

Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: Response to climate warming

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Abstract

We used three approaches to examine potential habitat loss in relation to climate warming for cold water species of fish in the North Platte River drainage in Wyoming. The projected loss of habitat varied among approaches, but all methods indicated a noticeable loss of habitat for even minor increases in temperature. An approach based on the use of summer air temperatures to define the thermal limits of cold water species estimated a loss of 9–76% of the present geographic range for temperature increases of 1–5°C. A second approach, also based on air temperature limits, projected a loss of 7–64% of the stream distance currently having thermally suitable habitat for cold water fish for temperature increases of 1–5°C. A third approach, based on the use of summer water temperatures to define the thermal limits of cold water species, projected a loss of 16–69% of the stream distance currently having thermally suitable habitat for temperature increases of 1–5°C. In addition to habitat loss, population fragmentation would occur as remaining enclaves of cold water fish are forced to retreat to increasingly isolated headwater stream reaches.

Temperature plays a critical role in determining the distribution of fish species in temperate regions. The importance of temperature is evident at spatial scales that range from regional to local (Shuter and Post 1990; Nielsen et al. 1994; Snucins and Gunn 1995). Fish species often are grouped into thermal guilds (Magnuson et al. 1979) that differ in the optimal temperature range for physiological function and ecological success. Cold water species typically have physiological optima $\leq 20^{\circ}\text{C}$ and generally are not found where summer water temperatures $>20\text{--}24^{\circ}\text{C}$ (Eaton et al. 1995). Trout and salmon (family salmonidae) are the dominant cold water species in northern or high elevation aquatic systems throughout North America and are of prime importance for both recreational and commercial fisheries.

Projections of climate change due to increased inputs of greenhouse gases into the atmosphere indicate that temperate latitudes in North America may experience increases in mean annual air temperatures of from 2 to 5°C (Houghton et al. 1990). Such increases in air temperature will likely result in increased surface water and groundwater temperatures and thus have profound effects on aquatic ecosystems (Regier and Meisner 1990; Schindler et al. 1990). Potential effects include alteration of fish production (Plante and Downing 1993) as well as changes in the distributional ranges of fish (Matthews and Zimmerman 1990; Meisner 1990a). In elevationally diverse regions such as the Rocky Mountains, warming stream temperatures would restrict cold water species to increas-

ingly higher elevations and thus reduce both the geographic range and stream distance they occupy. In an earlier analysis, we used relations between maximum summer air temperature and fish distributions to estimate the loss of thermally suitable habitat for salmonids in the Rocky Mountain region (Keleher and Rahel 1996). Here, we estimate habitat loss on a finer spatial scale (the North Platte River drainage in Wyoming) and compare approaches using thermal limits based on air temperature vs. stream water temperature. Also, we estimate the extent to which surviving populations will become fragmented into increasingly isolated enclaves.

We developed three approaches for estimating the extent of habitat loss associated with climate warming. Our first approach was to use the present relationship between salmonid distributions in streams and summer air temperature in Wyoming to estimate the loss of geographic range that would occur based on increases in summer air temperature. Historically, air temperatures have been associated with the geographic limits of fish species. For example, the native range of brook trout (*Salvelinus fontinalis*) is delimited to the north by a mean daily temperature of -15°C in January and to the south by areas where mean July air temperatures do not exceed 21°C (MacCrimmon and Campbell 1969). Our second approach was to use the same relationship between fish distribution limits and summer air temperature but to express habitat loss in terms of stream distance. Our third approach differed in that we used maximum summer water temperature rather than air temperature to define the present limit of salmonid distributions and to estimate the total stream distance that would be lost with increases in maximum summer water temperature.

We used all three approaches to estimate the extent of habitat loss in the North Platte River drainage in southeastern Wyoming (Fig. 1). This drainage was chosen because its fish fauna is well described and because of the

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availability of long-term water temperature records from streams across a wide elevational gradient (Rahel and Hubert 1991). Because of data availability, our analysis was confined to the portion of the drainage within the state of Wyoming. Thus, a small portion of the headwaters in northern Colorado was not considered. Habitat loss was estimated for warming scenarios of 1–5°C, which encompasses the range of temperature increase predicted to occur within the next century (Houghton et al. 1990).

In addition to habitat loss, fragmentation of cold water fish populations is likely to occur as remaining enclaves become increasingly isolated in headwater tributaries. We define an enclave as a group of interconnected streams having appropriate thermal habitat and isolated from other enclaves by downstream regions with thermally unsuitable water temperatures. The fragmentation of cold water fish populations is analogous to the restriction of terrestrial animals to mountain tops as low-lying areas become thermally unsuitable (Peters and Darling 1985). Fragmentation typically leads to small, isolated populations that have an increased risk of extinction because of stochastic population fluctuations and inbreeding depression (Mills and Smouse 1994). We examined the extent to which population fragmentation would happen in the North Platte River system as lower elevation stream reaches become thermally unsuitable for salmonids during summer.

Methods

Geographic area lost based on air temperature—The first approach involved estimating the geographic area currently occupied by the cold water fish guild in relation to summer air temperatures. We conducted our analysis at the guild level because there was overlap in the thermal limits of individual species in our data. In the North Platte River drainage, the cold water guild was composed of brook trout, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*. We used a mean July air temperature of 22°C to define the lower elevational limit of cold water species in the drainage. This value was based on a previous analysis that demonstrated that cold water fish were limited to areas where the mean July air temperature did not exceed 22°C (see Keleher and Rahel 1996).

We began by constructing a thermal map of the drainage based on contours of mean July air temperature. We began with a digital elevation matrix based on U.S. Geological Survey (USGS) data from 1:100,000 scale maps. This elevation matrix was converted to a grid in ARC/INFO where each grid cell had an elevation value rounded to the nearest 6.1 m. Grid resolution was 1,000 m. An additional grid with latitude values was constructed at the same resolution. A regression equation was used to create a grid of mean July air temperature from elevation and latitude information. The regression equation, which had been developed for a previous study (Keleher and Rahel 1996), was

$$\text{Mean July air temp.} = 66.86 - 0.0072 \text{ (elevation in m)} - 0.8096 \text{ (lat in decimal degrees).}$$

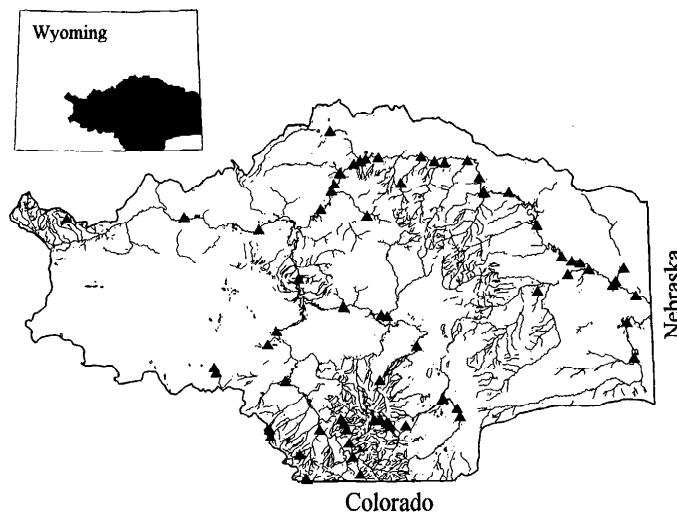


Fig. 1. Map of the North Platte River drainage in Wyoming. The river rises in northern Colorado (not shown), flows through southeastern Wyoming, and exits at the Nebraska stateline. Locations where records of stream temperature are available from the USGS—▲.

This equation was constructed from long-term meteorological data at 65 stations across Wyoming and had an R^2 value of 0.72 with $P < 0.0001$.

The area (km^2) contained within the 22°C contour of the thermal map was considered to represent the present geographic range of the cold water fish guild in the drainage. Future distributions of the cold water guild were predicted for temperature increases of 1–5°C by shifting current distributions the required amount of contours. We assumed that the rate of air temperature increase would be constant across elevation (McDonald and Brown 1992); thus if temperatures were to increase by 3°C, the 22°C contour would shift to where the 19°C contour is currently. The area lost as a result of warming by 3°C would equal the difference between the current 22°C and the current 19°C contours. We used a geographic information system (GIS) running ARC/INFO software to produce all maps and to calculate the geographic area within thermal contours.

Stream distance lost based on air temperature—The second approach was to estimate the stream distance (km) in the North Platte drainage that would be lost under various warming scenarios. As in the first approach, we used 22°C mean July air temperature to define the present lower elevational limit of the cold water fish guild in the drainage. We created a coverage using GIS that combined hydrologic features and contours of mean July air temperature. The hydrologic map was a commercially available digitized coverage of hydrologic features for Wyoming produced from 1:100,000 maps by the USGS. The total stream distance that is presently thermally suitable for cold water fish was determined by summing all the stream lengths contained within the 22°C contour of mean July air temperature. To determine thermally suitable stream distances after climate warming, we used the same logic as described for the first approach. Habitat lost in

terms of stream distance was determined by subtracting the future stream distance after warming from the present stream distance. For example, the stream distance thermally suitable for cold water species if temperatures increased by 3°C would equal the difference between stream distances contained within the present 22°C contour and the present 19°C contour of mean July air temperature.

Stream distance lost based on water temperature—The third approach was to examine habitat loss for the cold water fish guild in relation to increases in water temperature. This required identifying present distribution limits in relation to maximum summer water temperature. We began by developing a stream temperature model to predict maximum annual stream temperature as a function of elevation for the North Platte drainage. The model was developed from stream temperature data (available through STORET) provided by the Wyoming Water Resources Center at the University of Wyoming. Fifty-five sites (Fig. 1) were selected based on the criteria that temperature data had been collected by grab samples for at least 3 yr, the data covered the full annual cycle, and that locations were not influenced by major reservoir releases. These criteria were based on the fact that 95% of the variation of annual stream temperature cycles can be picked up in the first year (Song et al. 1973) and that grab samples can be a useful alternative to continuous record data for predicting annual thermal cycles (Lowham et al. 1975).

Annual temperature cycles in temperate regions follow a sinusoidal relationship that can be predicted with the harmonic function

$$T = M + A \{ \sin[(0.0172 \times t) + C] \}.$$

T is the stream temperature (°C) on day t of the water year and the harmonic function is described by its mean (M), amplitude (A), and phase angle (C) (Lowham et al. 1975; Lowham 1978). At each of the 55 sites, we fit a harmonic function to annual water temperature data and used it to predict the maximum annual stream temperature at that site by summing M and A . A harmonic function provided a statistically significant fit to annual temperature cycles for the sites with an average R^2 value of 0.73. Next, we used regression analysis to relate maximum stream-water temperature to elevation for the sites. The regression model was used to produce a map of maximum summer water temperature for all streams in the drainage. By combining the water temperature map with the hydrologic map, we could calculate the total stream distance contained within each 1°C contour of maximum summer water temperature.

We mapped the present distribution of cold water fish in the drainage based on extensive survey records of the Wyoming Game and Fish Department. At 481 sites where fish abundances were assessed by depletion-removal electrofishing, we estimated the maximum summer water temperature using the regression equation described above. We then examined a histogram of salmonid biomass vs. maximum summer water temperature to determine the upper thermal limit for the cold water fish guild

in the drainage. The stream distance presently within this thermal limit was determined from the stream temperature hydrocoverage map.

To estimate habitat loss due to climate warming, we assumed that increased air temperature would result in increased water temperature and that cold water fish would migrate to higher elevations to remain within their upper thermal limit. Thus, if the current thermal limit was 21°C maximum summer water temperature, the limit after 3°C warming would correspond to the present 18°C contour of maximum summer water temperature. The amount of habitat lost would correspond to the difference in stream length contained within the present 21 and 18°C contours. Future distributions of salmonids were predicted for temperature increases of 1–5°C by shifting current distributions the required number of thermal contours. We used GIS to produce all distribution maps and to calculate stream distances within contours of maximum summer water temperature.

Population fragmentation—Because cold water fish would be restricted to higher and higher elevations, populations in headwater tributaries would become increasingly fragmented into progressively smaller enclaves. We examined the extent of fragmentation that would accompany climate warming in the North Platte drainage. We limited our analysis to the portion of the drainage upstream of Seminoe Dam because it and other dams downstream currently block fish movements in the lower portion of the river. Upstream of Seminoe Reservoir, there are no major barriers to fish migration and thus population exchanges among streams is possible.

We used GIS to construct maps of the present distribution of cold water species and the future distribution after 3 and 5°C increases in maximum summer water temperature. As the thermal limit for cold water fish, we used 21°C maximum summer water temperature based on the results for the analysis of stream distance lost based on water temperature. At present, the entire drainage above Seminoe Reservoir contains thermally suitable habitat for cold water fish and we considered the entire drainage to be one large enclave. After climate warming, lower portions of the drainage would become thermally unsuitable, and the cold water fish guild would become fragmented into a series of smaller enclaves restricted to headwater tributaries. We determined the size of individual enclaves by delimiting each enclave using GIS and summing stream distances within the enclave.

Results

Geographic area lost based on air temperature—The 22°C mean July air temperature isopleth was used as the limit for cold water species in the North Platte River drainage. The total area currently contained within the 22°C isopleth of mean July air temperature is 60,435 km², which represents 90.4% of the geographic area of the drainage (Fig. 2A). For increases of 1–5°C, this area is reduced by 9–76% (Table 1; Fig. 2B–D).

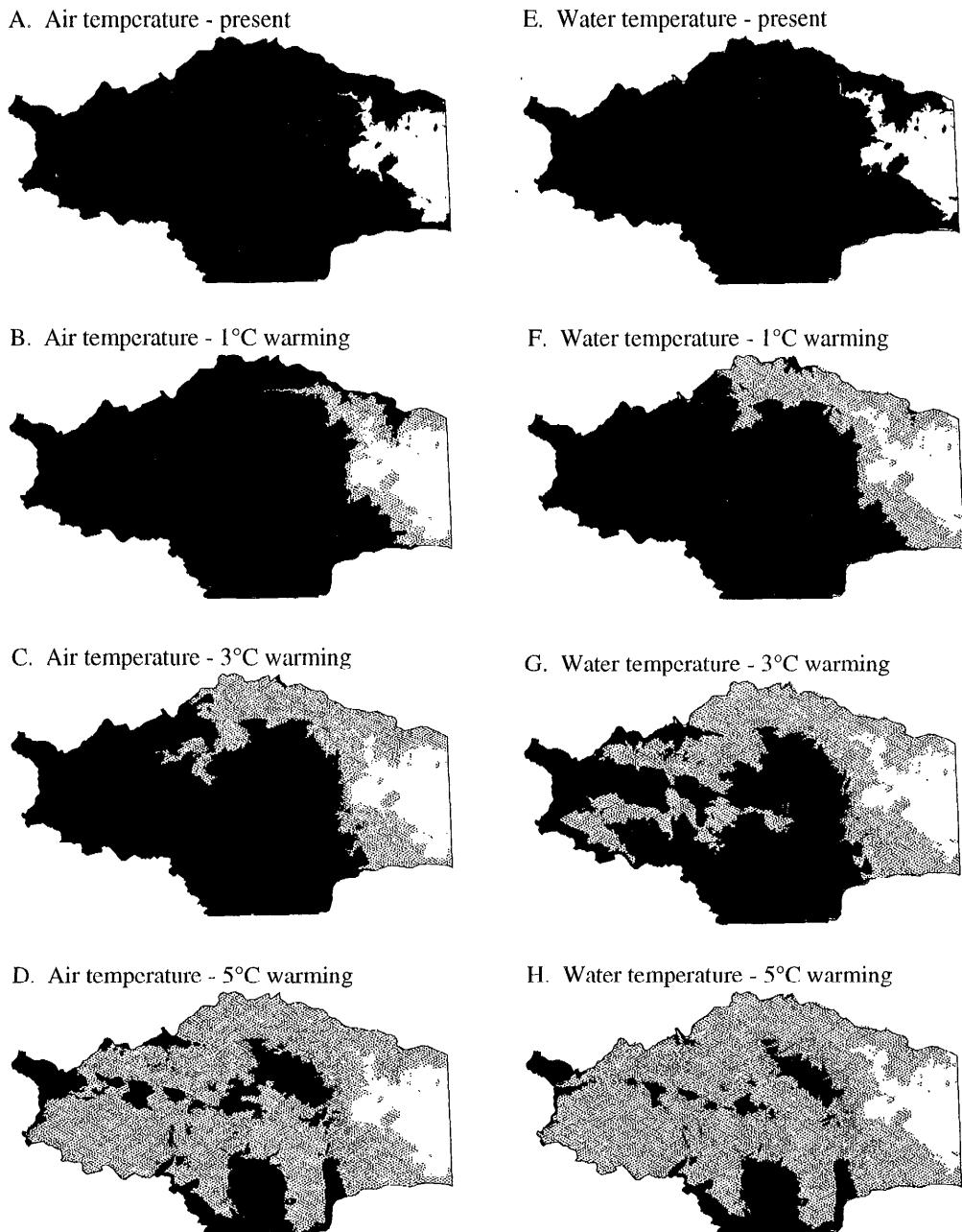


Fig. 2. Loss of habitat for cold water fish in the North Platte River drainage. Areas that are thermally unsuitable at present are shown in white, areas that would be lost with a given temperature increase are shown stippled. Areas that would remain thermally suitable after a given temperature increase are black. A-D. Habitat loss based on use of summer air temperature to define thermal limits. E-H. Habitat loss based on use of summer water temperatures to define thermal limits.

Stream distance lost based on air temperature—The 22°C mean July air temperature isopleth was used as the limit for cold water fish in the drainage. The total stream distance currently contained within the 22°C isopleth of mean July air temperature is 11,822 km, which represents 89.3% of the total stream distance within the drainage (Fig. 2A). For increases of 1–5°C, this distance is reduced by 7–64% (Table 1; Fig. 2B–D).

Stream distance lost based on water temperature—The relationship between elevation and maximum annual water temperature for the drainage was best described by the equation:

$$\begin{aligned}
 \text{JulyC} = & 11.05535 + 0.01526 \text{ (elevation in m)} \\
 & - 0.0000058 \text{ (elevation)}^2, \\
 R^2 = & 0.79 \quad P < 0.0001.
 \end{aligned}$$

Table 1. Loss of habitat for the cold water fish guild in the North Platte River drainage as estimated by three approaches. Habitat loss is the percent loss of habitat from current conditions for warming scenarios of 1–5°C.

Temp. increase (°C)	Geogr. area lost based on air temp. (%)	Stream distance lost based on	
		Air temp. (%)	Water temp. (°C)
1	9	7	16
2	18	15	26
3	26	24	39
4	48	42	54
5	76	64	69

JulyC is the predicted maximum July water temperature in °C. This equation was incorporated in the GIS to create a coverage of predicted maximum July stream temperatures for the drainage from a digital elevation model.

We used this equation to calculate the maximum July water temperature at every site in the drainage where a fish survey had been done. A histogram of salmonid biomass vs. maximum summer water temperature for all the sites in the drainage indicated that 21°C was the upper thermal limit for the cold water fish guild (Fig. 3). There were 26 sample sites in the database with predicted maximum summer water temperatures between 21 and 22°C. Twenty one of these sites lacked trout and the other five sites had only a few brown trout, comprising, on average, 3.4% of the individuals collected. Thus, 21°C maximum summer water temperature was selected as the upper thermal limit for the cold water fish guild in the drainage. Currently, the stream distance with predicted maximum July water temperatures $\leq 21^\circ\text{C}$ is 11,878 km, which represents 89.7% of the stream distance in the drainage (Fig. 2E). For increases of 1–5°C, this distance is reduced by 16–69% (Table 1; Fig. 2F–H).

To determine how sensitive our analysis was to the choice of the upper thermal limit for the cold water fish guild, we looked at the percent of current stream distance that would be lost if the thermal limit was 20, 21, or 22°C. We could not determine habitat losses for thermal limits

Table 2. Sensitivity of habitat loss estimates to the choice of thermal limit for the cold water fish guild. The thermal limits are based on maximum July water temperature. Habitat loss is expressed as the percent of stream distance that would be lost as thermally suitable habitat in the North Platte River drainage for warming scenarios of 1–5°C.

Temp. increase (°C)	Current stream distance that would be lost (%)		
	Limit of 20°C	Limit of 21°C	Limit of 22°C
1	12	16	9
2	27	26	24
3	46	39	33
4	63	54	45
5	71	69	59

>22°C because no streams within the drainage had maximum summer temperatures that high. There were slight differences in the amount of habitat that would be lost assuming different thermal limits (Table 2). As expected, the amount of habitat lost would be reduced as the thermal limit of the fish guild increases. However, whether 20, 21, or 22°C is used as the upper thermal limit for the cold water fish guild in the North Platte River, habitat loss clearly would be noticeable even for small increases in maximum summer water temperature.

Population fragmentation—The drainage above Seminoe Reservoir would remain thermally suitable for cold water species for a 1 or 2°C increase in maximum July water temperature. However, with a 3°C warming, the mainstem of the river above Seminoe Reservoir would become too warm and cold water fish would be restricted to upstream reaches and tributary streams (Fig. 4). The result would be fragmentation of a single large enclave into numerous smaller ones (Table 3). Fragmentation would be even greater if temperatures warmed by 5°C (Fig. 4, Table 3). The largest enclave would decline from 4,128 km at present to 2,191 km with a 3°C increase in maximum summer water temperature and to only 404 km with a 5°C increase.

Discussion

The three approaches give different predictions of habitat loss that would likely occur with climate warming. One reason for these differences is related to the density of streams in relation to elevation. In arid regions with high topographic relief, streams are more abundant at higher elevations relative to lower elevations (Derbyshire 1976; Chorley *et al.* 1984). Thus, as low elevation regions become too warm for cold water fish, a relatively small proportion of the total stream distance is affected. This would explain why estimates of stream distance lost were lower than estimates of geographic area lost for the analysis based on thermal limits defined by mean July air temperature (Table 1).

A second reason for differences in predicted habitat loss among the three approaches concerns differences in how water temperatures and air temperatures change with elevation. The relationship between summer air temperature and elevation is linear, with air temperatures steadi-

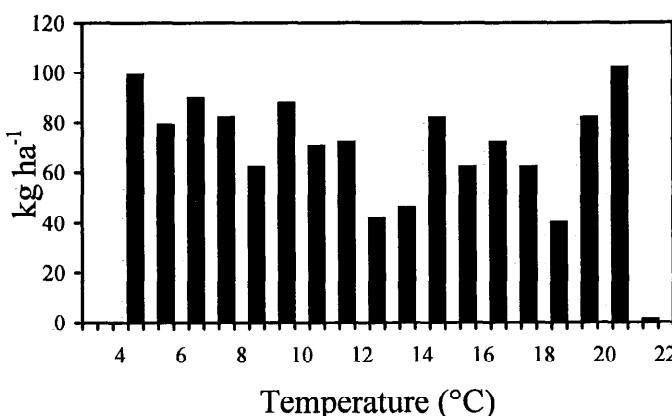


Fig. 3. Histogram showing biomass of the cold water fish guild as a function of maximum July water temperature for 481 sites in the North Platte River drainage.

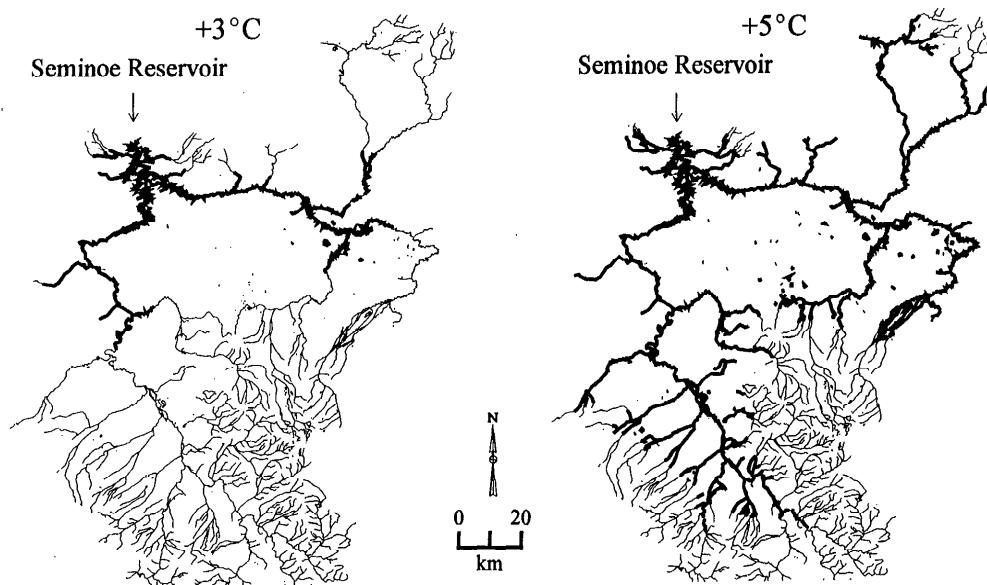


Fig. 4. Fragmentation of stream habitat for cold water fish in the North Platte River upstream of Seminoe Reservoir based on increases of 3 and 5°C in maximum July water temperature. Stream reaches that would become too warm for cold water species are shown by dark lines. The upper reaches of the river in Colorado were not included in the analysis.

ly warming as elevation declines (Fig. 5). This reflects the increased atmospheric pressure at lower elevations, which causes compression and warming of air (Smith 1990; McDonald and Brown 1992). By contrast, the relationship between summer stream temperature and elevation in mountainous regions often is curvilinear (Johnson 1971; Boon and Shires 1976; Theurer et al. 1984), with the rate of water temperature increase slowing at lower elevations (Fig. 5). This reflects the fact that upstream reaches of streams are strongly influenced by equilibration with air temperatures; downstream reaches do not reach equilibrium with air temperatures because of the thermal inertia of increased water volume and the increased influence of groundwater inputs that cool stream temperatures in summer (Boon and Shires 1976; Meisner et al. 1988).

The fact that air temperatures and stream temperatures respond differently to declining elevation explains why estimates of habitat loss based on water temperature vs. air temperature differed for the North Platte drainage. The present lower elevation limit for salmonids in the drainage occurs along the plateau portion of the stream temperature-elevation curve where a 1°C change in tem-

Table 3. Habitat fragmentation for cold water fish in the North Platte River drainage due to increases in maximum July stream temperature. All counted enclaves are nonnested and enclave sizes are expressed as stream distance.

Enclave size (km)	Warming scenario		
	Present	+3°C	+5°C
Largest enclave	4,128	2,191	404
No. >4,000 km	1	0	0
No. between 1,000 and 4,000 km	0	1	0
No. between 10 and 1,000 km	0	10	29
No. <10 km	0	2	19

perature involves a considerable distance along the water temperature-elevation line compared to a shorter distance along the air temperature-elevation line (Fig. 5). In this situation, analysis of habitat loss based on air temperature changes will underestimate the extent of habitat loss. For mountainous areas where the transition between cold water and warm water fauna occurs at elevations where stream temperatures have begun to plateau, the use of thermal limits based on water temperature would be a better approach for modeling changes in cold water fish habitat with climate warming.

Our analysis of fish distributions in relation to water temperature indicated that the cold water guild was limited to stream reaches where the maximum July water temperature was $\leq 21^{\circ}\text{C}$. This is similar to thermal limits reported by other researchers for cold water species. For

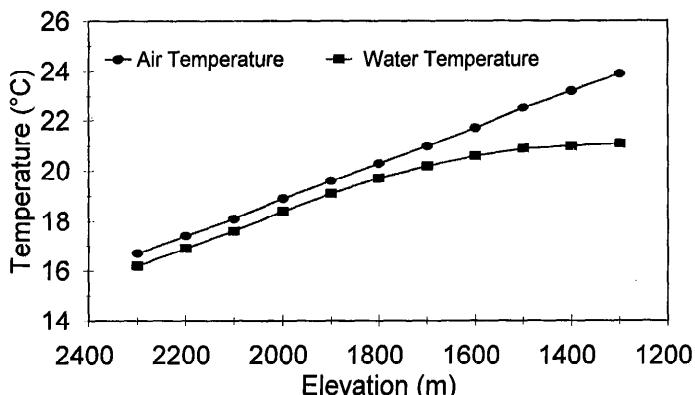


Fig. 5. Schematic relationship between elevation and mean July air temperature and maximum summer water temperature for streams in the North Platte River drainage basin. Relationships are based on temperature models discussed in the text.

example, a maximum summer water temperature $<22^{\circ}\text{C}$ was the critical factor distinguishing trout from nontROUT streams in Ontario (Barton et al. 1985). In extensive monitoring of fish distributions in two southern Ontario streams, the thermal limits of brook trout were $23\text{--}24^{\circ}\text{C}$ (Meisner 1990a). A comparison of fish distributions and stream temperature data throughout the U.S. found that the highest weekly mean water temperatures associated with the presence of cold water species was 22.3°C for brook trout, 24.1°C for brown trout, and 24.0°C for rainbow trout (Eaton et al. 1995). Our estimate of thermal limits is supported by fish survey data from the South Platte River drainage in Colorado. There, Propst (1982) reported that 1,524 m was the lowest elevation at which brown trout were found. On the basis of our regression models, this elevation would correspond to a maximum July water temperature of 20.8°C and a mean July air temperature of 23.1°C . Although the choice of thermal limit does influence the estimate of habitat loss (Table 2), it seems clear that even if the thermal limit of the cold water fish guild is slightly higher than our estimate, climate warming will noticeably reduce the amount of thermally suitable habitat for cold water fish in the Rocky Mountain region.

Loss of habitat for cold water species of stream fish has been predicted for other geographic regions following climate warming. Meisner (1990a) projected a significant reduction in the geographic range of brook trout in eastern North America if air temperature increased by 3.8°C . Stefan et al. (unpubl. rep.) examined the effects of climate warming on cold water fish in Minnesota and projected that this guild would become restricted to streams in the northern portion of the state that had riparian shading to moderate stream warming. In a detailed study of climate effects on Ontario streams, Meisner (1990b) predicted that thermally suitable habitat would be reduced by 30 and 42% in two streams if summer air temperatures were to increase by 4.1°C . In streams of the southern Great Plains, fish may be especially vulnerable to climate warming because the east–west orientation of many streams and the small elevational relief in the region would preclude migration northward or to higher elevations to escape increased water temperature (Matthews and Zimmerman 1990).

The negative effects of climate warming on cold water fish in streams contrast with projections that cold water species in some lakes may benefit from warming due to a lengthening of the growing season (Magnuson et al. 1990). In Lake Superior, doubling of atmospheric CO_2 concentrations was predicted to raise summer epilimnetic water temperatures and result in a 20–70% increase in growth rate for lake trout *Salvelinus namaycush* (Hill and Magnuson 1990). At present, the growing season in temperate or high-latitude lakes is limited by cold water temperatures for much of the year (i.e. temperatures below those optimal for growth, which is $\sim 10^{\circ}\text{C}$ for lake trout). Climate warming would result in the epilimnion warming earlier in spring and remaining warm later in autumn. If we assume that lake trout can thermoregulate by moving downward in the water column when epilimnion tem-

peratures become too warm, the proportion of the year when 10°C water is available will increase with climate warming. Fish unable to thermoregulate (e.g. in lakes with hypolimnetic oxygen depletion) would undergo decreased growth or suffer weight loss in summer when surface water temperatures increase above their optimum temperature (Hill and Magnuson 1990). Also, it is not known how altered food webs or hydrological regimes due to climate warming might affect cold water fish populations in lakes.

We expect that climate warming would restrict cold water populations in streams to increasingly higher elevations in the Rocky Mountain region. As a consequence, not only will the total amount of suitable habitat decline, but also the remaining habitat will become fragmented. These habitat fragments will consist of the headwater reaches of streams that are isolated from each other by thermally unsuitable downstream reaches (Fig. 4). Habitat fragmentation will result in population fragmentation, which is of major concern to conservation biologists. Small, isolated populations are susceptible to inbreeding depression and have an increased probability of extinction through environmental disturbances such as floods or droughts (Leary and Allendorf 1989; Mills and Smouse 1994). Increased extinction rates for small, isolated populations of cold-water fish would be another predicted consequence of climate warming.

One factor that might mitigate the effects of fragmentation is movement of fish among isolated populations. Movement during summer would be prevented by thermally unsuitable temperatures between enclaves. Winter movement would likely be limited because most salmonids show restricted activity as water temperatures approach 0°C (Cunjak and Power 1986; Griffith and Smith 1993). However, fish movement in spring or autumn may provide a mechanism for population exchange or recolonization of headwater enclaves. Meyers et al. (1992) reported that some brown trout in a Wisconsin drainage occupied distinct summer and winter habitats and were generally sedentary during these seasons, but exhibited fall–spring migrations of up to 20 km between the two areas. Gowan et al. (1994) reported that movements of brown trout in a Wyoming stream system were greatest in autumn, with a few fish moving 23–96 km. Such long-distance movements seem to be the exception for stream-resident salmonids, however, because many individuals are sedentary and those that migrate typically move <1 km (Bachman 1984; Riley et al. 1992; Gowan et al. 1994). Thus, small enclaves isolated by many kilometers of thermally inhospitable habitat would likely experience greatly restricted population exchange with other enclaves and thus be vulnerable to the consequences of population fragmentation.

In conclusion, although the three approaches we used varied in their results, all predict a noticeable decline in thermally suitable habitat for cold water fish with even modest increases in temperature due to climate warming. Remaining cold water fish populations would become restricted to increasingly higher elevations and would become fragmented, resulting in inbreeding effects and sto-

chastic environmental fluctuations that would increase the risk of population extinctions. Although our analysis centered on several species of salmonids, the results should apply to other cold water organisms including nongame fish species and benthic invertebrates.

References

BACHMAN, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Trans. Am. Fish. Soc.* **113**: 1-32.

BARTON, D. R., W. D. TAYLOR, AND R. M. BIETTE. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. *N. Am. J. Fish. Manage.* **5**: 364-378.

BOON, P. J., AND S. W. SHIRES. 1976. Temperature studies on a river system in north-east England. *Freshwater Biol.* **6**: 23-32.

CHORLEY, R. J., S. A. SCHUMM, AND D. E. SUGDEN. 1984. *Geomorphology*. Methuen.

CUNJAK, R. A., AND G. POWER. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* **43**: 1970-1981.

DERBYSHIRE, E. [ED.]. 1976. *Geomorphology and climate*. Wiley.

EATON, J. G., AND OTHERS. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* **20**(4): 10-18.

GOWAN, C., M. K. YOUNG, K. D. FAUSCH, AND S. C. RILEY. 1994. Restricted movement in resident stream salmonids: A paradigm lost? *Can. J. Fish. Aquat. Sci.* **51**: 2626-2637.

GRIFFITH, J. S., AND R. W. SMITH. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. *N. Am. J. Fish. Manage.* **13**: 823-830.

HILL, D. K., AND J. J. MAGNUSON. 1990. Potential effects of global climate warming on the growth and prey consumption of Great Lakes fish. *Trans. Am. Fish. Soc.* **119**: 265-275.

HOUGHTON, J. T., G. J. JENKINS, AND J. J. EPHRAUMS [EDS.]. 1990. *Climate change: The IPCC scientific assessment*. Cambridge.

JOHNSON, F. A. 1971. Stream temperatures in an alpine area. *J. Hydrol. (Amst.)* **14**: 322-336.

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. *Trans. Am. Fish. Soc.* **125**: 1-13.

LEARY, R. F., AND F. W. ALLENDORF. 1989. Fluctuating asymmetry as an indicator of stress: Implications for conservation biology. *Trends Ecol. Evol.* **4**: 214-217.

LOWHAM, H. W. 1978. An analysis of stream temperatures, Green River basin, Wyoming. *U.S. Geol. Surv. Water Resour. Invest.* **78-13**.

—, J. E. KIRCHNER, AND F. C. BONER. 1975. Temperatures of Wyoming streams: A basic-data report. *U.S. Geol. Surv. Rep.* **15**.

MACCRIMMON, H. R., AND J. S. CAMPBELL. 1969. World distribution of brook trout, *Salvelinus fontinalis*. *J. Fish. Res. Bd. Can.* **26**: 1699-1725.

MCDONALD, K. A., AND J. H. BROWN. 1992. Using montane mammals to model extinctions due to global change. *Conserv. Biol.* **6**: 409-415.

MAGNUSON, J. J., L. B. CROWDER, AND P. A. MEDVICK. 1979. Temperature as an ecological resource. *Am. Zool.* **19**: 331-343.

—, J. D. MEISNER, AND D. K. HILL. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. *Trans. Am. Fish. Soc.* **119**: 254-264.

MATTHEWS, W. J., AND E. G. ZIMMERMAN. 1990. Potential effects of climate change on native fishes of the southern Great Plains and the Southwest. *Fisheries* **15**(6): 26-32.

MEISNER, J. D. 1990a. 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.

—. 1990b. Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. *Trans. Am. Fish. Soc.* **119**: 282-291.

—, J. S. ROSENFIELD, AND H. A. REGIER. 1988. The role of groundwater in the impact of climate warming on stream salmonines. *Fisheries* **13**: 2-8.

MEYERS, L. S., T. F. THUEMLER, AND G. W. KORNELY. 1992. Seasonal movements of brown trout in northeast Wisconsin. *N. Am. J. Fish. Manage.* **12**: 433-441.

MILLS, S. L., AND P. E. SMOUSE. 1994. Demographic consequences of inbreeding in remnant populations. *Am. Nat.* **144**: 412-431.

NIELSEN, J. L., T. E. LISLE, AND V. OZAKI. 1994. Thermally stratified pools and their use by steelhead in northern California streams. *Trans. Am. Fish. Soc.* **123**: 613-626.

PETERS, R. L., AND J. DARLING. 1985. The greenhouse effect and nature reserves. *BioScience* **35**: 707.

PLANTE, C., AND J. A. DOWNING. 1993. Relationship of salmonine production to lake trophic status and temperature. *Can. J. Fish. Aquat. Sci.* **50**: 1324-1328.

PROFST, D. L. 1982. Warmwater fishes of the Platte River basin, Colorado: distribution, ecology, and community structure. Ph.D. thesis, Colorado State Univ.

RAHEL, F. J., AND W. A. HUBERT. 1991. Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: Biotic zonation and additive patterns of community change. *Trans. Am. Fish. Soc.* **120**: 319-332.

REGIER, H. A., AND J. D. MEISNER. 1990. Anticipated effects of climate change on freshwater fishes and their habitat. *Fisheries* **15**(6): 10-15.

RILEY, S. C., K. D. FAUSCH, AND C. GOWAN. 1992. Movements of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. *Ecol. Freshwater Fish* **1**: 112-122.

SCHINDLER, D. W., AND OTHERS. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* **250**: 967-970.

SHUTER, B. J., AND J. R. POST. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Trans. Am. Fish. Soc.* **119**: 314-336.

SMITH, L. S. 1990. *Ecology and field biology*, 4th ed. Harper and Row.

SNUCINS, E. J., AND J. M. GUNN. 1995. Coping with a warm environment: Behavioral thermoregulation by lake trout. *Trans. Am. Fish. Soc.* **124**: 118-123.

SONG, C. C., A. F. PABST, AND C. E. BROWN. 1973. Stochastic analysis of air and water temperatures. *J. Environ. Eng. Div. Proc. Am. Soc. Civ. Eng.* **99**: 785-800.

THEURER, F. D., K. A. VOOS, AND W. J. MILLER. 1984. Instream flow water temperature model. U.S. Fish Wild. Serv. Instream Flow Inform. Pap. **16**. FWS/OBS-84/15.