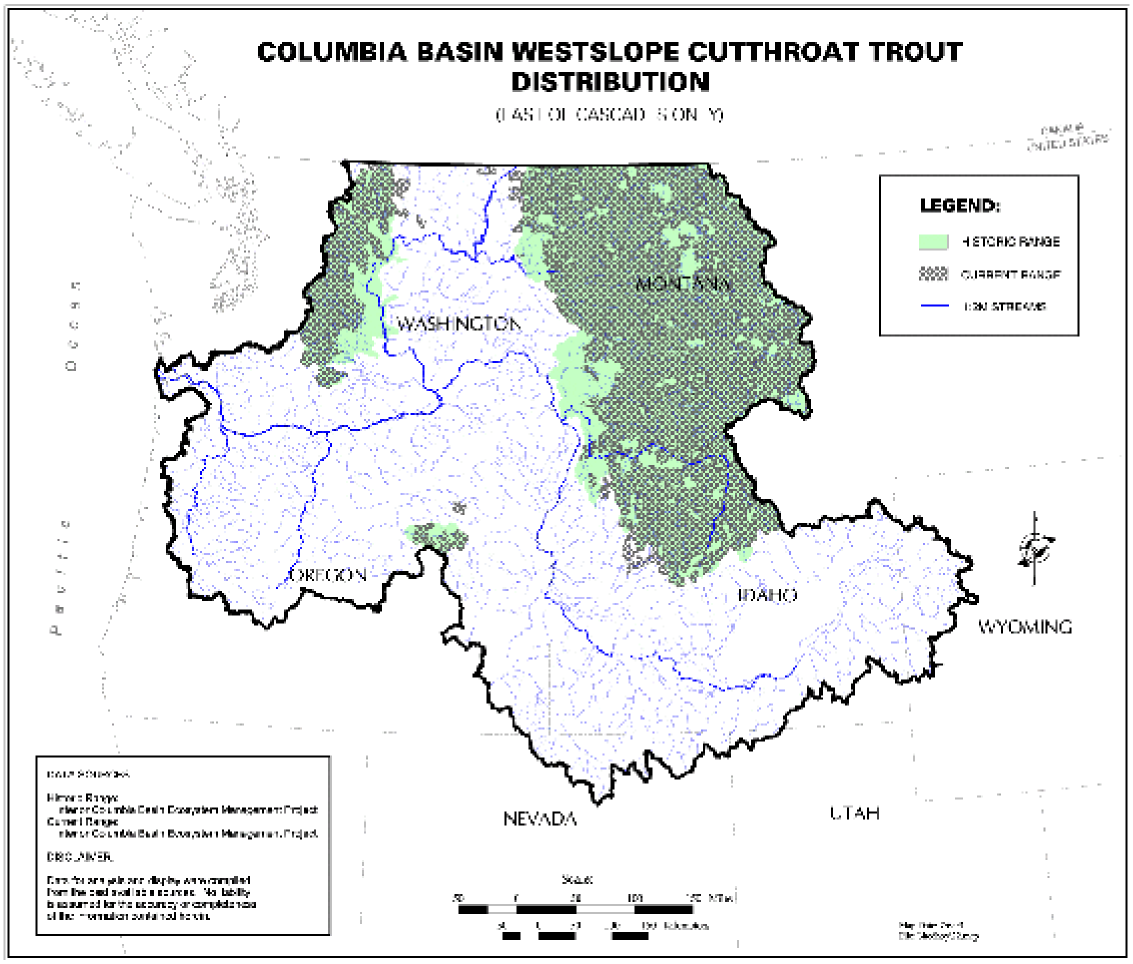

Figure 5. Columbia Basin westslope cutthroat trout distribution.

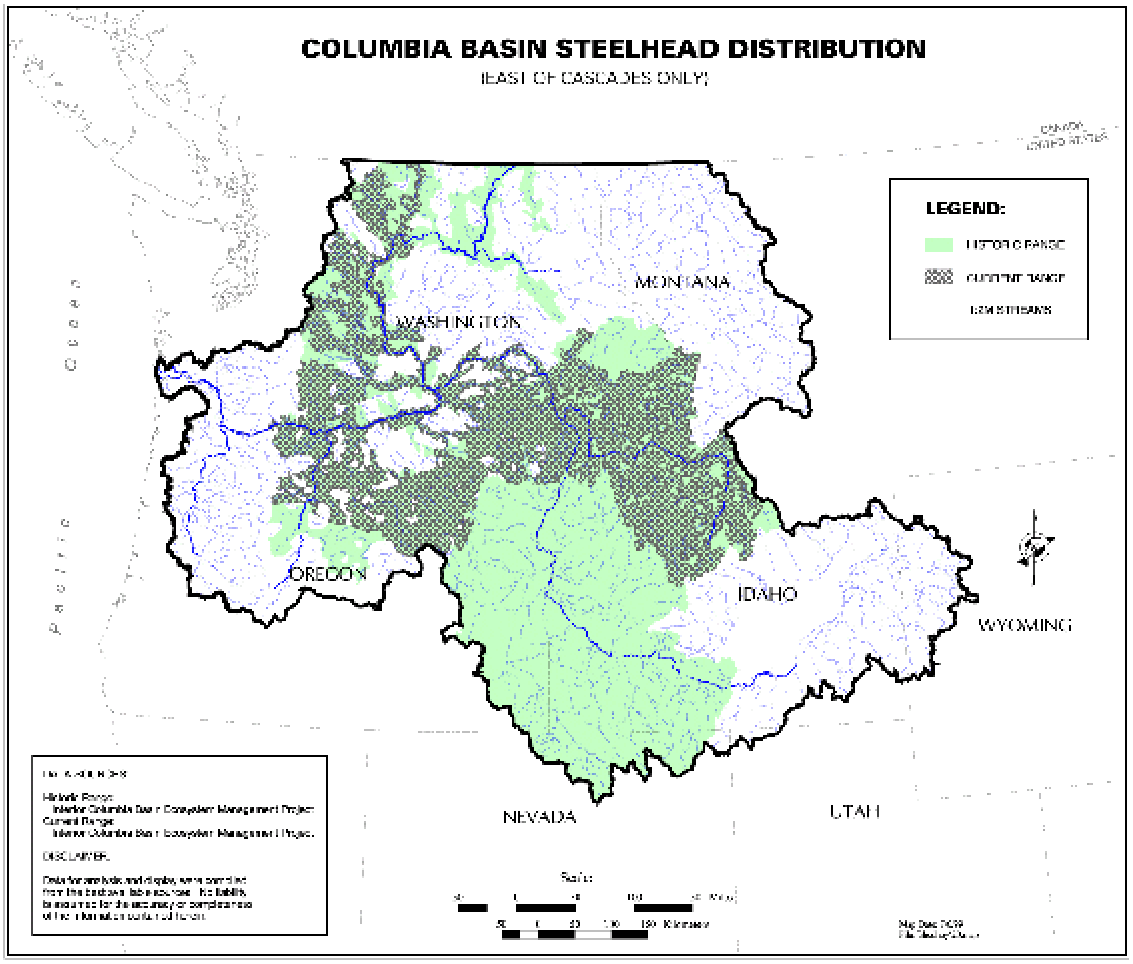

Figure 6. Columbia Basin steelhead distribution.

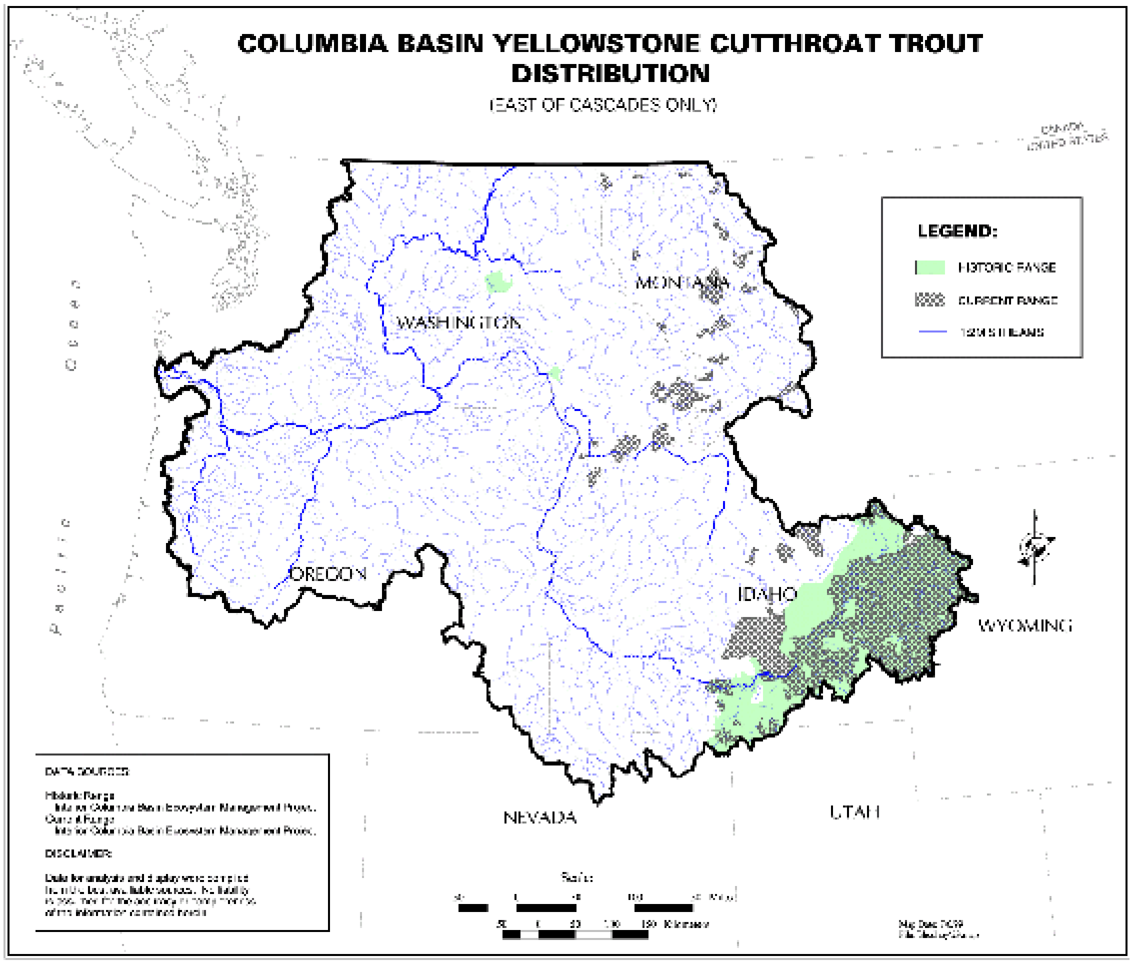

Figure 7. Columbia Basin Yellowstone cutthroat trout distribution.

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 6^{th} 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).

Point Observation of Cold-Water Fish in Relation to Temperature 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.

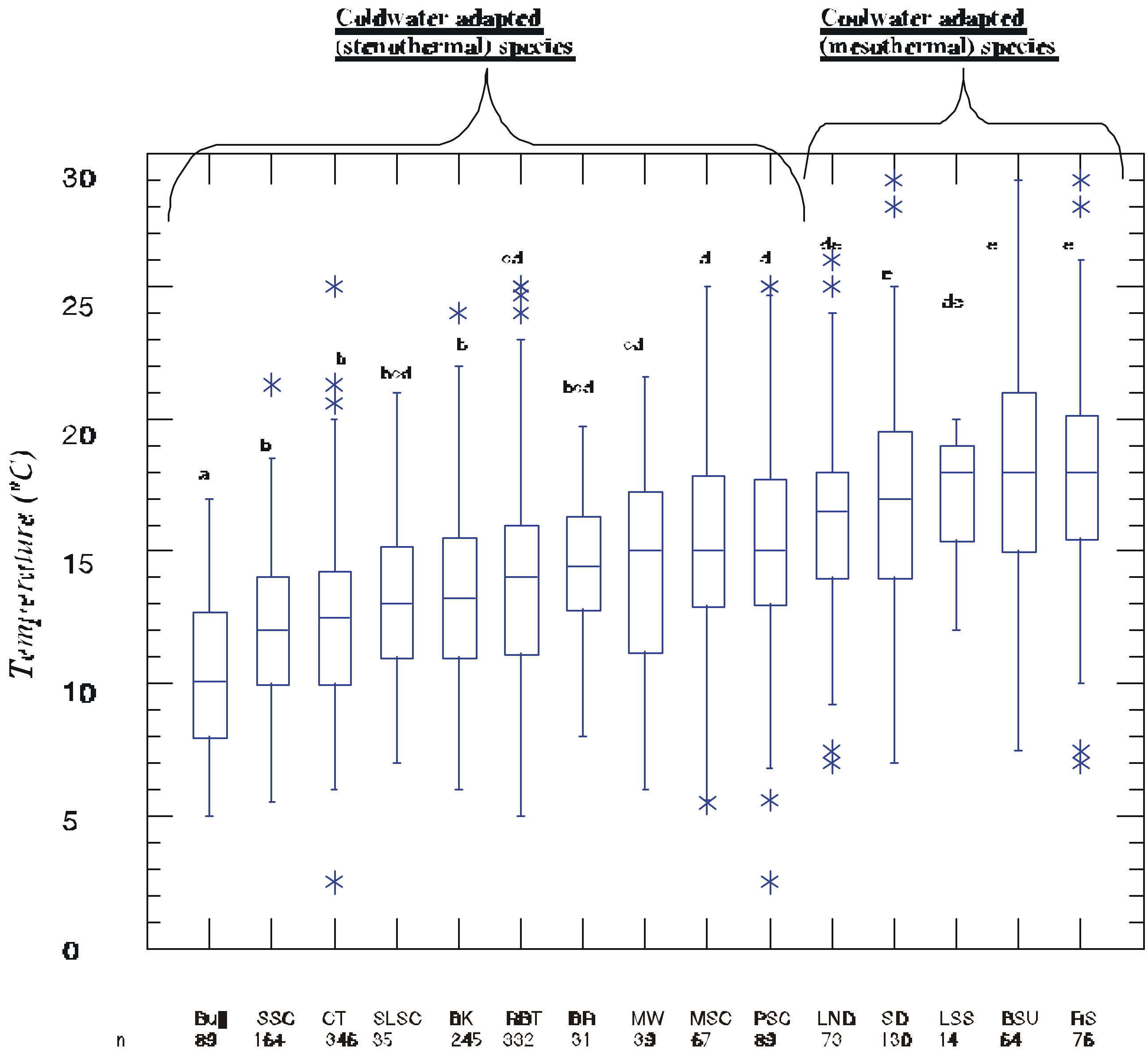

Figure 8. Distribution of summertime point temperatures at which selected fish species occurred in Idaho. Boxes indicate the median and upper and lower quartiles (the central 50% of the values), the whiskers extend up to 1.5X the interquartile value, and asterisks show outlying values. Plots marked with 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.

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