit. For water quality standards, a management unit is the type of geographic unit that is deemed either in or out of compliance with the standard. By convention, individual water bodies, stream reaches, or point locations are used as management units. Alternatively, a management unit could be defined as a basin or sub-basin. As long as enough well-distributed and connected cold water is present, these larger geographic units could be in compliance in spite of naturally warm water at some sites.

Number of measurements. Compliance can be determined based on different measurement conventions: individual samples, multiple samples, or a census of stream temperatures. Each of these conventions is applicable over both space and time. For instance, a temperature census over time is accomplished using a continuous recording data logger. A census over space might be accomplished using a remote sensing technique to map the distribution of water temperatures along the entire river.

Each of the approaches will have a unique set of opportunities and challenges. The flexibility associated with these different approaches may result in criteria that protect the thermal requirements of salmonids while accommodating naturally warm waters. Yet this flexibility could incrementally weaken protection and increase extinction risks. Thus, these alternatives must be considered with caution. The task before the Technical Workgroup is to identify criteria with characteristics that will best ensure the thermal conditions necessary to support viable salmonid population while reducing the instances where naturally warm water is deemed out of compliance.

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## Appendix A: Technical Interpretation of the Project Goals

The following project goals were identified by the Policy Workgroup to guide the Technical Workgroup in development of temperature criteria.

### **Project Goal Statements (from the Policy Workgroup)**

To Develop EPA Regional Temperature Criteria Guidance that:

- Meets the biological requirements of native salmonid species for survival and recovery pursuant to ESA, provides for the restoration and maintenance of surface water temperature to support and protect native salmonids pursuant to the CWA, and meets the salmon rebuilding needs of federal trust responsibilities with treaty tribes
- Recognizes the natural temperature potential and limitations of water bodies
- Can be effectively incorporated by states and tribes in water quality standards programs

The new criteria guidance will be jointly developed by EPA, USFWS, NMFS, States, and Tribes in the Pacific Northwest:

- States and tribes will use the new criteria guidance to revise their temperature standards, if necessary
- EPA and the Services will use the new criteria guidance to evaluate state and tribal standard revisions

### **Recovery Target (from the Policy Workgroup)**

The temperature criteria guidance that would support “sustainable and harvestable levels of salmonids.”

To facilitate communication and understanding between the Policy and Technical Workgroup, the Technical Workgroup developed the following interpretation of the project goals based on the literature reviewed in the five technical summaries described in the Preface to this document.

To meet the project goal, the Technical Workgroup believes it is necessary to develop EPA regional temperature criteria guidance that:

- if attained, would provide thermal habitat capable of supporting viable populations<sup>1</sup> (including a surplus for human harvest) of all native salmonids
- protects high quality thermal habitat while minimizing circumstances where compliance would require remediation beyond a system’s thermal potential can be implemented and enforced

Thus, temperature criteria should describe thermal regimes that promote the following characteristics of salmonid populations:

*Population size* is large enough to:

- Maintain genetic and phenotypic diversity<sup>2</sup> over the long term
- Survive environmental variation<sup>3</sup> and catastrophic disturbance
- Provide ecological functions;<sup>4</sup>
- Allow a population surplus that can be harvested by humans

*Population growth rate* is positive.<sup>5</sup>

*Population distributions:*

- Are extensive within and across sub-basins;<sup>6</sup>
- Allow full utilization of habitat potential<sup>7</sup> (temporally and spatially) of sub-basins, which allows natural expression of multiple life history strategies<sup>8</sup>.
- Are comprised of well-connected<sup>9</sup> sub-populations.

Additionally Temperature criteria should describe thermal regimes that promote the following features of salmonid habitats

- Natural thermal regimes are established across the maximum extent of the landscape.
- Habitats are well-connected.
- Habitat supports all life history stages and strategies.

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<sup>1</sup> The Technical Workgroup defines a “viable population” as a population where the population growth rate, size, and distribution are as described later in this appendix. See also McElhany et al. (2000) for a more comprehensive discussion of viable salmon populations.

<sup>2</sup> Small population sizes can result in loss of genetic information from the population gene pool such as run timing, age structure, size, fecundity, morphology behavior, and molecular genetic characteristics.

<sup>3</sup> “Environmental variation” includes the natural annual variations that can be summarized statistically. This also includes foreseeable cyclic patterns of climatic change.

<sup>4</sup> Salmon are a keystone species in ecosystems of the PNW. For example, nutrients from carcasses are vital in providing nutrients to riparian vegetation and for the feeding and growth of freshwater biological communities including juvenile salmonids.

<sup>5</sup> Most salmon populations that are currently listed under the ESA have population growth rates (e.g., spawner-spawner ratios) that are extremely depressed and static or are low and declining. Populations can recover only if these population growth rates have ratios of >1.0. A population is only fishable and sustainable if there are more adults returning to the spawning grounds to spawn than are needed to replace the numbers of the parent generation. Also, an excess is needed to compensate for natural fluctuations in environmental conditions throughout the geographic range of the salmon life cycle (including ocean conditions) that lead to periodic fluctuations in survival.

<sup>6</sup> This allows source sub-populations to be maintained so that they contribute to the stability of the overall population by providing centers of high productivity and contributing a source of strays to colonize other habitats within the sub-basin.

<sup>7</sup> Habitat potential is an inherent characteristic of a watershed that has a high level of ecosystem integrity. Elements of the watershed that define its potential include its potential natural vegetation, climate, lithology, geomorphology, biota, hydrology, and soils. These elements interactively set up instream habitat conditions (channel geomorphology, hydrologic regime, water temperature regime, riparian vegetation community types and dynamics, channel substrate characteristics). Given various levels of anthropogenic disturbance to the watershed, alterations to the watershed and/or stream channels and riparian areas can shift the processes that

produce in-stream habitats so that they disfavor salmonids. This can come about through alterations in the regimes for large wood input, water temperature, water routing, nutrient input, and sediment. Water temperature regime can be altered by the combined effects of shifts in the woody debris input, riparian vegetation condition (current state of the vegetation, given all possible states that are defined by its potential), sediment delivery to the channel (affecting intergravel flow, channel morphology, and pool depth and frequency).

<sup>8</sup> A life history strategy is one of the means by which a life cycle can be structured so that life functions are realized. Functions include growth, survival, development, mating, reproduction, incubation, emergence, rearing. When a watershed exhibits a state of high integrity, the ability of the watershed to develop high quality aquatic habitats is great and multiple life history strategies become available for salmonids to complete these functions. Watershed and habitat degradation tend to eliminate many life history strategies (e.g., those strategies that depend upon mainstem rivers, low elevation habitats, floodplain or off-channel habitats).

<sup>9</sup> When sub-populations are well connected, they are capable of interbreeding. This allows better maintenance of genetic integrity in the gene pool because the genes are maintained by a larger, more integrated population. Small, isolated populations with few or poorly connected sub-populations tend to be unstable over time and gradually disappear. They are not resistant to extreme environmental conditions because the entire population can be affected by a single event or disturbance. Populations comprised of well-distributed and connected sub-populations have greater resistance to perturbation because there is lesser likelihood that major portions of the population will be affected by a single event. Likewise, if some life history strategies involve spawning at a different time or in a different location, greater population stability results from this "hedging" against extinction.