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[Article]

Anticipated Climate Warming Effects on Bull Trout Habitats and Populations Across the Interior Columbia River Basin

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Abstract.—A warming climate could profoundly affect the distribution and abundance of many fishes. Bull trout *Salvelinus confluentus* may be especially vulnerable to climate change given that spawning and early rearing are constrained by cold water temperatures creating a patchwork of natal headwater habitats across river networks. Because the size and connectivity of patches also appear to influence the persistence of local populations, climate warming could lead to increasing fragmentation of remaining habitats and accelerated decline of this species. We modeled the relationships between (1) the lower elevation limits of small bull trout and mean annual air temperature and (2) latitude and longitude across the species' potential range within the interior Columbia River basin of the USA. We used our results to explore the implications of the climate warming expected in the next 50 or more years. We found a strong association between the lower elevation limits of bull trout distributions and longitude and latitude; this association was consistent with the patterns in mean annual air temperature. We concluded that climate does strongly influence regional and local bull trout distributions, and we estimated bull trout habitat response to a range of predicted climate warming effects. Warming over the range predicted could result in losses of 18–92% of thermally suitable natal habitat area and 27–99% of large (>10,000-ha) habitat patches, which suggests that population impacts may be disproportionate to the simple loss of habitat area. The predicted changes were not uniform across the species' range, and some populations appear to face higher risks than others. These results could provide a foundation for regional prioritization in conservation management, although more detailed models are needed to prioritize actions at local scales.

Distribution shifts in many species (Parmesan and Yohe 2003; Root et al. 2003) and environmental trends consistent with broad-scale warming (Mote et al. 2005a; Stewart et al. 2005; Westerling et al. 2006; Hamlet and Lettenmaier 2007) show that climate change is no longer an abstraction. Official statistics compiled by the Intergovernmental Panel on Climate Change (IPCC) suggest these trends were associated with a 0.6°C warming during the 20th century (IPCC 2007). Predictions of future global climates suggest larger and faster changes, and current models project a minimum warming of 1°C in mean annual or seasonal air temperatures over the next 50 years and possibly a 6°C increase in 100 years (Boer et al. 1992; Kerr 1997; IPCC 2007). Similar scenarios hold for predictions downscaled to the Columbia River basin, where models project warming of 1–2.5°C or more by 2050 (Leung et al. 2004; Mote et al. 2005b).

A warming climate can have important effects on the regional distribution and local extent of habitats available to salmonids (Meisner 1990; Keleher and Rahel 1996; Nakano et al. 1996; Rahel et al. 1996) and other fishes (Shuter and Meisner 1992; Eaton and Scheller 1996) because local climates influence surface water (Stephan and Preud'homme 1993; Stoneman and Jones 1996; Mohseni and Stefan 1999) and groundwater temperatures (Meisner 1990; Shuter and Meisner 1992). For coldwater fishes near the southern margins

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of their range and areas with substantial elevational relief (and thus gradients in local climate), warming could restrict distributions to smaller and more isolated fragments of suitable habitat (Flebbe 1993; Nakano et al. 1996; Rahel et al. 1996). Several studies have evaluated the potential effects of climate warming on salmonids over broad geographic regions ($>10^5$ km^2; Meisner 1990; Eaton and Scheller 1996; Keleher and Rahel 1996; Nakano et al. 1996; Flebbe et al. 2006; Hari et al. 2006). However, only Flebbe et al. (2006) considered both habitat area lost and habitat fragmentation at this scale, and their analysis did not resolve fragmentation at the level of individual stream networks or local populations.

Bull trout *Salvelinus confluentus* within the Columbia and Klamath River basins of the USA are a relatively recent and controversial addition to the list of species protected under the Endangered Species Act. Bull trout remain widely distributed throughout their potential range, but local extinctions, population declines, and habitat loss are apparent (Rieman et al. 1997). Precise estimation of actual losses is restricted by lack of distribution data on pre–Euro-American influence as well as of broad-scale models of suitable habitat (Rieman et al. 1997).

The optimal temperatures for bull trout appear to be substantially lower than those for other salmonids (Selong et al. 2001). Within-stream distributions of juvenile bull trout have been strongly associated with elevation and temperature (Dunham and Rieman 1999; Paul and Post 2001; Dunham et al. 2003). Although bull trout may move extensively and subadult or adult individuals have been observed throughout larger river basins (Rieman et al. 1997; Swanberg 1997; Muhlfeld and Marotz 2005), juveniles and resident individuals typically live in natal or associated tributary habitats for several years (Pratt 1992; Rieman and McIntyre 1995; Downs et al. 2006). The observed patterns lead us to conclude that spawning and initial rearing areas are constrained by temperature and define the spatial structuring of local populations or habitat "patches" across larger river basins (Rieman and McIntyre 1995; Dunham et al. 2002). Habitat patches in this sense represent networks of thermally suitable habitat that may lie in adjacent watersheds and are disconnected (or fragmented) by intervening stream segments of seasonally unsuitable habitat or by actual physical barriers.

Changes in habitat patch size and distribution are expected to have important effects on the persistence and dynamics of many species through the combined effects on population size, connectivity, and dispersal opportunities (Hanski and Simberloff 1997; Isaak et al. 2007). Rieman and McIntyre (1995) and Dunham and Rieman (1999) found that occurrence of bull trout populations was strongly associated with size and isolation of habitat patches (as defined here). Similar results have been observed for other chars (Morita and Yamamoto 2002; Koizumi and Maekawa 2004), and Isaak et al. (2007) showed that the size and isolation of spawning patches may be even more important than local habitat quality for the persistence of Chinook salmon *Oncorhynchus tshawytscha*. Warming associated with climate change would presumably lead to smaller and more isolated habitat patches for bull trout. It also could lead to loss of populations (i.e., local extinctions) that is disproportionate or accelerated relative to the simple loss of watershed area. Additionally, because bull trout are distributed across a broad range of environments and landforms of varied relief, the effects of climate change may be more pronounced in some regions than others.

In this paper we summarize the available information on bull trout distributions in individual streams and on mean annual air temperatures across the interior Columbia River basin within the USA (hereafter referred to as "the basin"; Figure 1). We used these data to examine evidence for a link between climate and bull trout distributions and then estimated current and potential future distributions of spawning and initial rearing habitats for the range of expected temperature increases. To consider whether the fragmentation of thermally suitable habitats implies risk for populations greater than that expected from loss of habitat area alone, we estimated both total area and size frequency distributions for habitat patches using digital elevation models (DEMs) and a geographical information system (GIS). We were especially interested in differential effects of climate warming among subregions and subbasins. Accordingly, we assigned a measure of risk associated with three levels of warming and then evaluated relative changes across subbasins. Understanding of the distribution of habitat suitable for bull trout and relative risks posed by climate change across the species' range could help prioritization of limited resources for conservation management and research (Peters and Darling 1985; Allendorf et al. 1997; Mattson and Angermeier 2007)

Methods

The general approaches used to predict the distribution of fishes in relation to climate and temperature patterns are varied (e.g., Meisner 1990; Keleher and Rahel 1996; Nakano et al. 1996; Flebbe et al. 2006). We regressed the lower elevation limit of fish occurrence against latitude and longitude, which was expected to reflect climate driven patterns in habitat use. We then modified the predicted distribution based on potential effects of warming. We chose this

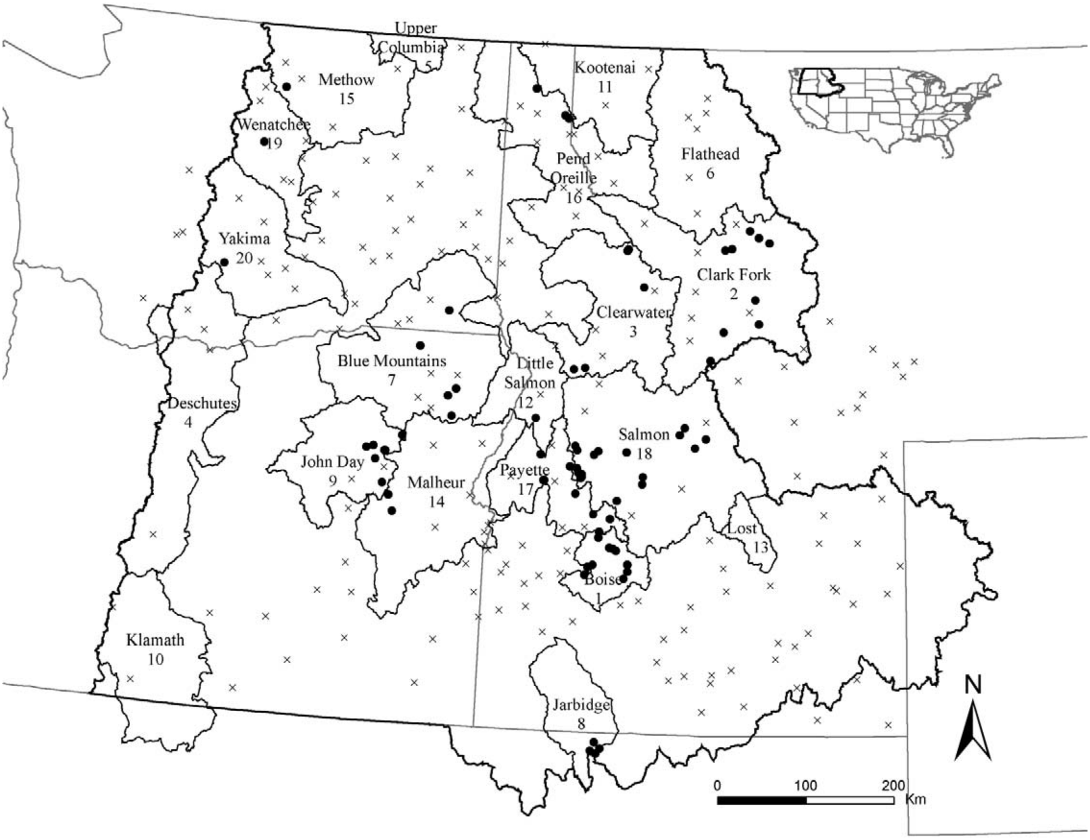

FIGURE 1.—Map of the interior Columbia River basin, showing the subregions (numbered and named after the dominant river) used for predicting bull trout habitat under current and future climates. The locations of air temperature stations (times signs) and of observations of lower elevation limits (circles) are also shown.

approach rather than directly modeling stream temperature and a presumed critical thermal limit because extensive data on fish distributions were available and we did not have the stream-scale environmental detail necessary to estimate stream temperatures directly. The influence of climate also could vary across the species' range because of interaction with other aspects of the environment (Rieman et al. 2006), and our approach allowed quantification of uncertainty in the estimates associated with these effects.

Our approach can be outlined in five general steps: (1) we summarized site-level observations of small bull trout (<150 mm) to identify the lower elevation limits of natal habitats across the basin; (2) we summarized the mean annual air temperatures for weather stations across the same area; (3) we regressed each set of observations against longitude and latitude (and elevation in the case of temperature) and compared the coefficients in the two regression models to assess whether climate could explain bull trout distributions; (4) we used a GIS to map the area and size distributions of thermally suitable habitat patches based on the predicted distribution limits; and (5) we used the GIS to explore changes in the distributions, area, and number of suitable habitat patches by elevating lower distribution limits by three levels of warming that bounded the range of recent predictions. We constrained our analysis to the potential range of bull trout in the basin, following Rieman et al. (1997). We considered suitable patches to be the area of a watershed above the predicted lower distribution limit of small bull trout because these individuals are strongly associated with natal habitat and a clear thermal gradient (Dunham and Rieman 1999; Dunham et al. 2003). The details of each step follow below.

Bull trout distribution.—We summarized observations of the occurrence of bull trout and brook trout *Salvelinus fontinalis* (an invading species that may displace bull trout) within streams sampled at multiple sites along an elevation gradient throughout the basin

(Figure 1). We obtained these observations directly from biologists responsible for fish inventory or monitoring and from published or archived data sets with clearly defined and controlled sampling methods (Platts 1974, 1979; Mauser 1986; Hoelscher and Bjornn 1988; Mauser et al. 1988; Clancy 1993; Adams 1994; Dambacher and Jones 1997; Dunham et al. 2003). We screened only those streams that contained bull trout smaller than 150 mm fork length (with the exception of one data set in which the closest recorded size break was 170 mm), streams with at least five sample sites distributed across 500 m of elevation, and sites represented by at least 45 m of sampled stream. For one data set we combined into single sites groups of three 15-m-long sites that were within 60 m of elevation of each other. Elevations were recorded for the midpoint of sites from 1:24,000 scale U.S. Geological Survey (USGS) topographic maps.

From the initial screening we selected for analysis only those streams in which there were at least two sites without small bull trout below the site with the lowest bull trout observation and at least two sites with small bull trout above that site. We restricted our sample rather than using the larger set of all lowest observations (i.e., bounded or not) because the appropriate model for the latter would require boundary or quantile regression (e.g., Flebbe et al. 2006), essentially forcing the model through the extreme observations. We believe the lower bounds of bull trout distributions among streams vary in response to temperature and its interaction with other environmental conditions, such as the presence of brook trout (Rieman et al. 2006). We assumed that changes in temperature associated with climate could displace other effects (e.g., brook trout would move up in elevation as well) or that similar effects at higher elevation would contribute to similar variability in the lower bound. As a result, regression through the extreme observations would produce an overly optimistic average (i.e., fish at lower elevations) of bull trout habitat use.

Mean annual air temperature.—We used "30-year normals" (i.e., averages of the mean annual air temperature for a 30-year period) from the period 1961 to 1990 to examine the regional spatial pattern in climate. We obtained records for 191 permanent weather stations distributed throughout the basin (Figure 1) from the 1993, 1994, or 1996 NOAA climatological data summaries for each state (e.g., NOAA 1993). We then determined 30-year normals by taking the mean annual air temperature at a station in a given year and substracting the "departure from normal" reported for that year and station. We used the normals for 1961–1990 to derive estimates appropriate for the period of bull trout sampling and to encompass any decadal variation in climate that might obscure regional patterns observed over shorter periods. All but three of our bull trout distribution observations were from data gathered between 1972 and 1996. The last three observations were from 1999 to 2001. Although we recognized that warming probably occurred over this time (e.g., Hari et al. 2006), we assumed that it had not substantively altered regional patterns and a general association of air temperature with elevation required by our analysis.

We chose mean annual air temperature as the simplest measure of climate and its potential effects on the species' distribution. We used the annual mean rather than summer mean because we were uncertain what characteristics of a temperature regime actually influence bull trout. Moreover, groundwater temperature is generally correlated with mean annual air temperature (Meisner 1990; Flebbe 1993; Nakano et al. 1996), has been strongly associated with the distributions of other chars (Meisner 1990; Flebbe 1993; Nakano et al. 1996), and has been shown to influence the survival of embryos and early juvenile growth of bull trout (McPhail and Murray 1979; Baxter 1997). Air temperatures are correlated with stream surface water temperatures (Rahel et al. 1996; BER unpublished data), which have been associated with juvenile bull trout distributions (Dunham et al. 2003) as well.

Regression models.—We used multiple linear regression to model the lower elevation limit of bull trout as a function of latitude and longitude (both in decimal degrees). Because brook trout may displace bull trout to higher elevations (Rieman et al. 2006), the presence or absence of brook trout also was evaluated as a categorical predictor. Although first-order interactions were assessed, they were not significant and were excluded from further consideration. Regression parameters were estimated using standard techniques that assumed spatial independence among residuals and were compared with estimates derived from spatial autoregressive techniques (Cressie 1993). Unbiased parameter estimates were obtained using restricted maximum likelihood procedures in the MIXED procedure in SAS (Littell et al. 1996). If residual errors were spatially correlated, the autoregressive models would provide the most accurate parameter estimates (Cressie 1993). Comparisons between aspatial and spatial models were made using likelihood ratio tests (Littell et al. 1996).

Diagnostic tests of regression residuals suggested no need for data transformations. Standardized residuals indicated four outlying observations (>2 SD), which were examined, found to be valid, and retained in the analysis. Cook's distance and DFFIT statistics indicated these observations did not strongly affect parameter estimates. Variance inflation factors less than 3 suggested that correlations among predictors did not artificially inflate standard error estimates.

Regression models for mean annual air temperature were developed using the same approach as for bull trout distribution limits. Mean annual air temperature was regressed against elevation, latitude, longitude, and first-order interactions. Residuals were normally distributed but were slightly heteroscedastic. A log transformation of air temperatures exacerbated the problem, so we proceeded with untransformed data. Standardized residuals indicated six outliers, but no observation strongly affected parameter estimates. Variance inflation factors indicated no problems with multicollinearity.

Geographical information system analysis.—We used a raster-based DEM along with rasterized latitude and longitude coordinates and our regression models to map potential bull trout habitat across the basin. The DEM data were originally referenced to the geographic coordinate system with a cell size of 3 arc seconds and were transformed to the Albers equal-area coordinate system with a spatial resolution of 90 m. Latitude and longitude coordinates were assigned to each cell in the raster with the same approximate spatial resolution and then input into the bull trout regression equation, along with the DEM data, to characterize each cell as at, above, or below the lower limit of predicted habitat. We converted the raster data to vector format so that cells at the predicted lower limits were delineated by an isopleth. The lower limit was then adjusted upward to create isopleths reflecting an upward shift in elevation with anticipated warming (see below).

We derived stream lines for the basin from the DEM using TauDEM software (Tarboton 1997). We clipped the DEM into 78 USGS fourth-level hydrologic unit codes (HUCs) or subbasins to reduce the data volume of the resultant GIS stream layers. TauDEM was run for every individual HUC to derive stream lines. We used these synthetic stream lines in the analysis because they are spatially coregistered to the DEM and because TauDEM generates a contributing area attribute for the watershed of each stream segment. The digital stream lines were overlain with each isopleth to delineate potential bull trout habitats. We identified watersheds that fell above the isopleth as thermally suitable habitat patches and recorded the area and number of patches.

Distributions and potential climate effects.—We estimated the potential effects of climate warming by manipulating the elevation limits of fish distributions over a range bounding the predicted effects of warming in the next 50 or more years. We used the regression models and patch derivation procedure to develop the recent or base habitat condition and three predictions of suitable area and patch size frequency distributions. For the base condition, we summarized results based on the bull trout lower-limit regression model. We assumed that as warming occurs, the lower limits of bull trout will move up in elevation by an amount equivalent to the mean lapse rate of air temperature (average change in temperature for a unit change in elevation) estimated from the temperature regressions. We then estimated new patch areas and numbers as above. We assumed that warming would not alter upper bounds of bull trout distributions because there have been no clear lower thermal limits (upper elevation limits) associated with bull trout distributions, and small stream size appears to be the more important upper constraint in headwater streams (Dunham and Rieman 1999).

We estimated the total area of patches and the number of patches of selected sizes. We summarized predictions across the 78 subbasins and within 20 USGS third-level HUCs to reduce the complexity of the subbasin pattern. The third-level HUCs are formally known as basins, but we refer to these as "subregions" to avoid confusing our "subbasin" and "basin" definitions.

To visualize the patterns and anticipated risks of climate change across the basin, we summarized patch sizes for each subbasin. Based on analyses of bull trout occurrence and patch size in the Boise River basin, Idaho (Rieman and McIntyre 1995; Dunham and Rieman 1999), we assumed that large patches (>10,000 ha) would support local populations large enough to have a high probability of persistence and that small patches (<5,000 ha) would face a substantially higher probability of local extinction. Multiple local populations can help ensure the persistence of a larger metapopulation (Hanski and Simberloff 1997), and current guidance for bull trout recovery planning suggests five or more local populations of modest size will be necessary to ensure persistence of the species in most of the larger core areas used for planning and management (W. Fredenberg, U.S. Fish and Wildlife Service, personal communication). Core areas are generally consistent with our subbasins. We defined subbasins having no medium (5,000–10,000 ha) or large habitat patches as high risk. Subbasins having five or more medium–large patches or two or more large patches were designated as low risk. Subbasins with an intermediate number of patches were considered at moderate risk.

Results

Regression Models

Bull trout.—From an initial collection of 292 streams with bull trout, 76 (Figure 1) were retained

TABLE 1.—Regression models predicting the lower elevation limit of bull trout from 76 streams across the interior Columbia River basin. The likelihood ratio test was used to compare the spatial and aspatial models based on differences in log likelihood. Significantly smaller values ($P < 0.001$) for the spatial models suggest that the data have spatial variability (Littell et al. 1996).

Model	Variable[a]	Coefficient (SE)[b]	R^2	−2 log likelihood	Residual error
Aspatial, no brook trout	Intercept	17,913 (1500)	0.745	983	33,674
	Latitude	−192.24 (14.7)			
	Longitude	66.29 (12.1)			
Spatial, no brook trout	Intercept	18,693 (1760)	0.744	966	1,248
	Latitude	−190.80 (19.1)			
	Longitude	73.58 (13.9)			
Aspatial, with brook trout	Intercept	17,754 (1480)	0.757	970	32,546
	Latitude	−204.22 (15.8)			
	Longitude	60.54 (12.2)			
	Brook trout	90.74 (48.3)			
Spatial, with brook trout	Intercept	18,558 (1730)	0.753	955	1,549
	Latitude	−197.56 (19.4)			
	Longitude	69.95 (13.9)			
	Brook trout	49.56 (39.5)			

[a] Latitude and longitude are in decimal degrees (longitude values are negative).

[b] All coefficients were statistically significant at $\alpha = 0.001$, except for the brook trout effect ($P = 0.06$ in the aspatial model, 0.22 in the spatial model).

for analysis based on our constraints defining the lower elevation limit. Brook trout occurred in 29 of these streams. Spatial autoregressive models for lower elevation limits performed better than traditional regression models, as indicated by the likelihood ratio tests and smaller residual errors (Table 1). Except for the brook trout effect, spatial models produced similar parameter estimates to aspatial models. Standard errors were usually larger in the spatial models, however, which indicated spatial redundancy in the data that aspatial models ignored. Models including a brook trout effect performed best, but this effect was relatively small (~50 m) and not statistically significant. Because brook trout status was unknown for much of the potential distribution of bull trout across the basin, we chose the simpler spatial model (no brook trout) for consideration of potential climate effects. Latitude and longitude were significant predictors in all models and accounted for most of the variation in bull trout lower elevation limits ($R^2 \approx 0.75$). We found a strong decline in the predicted lower limit elevation from south to north (191 m for every 1° change in latitude; Figure 2) and a more moderate decline from east to west (74 m for every 1° change in longitude).

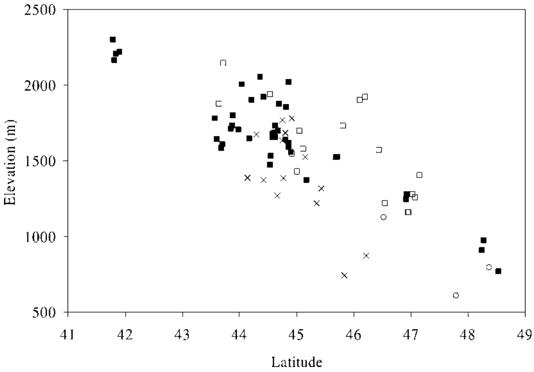

FIGURE 2.—Elevation and latitude of the lower elevation limits for bull trout in the Columbia River basin, by longitude: −113° to −115° (open squares), −115° to −117° (filled squares), −117° to −119° (times signs), and −119° or higher (circles).

Mean annual air temperature.—As with the bull trout models, a spatial autoregressive air temperature model performed better than the aspatial model (Table 2). Parameter estimates changed 5–15% in the spatial model, but standard errors were much larger (24–123%), which indicated considerable spatial redundancy not captured by the aspatial model. Elevation, latitude, and longitude all were significant predictors of mean annual air temperature and accounted for most of the variation ($R^2 = 0.89$).

Temperature model coefficients indicated south–north and east–west gradients that were consistent with the anticipated patterns of climate variation for the region (Mitchell 1976) and with the bull trout distribution (the predicted elevation change for a constant temperature and a 1° change in latitude was 138 m; that for a 1° change in longitude was 88 m). We inferred that climate provides a plausible explanation for bull trout distributions and used the temperature model to predict the changes in elevation that could result from climate warming. By rearranging the temperature model (Table 2) to predict elevation change from temperature change and assuming a uniform shift in temperature with warming (Halpin

TABLE 2.—Regression models predicting the mean annual air temperature at 191 weather stations across the interior Columbia River basin. The likelihood ratio test was used to compare the spatial and aspatial models based on differences in log likelihood. A significantly smaller value ($P < 0.001$) for the spatial model suggests that the data have spatial variability (Littell et al. 1996).

Model	Variable[a]	Coefficient (SE)[b]	R^2	−2 log likelihood	Residual error
Aspatial	Intercept	60.184 (3.56)	0.892	465.9	0.584
	Latitude	−0.7548 (0.0353)			
	Longitude	0.1046 (0.0246)			
	Elevation	−0.00596 (0.000176)			
Spatial	Intercept	67.062 (6.94)	0.888	437.9	0.366
	Latitude	−0.8618 (0.0786)			
	Longitude	0.1193 (0.0503)			
	Elevation	−0.00625 (0.000218)			

[a] Latitude and longitude are in decimal degrees (longitude values are negative); elevations are in meters.

[b] All coefficients were statistically significant at $\alpha = 0.05$.

1997), we estimated that a 1°C increase in temperature equated to an increase in elevation of 161 m. Accordingly, we used 100-m (~0.6°C), 250-m (~1.6°C), and 800-m (~5.0°C) elevation shifts to bound the general predictions of climate warming and estimate the effects on bull trout habitats as outlined above.

Total Area and Patch Number

Estimates of the total suitable area with a 100-, 250-, and 800-m rise in the distribution limits were about 82, 60, and 8%, respectively, of the area estimated for the base condition (Figure 3). Relative changes in patch area and number varied substantially across the subregions (Figure 4). Relative loss of area was most pronounced in the south-central part of the basin (i.e., subregions 7, 8, 9, 10, and 14), but the patterns did not reflect a simple progression with warming or regional gradients. Subregions 13 and 18, for example, appeared to be more resistant to loss of area than other nearby (i.e., south-central) subregions. Some subregions (e.g., 5 and 18) lost relatively little area initially but substantial area with more extreme warming, whereas other subregions (e.g., 6) showed the reverse. In the most extreme scenario, all but four subregions (3, 8, 5, 10) retained some suitable area, but only two (15 and 19) in the extreme northwestern part of the basin retained more than 12% of the original area estimated under current conditions.

Estimates of patch number produced changes similar to but more dramatic than those for area. We predicted that the total remaining number of large habitat patches would be about 73% of the base number given an elevation increase of 100 m, 36% for an increase of 250 m, and 0.6% for an increase of 800 m. For medium patches, the numbers remaining were about 70% of the base at 100 m, 40% at 250 m, and 0.9% at 800 m. Like area, patch number varied across the basin (Figure 4). In some cases the number of medium and large patches changed little or even increased with the first steps in the lower bound (e.g., patches 6, 15, 19), but that was a result of even larger patches being fragmented into multiple smaller ones (note the vertical axes are truncated to one in Figure 4). The more general result was a decline in number of medium or large patches that was substantially more pronounced than the decline in area (Figure 4). Risk, defined by absolute number of medium or large patches, also varied substantially across subbasins. Some subbasins, particularly in the south and central part of the basin, were already at high risk in the base condition (Figure 5). With limited or moderate warming, high and moderate risk was extended throughout the southern and interior part of the basin, although some refugia appeared to remain in central Idaho and around the margins of the basin to the north. Under the most extreme case, anticipated risk was high through virtually the entire basin.

Discussion

From our results and earlier work linking bull trout distributions to thermal gradients, we conclude that climate is, and will continue to be, an important factor in the distribution of bull trout. Our results are generally consistent with predictions for other chars at mid latitudes (Meisner 1990; Flebbe 1994; Nakano et al. 1996) and are also consistent with the view that aquatic ecosystems are influenced by pattern and processes across a hierarchy of scale (Fausch et al. 1994; Rabeni and Sowa 1996; Fausch et al. 2002). In this case, climate is probably a primary constraint on the distribution of bull trout through its effects on the availability, distribution, and size of thermally suitable habitats at both regional and landscape scales. Habitat quality and interaction with other species such as brook trout will have secondary influences at the scale of individual stream reaches (Rieman et al. 2006).

Context, then, is important. Biologists working to

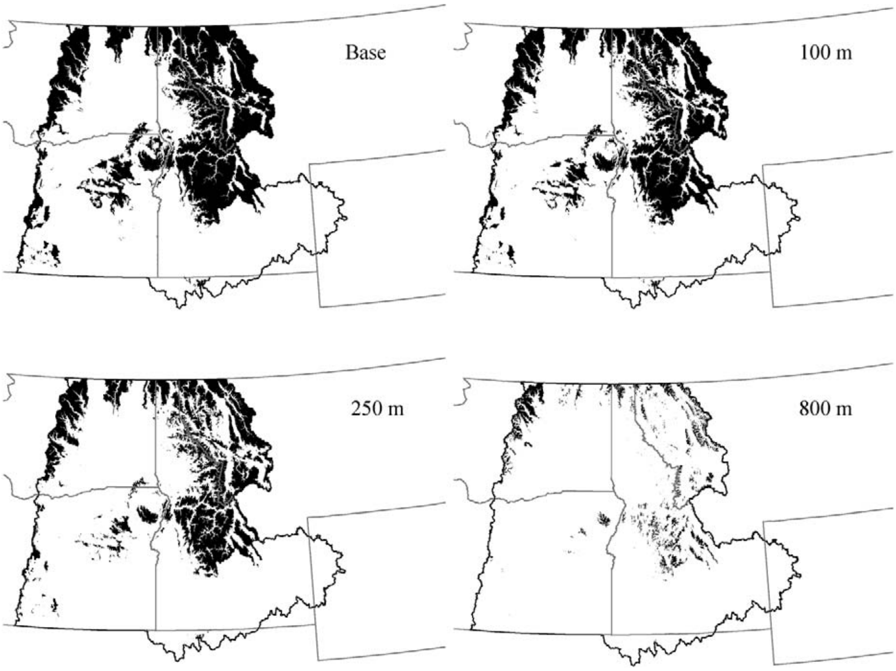

FIGURE 3.—Thermally suitable natal habitat area for bull trout in the interior Columbia River basin under baseline (current) conditions and assuming 100-, 250-, and 800-m increases in their lower elevation limits as a result of climate warming.

understand local distributions or fish–habitat associations must consider both regional and local variation in climate. Studies of bull trout across watersheds or basins (e.g., Watson and Hillman 1997) that fail to incorporate climate, its surrogates (latitude, elevation), or direct effects (stream temperature) may be confounded by spurious correlations (Dunham and Vinyard 1997). For example, an apparent influence of geomorphic conditions (gradient, confinement) or habitat characteristics (stream size, substrate, habitat unit frequency) might emerge because geomorphic patterns also are correlated with elevation and thus with local climate. Management and research directed toward bull trout also will be more effective and efficient if focused in areas most likely to support existing or future populations. Biologists conducting basic inventories, for example, might initiate their surveys in habitats that encompass the estimated lower limits of thermally suitable habitat. Where inventory is lacking, risky management or expensive restoration projects might be more carefully reviewed in watersheds predicted to support spawning and rearing habitats.

Our results also support earlier observations (Rieman and McIntyre 1995; Dunham et al. 2003) indicating that the important patterns in bull trout distributions are specific to life stages. Using the air temperature model presented here, natal habitats for bull trout could be approximated by mean annual air temperatures less than 4–6°C. Small fish distributions appear far more restricted than those for older and larger fish that can move throughout larger river basins with potentially warmer waters (Rieman and McIntyre 1995; Swanberg 1997; Muhlfeld and Marotz 2005). Studies that simply pool all life stages may hide important effects. Because the extent of natal habitat can effectively delimit the structure of local populations, evaluation of critical habitat could be more effectively stratified by considering life-stage-specific patterns in habitat use. Our prediction of habitat area currently suitable for small bull trout (Figure 3), for example, appears to be only a fraction of that mapped as suitable for salmonids in general (see Figure 6 in Keleher and Rahel 1996).

Loss and fragmentation of habitats with warming has important implications for bull trout conservation. We estimated that loss of large habitat patches for bull trout in the interior Columbia River basin would be more pronounced than the simple loss of thermally suitable area. Overall, our estimates of areal loss (18% to 92%) were similar to the losses estimated with climate warming for salmonids in general (Keleher and Rahel 1996; Rahel et al. 1996). In our analysis, however, medium and large habitat patches were lost more quickly than total habitat area. If populations restricted

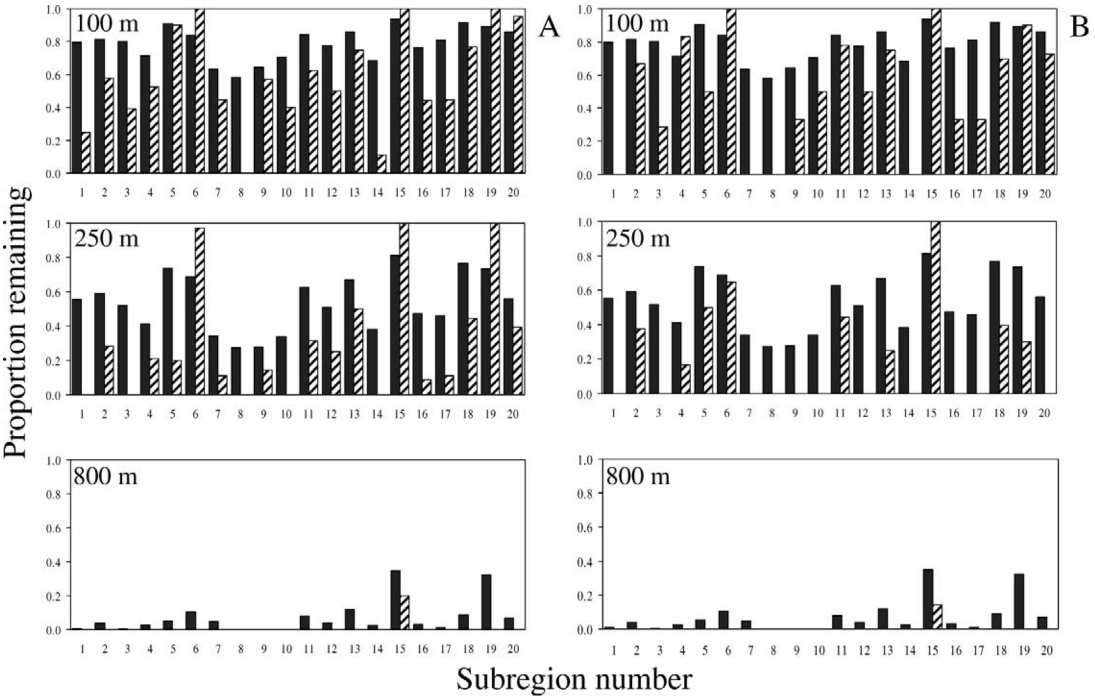

FIGURE 4.—Predicted changes (proportions remaining) of thermally suitable area for bull trout in the interior Columbia River basin (black bars) and the number of habitat patches (hatched bars) of **(A)** medium (5,000–10,000 ha) and **(B)** large size (>10,000 ha), by subregion assuming 100-, 250-, and 800-m increases in the species' lower elevation limits as a result of climate warming. Note that the changes in area are the same in both (A) and (B). The bars for patch number proportions exceeding 1.0 as a result of larger patch fragmentation were truncated.

to smaller or more isolated patches of habitat are more vulnerable to local extinction (Dunham et al. 1997; Dunham and Rieman 1999; Morita and Yamamoto 2002; Rich et al. 2003; Isaak et al. 2007) losses could proceed more quickly than implied by the loss of thermally suitable area alone. Even limited warming may produce dramatic increases in the extirpation of local populations of bull trout in some areas of the interior Columbia River basin.

The predicted changes with any warming varied substantially across the basin. Owing to both local land form (i.e., topographic relief) and geographic location within the climatic gradient of the region, it appears that some bull trout populations face higher risks than others. The relative differences in existing conditions and predicted changes among subregions and subbasins could be important in development of conservation priorities. For example, the Jarbidge River subbasin on the Idaho–Nevada border, other tributaries to the Snake River near the Oregon, Washington, and Idaho borders, and those associated with the northeastern flank of the Cascades in Oregon (west-central portion of the basin) appear to be at high risk already. If they are to persist with climate warming, aggressive measures in habitat conservation or restoration may be needed. This assumes, of course, that mitigation of existing habitat problems could also mitigate the risks associated with climate change.

As the resources for conservation management are limited and not expected to expand dramatically in the foreseeable future, effective prioritization will be important. Our results suggest moderate to high risks will extend across the basin with even modest warming. Consideration of ecological and evolutionary significance, as well as risk related to climate change, could highlight areas as regional priorities (Allendorf et al. 1997). For example, by virtue of their extended isolation from other bull trout populations and location on the extreme margins of the species' range, both the Jarbidge and Klamath subregions could represent distinct and thus evolutionarily important populations (Leary et al. 1993; Lesica and Allendorf 1995; Rieman et al. 1997) worthy of extraordinary efforts.

Effectively weighting and acting on the risks associated with climate and other anthropogenic changes will be no simple task. In some cases different

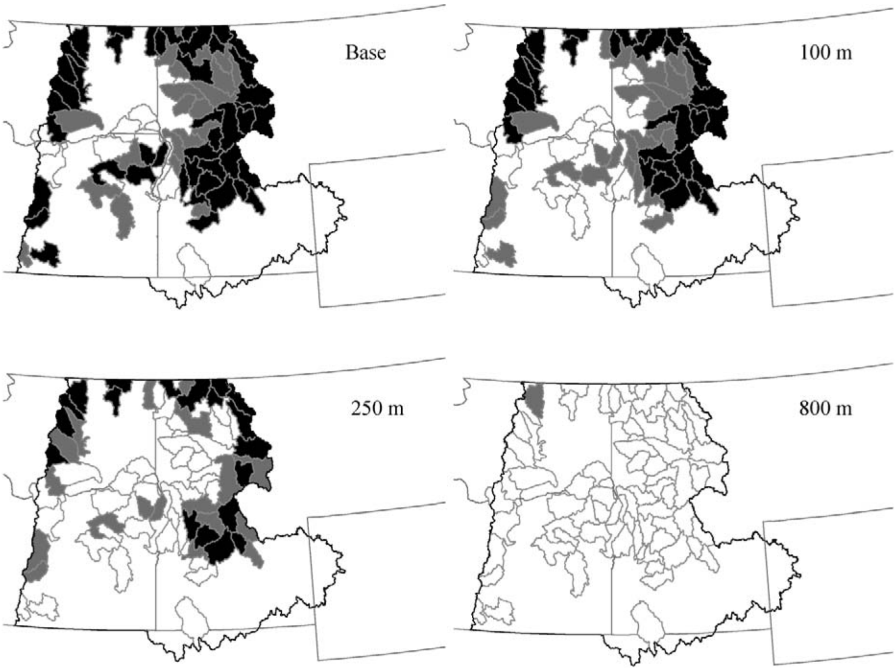

FIGURE 5.—Risk of bull trout extirpation according to the number of medium or large habitat patches remaining in individual subbasins of the interior Columbia River basin assuming 100-, 250-, and 800-m increases in the lower elevation limits for this species as a result of climate warming. Risk was considered high (no shading) if no medium or large patches remained, moderate (gray shading) if one to four medium patches or one large patch remained, and low (black shading) if five or more medium–large patches or two or more large patches remained.

risks may increase confusion surrounding management alternatives. In one view, to be most efficient and to assure a core of healthy populations for the long term, investment of limited conservation resources should be focused on securing areas where there is a good chance of success, not on those facing the highest risk. Extensive investment may be pointless if climate change is expected to eliminate most suitable habitat (Halpin 1997). Alternatively, land use management and habitat restoration in areas with already degraded habitats may become critical if remnant populations are to retain enough resilience to persist under the challenges posed by even modest climate change. Resolution of these issues will depend on the scale and scope of management. Regional priorities might be focused both by the potential for short-term loss of ecological and evolutionary significance in marginal populations and the potential for long-term persistence in core habitats. Local priorities might be based on short-term urgency implied by the interactions between land use and climate change. Short-term habitat conservation and restoration for bull trout could be far more urgent in subregions of central Oregon or southwestern Idaho, for example, than in areas less vulnerable to change. Long-term goals may focus on conserving, restoring, or even expanding high-quality habitats in subbasins and patches that have the best chance for persistence, especially if climate change proceeds as quickly as some anticipate.

Our analysis has important limitations. We focused only on potential habitat and did not consider other factors that may limit bull trout in some areas. Indeed, bull trout may already be gone or severely depressed in regions that still appear to sustain suitable habitat and even large patches. The regression models are limited by the number and distribution of observations and unexplained variation in the observations. The mean error in the predicted lower elevation limit (142 m), for example, was roughly equivalent to the anticipated effect of a 1°C warming (161 m increase in comparable elevation). Clearly, local effects, including small-scale variation in climate, linkages between air and water temperatures, behavior, ecological interactions, evolutionary history and potential, and sampling error and bias may confound our results and predictions of both current and future patterns. Although the influence of brook trout was not clear in our analyses, more detailed analyses do suggest that brook trout can displace bull trout (Rich et al. 2003; Rieman et al. 2006). Future warming might favor an expanding invasion of species like brook trout that could exacerbate our predicted losses and fragmentation of bull trout habitats. Climate changes also are anticipated to be more complex than a uniform, vertical displacement of mean annual isotherms (Halpin 1997). Climate may warm more in some regions than others (Leung et al. 2004). Important changes are likely to include seasonal and spatial patterns in precipitation that will in turn influence patterns of stream flow and flooding (Lettenmaier et al. 1992; Poff et al. 1996; Stewart et al. 2005; Knowles et al. 2006). Winter floods that can dramatically influence the dynamics of fall-spawning fishes (Seegrist and Gard 1972) like bull trout may become more common in some areas (Lettenmaier et al. 1992). Others predict increased frequency or extent of wildfire (McKenzie et al. 2004; Westerling et al. 2006) that can directly remove riparian vegetation or catalyze severe channel disturbances such as debris flows (Luce 2005). Given the large component of a stream heat budget driven by solar radiation (Johnson 2003), riparian disturbances may exacerbate stream warming beyond the direct climate effect. Conceivably, the combined effects of shrinking patch size and increasing frequency or magnitude of stream channel disturbance could even accelerate the rate of local extinctions beyond that driven by temperature alone.

Our work is clearly a first approximation of the potential influence of regional climate patterns on the distribution of bull trout habitat and the risks that implies. Our intent was to look for broad patterns and compare relative effects of habitat loss and fragmentation. We conclude that the effects of climate change will be important and vary substantially across the basin. We acknowledge the uncertainty and limited resolution of our analysis. These results can serve as a basis for regional discussion and more detailed study. They should not be extrapolated directly, however, for management of bull trout populations or habitats within individual subbasins without consideration of the local effects such as habitat degradation, hydrology and stream temperature, migration barriers, and nonnative species.

Most climate models have limited resolution, making application at the watershed and landscape scales problematic. Finer resolution extrapolations that incorporate local drivers such as topographic effects are now being developed (Bartlein et al. 1997; Ferguson 1997; Leung et al. 2004), and whole climate regimes (i.e., temperature, precipitation and their seasonal timing) offer an approach for more complete analyses (Halpin 1997). Detailed studies of individual stream networks and watersheds should provide better resolution of the local climatic, hydrologic (e.g., Lettenmaier et al. 1992), and ecological processes likely to influence the distribution and persistence of bull trout at this scale and identify the sources of variability underlying the uncertainty of general predictions. Replication of existing data sets and representative sampling based on probabilistic designs could help resolve the rate of change that may already be occurring and the accuracy of further predictions.

In the interim, efforts to study, conserve, and restore bull trout populations and habitats will proceed based on existing information, resources, and agency commitment. The capability to do that work effectively and efficiently will depend on an ability to focus and prioritize resources. Climate patterns should be an important consideration in any analysis. Our results indicate that climate is a first-order determinant of bull trout distributions. From this, we also infer that climate warming may lead to an important loss of bull trout habitats and that the resulting fragmentation can lead to local extinctions more quickly than anticipated from a simple loss of thermally suitable watershed area. Occurrence and persistence of bull trout will vary with climate gradients and with landscape characteristics likely to modify local climate, stream temperatures, and the extent of thermally suitable habitats within and among streams across the species' range.

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References

Adams, S. B. 1994. Bull trout distribution and habitat use in the Weiser River drainage, Idaho. Master's thesis. University of Idaho, Moscow.

Allendorf, F. W., D. W. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11:140–152.

Bartlein, P. J., C. Whitlock, and S. L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11:782–792.

Baxter, J. S. 1997. Aspects of the reproductive ecology of bull trout in the Chowade River, British Columbia. Master's thesis. University of British Columbia, Vancouver.

Boer, G. J., N. A. McFarlane, and M. Lazare. 1992. Greenhouse gas–induced climate change simulated with the CCC second generation general circulation model. Journal of Climate 5:1045–1077.

Clancy, C. G. 1993. Statewide fisheries investigation, Bitterroot Forest inventory. Montana Department of Fish, Wildlife and Parks, Job Completion Report F-46-R-4, Helena.

Cressie, N. 1993. Statistics for spatial data, revised edition. Wiley, New York.

Dambacher, J. M., and K. K. Jones. 1997. Stream habitat of juvenile bull trout populations in Oregon and benchmarks for habitat quality. Pages 353–360 *in* W. C. Mackay, M. K. Brewin, and M. Monita, editors. Friends of the Bull Trout conference proceedings. Trout Unlimited, Canada, Calgary, Alberta.

Downs, C. C., D. Horan, E. Morgan-Harris, and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190–200.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642–655.

Dunham, J. B., B. E. Rieman, and G. L. Chandler. 2003. Influences of temperature and environmental variables on the distribution of bull trout at the southern margin of its range. North American Journal of Fisheries Management 23:894–904.

Dunham, J. B., B. E. Rieman, and J. T. Peterson. 2002. Patch-based models to predict species occurrence: lessons from salmonid fishes in streams. Pages 327–334 *in* J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall, editors. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California.

Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Transactions of the American Fisheries Society 126:323–329.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17:1126–1133.

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., S. Nakano, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia 100:1–12.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Ferguson, S. A. 1997. A climate change scenario for the Columbia River basin. U.S. Forest Service, Pacific Northwest Research Station, PNW RP 499, Portland, Oregon.

Flebbe, P. A. 1993. Comment on Meisner (1990): Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 50:883–884.

Flebbe, P. A. 1994. A regional view of the margin: salmonid abundance and distribution in the southern Appalachian mountains of North Carolina and Virginia. Transactions of the American Fisheries Society 123:657–667.

Flebbe, P. A., L. D. Roghair, and J. L. Bruggink. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Transactions of the American Fisheries Society 135:1371–1382.

Halpin, P. N. 1997. Global climate change and natural area protection management responses and research directions. Ecological Applications 7:828–843.

Hamlet, A. F., and D. P. Lettenmaier. 2007. Effects of 20th century warming and climate variability on flood risk in the western U.S. Water Resources Research 43(6): W06427. DOI:10.1029/2006WR005099.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology, ecology, genetics, and evolution. Academic Press, San Diego, California.

Hari, R. E., D. M. Livingstone, R. Siber, P. Burkhardt-Holm, and H. Guttinger. 2006. Consequences of climatic change for water temperature and brown trout populations in alpine rivers and streams. Global Change Biology 12:10–26.

Hoelscher, B., and T. C. Bjornn. 1988. Habitat, densities of trout and char, and potential production in Pend Oreille Lake tributaries. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-71-R-10, Boise.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: the physical science basis. Available: www.ipcc.ch. (February 2007).

Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B. Dunham. 2007. Relative roles of habitat size, connectivity, and quality on Chinook salmon use of spawning patches. Ecological Applications 17:352–364.

Johnson, S. L. 2003. Stream temperature: scaling of observations and issues for modeling. Hydrological Processes 17:497–499.

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.

Kerr, R. A. 1997. Greenhouse forecasting still cloudy. Science 276:1040–1042.

Knowles, N., M. D. Dettinger, and D. R. Cayan. 2006. Trends in snowfall versus rainfall in the western United States. Journal of Climate 19:4545–4559.

Koizumi, I., and K. Maekawa. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. Freshwater Biology 49:973–981.

Leary, R. F., F. W. Allendorf, and S. H. Forbes. 1993.

Conservation genetics of bull trout in the Columbia and Klamath river drainages. Conservation Biology 7:856–865.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9:753–760.

Lettenmaier, D. P., L. W. Vail, S. B. Yabusaki, K. L. Brettmann, and M. J. Scott. 1992. Sensitivity of Pacific Northwest water resources to global warming. Northwest Environmental Journal 8:265–283.

Leung, L. R., Y. Qian, X. Bian, W. W. Washington, J. Han, and J. O. Roads. 2004. Midcentury ensemble regional climate change for the western United States. Climatic Change 62:75–113.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina.

Luce, C. H. 2005. Fire effects on runoff generation processes. Pages 1831–1838 *in* M. G. Anderson and J. J. McDonnell, editors. Encyclopedia of hydrological sciences, volume 3. Wiley, Chichester, UK.

Mattson, K. M., and P. L. Angermeier. 2007. Integrating human impacts and ecological integrity into a risk-based protocol for conservation planning. Environmental Management 39:125–138.

Mauser, G. R. 1986. Enhancement of trout in large north Idaho lakes. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-73-R-8, Boise.

Mauser, G. R., R. W. Vogelsang, and C. L. Smith. 1988. Enhancement of trout in large north Idaho lakes. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Study Completion Report, Project F-73-R-10, Boise.

McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climate change, wildfire, and conservation. Conservation Biology 18:890–902.

McPhail, J. D., and C. B. Murray. 1979. The early life history and ecology of Dolly Varden (*Salvelinus malma*) in the upper Arrow Lakes. Department of Zoology and Institute of Animal Resource Ecology, University of British Columbia, Manuscript Report, Vancouver.

Meisner, J. D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 47:1065–1070.

Mitchell, V. L. 1976. The regionalization of climate in the western United States. Journal of Applied Meteorology 15:920–927.

Mohseni, O., and H. G. Stefan. 1999. Stream temperature–air temperature relationship: a physical interpretation. Journal of Hydrology 218:128–141.

Morita, K., and S. Yamamoto. 2002. Effect of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. Conservation Biology 16:1318–1323.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005a. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Mote, P. W., E. Salathe, and C. Peacock. 2005b. Scenarios of future climate for the Pacific Northwest. University of Washington, Seattle.

Muhlfeld, C. C., and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797–810.

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.

NOAA (National Oceanic and Atmospheric Administration). 1993. Climatological data annual summary, Idaho 96(13). NOAA, Asheville, North Carolina.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature (London) 421:37–42.

Paul, A. J., and J. R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. Transactions of the American Fisheries Society 130:417–430.

Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. BioScience 35:707–717.

Platts, W. S. 1974. Geomorphic and aquatic conditions influencing salmonids and stream classification in the Salmon River drainage, Idaho, 1970–1972. U.S. Forest Service, Progress Report III, Boise, Idaho.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries 4(2):5–9.

Poff, N. L., S. Tokar, and P. Johnson. 1996. Stream hydrological and ecological responses to climate change assessed with an artificial neural network. Limnology and Oceanography 41:857–863.

Pratt, K. L. 1992. A review of bull trout life history. Pages 5–9 *in* P. J. Howell and D. V. Buchanan, editors. Proceedings of the Gearhart Mountain Bull Trout Workshop. American Fisheries Society, Oregon Chapter, Corvallis.

Rabeni, C. F., and S. P. Sowa. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):252–259.

Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and population fragmentation for coldwater fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography 41:1116–1123.

Rich, C., T. McMahon, B. Rieman, and W. Thompson. 2003. Influence of local habitat, watershed, and biotic features on bull trout occurrence in Montana streams. Transactions of the American Fisheries Society 132:1053–1064.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:895–909.

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.

Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have brook trout displaced bull trout along longitudinal gradients in central Idaho streams? Canadian Journal of Fisheries and Aquatic Sciences 63:63–78.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C.

Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature (London) 421:57–60.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478–482.

Selong, J. H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026–1037.

Shuter, B. J., and J. D. Meisner. 1992. Tools for assessing the impact of climate change on freshwater fish populations. Geojournal 28:7–20.

Stephan, H. G., and E. B. Preud'homme. 1993. Stream temperature estimation from air temperatures. Water Resources Bulletin 29:27–45.

Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18:1136–1155.

Stoneman, C. L., and M. J. Jones. 1996. A simple method to classify stream thermal stability with single observations of daily maximum water and air temperature. North American Journal of Fisheries Management 16:728–737.

Swanberg, T. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 126:735–746.

Tarboton, D. G. 1997. A new method for the determination of flow directions and contributing areas in grid digital elevation models. Water Resources Research 33:309–319.

Watson, G., and T. W. Hillman. 1997. Factors contributing to the distribution and abundance of bull trout: an investigation of ecologic hierarchies. North American Journal of Fisheries Management 17:237–252.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science 313:940–943.