

## Using Current Biogeographic Limits to Predict Fish Distributions Following Climate Change

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**Abstract.**—There is a long history in fisheries biology of relating biogeographic distribution patterns of fish to thermal conditions. The association of distribution boundaries with thermal limits reflects the fact that temperature has a major influence on the physiology, growth, and behavior of ectothermic animals such as fish. Approaches used to relate species distributions to thermal limits can be grouped into four categories: air temperatures, surface water temperatures, groundwater temperatures, and correlates of temperature such as agricultural growing season. Air temperature limits typically focus on mean daily air temperature for the warmest month of the year and are based on the assumption that air and water temperatures are correlated. Water temperatures limits include measures of daily mean as well as daily maximum temperature, both averaged over periods of weeks to a month. Groundwater temperature limits are based on the observation that groundwater integrates annual temperature conditions and is usually within 1–2°C of the mean annual air temperature. Correlates of air or water temperature include measures of the agricultural growing season or elevation. Biogeographic limits can be used to infer thermal limits that can be used to model fish distribution changes following climate change. The assumption is that fish populations will migrate pole-ward or up in elevation to remain within suitable thermal envelopes. Several studies that have used this approach predict a substantial loss of habitat for coldwater fishes due to climate warming. When using biogeographic limits to model species responses to climate change, researchers should ensure that distribution patterns reflect thermal limits rather than other limiting factors and should recognize that changes in other factors, especially hydrological regime, also may alter fish distribution patterns in the future.

### Introduction

Biogeography is the study of species distribution patterns at large spatial scales (Cox and Moore 1980). Early naturalists were interested in describing species distributions and as the science of ecology developed, mere description was replaced by the desire to identify which environmental factors determine species distribution patterns. Temperature has long been a focus of biogeographic studies because of its overwhelming influence on the physiology of ectothermic organisms (Hutchins 1947). Because fish are ectothermic, their survival, growth, egg development, and even competitive ability all are temperature-dependent (Magnuson and DeStasio 1996; Taniguchi et al. 1998; King et al. 1999; Power and van den Heuvel 1999). Hence, it was logical for early workers to consider how temperature influenced fish distribution patterns (Radforth 1944).

Most of the early studies involving freshwater fishes focused on air temperature limits because of the paucity of temperature data for lakes and streams. For example, Weatherley (1963) investigated the world distribution of yellow perch *Perca flavescens* and noted

that the southern margin of their distribution in the United States corresponded with mean maximum mid-summer air temperatures of 31°C (Figure 1). Many other investigators reported associations between biogeographic distributions and air temperature isotherms (Radforth 1944; MacCrimmon and Marshall 1968; MacCrimmon and Campbell 1969; Shuter et al. 1980). With the accumulation of water temperature records, associations between fish distributions and water temperatures became of interest (Eaton et al. 1995). Today, the interest in thermal limits to fish distributions continues both for understanding the basic ecology of species (Fausch et al. 1994; Rahel and Nibbelink 1999; Welsh et al. 2001) and for predicting how fish distributions may be altered by climate warming (Shuter and Post 1990; Rahel et al. 1996; Stefan et al. 2001). In this chapter, the types of thermal limits that have been associated with fish species distributions are described, an example of how thermal limits can be used to forecast the loss of habitat for coldwater fishes in the Rocky Mountain region is discussed, and caveats in using biogeographic limits to model the response of fish to climate change are discussed.

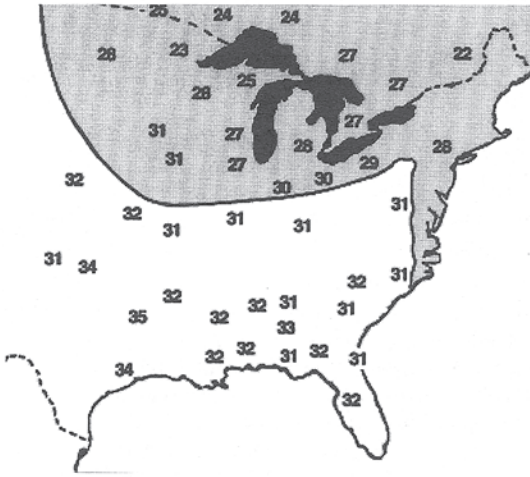


Figure 1. Shaded area indicates the native distribution of yellow perch *Perca flavescens* in eastern North America. The southern limit corresponds to areas where mean maximum summer air temperatures do not exceed 31°C. Adapted from Weatherley (1963).

## Types of Thermal Limits Used

A large number of approaches have been used to relate species distributions to thermal limits. They were grouped into four categories: air temperature limits; surface water temperature limits; groundwater temperature limits, and correlates of air or water temperature such as agricultural growing season (Table 1). However, as noted below, there is considerable variation even within categories.

Air temperature limits typically focus on mean daily air temperature for the warmest month of the year on the assumption that air and water temperatures will be correlated. This assumption appears to be reasonable, especially over time scales of a week or longer and when mean daily air temperatures are less than 25°C (Mohseni et al. 1998).

Water temperature limits include measures of daily mean temperature, e.g. studies 1–3, Table 1, as well as daily maximum temperatures both averaged over some time period, usually a week or a month (studies 4–6, Table 1). The focus on daily maximum temperatures reflects the idea that it is exposure to high temperatures that kills fish. However, it is not clear whether physiological stress is related more to the mean or to the maximum daily temperature experienced by fish. Fish can survive daily exposures to temperatures that would be lethal over extended periods, provided that temperatures cool off at night as is often the case in streams (Dickerson and Vinyard 1999).

Groundwater temperatures integrate annual temperature conditions and are usually within 1–2°C of the mean annual air temperature (Meisner 1990b). Groundwater isotherms would be expected to be correlated with the distribution of coldwater fishes living in headwater streams where groundwater inputs are a major source of summer streamflows.

Correlates of air temperature such as measures of the agricultural growing season also have been related to the distributional limits of some fish species. These measures integrate thermal conditions over the annual cycle and have proven useful in the absence of water temperature information. Scheller et al. (1999) argue that measures of degree-week accumulations based on water temperatures are a suitable method for delimiting the distribution of warmwater fishes because such species are more likely limited by the length of the growing season than lethal high or low temperatures. In mountainous regions, water temperatures are correlated with elevation and thus elevational limits have been used as a surrogate for thermal limits (Rieman and McIntyre 1995).

The thermal limits summarized in Table 1 indicate that the biogeographic distributions of coldwater species across North America often are associated with excessively warm summer temperatures that cause physiological stress leading to mortality. By contrast, the biogeographic distribution of warmwater species often is limited by cold summer temperatures that limit growth although some species may experience mortality at cold temperatures, e.g. threadfin shad *Dorosoma petenense* (Griffith 1978). Interestingly, there are situations where water temperatures are too cold even for some coldwater fish species to persist. Harig and Fausch (2002) reported that mean daily July water temperatures greater than or equal to 8°C were necessary for cutthroat trout *Oncorhynchus clarki* populations to become established in Rocky Mountain streams. At colder temperatures, larval trout failed to grow enough during their first summer to survive overwinter.

### *Using Biogeographic Distributions to Infer Thermal Limits and Model Habitat Loss for Coldwater Fishes Following Climate Change*

Keleher and Rahel (1996) used the relationship between fish distributions and mean July air temperature to predict potential habitat loss for salmonids in the Rocky Mountains of the United States under various climate-warming scenarios. The first step was to develop a regression relation between latitude, elevation and mean July air temperature based on 615 meteorological stations across the Rocky Mountain region. The resultant multiple regression equation allowed mean July air tem-



Table 1. Types of thermal limits associated with species biogeographic distributions.

Species and type of thermal limit	Reference
<b>I. Air temperature limits</b>	
1. Mean daily air temperature in July of 21°C associated with southern limit and -15°C in January associated with northern limit of brook trout in North America.	MacCrimmon and Campbell 1969
2. Mean daily air temperature in July of 21°C associated with southern limit and -12°C in January associated with northern limit of brown trout in North America.	MacCrimmon and Marshall 1968 Keleher and Rahel 1996 Shuter et al. 1980
3. Mean daily air temperature in July $\leq$ 21°C associated with lower elevational limit of salmonids in the western United States.	Meisner et al. 1987
4. Mean daily air temperature in July $>$ 16.6°C associated with northern limit of smallmouth bass in Canada.	Johnson and Evans 1990
5. Mean daily air temperature in July associated with northern limit of fish species in Ontario, (13 species have limit of 21.0°C; 9 species have limit of 18.0°C; 10 species have limit of 16.7°C).	Weatherley 1963
6. Mean daily air temperature December-February $>$ -5°C associated with northern limit of white perch distributions in North America.	
7. Mean maximum daily air temperature in July/August $<$ 31°C associated with the southern limit of yellow perch distribution in the United States.	
<b>II. Surface water temperature limits</b>	
1. Mean daily water temperature in July $\geq$ 8°C necessary for establishment of cutthroat trout populations in small Rocky Mountain streams.	Hartig and Fausch 2002
2. Maximum weekly mean water temperature during the year associated with distributional limits for 57 fish species across the United States.	Eaton and Scheller 1996
3. Maximum daily mean water temperature during the summer $\leq$ 21°C associated with lower elevational limit of salmonids in Wyoming streams.	Rahel et al. 1996
4. Trimean (approximate median) weekly maximum water temperature $<$ 22°C during summer associated with distributional limit of trout in southern Ontario (Canada) streams.	Barton et al. 1985
5. Mean weekly maximum water temperatures during July/August $\leq$ 24°C associated with downstream distributional limit of brook trout in two Ontario (Canada) streams.	Meisner 1990a
6. Mean maximum daily temperature over a 7-day period $\leq$ 18°C and mean daily temperature over 7-day period $\leq$ 16.7°C associated with distribution of juvenile coho salmon in California.	Welsh et al. 2001
7. Winter temperature $>$ 8°C required for survival of threadfin shad in North American lakes and reservoirs.	Griffith 1978.
8. Winter temperatures $<$ 13°C required for naturally-reproducing populations of rainbow trout.	MacCrimmon 1971
<b>III. Groundwater temperature limits</b>	
1. Groundwater isotherm of 15°C associated with southern limit of brook trout distribution in North America.	Meisner 1990b
2. Groundwater isotherms of 8°C and 16°C associated with lower elevational limits of Dolly Varden and white-spotted char, respectively, in Japan.	Nakano et al. 1996
<b>IV. Correlates of thermal regime</b>	
1. Agricultural growing season (number of frost free days) $\geq$ 100 days necessary for self-sustaining populations of largemouth bass in Wyoming.	Hubert 1988
2. Warmth index (annual sum of mean monthly temperatures exceeding 5°C $\leq$ 50) associated with distributional limit of allopatric populations of Dolly Varden in Japan.	Fausch et al. 1994
3. Annual degree-days above 10°C must exceed 550 to maintain a viable population of largemouth bass in North America.	McCaughey and Kilgour 1990
4. Total degree-weeks (sum of the average weekly water temperature over the annual cycle) related to the distribution of 8 warmwater fish species across the U.S.A.	Scheller et al. 1999.
5. Elevation must exceed 1,600 m in order for bull trout populations to persist in the Boise River basin of Idaho (U.S.A.).	Rieman and McIntyre 1995

perature to be estimated for any site based on latitude and elevation ( $R^2 = 0.90$ ; details in Keleher and Rahel 1996). Next, a fisheries database maintained by the Wyoming Game and Fish Department was queried to determine the biomass of all salmonid species at 736 sites that had been sampled by depletion-removal electrofishing. At each of these sites, the mean July air temperature was estimated from the regression equation. A histogram indicated that salmonids were absent or extremely rare at 30 sites where mean July air temperatures exceeded  $22^\circ\text{C}$  (Figure 2). This value was used as the thermal limit for the distribution of salmonids in the Rocky Mountain region.

Using a geographic information system, a thermal map of the Rocky Mountain region was constructed based on the regression equation predicting mean July air temperature from latitude and elevation. The map depicted thermal conditions by  $1^\circ\text{C}$  contours of mean July air temperature. The area within the  $22^\circ\text{C}$  contour represented the current potential geographic range for salmonids in the Rocky Mountain region (Figure 3A). Future distributions of the coldwater fish guild were predicted for temperature increases of  $1$ – $5^\circ\text{C}$  by shifting the current distribution by the required amount of contours. For example, if temperatures were to increase by  $3^\circ\text{C}$ , the  $22^\circ\text{C}$  contour would shift to where the  $19^\circ\text{C}$  contour is currently. The area lost as a result of warming by  $3^\circ\text{C}$  would equal the difference between the current  $22^\circ\text{C}$  and the current  $19^\circ\text{C}$  (Figure 3B). The extent of geographic area lost as potential salmonid habitat was calculated for temperature increases of  $1$ – $5^\circ\text{C}$  (Figure 4). Even a slight warming of  $1^\circ\text{C}$  would reduce the geographic area containing suitable salmonid habitat by 17%. A common projection is that a doubling of atmospheric carbon dioxide concen-

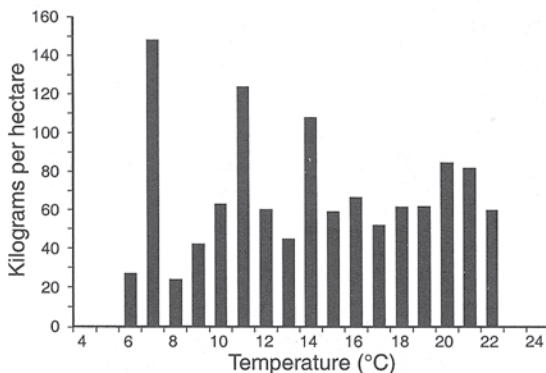


Figure 2. Average salmonid biomass (kilograms per hectare) in relation to predicted mean July air temperature. Averages were calculated from Wyoming Game and Fish Department data for  $1^\circ\text{C}$  increments of predicted mean July air temperature. From Keleher and Rahel (1996).

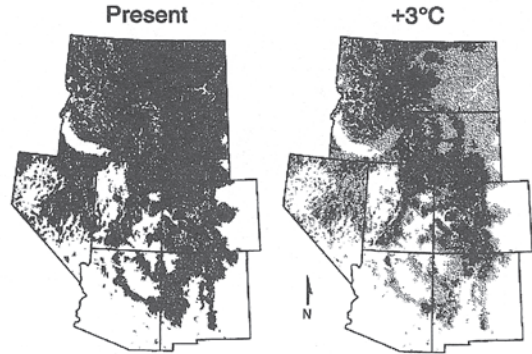


Figure 3. A) Present day potential distribution of the coldwater fish guild in the Rocky Mountain region as limited by the  $22^\circ\text{C}$  isocline of mean July air temperature (shaded area). B) Future potential distribution of the coldwater fish guild (dark shade) and habitat loss (light shade) in the Rocky Mountain region after a  $3^\circ\text{C}$  increase in mean July air temperature. There would be a 50% loss of geographic range following such a temperature increase. From Keleher and Rahel (1996).

tration will cause air temperature increases of about  $3^\circ\text{C}$  across much of the United States (Eaton and Scheller 1996). A  $3^\circ\text{C}$  temperature increase was predicted to cause a 50% reduction in the geographic area containing thermally-suitable habitat for salmonids in the Rocky Mountain region (Figure 4).

The prediction of extensive loss of habitat for coldwater fishes in the Rocky Mountain region agrees with predictions from other studies (Table 2). For example, Eaton and Scheller (1996) used an extensive database matching fish occurrence across the United States with stream temperature records to identify upper thermal limits for ten coldwater fish species. They then used projections of stream warming following a doubling of atmospheric  $\text{CO}_2$  concentrations to estimate how many stream locations would become too warm for the species. On average, there was a 47% loss of stations having thermally-suitable habitat for these coldwater fishes. Stefan et al. (2001) modeled the response of the coldwater fish guild in lakes across the United States to climate change. Climate warming was projected to reduce the number of lakes having suitable coldwater fish habitat by up to 45%. In Japan, Nakano et al. (1996) associated the distribution of coldwater fish species with groundwater isotherms and used current thermal limits to project habitat loss following climate change. With a  $3^\circ\text{C}$  increase in mean annual air temperature, the geographical ranges of Dolly Varden *Salvelinus malma* and white-spotted char *S. leucomaenis* were projected to decline by 80% and 34%, respectively.

In addition to habitat loss, fragmentation of remaining populations of coldwater fishes will occur. Fragmentation



Table 2. Projected responses of coldwater fishes to climate change.  $2 \times \text{CO}_2$  refers to climate change scenarios based on a doubling of atmospheric carbon dioxide concentrations.

Geographic region	Extent of habitat loss	Thermal limit for coldwater fish guild	Reference
Rocky Mountain region of the United States.	A 50% loss of the geographic range for salmonids with a 3°C increase in summer air temperatures	Mean July air temperature $\leq 22^\circ\text{C}$	Keleher and Rahel 1996
Streams across the United States	Average 47% loss of stream sites with suitable habitat for ten species with $2 \times \text{CO}_2$	Maximum weekly average water temperature 19.8–24.3°C	Eaton and Scheller 1996
Lakes across the United States	A 45% loss of lakes with suitable habitat for coldwater fish guild with $2 \times \text{CO}_2$	Maximum water temperature $\leq 23.4^\circ\text{C}$	Stefan et al. 2001
Japanese archipelago	Geographical range of Dolly Varden and white-spotted char reduced by 80% and 34% respectively for 3°C increase in mean annual air temperature	Groundwater isotherm of 8°C for Dolly Varden and 16°C for white-spotted char.	Nakano et al. 1996.

tation is detrimental because small, isolated populations are susceptible to inbreeding and have an increased probability of extinction through environmental disturbances such as floods or droughts. Rahel et al. (1996) explored this issue for coldwater fishes in the North Platte River drainage of Wyoming. The current distribution of coldwater fishes was limited to streams with a mean daily water temperature in July less than or equal to 21°C. With a 3°C increase in summer water temperatures, the 4,128 km of interconnected streams that currently provide thermally-suitable habitat for coldwater fish was projected to decline by 13% and become fragmented into smaller and more isolated enclaves (Figure 5). Nakano et al. (1996) predicted a similar phenomenon for trout populations in Japan.

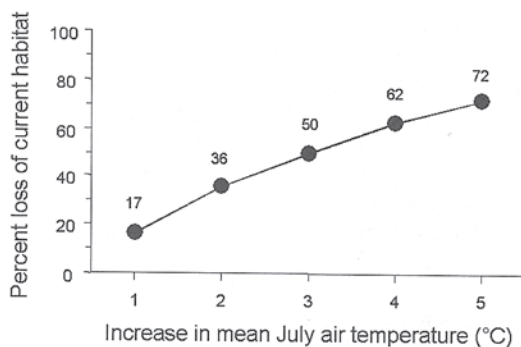


Figure 4. Percent loss of current habitat for the coldwater fish guild in the Rocky Mountain region under climate change scenarios of 1–5°C increases in mean July air temperature. The numbers above each point indicate the percent of the current geographic range that would become too warm based on a current distribution limit of 22°C mean July air temperature. Based on data from Keleher and Rahel (1996).

## Considerations in Using Biogeographic Limits to Model Species Responses to Climate Change.

### *Ensuring that Distribution Patterns Reflect Thermal Limits Rather than Other Factors*

Perhaps the major concern in using biogeographic distributions to model species responses to climate warming is to ensure that temperature and not some other factor is primarily responsible for the observed patterns. This should not be a major problem for other abiotic factors because most of them do not produce clinal gradients across large spatial scales. For example, low pH, high salinity, or winter anoxia conditions are distributed heterogeneously across the landscape whereas thermal conditions typically follow clinal gradients associated with latitude or altitude (Rahel 1984, 1986). Another factor that can confound distribution patterns is postglacial dispersal (Mandrak and Crossman 1992). Shuter and Post (1990) predicted that the northern distribution of yellow perch should extend onto the Quebec peninsula based on thermal limits. The absence of yellow perch was attributed to physical barriers to postglacial dispersal that have prevented yellow perch and many other fish species from colonizing this region. Thus, knowledge of postglacial dispersal routes and biogeographic history will aid in determining factors that limit fish distributions. Distribution patterns that suggest temperature limits rather than dispersal limits include distributions that transcend drainage divides, do not coincide with zoogeographic barriers to range expansion, or that are associated with similar thermal conditions in different regions (Cross

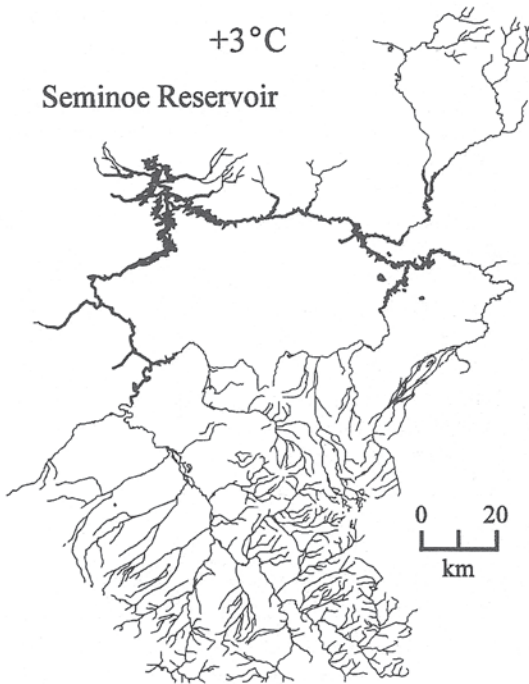


Figure 5. Fragmentation of stream habitat for coldwater fishes in the North Platte River upstream of Seminoe Reservoir in Wyoming, U.S.A. based on a 3°C increase in July water temperatures. At present, the entire drainage provides thermally-suitable habitat. Stream reaches that would become too warm for coldwater species are shown by dark lines. From Rahel et al. (1996).

et al. 1986). For example, Weatherley (1963) noted that the distribution of yellow perch in Australia (where they are introduced) corresponds to the same thermal limit as in North America (where they are native).

Biotic interactions also may complicate biogeographic distribution patterns (Davis et al. 1998). The distribution of coldwater fish species may be determined by a combination of thermal tolerance and competitive interactions with other species (Taniguchi et al. 1998). In the Rocky Mountain region, native cutthroat trout *Oncorhynchus* spp. often are restricted to headwater reaches because of competitive displacement at lower elevations by introduced brook trout *Salvelinus fontinalis* (Fausch 1989; De Staso and Rahel 1994). Because models of cutthroat trout distribution patterns emphasize the association of this species with high elevations (Bozek and Hubert 1992), one might assume they are restricted from occurring at lower elevations because of warm temperatures. Historically, however, cutthroat trout occurred at lower elevations. Thus, thermal limits inferred from current distribution patterns would underestimate the thermal tolerance of cutthroat trout.

### *Standardized approaches would facilitate comparisons among studies but may not be feasible*

As indicated in Tables 1 and 2, a variety of thermal limits have been used to model how fish distributions will be affected by climate change. The lack of standardized methods makes it difficult to compare studies, even for the same species. Consider, for example, efforts to model the response of brook trout to climate change (Table 3). Each of the four studies used a different thermal limit for brook trout distributions and different estimates of climate warming. For studies using air temperature limits, mean air temperature during the warmest month of the year (July in the northern hemisphere) would be a good metric because air and water temperatures are typically highly correlated over periods greater than a week and long-term air temperature data are available for most regions of the world. Studies using water temperature data could utilize the daily average temperature or the daily maximum temperature both averaged over a seven day period during the warmest part of the year. However, as discussed earlier, it is not clear whether the average or maximum daily temperature is most critical for fish in environments with pronounced diel temperature fluctuations.

For coldwater fishes, mean or maximum summer temperature are associated with both upper limits to survival (Eaton and Scheller 1996) and lower limits for sufficient growth (Harig and Fausch 2002). For warmwater fishes, mean or maximum summer temperatures are associated with lower limits for growth (Shuter and Post 1990), although there may be merit in considering the accumulation of degree-days during the growing season rather than a single thermal limit (Scheller et al. 1999). For some warmwater fishes, lethal cold temperatures may be the most important determinant of distribution patterns and thus winter temperature limits should be used in modeling how these species will respond to climate warming, e.g. threadfin shad (Griffith 1978).

Given the variability in temperature data available to researchers and the fact that different thermal limits may be appropriate for different thermal guilds, it seems unlikely that complete standardization of thermal limits will be possible. Also, a better understanding of the relative importance of average versus maximum daily temperature in determining fish distributions in streams is needed.

### *Shifts along air or water isotherms do not capture local scale variation in temperatures or species distributions*

A common approach in modeling the effects of climate change on fish distributions is to identify current thermal



Table 3. Current thermal limits and projected responses of brook trout to climate change.  $2 \times \text{CO}_2$  refers to climate change scenarios based on a doubling of atmospheric carbon dioxide concentrations.

Geographic Region	Predicted response to climate change	Thermal limit	Reference
Streams across the United States	A 55% loss of stream sites with suitable habitat for $2 \times \text{CO}_2$	Maximum weekly average water temperature $\leq 22.4^\circ\text{C}$	Eaton and Scheller 1996
Southeastern United States	Significant reduction in geographic range with a $3.8^\circ\text{C}$ increase in air temperature. (Reduction estimated to be 40–50% by Clark et al. 2001).	$15^\circ\text{C}$ groundwater isotherm	Meisner 1990b
Southern Appalachian Mountains in U.S.A.	A 24% loss of habitat for a $1.5^\circ\text{C}$ increase in summer water temperatures and more floods.	$< 19^\circ\text{C}$ mean summer water temperature	Clark et al. 2001
Two streams in Ontario, Canada	A 30 and 42% loss of stream length suitable as habitat with a $4.1^\circ\text{C}$ increase in summer air temperature.	Average weekly maximum summer water temperature $\leq 24^\circ\text{C}$ .	Meisner 1990a

limits and then assume fish will track the latitudinal or elevational shifts in isotherms with climate warming (Shuter and Post 1990; Keleher and Rahel 1996; Nakano et al. 1996). This approach assumes the entire area between isotherms is either thermally suitable or unsuitable as habitat for the species of interest. It also assumes that temperatures change monotonically with changes in latitude or elevation. But much local-scale variation in temperature can occur as a result of local landforms, groundwater inputs or land-use practices (Torgersen et al. 1999; Isaak and Hubert 2001). Assessments of climate change impacts based on species shifts along air, surface water or groundwater temperature isotherms will not capture such local-scale variation. Instead, assessments at the scale of individual streams or lakes will need to use site-specific models of how stream or lake temperature regimes will respond to climate change (Meisner 1990a; Magnuson and DeStasio 1996; Stefan et al. 2001).

*Assessments based on biogeographic shifts along isotherms do not take into account interaction of multiple factors*

Climate change is predicted to have multifaceted consequences for aquatic ecosystems that extend beyond warming (Schindler 1997). For streams in North America, alteration of streamflow patterns is likely with a tendency for reduced annual discharge and a shift in peak flows from spring to winter in many areas (Hauer et al. 1997). Such changes in hydrological regime will interact with changes in thermal regime to influence stream fish populations in complex ways.

Clark et al. (2001) used an individual-based modeling approach to explore how temperature increases and altered streamflow would impact rainbow trout *Oncorhynchus mykiss* populations in the Appalachian Mountains of the United States. They considered three climate change scenarios. The first involved tempera-

ture increase only and was accomplished by increasing daily stream temperatures by  $2.0^\circ\text{C}$  in the spring,  $1.5^\circ\text{C}$  in the summer and fall, and  $2.5^\circ\text{C}$  in the winter. The second scenario involved temperature increases plus altered streamflow in the form of increased winter and decreased summer flows. The third scenario added episodic high-flow events that would scour trout redds to the temperature and streamflow changes. The response of rainbow trout varied among the three scenarios of climate change (Figure 6). Temperature change by itself caused an increase in the simulated population because warmer spring temperatures increased the development rate of eggs, which, with constant mortality rates, resulted in increased egg survival. More eggs hatching ultimately lead to higher numbers of adult rainbow trout. However, the benefit of higher temperatures on egg survival was offset by flow alterations. Higher peak flows in winter when rainbow trout spawn disrupted spawning activity and eliminated suitable spawning areas. The result was a lower number of eggs being produced that negated the higher egg survival due to temperature changes. When high-flow episodes were added to the model, rainbow trout abundance decreased over baseline levels because the flood events scoured nests and caused mortality of fry. Thus, changes in streamflow were an important factor in how trout populations would be impacted by climate change. Jager et al. (1999) also concluded that temperature and hydrological alterations due to climate change would interact in complex ways to influence fish populations in a California stream.

**Conclusion**

Biogeographic distributions often provide insight into thermal limits for ectotherms such as fish whose physiology and reproductive success are strongly influenced

## Appalachian Rainbow Trout

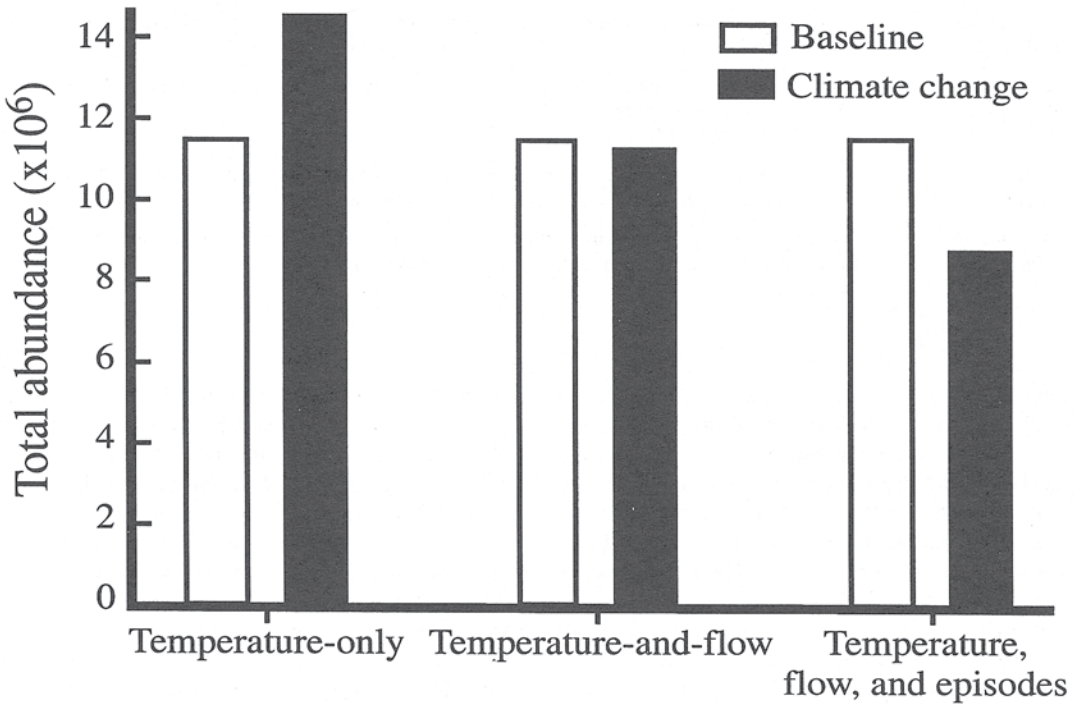


Figure 6. Response of a simulated population of rainbow trout in the Appalachian Mountains to three climate change scenarios: an increase in temperature only; an increase in temperature plus higher winter streamflow; and an increase in temperature and winter streamflow plus episodic floods. Relative to baseline conditions, temperature-only changes caused an increased in trout population size due to better survival of eggs. This increase was negated by lower spawning success when high winter streamflows were added to the simulation. Adding episodic floods caused the population size to decline due to destruction of redds. Adapted from Clark et al. 2001.

by temperature. These thermal limits can be used to project distributional changes following climate change by assuming fish will migrate along isotherms to remain within a suitable thermal envelope. These distributional shifts can include abandonment of areas currently occupied if future temperatures exceed physiological tolerances (Rahel et al. 1996) as well as colonization of new areas if previously unsuitable temperature conditions are ameliorated (Shuter and Post 1990). This approach has been termed "forecasting from historical analogy" and has been used to predict how marine fish stocks will respond to alterations in ocean temperatures (Murawski 1993). In freshwaters, we should expect to see fish distributions migrate poleward or higher in elevation as species track suitable temperatures. Areas now supporting high yields of sport or commercial species may become marginal, whereas areas at the margins of species distributions may become op-

timal (Minns and Moore 1995). Of course, such changes in fish distributions assume species will be able to migrate along watercourses to find suitable thermal habitat. But such migrations may be limited by the extensive damming of rivers that has occurred in North America (Nehlsen et al. 1991; Porto et al. 1999). Also, such a strategy is not possible for Great Plains fishes in the United States where the east-west orientation of most rivers and the lack of elevational relief would prevent migrations to northern or higher elevation thermal refuges (Matthews and Zimmerman 1990)

A variety of approaches have been used to identify thermal limits including measures of air, surface water and groundwater temperatures as well as agricultural growing season. Although measures of water temperature are the best indication of thermal conditions experienced by fish, data are not always available and air temperature limits have been used in many assessments



of climate change impacts on fish populations (Tables 1, 2). Measures of summer temperature have been correlated with the distributions of both coldwater species (where high summer temperatures typically limit fish occurrence) and warmwater species (where low summer temperatures typically limit fish occurrence).

Caveats in using biogeographic limits to infer species' thermal limits include making sure that other abiotic factors, postglacial colonization, or species interactions are not primarily responsible for current distribution limits. Also, models based on species tracking changes in temperature isoclines do not consider the impacts of hydrological alterations that may accompany climate change. Models that incorporate hydrological alterations predict additional negative effects on coldwater fish populations due to shifts in the timing of floods and increased flood events (Clark et al. 2001). However, such models require extensive parameterization and simplifying assumptions, hence their use is limited to species for which extensive life history and physiological data are available.

In conclusion, inferring thermal limits based on biogeographic distributions has a long history in fisheries ecology and is a useful approach for predicting how fish species will respond to climate change. The approach is especially strong when combined with detailed mechanistic studies that provide the physiological underpinnings of why biogeographic limits are correlated with thermal conditions for many fish species (Shuter and Post 1990; Power and van den Heuvel 1999). Forecasting from historical analogy will be especially important for the many fish species for which absence of detailed life history and bioenergetic data will limit the use of other modeling approaches.

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## References

- Barton, D. R. W. W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. *North American Journal of Fisheries Management* 5:364–378.
- Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70:886–890.
- Clark, M. E., K. A. Rose, D. A. Levine and W. W. Hargrove. 2001. Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. *Ecological Applications* 11:161–178.
- Cox, C. B. and P. D. Moore. 1980. *Biogeography: an ecological and evolutionary approach*. Wiley, New York.
- Cross, F. B., R. L. Mayden and J. D. Stewart. 1986. Fishes in the western Mississippi basin (Missouri, Arkansas and Red rivers). Pages 363–412 in C. H. Hocutt and E. O. Wiley, editors. *The zoogeography of North American freshwater fishes*. Wiley, New York.
- De Staso, J. III, and F. J. Rahel. 1994. Influence of water temperature on interactions between young Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 123:289–297.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature (London)* 391:783–786.
- Dickerson, B. R., and G. L. Vinyard. 1999. Effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 128:516–521.
- Eaton, J. G., and J. H. McCormick, B. E. Goodno, D. G. O'Brien, H. G. Stefany, M. Hondzo, and R. M. Scheller. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* 20(4):10–18.
- Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41:1109–1115.
- Fausch, K. D. 1989. Do gradient and temperature affect distributions, and interactions between brook char (*Salvelinus fontinalis*) and other resident salmonids in streams? *Physiology and Ecology, Japan 1 (special volume)*:303–322.
- Fausch, K. D., S. Nakano, K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. *Oecologia* 100:1–12.
- Griffith, J. S. 1978. Effects of low temperature on the survival and behavior of threadfin shad, *Dorosoma petenense*. *Transactions of the American Fisheries Society* 107:63–70.
- Hartig, A. L., and K. D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535–551.
- Hauer, F. R., J. S. Baron, D. H. Campbell, K. D. Fausch, S. W. Hostetler, G. H. Leavesley, P. R. Leavitt, D. M. McKnight and J. A. Stanford. 1997. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrological Processes* 11:949–970.
- Hubert, W. A. 1988. Altitude as the determinant of distribution of largemouth bass and smallmouth bass in Wyoming. *North American Journal of Fisheries Management* 8:386–387.
- Hutchins, L. W. 1947. The basis for temperature zonation in geographical distribution. *Ecological Monographs* 17:325–335.

- Isaak, D. J., and W. A. Hubert. 2001. A hypothesis about factors that affect maximum summer stream temperatures across montane landscapes. *Journal of the American Water Resources Association* 37(2):1-16.
- Jager, H. I., W. Van Winkle, and B. D. Holcomb. 1999. Would hydrologic climate changes in Sierra Nevada streams influence trout persistence? *Transactions of the American Fisheries Society* 128:222-240.
- Johnson, T. B., and D. O. Evans. 1990. Size-dependent winter mortality of young-of-year white perch: climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society* 119:301-313.
- Keleher, C. J., and F. J. Rahel. 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. *Transactions of the American Fisheries Society* 125:1-13.
- King, J. R., B. J. Shuter, and A. P. Zimmerman. 1999. Empirical links between thermal habitat, fish growth, and climate change. *Transactions of the American Fisheries Society* 128:656-665.
- MacCrimmon, H. R. 1971. World distribution of rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* 28:663-704.
- MacCrimmon, H. R., and T. L. Marshall. 1968. World distribution of brown trout, *Salmo trutta*. *Journal of the Fisheries Research Board of Canada* 25:2527-2548.
- MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 26:1699-1725.
- Magnuson, J. J. and B. T. DeStasio. 1996. Thermal niche of fishes and global warming. Pages 377-408 in C. M. Wood and D. G. McDonald, editors. *Society for Experimental Biology Seminar Series 61: Global warming: implications for freshwater and marine fish*. Cambridge University Press.
- Mandrak, N. E., and E. J. Crossman. 1992. Postglacial dispersal of freshwater fishes into Ontario. *Canadian Journal of Zoology* 70:2247-2259.
- Matthews, W. J., and E. G. Zimmerman. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the southwest. *Fisheries* 15(6):26-32.
- McCauley, R. W., and D. M. Kilgour. 1990. Effect of air temperature on growth of largemouth bass in North America. *Transactions of the American Fisheries Society* 119:276-281.
- Meisner, J. D. 1990a. Potential loss of thermal habitat for brook trout, due to climate warming, in two southern Ontario streams. *Transactions of the American Fisheries Society* 119:282-291.
- Meisner, J. D. 1990b. Effect of climatic warming on the southern margin of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1065-1070.
- Meisner, J. D., J. L. Goodier, H. A. Regier, B. J. Shuter, and W. J. Christie. 1987. An assessment of the effects of climate warming on Great Lakes basin fishes. *Journal of Great Lakes Research* 13:340-352.
- Minns, C. K. and J. E. Moore. 1995. Factors limiting the distribution of Ontario's freshwater fishes: the role of climate and other variables, and the potential impacts of climate change. Pages 137-160 in R. J. Beamish, editor. *Climate change and northern fish populations*. Canadian Special Publication Fisheries and Aquatic Sciences 121.
- Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. *Water Resources Research* 34:2685-2692.
- Murawski, S. A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. *Transactions of the American Fisheries Society* 122:647-658.
- Nakano, S., F. Kitano, and K. Maekawa. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshwater Biology* 36:711-722.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks of salmon at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- Porto, L. M., R. L. McLaughlin and D. L. G. Noakes. 1999. Low-head barrier dams restrict the movements of fishes in two Lake Ontario streams. *North American Journal of Fisheries Management* 19:1028-1036.
- Power, M., and M. R. van den Heuvel. 1999. Age-0 yellow perch growth and its relationship to temperature. *Transactions of the American Fisheries Society* 128:687-700.
- Radforth, I. 1944. Some considerations on the distribution of fishes in Ontario. *Contribution of the Royal Ontario Museum (Zoology)* 25, Toronto, Canada.
- Rahel, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. *Ecology* 65:1276-1289.
- Rahel, F. J. 1986. Biogeographic influences on fish species composition of northern Wisconsin lakes with applications for lake acidification studies. *Canadian Journal of Fisheries and Aquatic Sciences* 43:124-134.
- Rahel, F. J. and N. P. Nibbelink. 1999. Spatial patterns in relations among brown trout distribution, summer air temperature, and stream size in Rocky Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 56(Supplement 1):43-51.
- Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and populations fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. *Limnology and Oceanography* 41:1116-1123.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285-296.
- Scheller, R. M., V. M. Snarski, J. G. Eaton and G. W. Oehlert. 1999. An analysis of the influence of annual thermal variables on the occurrence of fifteen warmwater fishes. *Transactions of the American Fisheries Society* 128:257-264.
- Schindler, D. W. 1997. Widespread effects of climate warming on freshwater ecosystems in North America. *Hydrological Processes* 11:1043-1067.



- Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109:1-34.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314-336.
- Stefan, H. G., X. Fang, and J. G. Eaton. 2001. Simulated fish habitat changes in North American lakes in response to projected climate warming. *Transactions of the American Fisheries Society* 130:459-477.
- Taniguchi, Y., F. J. Rahel, D. C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1894-1901.
- Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* 9:301-319.
- Weatherley, A. H. 1963. Zoogeography of *Perca fluviatilis* (Linnaeus) and *Perca flavescens* (Mitchill) with special reference to the effects of high temperature. *Proceedings of the Zoological Society of London* 141:557-576.
- Welsh, H. H., Jr., G. R. Hodgson, B. C. Harvey, and M. F. Roche. 2001. Distribution of juvenile coho salmon in relation to water temperatures in tributaries of the Mattole River, California. *North American Journal of Fisheries Management* 21:464-470.