United States
Environmental Protection
Agency

EPA-910-D-01-002
May 2001

Issue Paper 2

Salmonid Distributions and Temperature

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

Jason Dunham, U.S. Forest Service

Jeff Lockwood, National Marine Fisheries Service

Chris Mebane, Idaho Department of Environmental Quality

Contents

Abstract 1

Introduction 1

What is a “distribution”? 2
  Ontogenetic variation 2
  Life history variation 3
  Historical vs. contemporary vs. potential distribution 3
  Examples 4

What are the direct effects of temperature? 12
  Examples 12

What are indirect effects of temperature on fish distributions? 13
  Biotic interactions 13
  Habitat size and isolation 13

What is meant by “scale” and “level?” At what “level” should we be concerned with temperature criteria to protect fish distributions? 13

Information on thermal relationships of salmonids comes from a variety of laboratory and field studies—how do we integrate work conducted at different scales or levels of organization (e.g., population vs. individuals)? 14
  EPA Fish and Temperature Database Matching System (FTDMS) 15
  “I saw fish in hot water.” 15

Is unoccupied habitat relevant to temperature requirements of salmonids? 15

Conclusion 17

Literature Cited 18

Issue Paper 2

Salmonid Distributions and Temperature

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

Jason Dunham, Jeff Lockwood, and Chris Mebane

Abstract

Distributions of native salmonid fish in the Pacific Northwest are strongly tied to temperature conditions in their habitat. Salmonid populations have declined in conjunction with thermal changes and the loss and fragmentation of large and interconnected cold-water habitats. Temperature affects the health of not only individual fish but also entire populations and groups of species. Temperature changes have obvious direct effects, and also interact with other factors to indirectly affect salmonids.

The best way to protect existing populations and restore depleted populations is to create temperature criteria that explicitly consider salmonids' temperature requirements at different times and places. Natural temperature conditions must be preserved whenever possible. Because current fish distributions and populations are significantly reduced from their historical numbers, protection and restoration of their thermal environment must often extend beyond the boundaries of their existing or suitable habitat.

Attempts to set temperature criteria must balance what is known and *not* known about the habitat and biological requirements of salmonids. Full consideration of current and potential fish distribution and habitat, including thorough documentation of assumptions and knowledge gaps, is needed in establishing and implementing temperature criteria to support healthy (viable, productive, and fishable) salmonid populations.

Introduction

Under natural conditions, freshwater salmonid habitat is defined by physical and chemical characteristics of the environment, including water quality, flow, geological and topographic features of the stream and its valley, and cover (National Research Council 1996). Common factors influencing fish distribution include size and accessibility of suitable habitat, connectivity between areas of suitable habitat, biological interactions, and "historical" factors (e.g., postglacial dispersal and geographic barriers) (Matthews 1998). Many of these factors act directly or indirectly with temperature to determine the distribution of a species. This is especially true for cold-water fishes such as salmonids.

This paper is not intended to be an exhaustive review of the status or declines in salmonid populations or distributions. These are widely documented elsewhere. We briefly review some examples of declines in salmonid populations and habitats to provide some context for these issues, but our focus is not on declines per se. Furthermore, this issue paper is not intended to be an exhaustive review of the effects of temperature on salmonid distributions in the Pacific Northwest (see McCullough 1999). Rather, it is intended to describe a basic framework for thinking about salmonid distributions and appropriate biological criteria to protect salmonid populations from adverse effects of altered factors affecting thermal regimes.

This paper describes in a question-and-answer format five main issues related to salmonid distributions and temperature criteria:

1. Definition of a "distribution"
2. Direct effects of temperature
3. Indirect effects of temperature
4. Relevance of scale
5. Importance of unoccupied habitat

What is a "distribution"?

Often, the word "distribution" is used without reference to what is specifically meant. Like any other organism, salmonid fishes (and temperatures) are not distributed equally across landscapes. Within stream basins, limits to fish distributions may be obvious, but even within continuous areas of suitable habitat, discontinuities in distributions may arise (Angermeier et al. in press, Dunham et al. in press).

A common example of "distribution" for animals can be found in popular bird identification and field guides. Distribution maps for birds often cover broad areas. In some cases, ranges of different "races" or recognized subspecies are distinguished. Within these areas, it is obvious that birds do not occur everywhere. For example, a wading bird may only be found in wetland areas, though it is broadly distributed across the continent (because wetlands are broadly distributed). Furthermore, this bird may only be found in particular kinds of wetlands (those with sufficient cover and food to support reproduction). This bird may be found in different areas, depending on the season. Birds may appear in "unusual" habitats while migrating, or may shift habitat use from year to year, depending on climate (wet vs. dry years). Similar analogies apply to salmonid fishes. There are several things to consider when using the term "distribution" for salmonids: ontogenetic variation; life history variation; and historical, contemporary, and potential distribution.

Ontogenetic variation. "Ontogenetic variation" refers to changes in habitat use during the life cycle of an individual. Here, the term "life cycle" refers to the sequence of events (egg → alevin → parr → smolt → juvenile → adult) that must occur within an individual's life for successful reproduction. Ideally, temperature criteria established for salmonids should address spatial and temporal distribution of thermal habitats that protect all life stages.

Habitat requirements vary considerably as salmonids begin their lives as eggs in (or on) the substrate and progress through developmental stages to reproduction as an adult. Different life stages may have different thermal requirements (Magnuson et al. 1979; Physiology issue paper). However, thermal requirements may also overlap considerably among life stages.

Furthermore, some life stages are relatively insensitive to temperature whereas others (such as egg incubation) are extremely sensitive (see Physiology issue paper).

Life stage requirements may be tied to specific spatial or temporal frames. Many salmonids' life stages may use certain habitats only on a seasonal or intermittent basis. For example, the timing of migration and spawning for most species is strongly tied to temperature (Bjornn and Reiser 1991).

Often, assessments for salmonids focus on the distribution of areas used for spawning and early rearing (Dunham et al. 2001). Even though the importance of spawning and rearing habitat is obvious, other components of the life cycle may be key to viability or productivity, particularly for species with obligate life histories. Such habitats can include migratory corridors, feeding areas, and seasonal refuges (Northcote 1997). In many species, loss or severe degradation of these habitats can cause extinction even if spawning and rearing habitats are in good condition. An obvious example is extinction of migratory salmonid populations that used spawning habitats now blocked by dams. As of 1991, at least 106 major populations of salmon and steelhead on the West Coast of the United States had become extinct, with inadequate fish passage at dams a primary cause (Nehlsen et al. 1991).

Life history variation. Life history refers to how an individual completes the life cycle. Salmonids may adopt a "resident" or "migratory" life history. Resident fish remain very close to their natal habitats throughout their life cycle, whereas migratory fish use a much broader range of habitat. Each of these broad categories has its own variations. For example, spawning migrations vary by time and location (e.g., summer vs. winter steelhead; fall vs. winter chinook). The length of juvenile residence in natal areas may also be important (e.g., "stream" vs. "ocean" type chinook).

Some species have relatively fixed life cycles and life history patterns (e.g., pink salmon, Groot and Margolis 1991); others exhibit considerable variation or polymorphism (e.g., cutthroat trout). Most Pacific salmon die after spawning, whereas most species of trout and char do not (iteroparous). Some species, subspecies, races, or populations have flexible life histories (referred to as "facultative"); others have fixed life history patterns (referred to as "obligatory") (Rieman and Dunham 1999). Species in the latter category may be less resistant to environmental change.

Historical vs. contemporary vs. potential distribution. Both fish distributions and stream temperatures can be considered in terms of "historical," "contemporary," or "potential" distribution. Historical refers to the distribution of native salmonids before European settlement. Contemporary refers to the present distribution of native salmonids. Potential refers to the distribution of native salmonids we would expect if natural habitat conditions were restored to the fullest extent possible, given the current natural capacity (Ebersole et al. 1997) of the system. In other words, potential distribution allows for the possibility that physical systems have been altered such that historical distributions are no longer attainable. Widespread declines of salmonids observed in most areas (Nehlsen et al. 1991, Lee et al. 1997, Thurow et al. 1997) suggest that many streams are not currently at their full natural potential or capacity.

A primary concern of managers is protecting or restoring fish distributions that maximize population viability (most recently reviewed by McElhany et al. 2000). Many efforts are under way to define thermal habitat potential using predictive physical models (reviewed by Bartholow 2000). Prediction of physical responses is complex, but is much simpler than predicting biological responses.

Restoration of the physical system (temperature, thermal regime) should be considered together with biological requirements (viability, productivity) of a species. The physical potential of a system constrains what can be achieved biologically. There are four possible scenarios in which physical system potential and biological requirements or potential are considered:

1. System potential attained, biological goal attained. This is the best of all worlds, where protection to maintain existing conditions would be a prudent management option.

2. System potential attained, biological goal **not** attained. This is a situation where nothing can be done to enhance the potential of the natural system to attain a biological goal.

3. System potential **not** attained, biological goal **not** attained. This is a situation where enhancement of system potential could result in a biological benefit.

4. System potential **not** attained, biological goal attained. This is a situation where enhancement of system potential could result in a biological benefit, but the current state of the biological system is satisfactory from a regulatory viewpoint.

It may be difficult to balance the attainment of biological goals versus physical system potential, but the answer is essential to long-term viability and productivity of salmonid populations. In reality, these four scenarios represent extremes along a continuum of biological requirements and physical system potential. In practice, it is much easier to define physical system potential than to define “how much is enough?” from a biological perspective. Thus, it may be difficult to discern different scenarios based on biological requirements. In practice, most management to date has focused on system potential.

Defining of system potential can be challenging. First, it is critical to realize that perspectives on attainment of system potential may depend on scale. For example, a local reach of stream may be at system potential, but part of a larger degraded system in need of restoration. Second, it is difficult, if not impossible, to restore all aquatic habitats to their historic condition. There usually are insufficient data to definitively document “historic” conditions, but even limited information on historic habitat conditions and fish populations can provide a useful perspective. Such determination involves finding what is “irreversible” (e.g., removal of major dams and urban centers) and what can likely be accomplished through basin management.

Examples. The historical and contemporary distributions of resident and anadromous fish have been documented in the Columbia River Basin (CRB) by the Interior Columbia Basin Ecosystem Management Project (Figures 1 to 7). About 12,452 km of the 16,935 km of streams that originally were accessible are now blocked (Quigley and Arbelbide 1997), including some large subbasins and many smaller watersheds. Other factors contributing to the decline of

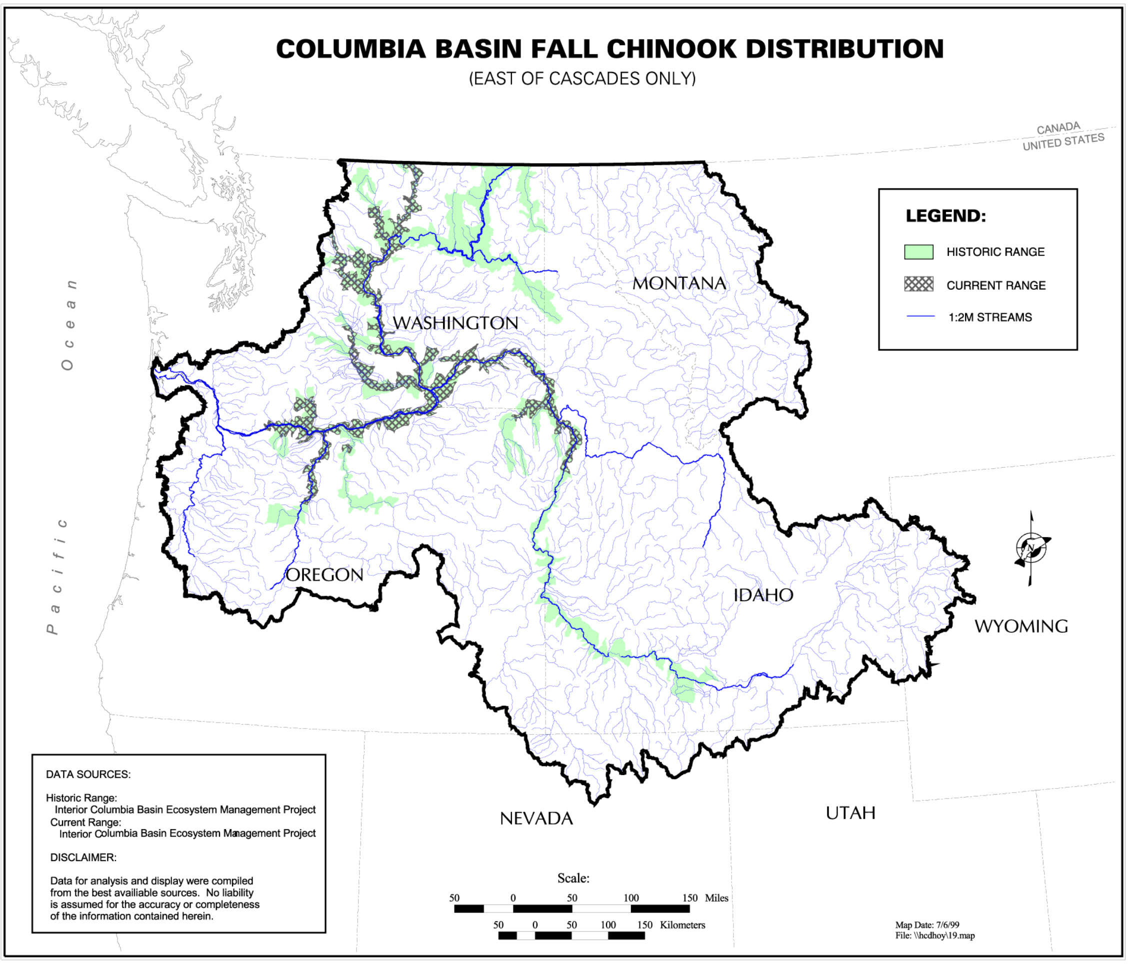
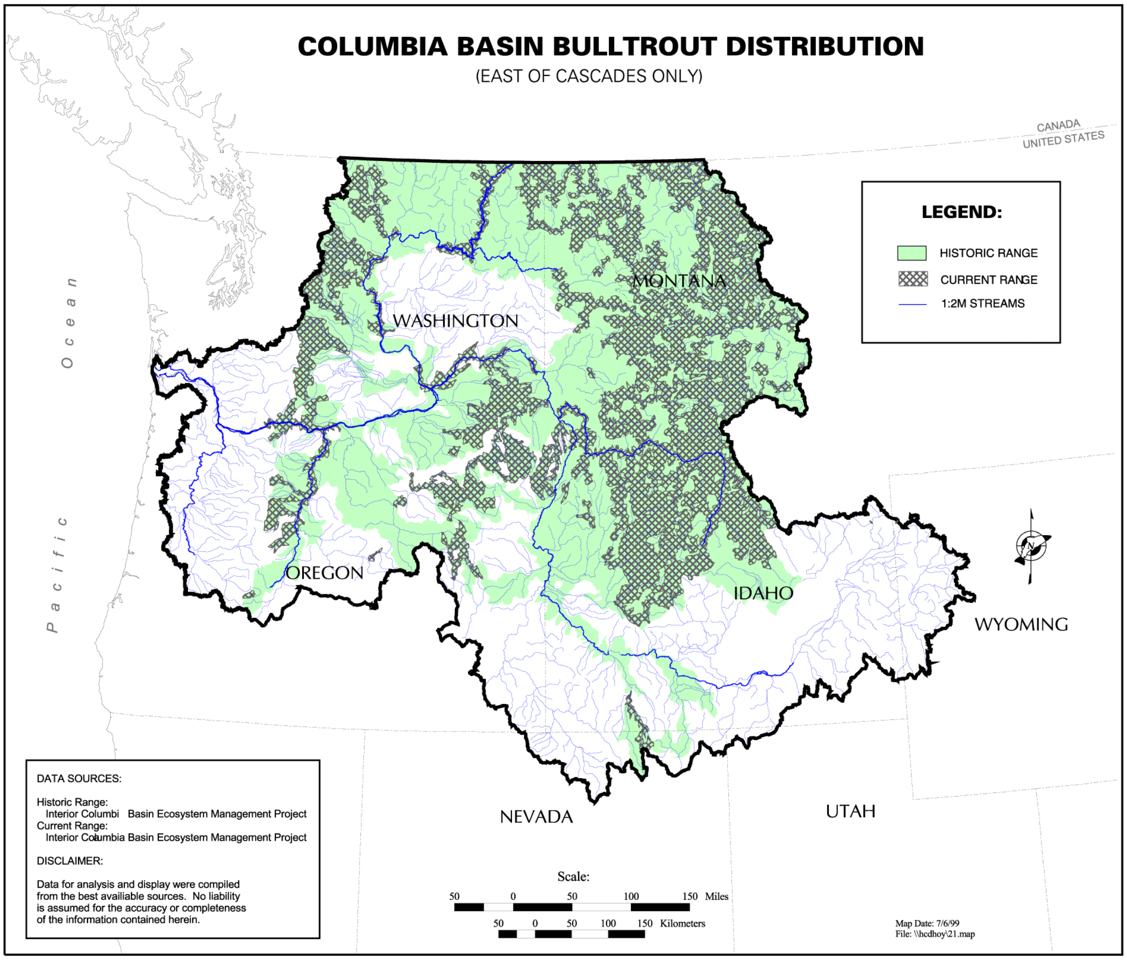


Figure 1. Columbia Basin fall chinook distribution.



DATA SOURCES:

Historic Range:
Interior Columbi Basin Ecosystem Management Project
Current Range:
Interior Columbia Basin Ecosystem Management Project

DISCLAIMER:

Data for analysis and display were compiled from the best availiable sources. No liability is assumed for the accuracy or completeness of the information contained herein.

Map Date: 7/6/99
File: \\hcdhoy\21.map

Figure 2. Columbia Basin bulltrout distribution.

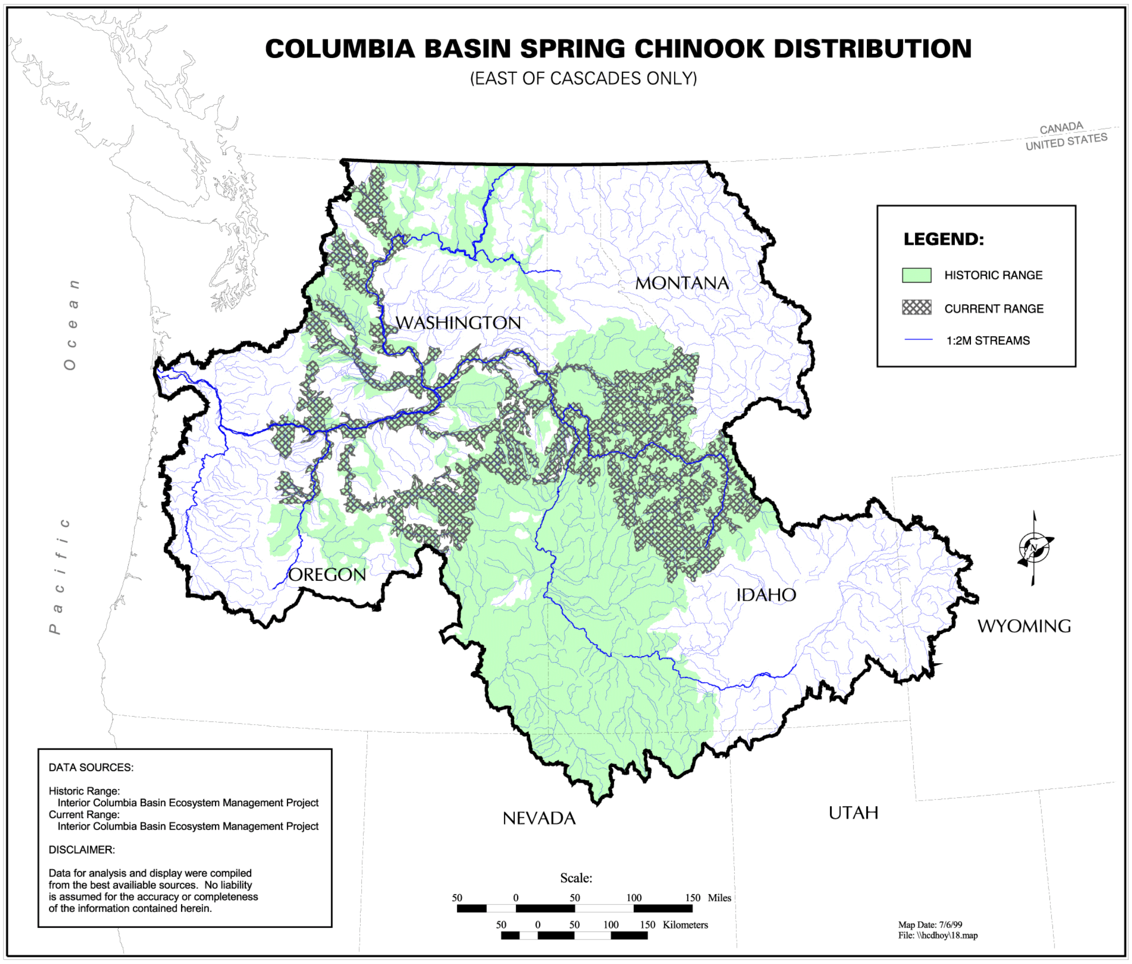
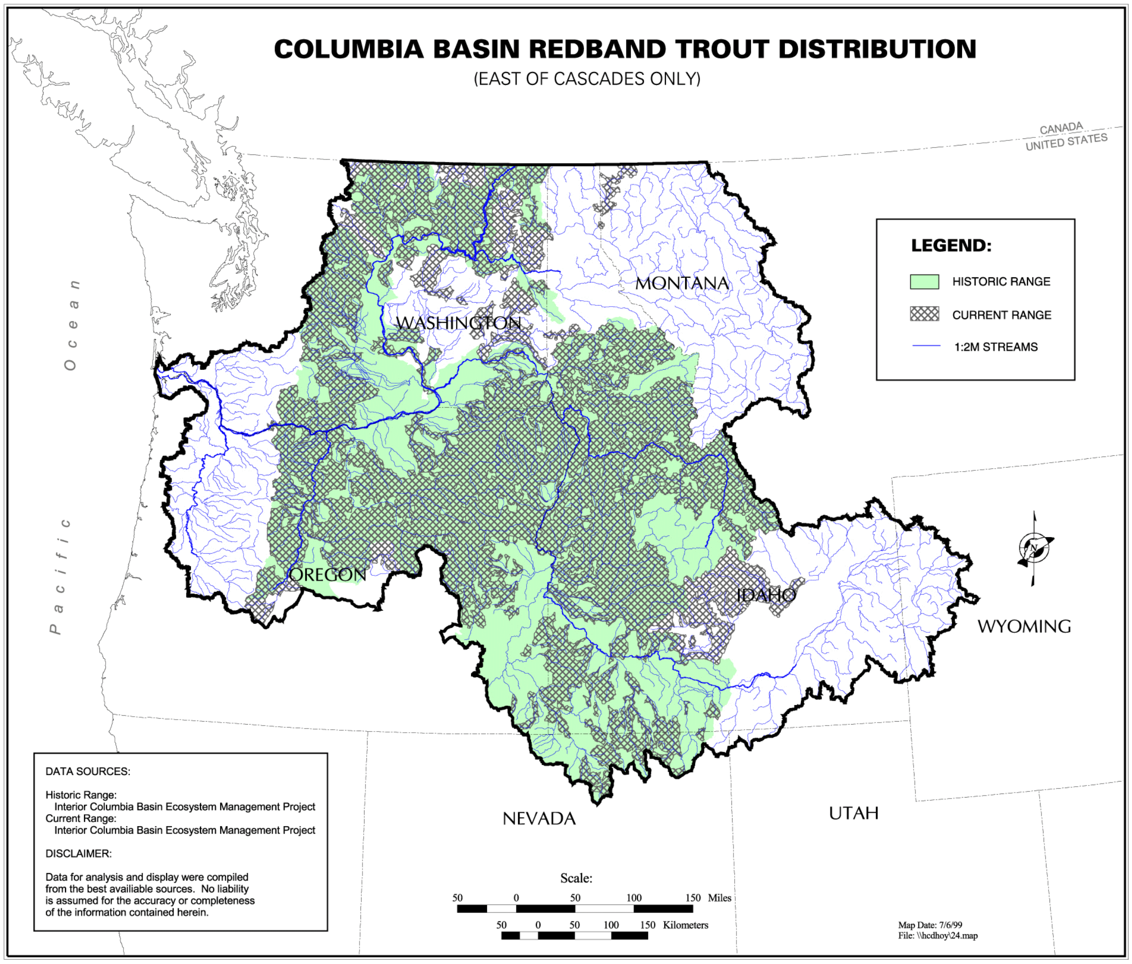


Figure 3. Columbia Basin spring chinook distribution.



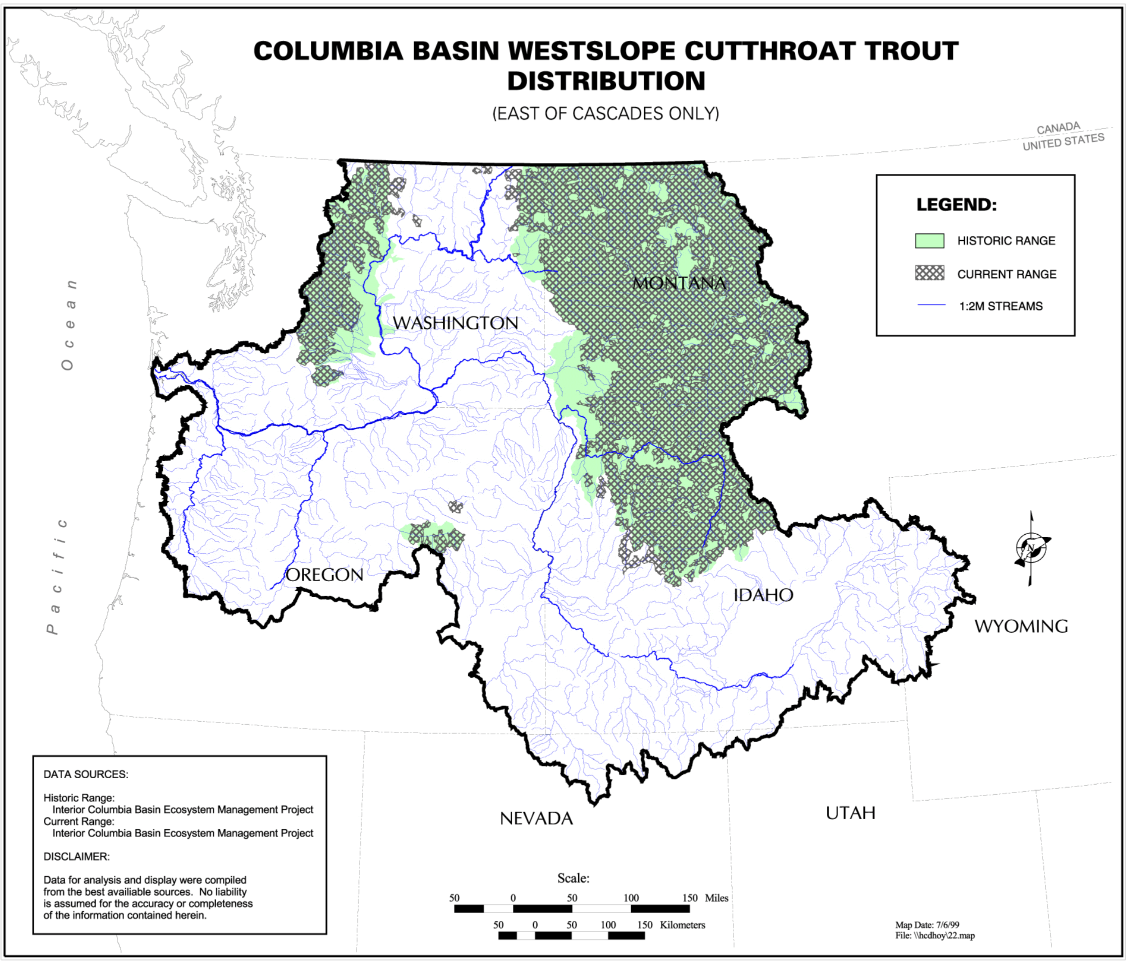
DATA SOURCES:

Historic Range:
Interior Columbia Basin Ecosystem Management Project
Current Range:
Interior Columbia Basin Ecosystem Management Project

DISCLAIMER:

Data for analysis and display were compiled from the best availiable sources. No liability is assumed for the accuracy or completeness of the information contained herein.

Figure 4. Columbia Basin redband trout distribution.


COLUMBIA BASIN WESTSLOPE CUTTHROAT TROUT DISTRIBUTION

(EAST OF CASCADES ONLY)

DATA SOURCES:

Historic Range:
Interior Columbia Basin Ecosystem Management Project
Current Range:
Interior Columbia Basin Ecosystem Management Project

DISCLAIMER:

Data for analysis and display were compiled from the best availiable sources. No liability is assumed for the accuracy or completeness of the information contained herein.

Map Date: 7/6/99
File: \\hcdhoy\22.map

Figure 5. Columbia Basin westslope cutthroat trout distribution.

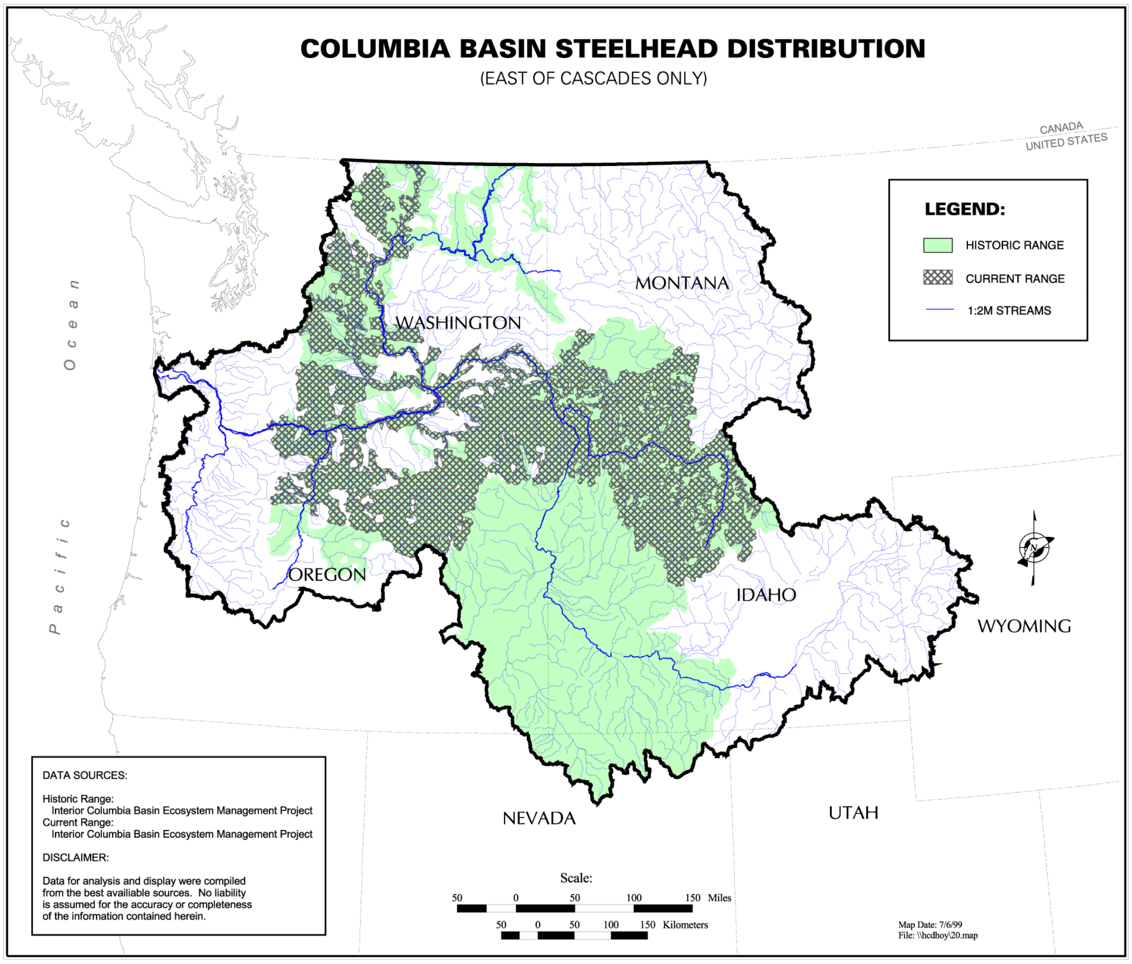


Figure 6. Columbia Basin steelhead distribution.

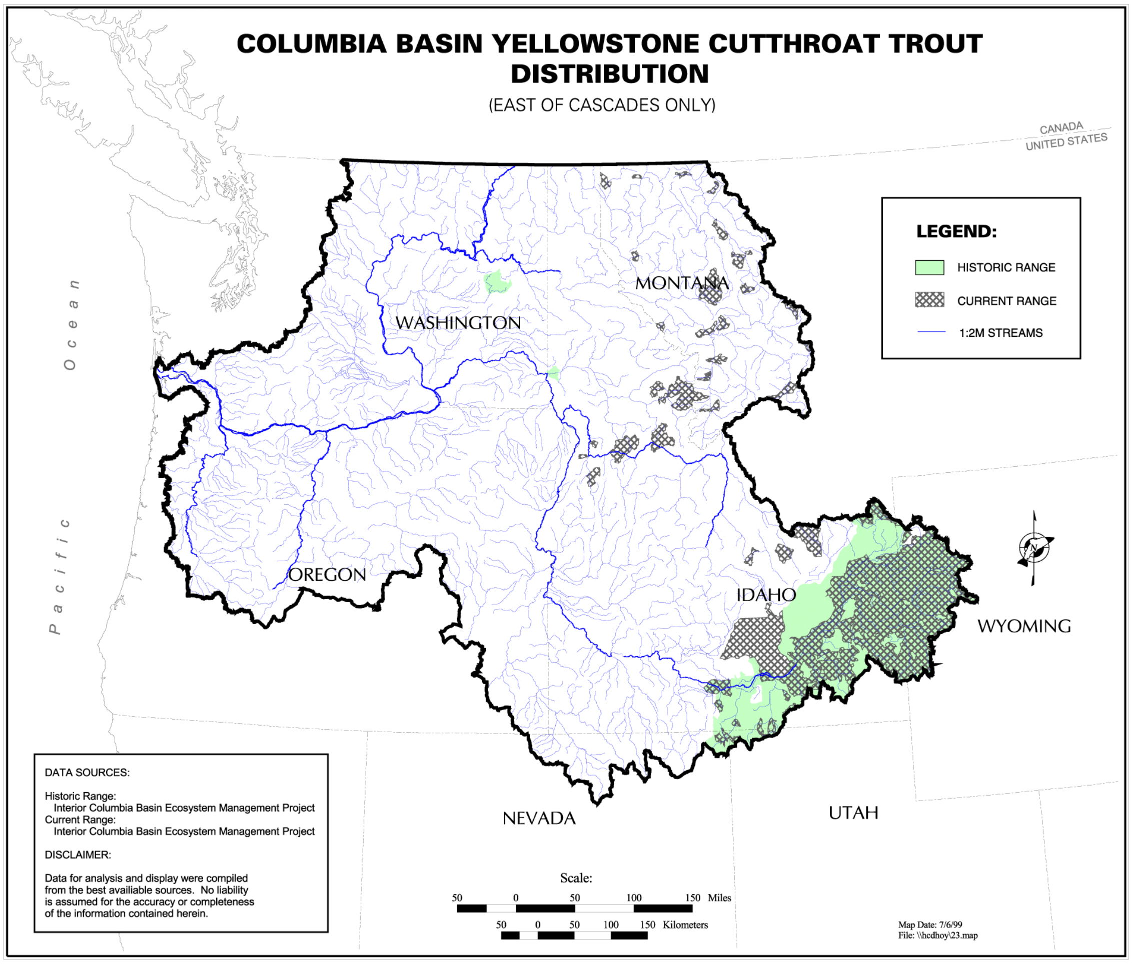


Figure 7. Columbia Basin Yellowstone cutthroat trout distribution.

salmonids in the CRB are habitat loss (including thermal degradation), harvest, and direct and indirect effects of hatcheries (Lichatowich 1999). The current known and predicted distribution of steelhead trout in the CRB encompasses 46% of the historical range. For chinook salmon, the current known and predicted distribution encompasses 28% of the historical range for stream-type chinook and 29% for ocean-type chinook (Quigley and Arbelbide 1997). For many of these species and populations, it is likely that both system potential and biological goals are not attained (scenario 3). In other words, widespread enhancement of system physical potential to minimize adverse effects of altered temperature conditions is needed in the region.

What are the direct effects of temperature?

Temperature may constrain the distribution of fish through direct effects on physiological function. If temperatures are too warm, metabolic rates may rise to the point at which energy intake (e.g., food consumption) is insufficient to maintain basic physiological functions. Growth ceases, and compounding effects of temperature may result in death. Cold temperatures may also be important, particularly where growing seasons are short and fish must endure a long season (e.g., winter) of scarce resources (Shuter and Post 1990). For salmonids in the Pacific Northwest, the concern is unsuitably warm summer temperatures. Currently, there are no criteria that directly address excessively cool temperatures.

Examples. Studies of thermal effects on regional salmonid distributions are numerous (see McCullough 1999). These studies use a wide variety of indicators. At larger scales, it is common to use climate indicators of thermal regimes, such as air temperature, elevation, or geographic location (e.g., Meisner 1990, Flebbe 1994, Keleher and Rahel 1996, Dunham et al. 1999). Geographic variation in distribution of fish populations is typically studied with these large-scale indicators. At finer scales, air temperature can be a poor indicator of fish distributions. Within streams, variation in local climate is minimal, but variation in water temperatures is often obvious. For example, geographic variation in the distribution of cutthroat trout is strongly tied to climate gradients (Dunham et al. 1999). At a smaller scale within streams, water temperature is the best indicator (in terms of water temperature) of suitable conditions for fish (Dunham 1999). At even smaller scales (e.g., stream reach or unit) it may be possible to distinguish habitat use patterns, if local variation in water temperature is large enough to elicit a biologically significant response (e.g., Torgerson et al. 1999; Ebersole et al., in press).

Most attempts to relate salmonid distributions to temperature are based on air temperatures, which are widely available. Air temperature and groundwater temperature are known to be related (either directly or indirectly), which is believed to explain the association between air temperatures and salmonid distributions on a regional scale (e.g., $>10^4$ m, or 6th field hydrologic unit code; see Rieman et al. 1997). However, air temperature generally has only a weak direct influence on surface water temperature (Poole and Berman in press).

More recent studies have focused on direct associations between fish distributions and surface water temperatures. As digital data loggers and remote sensing (e.g., forward-looking infrared ideography, Torgerson et al. 1999) become more accessible, reliance on indirect measures of aquatic thermal regimes (e.g., regional climatic or air temperatures) will be less necessary.

What are indirect effects of temperature on fish distributions?

The direct effects of temperature are obvious, but indirect effects can be important as well. Multiple stressors (see Multiple Stressors issue paper) can modify the effect of temperature on probability of survival under different thermal regimes. In colder seasons, fish may be vulnerable to warm-blooded predators, including birds and mammals (Conduce et al. 1998). In warm seasons, thermal stress may similarly render fish susceptible to predators, competitors, or disease. Patterns of habitat use may change. Abundance of prey may also change (e.g., Li et al. 1994). Interactions of these factors with temperature may affect fish distributions and responses to temperature, as in the following examples.

Biotic interactions. The response of a species to a given thermal environment can be modified dramatically by biotic interactions (e.g., competition, disease, predation) within or among species. In some cases, this influence may affect the distribution of a species.

Within a species, temperature may affect important life history attributes, such as size and age at emigration and return times for spawning adults. Within cohorts, intraspecific competition for limited resources (e.g., food, shelter, mates) may be affected, possibly leading to variation in competitive ability and fitness of individuals and changing patterns of growth and survival. The subtle influences of these factors on the distribution of fish within aquatic habitats has not been documented in the published literature.

There is better evidence for the influence of temperature on distribution of fishes among different species. In studies by Reeves et al. (1987), juvenile steelhead production was the same at water temperatures of 53.6-59°F (12-15°C) whether red shiners were present or not. At warmer temperatures (66.2-71.6°F [19-22°C]), steelhead production was lower when shiners were present than when shiners were absent. Additional examples can be found in the Behavior and Multiple Stressors issue papers.

Habitat size and isolation. Thermal gradients often result in erratic distribution of fish populations (Dunham et al. 2001). Changes in the size and distribution of habitats result in habitat fragmentation, which has been documented for several species (e.g., Rieman and Dunham 2000). Generally, as habitat size decreases and isolation increases, the occurrence of fish decreases. For bull trout *(Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) limited evidence suggests these species are unlikely to be found in watersheds with surface areas of less than roughly 10^5 ha (Dunham et al., in press). Available data are not sufficient to propose minimum area requirements for any species (Rieman and Dunham 2000). Populations in smaller habitats are assumed to be more vulnerable to chance extinction, or extinction caused by deterministic factors such as replacement by competitors or land use impacts (see McElhany et al. 2000).

What is meant by "scale" and "level?" At what "level" should we be concerned with temperature criteria to protect fish distributions?

Temperature can affect fishes at several scales and levels. Scale refers to the space or time dimensions of a problem, whereas level refers to the ways in which physical or biological processes are organized (for details, see Allen 1998). A local population may be considered as a level of biological organization, for example. Local populations for salmonids may correspond to the distribution of spawning and rearing areas (Dunham et al. in press). In terms of scale, local populations can occupy very small or very large watersheds. Thus, "scale" and "level" are not exactly synonymous.

Research on salmonid habitat has addressed a wide variety of spatiotemporal scales and levels. In the 1970s and 1980s, research often focused on fishery production. Numerous studies addressed the relationship between standing crop of salmonids and site-specific habitat characteristics (e.g., pools, cover, substrate). These models were often limited by their lack of transferability in space or time and poor predictive ability (Fausch et al. 1988). Existing EPA temperature criteria (U.S. EPA 1998) are site-specific and do not address larger scale issues of landscape processes and fish distributions.

Recent models have addressed aquatic habitat at larger spatial scales (Johnson and Gage 1997; see Spatial-Temporal Issue Paper) and focused more on patterns of species diversity, distribution, and occurrence than on standing crop (Dunham et al. in press, Angermeier et al. 2001). Larger scale approaches to salmonid habitat focus on both habitat characteristics and the spatial context of a habitat in the landscape (Rieman and Dunham 1999). Part of the motivation for a larger scale approach is the need for models that address habitat requirements at the population level. Population-level concerns (e.g., occurrence, persistence, diversity) are increasingly critical in this region as the list of threatened, endangered, and sensitive salmonids grows.

Information on thermal relationships of salmonids comes from a variety of laboratory and field studies—how do we integrate work conducted at different scales or levels of organization (e.g., population vs. individuals)?

One important issue related to scaling is the connection between laboratory studies of thermal tolerance and thermal habitat use in the field. EPA criteria for temperature (Federal Register 1998, Brungs and Jones 1977) are based on laboratory tests of individual fish responses to temperature. These experiments provide a mechanistic basis for understanding the effects of temperature on individual fish. In the laboratory, a rigorous experimental design can isolate the effects of specific factors and test for interactions among factors.

It is difficult to extrapolate results obtained under laboratory conditions to the field, where many uncontrolled factors interact simultaneously. Nonetheless, it is in the field that temperature has a potentially important role. Although it is sometimes possible to conduct large-scale field experiments, field studies more often involve analyses of correlation or association between factors, such as fish distribution and temperature. Obviously, such correlations do not necessarily constitute cause and effect. Development of temperature criteria must therefore involve a combination of approaches, including laboratory experiments and field studies. Integrating pattern and process across multiple scales or levels of biological organization is essential for correct ecological inference (Werner 1998). Following are several examples.

EPA Fish and Temperature Database Matching System (FTDMS). A simple example of integrating field and laboratory studies comes from results of the EPA's FTDMS, Eaton et al. 1995). Eaton et al. (1995) found a close correspondence between laboratory-derived thermal tolerance limits and maximum water temperatures in the field. For salmonids, maximum water temperatures in the field were 33.8-39.2°F (1-4°C) cooler than limits indicated by laboratory studies. The fact that fish distributions in the field corresponded to cooler temperatures suggests that sublethal effects may be important. This may occur when temperature directly or indirectly acts as one of multiple stressors (see Temperature Interaction issue paper).

"I saw fish in hot water." Sometimes simple observations of fish in unusually warm water are used to support (or reject) proposed temperature criteria or thresholds. Such observations do not indicate anything about individual fitness or population health. Furthermore, they ignore the essential chain of inference that should be made using both laboratory and field observations (Werner 1998). Observations of fish in "unusual" (or *any*) conditions should be interpreted in a probabilistic context. For example, given the observed thermal regime, what is the *probability* that a given species will occur? Determining this requires information (and evidence) on a fuller range of thermal conditions and is much more informative. Salmonid fish may occasionally occur in "hot" water, but in general they are much more likely to occur when temperatures are cooler. This is illustrated by the wide range of temperatures where salmonids and other species are observed to occur (Figure 8).

A useful perspective can be found in humans' use of high-temperature environments. In many cultures, it is common to engage in recreational or ritual use of steam baths, saunas, sweat lodges, hot springs, or other extremely warm microclimates. Although limited use of these environments is common, they are by no means suitable in the long term; the negative health effects are obvious to humans. Fish, like humans, will occasionally be found in thermal habitats that are unsuitable for long-term (and sometimes even short-term) health. In some cases, short forays into physiologically stressful habitats may provide a net benefit. Many prey organisms make use of predator-free space, which often exists at the extremes of physiological tolerance for predators (e.g., Rahel et al. 1994).

Is unoccupied habitat relevant to temperature requirements of salmonids?

Thermal habitat can be utilized at a variety of spatial and temporal scales (see also Spatial/Temporal issue paper). Spatial and temporal variation in the availability of thermal habitat may be an important constraint. Temperature criteria should address all temperatures likely to be used by fish, not just upper, lower, or "optimal" temperatures. It is the full range of thermal variability that provides a context for continued evolution of species (Lichatowich 1999). Distribution of "habitat" can extend well beyond that which is currently occupied by a species or population.

Because of natural variation in space and time, most fish occupy landscapes with a considerable amount of suitable but unoccupied habitat. Unoccupied habitat is a natural consequence of extinction and recolonization, natural habitat succession, and human influences on fish populations and habitats (Reeves et al. 1995, Rieman and Dunham 2000). Therefore, the distribution of habitat needed by fish may extend well beyond that which is currently occupied.

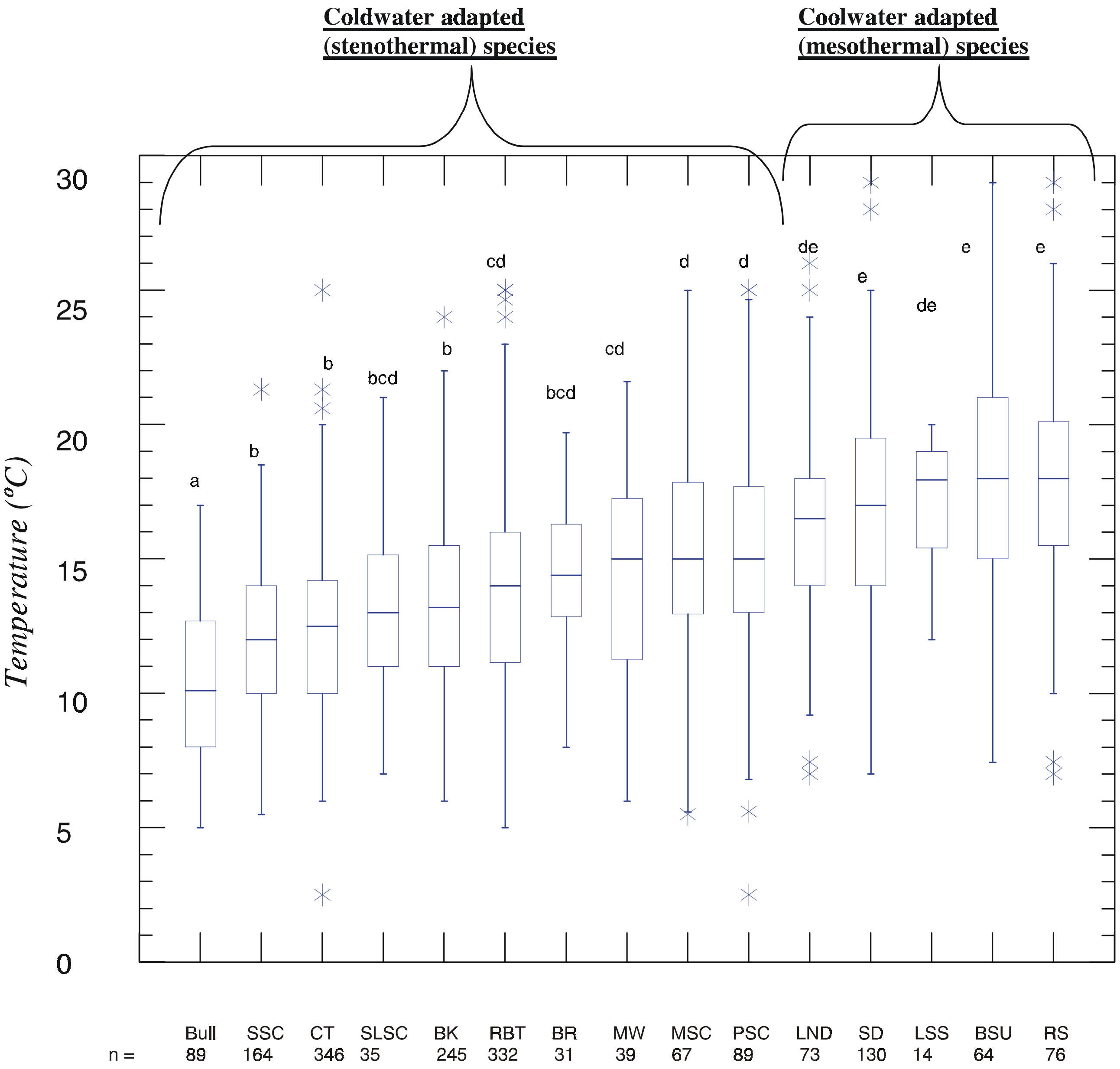


Figure 8. Distribution of summertime point temperatures at which selected fish species occurred in Idaho. Boxes indicate the median and upper and lower quartiles (the central 50% of the values), the whiskers extend up to 1.5X the interquartile value, and asterisks show outlying values. Plots marked with the same letter indicate that their means are not significantly different at P<0.05 using Tukey's multiple comparison procedure. Data from the Idaho Department of Environmental Quality beneficial use reconnaissance program.

Code	Common Name	Scientific Name	Code	Common Name	Scientific Name
Bull	Bull trout	*Salvelinus confluentus*	MW	Mountain whitefish	*Prosopium williamsoni*
SSc	Shorthead sculpin	*Cottus confusus*	MSC	Mottled sculpin	*Cottus bairdi*
Cutt	Cutthroat trout	*Oncorhynchus clarki*	PSC	Paiute sculpin	*Cottus beldingi*
SLSC	Slimy sculpin	*Cottus cognatus*	LND	Longnose dace	*Rhinichthys cataractae*
BK	Brook trout	*Salvelinus fontinalis*	SD	Speckled dace	*Rhinichthys osculus*
RBT	Rainbow trout	*Oncorhynchus mykiss*	LSS	Largescale sucker	*Catostomus macrocheilus*
BR	Brown trout	*Salmo trutta*	BSU	Bridgelip sucker	*Catostomus columbianus*
			RS	Redside shiner	*Richardsonius balteatus*

This is especially true for most threatened and endangered species because current distributions are reduced or declining.

Unoccupied habitat is a potentially controversial issue, particularly because it can be difficult to identify areas needing protection. When fish are present, the choice of habitat to protect or restore can be relatively obvious. When fish are not present, the choice must be guided by information on historical and potential distributions of fish and suitable habitat, and potential sources of natural recolonization.

Conclusion

Salmonids in the Pacific Northwest evolved in habitats with large amounts of cold, clean water. Their life histories and ecology are strongly tied to natural thermal regimes. Region-wide declines in salmonids have paralleled the loss and fragmentation of formerly large and interconnected cold water habitats, and changes in thermal regimes (see Spatial/Temporal issue paper). Temperature is widely appreciated as an important factor affecting not only the health of individual fish, but also entire populations and species assemblages. Direct effects of temperature may be obvious, or temperature may interact with other important variables to indirectly affect salmonids.

Temperature criteria that explicitly consider the thermal requirements of salmonids at multiple spatial and temporal scales (see also Spatial/Temporal issue paper), and the connection between salmonids and natural thermal regimes, will be most protective of existing populations and offer a means for restoring depressed populations. In many cases, protection and restoration of thermal habitat must extend beyond the current boundaries of existing occupied and/or suitable habitat, because current fish distributions are significantly reduced from their historical extent.

Attempts to set temperature criteria must balance what is known and *not* known about the physical system potential and biological requirements of salmonids. Consideration of unknown factors is essential in determining precautionary measures to avoid adverse effects related to temperature criteria. General guidelines for assessing salmonid populations (e.g., McElhany et al. 2000) provide a means for determining the "knowns" and "unknowns." Full consideration of the weight of evidence about current and potential fish distribution and physical system potential, including thorough documentation of assumptions and knowledge gaps, is needed in establishing and implementing temperature criteria to support healthy (viable, productive, and fishable) salmonid populations.

Literature Cited

Allen TFH. 1998. The landscape "level" is dead: Persuading the family to take it off the respirator. In: Peterson DL, Parker VT, eds. Ecological Scale: Theory and Applications. New York: Columbia University Press, pp. 35-54.

Angermeier PL, Krueger KL, Dolloff CA. In Press. Discontinuity in stream-fish distributions: Implications for assessing and predicting species occurrences. In: Scott JM, Heglund PJ, Samson F, Haufler J, Morrison M, Raphael M, Wall B, eds. Predicting Species Occurrences: Issues of Accuracy and Scale. Covelo, CA: Island Press.

Bartholow JM. 2000. The stream segment and stream network temperature models: A self-study course. Version 2.0. U.S. Geological Survey Open File Report 99-112.

Bjornn TC, Reiser DW. 1991. Habitat requirements for salmonids. Am Fish Soc Special Pub 19:83-138.

Brungs WA, Jones BR. 1977. Temperature criteria for freshwater fish: Protocol and procedures. Environmental Research Laboratory-Duluth, Office of Research and Development, U.S. Environmental Protection Agency, EPA-600/3-77-061, Duluth, MN.

Cunjak RA, Prowse TD, Parrish DL. 1998. Atlantic salmon (*Salmo salar*) in winter: “The season of parr discontent?” Can J Fish Aquat Sci 55(Suppl. 1):161-180.

Dunham JB. 1999. Temperature criteria for Oregon’s Lahontan cutthroat trout. Report to Oregon Department of Environmental Quality, Portland, OR.

Dunham JB, Rieman BE. 1999. Metapopulation structure of bull trout: Influences of physical, biotic, and geometrical landscape characteristics. Ecol Appl 9:642-655.

Dunham JB, Rieman BE, Peterson JT. In Press. Patch-based models to predict species occurrence: Lessons from salmonid fishes in streams. In: Scott JM, Heglund PJ, Morrison M, Raphael M, Haufler J, Wall B, eds. Predicting Species Occurrences: Issues of Accuracy and Scale. Covelo, CA: Island Press.

Dunham JB, Peacock MM, Rieman BE, Schroeter RE, Vinyard GL. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Trans Am Fish Soc 128:875-889.

Eaton JG, et al. 1995. A field information-based system for estimating fish temperature tolerances. Fisheries 20(4):10-18.

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

Ebersole JL, Liss WJ, Frissell CA. 1997. Restoration of stream habitats in the western United States: Restoration as reexpression of habitat capacity. Environ Manage 21:1-14.

Fausch KD, Hawkes CL, Parsons MG. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. USDA Forest Service General Technical Report PNW-GTR-213. USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Flebbe PA. 1994. A regional view of the margin: Salmonid abundance and distribution in the southern Appalachian mountains of North Carolina and Virginia. Trans Am Fish Soc 123:657-667.

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

Johnson LB, Gage SH. 1997. Landscape approaches to the analysis of aquatic ecosystems. Freshwater Biol 37:113-132.

Keleher CJ, Rahel FJ. 1996. Thermal limits to salmonid distributions in the Rocky

Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Trans Am Fish Soc 125:1-13.

Lee D, Sedell CJ, Rieman B, Thurow R, Williams J. 1997. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR, Report Number PNW-GTR-405.

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.

Lichatowich J. 1999. Salmon without rivers: A history of the Pacific salmon crisis. Covelo, CA: Island Press.

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

Matthews WJ. 1998. Patterns in freshwater fish ecology. New York: Chapman and Hall.

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. Prepared for the U.S. Environmental Protection Agency, Region 10, Seattle, WA.

McElhany P, Ruckleshaus M, Ford MJ, Wainwright T, Bjorkstedt E. 2000. Viable salmon populations and the recovery of evolutionarily significant units. U.S. Dept. of Commerce, NOAA Technical Memorandum NMFS-NWFSC-42.

Meisner JD. 1990. Effect of climate warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Can J Fish Aquat Sci 47:1065-1070.

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

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.

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

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

Quigley TM, Arbelbide SJ, eds. 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins: vol. 3. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Rahel FJ, Nutzman JW. 1994. Foraging in a lethal environment: Fish predation in hypoxic waters of a stratified lake. Ecology 75:1246-1253.

Reeves GH, Benda LE, Burnett KM, Bisson PA, Sedell JR. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. In: Nielsen JL, ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17, Bethesda, MD. pp. 334-349.

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

Rieman BE, Dunham JB. 2000. Metapopulations and salmonids: A synthesis of life history patterns and empirical observations. Ecol Freshwater Fish 9:51-64.

Rieman BE, Lee DC, Thurow RF. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath Basins. N Am J Fish Manage 17:1111-1125.

Shuter BJ, Post JR. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans Am Fish Soc 119:314-336.

Thurow RF, Lee DC, Rieman BE. 1997. Distribution and status of seven native salmonids in the Interior Columbia River Basin and portions of the Klamath River and Great Basins. N Am J Fish Manage 17:1094-1110.

Torgersen CE, Price DM, Li HW, McIntosh BA. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecol Appl 9:301-319.

U. S. Environmental Protection Agency. 1998. National recommended water quality criteria; republication. Federal Register 63:68354-68364.

Werner EE. 1998. Ecological experiments and a research program in community ecology. In: Resetarits WJ, Bernardo J, eds. Experimental ecology: Issues and perspectives. New York: Oxford University Press.