North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 09 Jan 2011.

North American Journal of Fisheries Management 25:225–237, 2005

DOI: 10.1577/M03-165.1

[Article]

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Abstract.—Stream temperature is an important factor influencing habitat suitability for cutthroat trout *Oncorhynchus clarkii*, but temperature data from headwater habitats are difficult to obtain. We tested the ability of easily obtained landscape and meteorological data to predict the mean daily temperature measured at 79 sites in tributaries to the Madison River, Montana. We also evaluated stream habitat suitability by using temperature predictions to estimate growth potential for age-0 westslope cutthroat trout *O. c. lewisi*. A model using mean daily air temperature, elevation, and channel gradient explained approximately 75% of the observed variation in mean daily stream temperatures. Classifications of habitat suitability based on predicted fish growth indicated that the majority (78%) of stream habitat in Madison River tributaries provides suitable or highly suitable habitat for westslope cutthroat trout. However, these higher-quality habitats occur primarily in lower-elevation reaches where westslope cutthroat trout have been displaced by nonnative salmonids. Linking potential fish growth to stream temperature predictions will help managers prioritize conservation efforts for this declining subspecies by predicting habitat suitability at potential reintroduction or population expansion sites.

Westslope cutthroat trout *Oncorhynchus clarkii lewisi* have undergone substantial reductions in distribution and abundance throughout their historical range (Liknes and Graham 1988; Behnke 1992). Impacts such as habitat alteration, overharvest, and introductions of nonnative fishes have restricted most westslope cutthroat trout populations to isolated headwater habitats (Liknes and Graham 1988; Shepard et al. 1997). Interactions (such as predation, competition, or hybridization) with nonnative salmonid species probably constitute the greatest contemporary factor responsible for the loss of westslope cutthroat trout populations (Allendorf and Leary 1988; Liknes and Graham 1988; USFWS 1999). As with other interior subspecies of cutthroat trout, primary management strategies for westslope cutthroat trout include identifying and maintaining remnant populations and establishing new populations through translocations of genetically pure fish (MFWP 1999). When new populations of cutthroat trout are established they are introduced into historically fishless stream reaches or streams in which nonnative salmonids have been removed through chemical or mechanical (i.e., physical removal by electrofishing) treatment (Harig et al. 2000; Shepard et al. 2001). However, translocations of cutthroat trout have sometimes failed to produce viable populations, often at great expense in terms of both labor and financial cost (Thompson and Rahel 1998; Harig 2000). Developing basinwide restoration strategies for cutthroat trout requires fish managers to assess habitat suitability across large spatial scales and to identify sites with relatively high chances of translocation success.

Environmental temperature is a fundamental element defining habitat suitability for aquatic organisms (Magnuson et al. 1979). Temperature, through its direct effect on metabolism, is a primary factor controlling fish growth (Railsback and Rose 1999; Edmundson and Mazumder 2001). Growth potential is an important indicator of habitat suitability because fish growth incorporates much of the variability in thermal conditions experienced by individual fish. The distribution and abundance of salmonids have been positively as-

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Received August 24, 2003; accepted June 17, 2004
Published online February 28, 2005

sociated with the potential for stream habitat to provide positive growth (Nislow et al. 2000).

In streams with limited growth opportunities, salmonid fry face overwinter starvation if they cannot grow enough to withstand metabolic deficits at low winter temperatures (Shuter and Post 1990; Harig et al. 2000). Translocations of cutthroat trout sometimes fail because low stream temperatures limit juvenile recruitment (Harig et al. 2000). Information on stream temperature and its potential effects on fish growth, therefore, are useful to fish managers who wish to assess the suitability of streams for reintroduction of westslope cutthroat trout.

Stream temperature data are usually limited and difficult to obtain in headwater stream habitats. When stream temperatures are unavailable, air temperature data, which are typically more abundant, are often used to approximate the thermal behavior of a stream (Brown 1969; Cluis 1972; Smith and Lavis 1975; Stefan and Preud'homme 1993). However, large differences in water temperature can exist both within and among adjacent streams as a result of local landscape characteristics (Smith and Lavis 1975). For example, relief and aspect, in combination with riparian vegetation, may determine the extent to which the stream surface is shielded from direct solar radiation (Smith and Lavis 1975). Therefore, knowledge of how landscape features and meteorological conditions interact to affect stream temperatures is necessary to understand and predict thermal regimes across broad, geomorphically complex areas (Isaak and Hubert 2001).

In this study, we focused on the summer temperatures of small streams within the Madison River basin, Montana, and the possible influence of temperature on potential growth for juvenile westslope cutthroat trout. We tested the ability of easily obtained landscape and meterological data to predict daily stream temperatures by calibrating multiple-regression models against empirical observations of daily summer stream temperatures. We linked mean daily stream temperature predictions to a temperature-dependent growth model for juvenile salmonids (Selong et al. 2001) by predicting daily growth within individual stream reaches and summing these growth increments over the growing season. We use this link between environmental temperature and fish growth to evaluate current habitat suitability for westslope cutthroat trout across the Madison River basin. This linkage can help fishery managers prioritize conservation efforts and refine water temperature criteria to support this declining cutthroat trout subspecies.

Study Area

The Madison River valley is a 906-km^2, north-trending, intermontane basin located in southwest Montana. The Madison River is formed at the confluence of the Firehole and Gibbon rivers in Yellowstone National Park, Wyoming, and flows approximately 195 km northward before joining the Gallatin and Jefferson rivers to form the Missouri River near the town of Three Forks, Montana. Our study focused on tributaries to the 101-km section of the Madison River between Hebgen and Ennis reservoirs (Figure 1).

The Madison Range, which forms the eastern border of the study area, is within the Absaroka–Gallatin–Madison–Bridger Sedimentary Mountain ecoregion, a carbonate-rich, mostly forested, and partially glaciated region (Woods et al. 1999). The Madison Range rises sharply from the valley floor to peak elevations exceeding 3,200 m. The Gravelley Mountain Range, which forms the western border of the study area, is part of the Eastern Gravelley Mountain ecoregion and is less rugged than the Madison Range, with elevations not exceeding 2,900 m. The lower slopes of the Gravelley and Madison ranges and floor of the Madison River valley lie within the Dry Intermontane Sagebrush Basins ecoregion, which is composed of alluvial, fan, and valley fill deposits with natural vegetation of sagebrush steppe (Woods et al. 1999). Although the alluvial plain in the Madison River valley is predominately privately owned, most of the basin is public and managed by the U.S. Forest Service (USFS). The primary land use in the Madison River valley is livestock grazing, with localized dryland and irrigated agriculture. While limited logging has occurred on USFS land in the Gravelley Mountains, we observed very little evidence of timber clearing adjacent to any study streams. Land use is restricted in the majority of the Madison Range through wilderness designation of USFS land.

Study streams ranged from first to fourth order (measured from 1:24,000-scale topographic maps after Strahler 1957), with drainage areas between 9.2 and 128.8 km^2. Flow regimes in tributary streams are driven by snowmelt, with peak discharges occurring in May and June. Study stream discharges are 0.02–0.92 m^3/s during the late summer when streamflows are at their lowest (Sloat 2001). Riparian vegetation adjacent to study streams was dominated by mixed conifer stands in

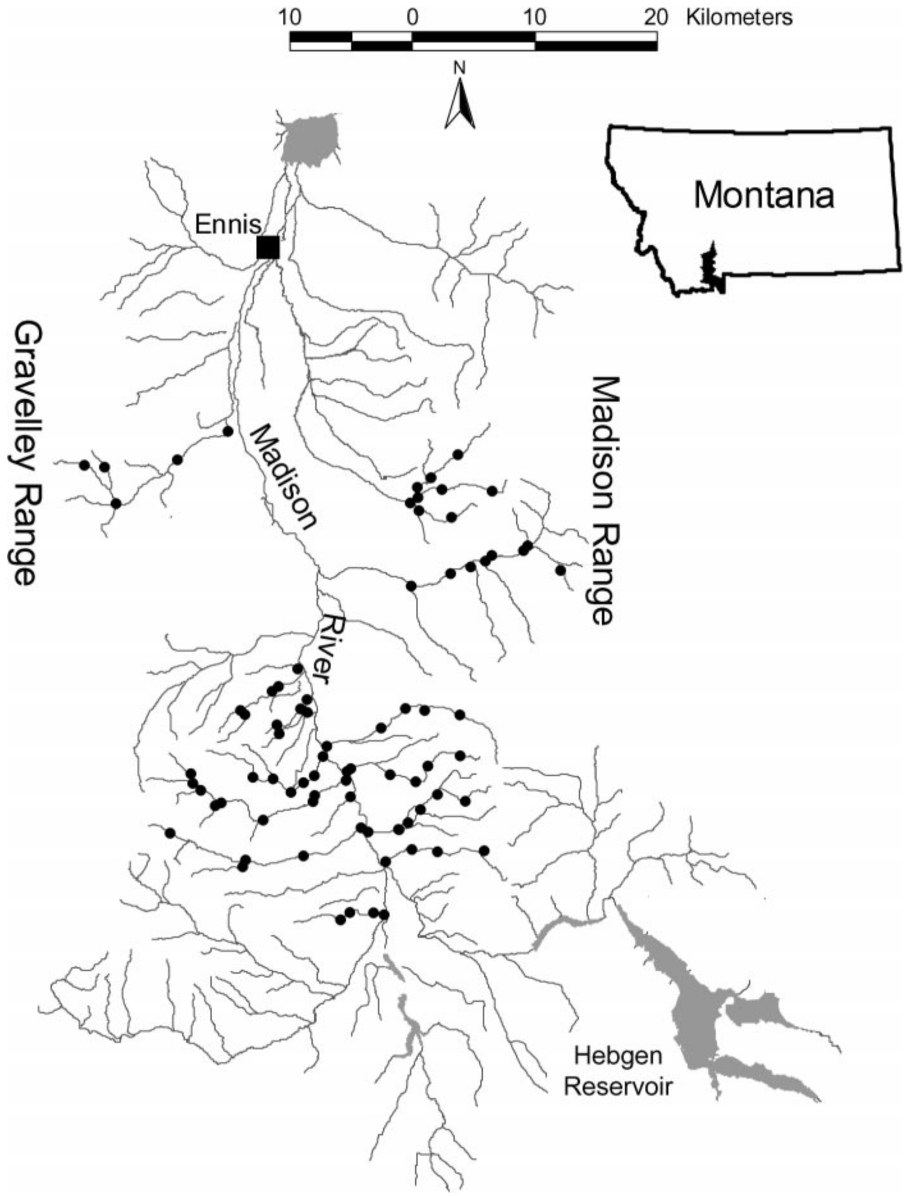

FIGURE 1.—Map of the Madison River basin, Montana, showing the locations of temperature sampling sites (pound signs).

headwater reaches and black cottonwood *Populus balsamifera* and willow *Salix* spp. along lower elevation reaches in the Madison River valley. The climate of the Madison River valley is typical of high elevation basins in the Rocky Mountains, with mild summers and cold winters. The mean annual precipitation is 33.7 cm, and the mean annual air temperature is 6.4°C on the valley floor (NOAA 2000).

Fish communities in study streams consist of native populations of westslope cutthroat trout and mottled sculpin *Cottus bairdii*, and introduced populations of Yellowstone cutthroat trout *O. c. bouvieri*, rainbow trout *O. mykiss*, and brown trout *Salmo trutta* (Sloat et al. 2001).

Methods

Temperature modeling.—Water temperatures were measured with continuously recording digital thermographs. Stream temperatures were sampled at two sites in 1997, six sites in 1998, and 71 sites in 1999 (Figure 1). The thermographs we used (Onset Computer Corporation, Pocasset, Massachusetts; Hobo and Stowaway Models) measure temperatures ranging from −5°C to +37°C with an accuracy of ±0.2°C. Before sampling, we tested thermographs against a National Institute of Science and Technology handheld thermometer at 3, 9, and 20°C to correct for instrument bias. During all years, water temperatures were sampled from 1 July to 15 September. We placed thermographs in well-mixed run or pool habitats shielded from direct solar radiation. Thermographs recorded stream temperatures at 1- or 2-h intervals, depending on the memory capacity of the thermograph model. Sample sites were referenced by kilometer above the stream's mouth and by latitude and longitude obtained from a handheld global positioning system (GPS) and input into an ArcView-based geographic information system (GIS; ESRI 1999).

Prior to data analysis, hourly and bihourly stream temperature measurements were summarized into daily means. We used multiple regression to relate stream temperatures to meterological and landscape variables for study streams, using mean daily water temperature as the response variable. Mean daily air temperatures, elevation, aspect, channel gradient, riparian forest cover, and drainage area were included as possible predictor variables. Mean daily air temperatures were obtained from published National Oceanic and Atmospheric Administration (NOAA) meterological records from the Ennis, Montana, weather station (Figure 1; NOAA 1997, 1998, 1999). All other variables were quantified with the aid of a GIS that used several different data layers for the Madison River basin. Data layers included a 1:24,000 hydrography layer that included stream channel locations for study streams, a 30-m resolution digital elevation matrix (DEM) of the Madison River basin based on U.S. Geological Survey (USGS) data, and a 90-m grid of land cover types obtained from the Montana Gap Analysis Project (GAP; Redmond et al. 1998).

To assess landscape characteristics associated with each sample site, polygons encompassing the drainage area above each sample site were created. First, the lowermost thermograph sample site within each stream was defined as a ''pour point'' in ArcView. These pour points were used by the Surface Water Modeler extension in ArcView to automatically delineate the watershed boundaries upstream from each pour point using a 30-m DEM of the study area (ESRI 1999). Drainage boundaries delineated by the Surface Water Modeler were visually verified by plotting them, overlaying them onto USGS contour maps (1:24,000 scale), and adjusting drainage boundaries (where necessary) to conform to observed drainage divides. Errors in watershed delineation occurred in approximately 16% of the watersheds and occurred primarily in extreme headwater portions of watersheds or in areas of low topographic variability on the alluvial plane of the Madison River valley. After verifying the correct delineation of drainage areas for entire tributaries, the pour point procedure was repeated for each sample site to create subdrainage polygons above each site.

Channel elevation, channel gradient, channel aspect, riparian forest cover, and drainage size were estimated for each sample site once subdrainage boundaries were defined. Elevation was quantified as the mean elevation of the entire stream channel network upstream from the site. To assign elevation values to the stream channel, the hydrography data layer was converted to a 30-m grid and intersected with the DEM grid in ArcView. Mean channel elevation was then calculated from elevation values for each cell in the resulting grid. Mean channel gradient (the change in elevation divided by the stream channel length) was calculated for the entire stream network above each thermograph site from a slope coverage derived from the DEM. Channel aspect was defined as the downslope direction (the maximum rate of change in elevation along the stream channel) from each cell to its neighboring cells within the DEM, expressed in positive degrees from 0 to 360, measured clockwise from the north. Numeric ranks indicative of the relative solar radiation the drainage likely received were then assigned to compass directions (north = 0, northeast = 1, east = 2, southeast = 3, south = 4, southwest = 3, west = 2, and northwest = 1). Drainage area was calculated for the portion of the watershed above each thermograph sample site in ArcView. A 90-m grid of land cover types obtained from Redmond et al. (1998) was used to determine the influence of riparian vegetation shading on stream temperatures. The land cover data set was composed of 45 vegetation types based on remotely sensed imagery collected from 1991 to 1993. Estimated mean accuracy of cover type classification exceeded 80% within our study area (Redmond et al. 1998). Because we were only interested in potential shading effects of riparian vegetation, we reclassified vegetation cover types into either ''tree'' or ''nontree'' categories. We then applied a 200-m buffer centered on the stream channel and calculated the percentage of land area that had tree cover within the buffer.

Best-subsets regression was used to analyze variable combinations in the stream temperature models. We used a variety of model selection criteria, including Akaike's information criteria (AIC), Mallows' C_p, and adjusted coefficient of determination for the selection of alternative regression models (Neter et al. 1996; Burnham and Anderson 1998). Variance inflation factors were calculated to identify multicollinearity among predictor variables (Neter et al. 1996). Distributions of residuals were analyzed to ensure assumptions of normality were satisfied. Tests for normality used studentized residuals and the *W* statistic, following the method of Shapiro and Wilk (1965). The Durbin–Watson test for autocorrelation of error terms was used to evaluate the influence of the time series nature of the data (Neter et al. 1996). We tested for the effects of additional correlation between observations occurring within the same subdrainage or sample year on mean daily stream temperatures using the variables from the most plausible regression model entered as fixed variables, and subdrainage and year as random variables (SAS Institute 1999). We used the Wald statistic to test for significance of random effects (Littel et al. 1996).

Model performance was assessed by means of a jackknife procedure that did not require the collection of an independent set of reference data (Olden and Jackson 2000). Each sample site was systematically excluded from the data set and the model was fit to the remaining observations. The refitted model was then used to predict temperatures for the site that was removed. This procedure avoids using observations to simultaneously create and evaluate the predictive performance of the regression model. The agreement between observed and predicted values was summarized to evaluate model predictions.

Growth prediction.—After selecting the model that appeared most plausible according to our selection criteria, we input 30-year mean air temperatures (1971–2000; NOAA 2000) into that model to estimate daily stream temperatures at 2.0-km reaches along each stream within the study area. Thirty-year mean air temperatures were used to approximate average recent climatic conditions and to eliminate the effect, if any, of sample year on temperature predictions. These analyses were not completed for the lower portions of major tributaries (West and South forks of the Madison River), the main stem of the Madison River, or for spring creeks. Temperatures in these streams were expected to differ from study streams in their response to meterological and landscape characteristics because of either their larger size or higher contribution of groundwater to their streamflow.

Mean daily stream temperature predictions were then input into a growth model developed for juvenile (age-0) bull trout *Salvelinus confluentus* that predicts daily growth with an unlimited food ration across a range of water temperatures (Selong et al. 2001). The bull trout model was used because published models are not currently available for westslope cutthroat trout and preliminary laboratory results have shown close similarities between the growth of westslope cutthroat trout and bull trout in response to temperature (Beth Bear, Montana State University, personal communication). Potential daily fish growth was estimated using the mean daily water temperature and fish growth equation (Selong et al. 2001),

$$\text{Growth (g/d)} = 0.0625(\text{temperature}) - 0.0024(\text{temperature})^2 - 0.2634.$$

Based on this temperature–growth relationship we calculated and summed potential daily growth during the summer (1 July–15 September) for all 2.0-km stream reaches within the study area. Sites with negative growth predictions were assigned a growth potential of zero. We then ranked habitat suitability for each stream reach based on predicted fish growth, with sites where potential annual fish growth (weight gain) was less than 5 g/year considered unsuitable, sites with predicted weight gain of 5–10 g/year considered suitable, and sites with weight gain greater than 10 g/year considered highly suitable. Growth-classes used for habitat suitability rankings were based on temperature-specific growth observed in 60-d trials by Selong et al. (2001) adjusted for the slightly longer time period of our study (77 d).

Results

Temperature Modeling

Mean daily stream temperature was 8.3°C (SD, 2.4°C; range, 2.3–16.6°C), and mean daily air temperature was 17.2°C (SD, 3.8°C; range, 6.9–23.0°C) during the study period. The values of landscape variables ranged widely among sample sites (Table 1). The regression analysis of meteorological and landscape variables on mean daily stream temperature resulted in multiple significant

TABLE 1.—Summary of descriptive statistics associated with variables used to model mean daily stream temperature.

Variable	Mean	SD	Minimum	Maximum
Mean stream temperature (°C)	8.3	2.4	2.3	16.6
Mean air temperature (°C)	17.2	3.8	6.9	23.0
Elevation (m)	2,411	183	1,918	2,827
Riparian tree cover (%)	69.7	28.0	0	100
Channel gradient (%)	10.7	2.9	6.6	21.8
Drainage area (km^2)	22.3	25.2	1.3	128.8

models (Table 2). The model including all predictor variables considered in this study was the most plausible in terms of both AIC values and Mallows' C_p, but models with fewer variables explained a similar percentage of the variation in stream temperatures (Table 2). The model that included only mean air temperature, elevation, and channel gradient was more plausible in terms of both AIC values and Mallows' C_p when compared with competing models with the same number of parameters (Table 2). These variables were also included in all of the most plausible models that contained greater than three variables (Table 2). The addition of variables including mean air temperature, elevation, and channel gradient to the model introduced multicollinearity among predictors, as measured by variance inflation factors (Table 3). Although alternative models were plausible in terms of other criteria (such as AIC values and Mallow's C_p), because of relatively small increases in the adjusted coefficient of determination and the introduction of multicollinearity among predictors as more variables were included, we chose the three-variable model including mean air temperature, elevation, and channel gradient for further analysis.

Most stream temperatures estimated by the model, including mean air temperature, elevation, and channel gradient, closely corresponded with observed stream temperatures (Figure 2). The maximum raw residual value was 4.2°C. The standard deviation of raw residual values was 1.2°C. Tests for normality of Studentized residuals indicated model errors were normally distributed ($W = 0.99$; $P < 0.01$). As expected, the Durbin–Watson test statistic ($d = 0.3023$; $n = 6{,}210$) indicated positive correlation of error terms, confirming that the time series nature of the data prevented independence of daily stream temperature observations. However, cross-correlation results from the jackknife procedure indicated that parameter estimates for model variables were stable, as evidenced by close concordance between predicted and observed mean daily stream temperatures, and that the model was robust. The mean prediction error when sample sites were iteratively removed from the data set was −0.03°C (SD, 1.3°C; range, −5.4 to +5.5°C). When the effect of sample year and subdrainage were included as random effects in a mixed regression model, all variables considered in the linear model retained their significance (Table 4). Mean daily stream temperature was not significantly associated with sample year but was significantly associated with subdrainage ($P = 0.004$; Table 4).

Growth Prediction

Potential fish growth was estimated for 1,453 km of tributaries in the Madison River basin using

TABLE 2.—Candidate models for predicting mean daily stream temperature. The two best-fitting models for each number of variables are listed. A base model (including air temperature [air] and elevation [elev]) is provided for comparison. Other variables include riparian tree cover (tree [%]), channel gradient (gradient [%]), downslope direction (aspect), and drainage area (area [km^2]). Models are listed in ascending order by Akaike's information criterion (AIC), Mallows' C_p, and adjusted coefficient of determination (R^2).

Model variables	Number of variables	F	P	AIC	ΔAIC	Mallows' C_p	R^2
Air + elev	2	5,301.96	<0.0001	22,242.09	2,710.94	3,406.6	63.1
Air + elev + tree	3	4,926.05	<0.0001	20,866.10	1,334.95	1,496.1	70.4
Air + elev + gradient	3	6,091.73	<0.0001	19,908.90	377.75	396.4	74.6
Air + elev + gradient + aspect	4	3,718.77	<0.0001	20,838.77	1,307.62	251.9	75.2
Air + elev + gradient + tree	4	4,843.96	<0.0001	19,637.04	105.89	113.7	75.7
Air + elev + gradient + tree + area	5	3,894.24	<0.0001	19,615.17	84.02	91.5	75.8
Air + elev + gradient + tree + aspect	5	3,939.45	<0.0001	19,600.02	68.87	36.6	76.0
Air + elev + gradient + tree + area + aspect	6	3,304.36	<0.0001	19,531.15	0.00	7.0	76.1

TABLE 3.—Multiple-regression parameter estimates, confidence intervals (CIs), and variance inflation factors for eight models of mean daily stream temperature (MDST). See Table 2 for definitions of the variables.

Parameter	Parameter estimate	95% CI Lower	95% CI Upper	Variance inflation factor
MDST = air + elevation				
Intercept	21.003	20.517	21.489	
Air	0.328	0.318	0.338	1.0
Elevation	−0.008	−0.008	−0.008	1.0
MDST = air + elevation + channel gradient				
Intercept	25.649	25.211	26.087	
Air	0.329	0.321	0.337	1.0
Elevation	−0.008	−0.008	−0.008	1.0
Channel gradient	−0.283	−0.293	−0.273	1.0
MDST = air + elevation + tree				
Intercept	22.602	22.159	23.045	
Air	0.333	0.324	0.342	1.0
Elevation	−0.007	−0.007	−0.007	1.0
Tree	−3.097	−3.252	−2.942	1.0
MDST = air + elevation + channel gradient + tree				
Intercept	25.470	25.041	25.899	
Air	0.331	0.323	0.339	1.1
Elevation	−0.008	−0.008	−0.008	1.0
Channel gradient	−0.228	−0.240	−0.216	1.4
Tree	−1.417	−1.583	−1.251	1.4
MDST = air + elevation + channel gradient + aspect				
Intercept	24.859	24.407	25.311	
Air	0.330	0.322	0.338	1.0
Elevation	−0.008	−0.008	−0.008	1.1
Channel gradient	−0.281	−0.291	−0.271	1.0
Aspect	0.152	0.127	0.177	1.1
MDST = air + elevation + channel gradient + tree + area				
Intercept	25.322	24.890	25.754	
Air	0.331	0.323	0.339	1.1
Elevation	−0.008	−0.008	−0.008	1.0
Channel gradient	−0.218	−0.231	−0.205	1.6
Tree	−1.578	−1.756	−1.400	1.2
Area	0.003	0.002	0.004	1.6
MDST = air + elevation + channel gradient + tree + aspect				
Intercept	24.890	24.445	25.335	
Air	0.332	0.324	0.340	1.0
Elevation	−0.008	−0.008	−0.008	1.1
Channel gradient	−0.223	−0.391	−0.055	1.5
Tree	−1.264	−1.276	−1.252	1.5
Aspect	0.114	0.089	0.139	1.1
MDST = air + elevation + channel gradient + tree + area + aspect				
Intercept	24.699	24.250	25.148	
Air	0.331	0.323	0.339	1.1
Elevation	−0.008	−0.008	−0.008	1.0
Channel gradient	−0.221	−0.234	−0.208	1.7
Tree	−1.440	−1.619	−1.261	1.2
Area	0.003	0.002	0.004	1.6
Aspect	0.119	0.094	0.144	1.1

the model that included mean daily air temperature, elevation, and channel gradient, with air temperature values based on 30-year averages. Potential fish growth ranged from zero to 13.1 g, with the majority of stream reaches providing suitable or highly suitable habitat based on predicted growth potential (Figure 3). Approximately 547 km (38%) of stream habitat had a predicted annual growth greater than 10 g/year, 536 km (37%) had a predicted growth of from 5 to 10 g/year, and 369 km (25%) had a predicted growth of less than 5 g/year (Figure 4). Growth potential generally de-

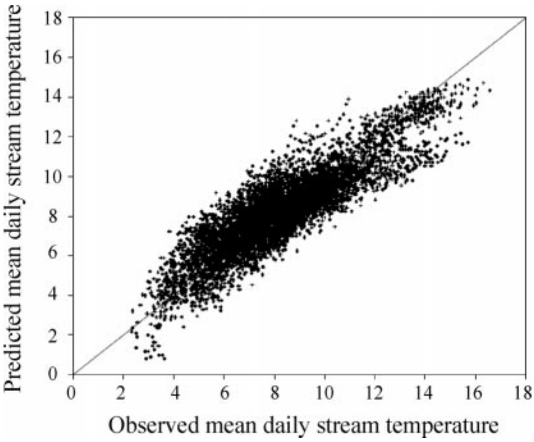

FIGURE 2.—Comparison between observed and predicted mean daily stream temperatures (°C) from a multiple-regression model using air temperature, elevation, and channel gradient. A 1:1 line is included for reference.

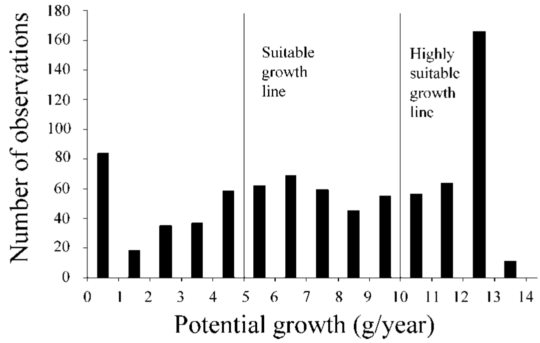

FIGURE 3.—Frequency distribution of westslope cutthroat trout growth potential in 2-km reaches of stream habitat in the Madison River basin.

clined with increases in elevation, with the highest mean growth predictions between 1,700 and 2,100 m (Figure 5). No stream reaches over 2,900 m had positive growth predictions (Figure 5).

Discussion

We found that the majority of the variation in mean daily stream temperatures in the Madison River basin could be explained by mean air temperature, elevation, and channel gradient. These model components have been widely recognized to influence stream temperatures (Smith and Lavis 1975; Stefan and Preud'homme 1993; Isaak and Hubert 2001). Mean daily air temperature is positively correlated with stream temperatures, and in areas with little topographic complexity accurate stream temperature predictions can be obtained using only air temperature (Cluis 1972; Cassie et al. 2001). Because we used a fixed source for air temperature values to predict stream temperatures across a large study area, we expected the influence of this variable on stream temperatures to vary between sample sites. Including elevation and channel gradient as predictor variables with mean air temperature improved model fit, likely because localized landscape conditions affected the correlation of stream temperatures and fixed-source air temperatures. Both elevation and channel gradient negatively influenced stream temperatures.

TABLE 4.—Results of a multiple-linear-regression model (linear) and a mixed-regression model (mixed) to predict mean daily stream temperatures. The linear model included elevation, average daily air temperature, and channel gradient. The mixed model included all variables in the linear model plus the ''random'' variables, year and subdrainage. See Table 2 for more on the variables used. The type III *F*-values and associated *P*-value are shown for fixed effects, and the component of variance, Wald's *Z*-value, and the associated *P*-value are shown for random effects. There were a total of 6,210 observations within 16 subdrainages over 3 years.

Model and variables	Fixed effects		Random effects		
	Type III *F*	*P*	Component of variance	*Z*-value	*P*
Linear					
Air	6,770.07	<0.001			
Elevation	9,811.02	<0.001			
Channel gradient	1,123.24	<0.001			
Residual			1.37	55.7	<0.001
Mixed					
Air	8,052.85	<0.001			
Elevation	3,660.52	<0.001			
Channel gradient	482.22	<0.001			
Year			0.034	0.93	0.172
Subdrainage			0.529	2.67	0.004
Residual			1.17	55.62	<0.001

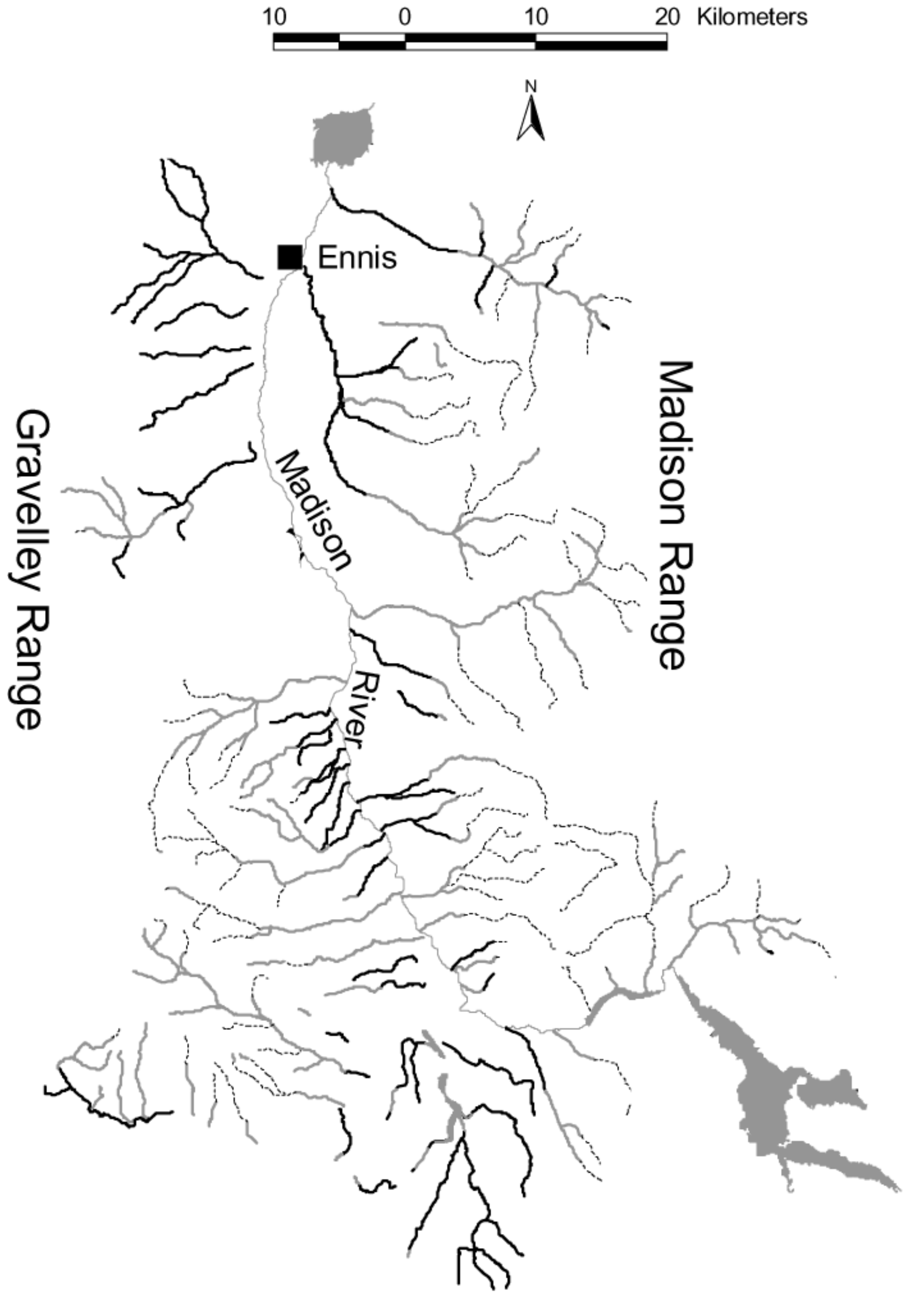

FIGURE 4.—Habitat suitability based on growth potential for age-0 westslope cutthroat trout in the Madison River basin (dark lines = highly suitable; broad gray lines = suitable; dotted black lines = unsuitable). Habitat suitability was not assessed for the Madison River itself (light gray line) or for the lower portions of major tributaries and spring creeks (not shown).

Elevation can be predicted to have a direct negative effect on stream temperatures because of the lapse rate of air temperature with elevation (Isaak and Hubert 2001). Channel gradient is correlated with velocity and may indicate the amount of time that water spends in the channel as it travels downstream (Wehrly et al. 1998). The time required for water to move downstream is the time a unit volume of water is exposed to heat exchange with the atmosphere (Smith and Lavis 1975; Theurer et al.

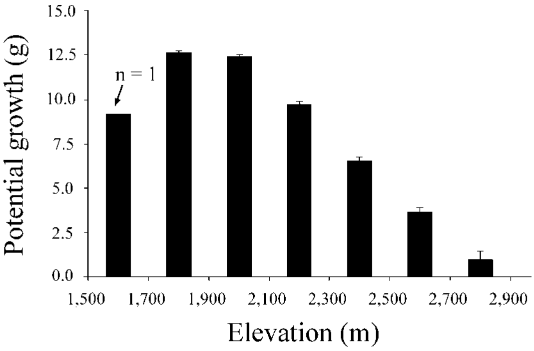

FIGURE 5.—Mean growth potential (+SE) for age-0 westslope cutthroat trout averaged across 200-m changes in elevation.

1984; Bartholow 1989). In general, as travel time increases, streams accumulate heat and approach an equilibrium temperature at which net heat exchange with the atmosphere is zero (Brown 1969; Theurer et al. 1984; Bartholow 1989). Factors that reduce travel time, such as higher channel gradients, reduce the amount of time a unit volume of water is exposed to sources of heat.

Other variables considered in this study—drainage area, riparian vegetation, and channel aspect—have also been shown to influence stream temperatures (Brown 1969; Smith and Lavis 1975; Isaak and Hubert 2001). However, these variables did not substantially increase predictability (improvement in adjusted R^2) when added to the model including mean air temperature, elevation, and channel gradient or when used in other variable combinations. Generally, lower values for AIC and Mallows' C_p indicate improved model fit when used in conjunction with well-formulated a priori hypotheses (Burnham and Anderson 1998). However, post hoc analysis and autocorrelation of environmental variables may introduce bias into these model selection procedures (Burnham and Anderson 1998). Although these measures of model performance suggested that increasing the number of variables included in alternative models improved model fit, we observed very small increases in predictability and the introduction of multicollinearity between predictor variables. Consequently, the model including only mean air temperature, elevation, and channel gradient was used for stream temperature predictions.

Despite considerable variation in observed temperatures within some streams, random effects of drainage were detected in a mixed-regression model, indicating that spatial correlation of stream temperatures occurred among sites within the same drainage. Positive spatial autocorrelation may not bias parameter estimates but may underestimate variances, inflating the chance of finding a significant result when in fact one does not exist: a type I statistical error (Zar 1984; Dunham and Vinyard 1997). However, after accounting for the effects of drainage in a mixed-regression model, mean air temperature, elevation, and channel gradient retained their statistical significance, indicating that temperature predictions from these variables were reliable.

Modeling mean daily stream temperatures allowed us to link stream temperature predictions to temperature-dependent growth models for juvenile salmonids. Our study focused on stream temperatures, but growth of juvenile salmonids depends on several other factors, including microhabitat availability, prey availability, and foraging success (Elliot 1994; Hayes et al. 2000; Nislow et al. 2000). Limited evidence also suggests that local adaptations to thermal regimes may play a role in the regulation of growth (Lobon-Cervia and Rincon 1998). However, our goal was to use temperature-based predictions of growth potential as an indicator of habitat quality, rather than to provide quantitative estimates of growth rates for westslope cutthroat trout.

Since temperature–growth relationships have not been developed for westslope cutthroat trout, we used data for bull trout (Selong et al. 2001) to approximate the effect of temperature on potential growth for juvenile westslope cutthroat trout. Although the temperature requirements for westslope cutthroat trout are not well studied, both empirical and theoretical evidence suggests that bull trout and westslope cutthroat trout have similar thermal preferences. Temperature–growth relationships are available for species more closely related to westslope cutthroat trout (e.g., rainbow trout; Hokanson et al. 1977), but we assumed that bull trout more closely approximated the thermal preferences of westslope cutthroat trout because bull trout and westslope cutthroat tend to have sympatric distributions where the historical ranges of the two species overlap (Mullan et al. 1992). Where the historical ranges of rainbow trout and westslope cutthroat trout overlap the species tend to segregate, with westslope cutthroat trout occupying colder, upstream reaches (Mullan et al. 1992). Available laboratory evidence also suggests a close concordance between bull trout and westslope cutthroat trout thermal preferences. In laboratory conditions, peak growth for juvenile bull trout occurs at 13.2°C (10.9–15.4°C, 95% confidence interval; Selong et al. 2001). Preliminary growth trials conducted with westslope cutthroat trout indicate that maximum growth for juvenile westslope cutthroat trout occurs at approximately 12°C (Beth Bear, Montana State University, personal communication). Therefore, we suggest that similarities between bull trout and westslope cutthroat trout are sufficient to direct management decisions until the thermal requirements of westslope cutthroat trout are better understood.

Spatial and temporal variation in growth conditions for juveniles may determine the ultimate success of salmonid populations (Nislow et al. 2000). Averett (1963) documented higher growth rates for westslope cutthroat trout from lower versus higher elevation tributaries of the St. Joe River, Idaho. Similarly, in the Madison River basin growth potential showed a declining trend with increasing elevation. Reaches with lower growth potential were associated with headwater habitats where growth was limited by cold stream temperatures. Stream habitats with higher growth potential occurred primarily in lower elevation reaches of study streams (Figure 4). Overall, our analysis indicates that the majority (78%) of stream habitat in Madison River tributaries provides potentially suitable or highly suitable habitat for westslope cutthroat trout. However, higher quality habitats exist primarily in lower elevation reaches where westslope cutthroat trout populations have largely disappeared (Sloat et al. 2001).

Historically, westslope cutthroat trout inhabited a broad range of habitats, including small headwater streams, large rivers, and mid- to low-elevation lakes (Liknes and Graham 1988; Marnel 1988; Behnke 1992). Extant populations in the Madison River basin are now restricted to headwater reaches, often above the upstream distribution limit of nonnative salmonids (Sloat et al. 2001). Fausch (1989) hypothesized that colder, higher-gradient headwater habitats provide refuges for cutthroat trout, where nonnative salmonids either cannot persist or where environmental conditions tip the balance of interspecific competition to favor cutthroat trout. Likewise, Behnke (1992) suggested that cutthroat trout might have a selective advantage over nonnative salmonids in headwater areas because they may function better in colder environments. De Staso and Rahel (1994) found that differences in critical thermal maxima between brook trout *Salvelinus fontinalis* and Colorado River cutthroat trout *O. c. pleuriticus* correlated with greater competitive ability of brook trout at warmer temperatures. While the colder stream temperatures characteristic of headwater habitats may provide a competitive advantage for westslope cutthroat trout relative to nonnative salmonids, our study suggests that in the Madison River basin many of these habitats are marginal because of poor growing conditions.

Because low population sizes and isolation place many populations at risk, the long-term persistence of westslope cutthroat trout in the Madison River basin will require replication and expansion of existing populations into high-quality habitats (Shepard et al. 1997; Sloat et al. 2001). Besides stream temperature, a variety of factors appear to influence the translocation success of cutthroat trout, including the presence of critical habitat components such as suitable spawning substrate (Harig et al. 2000), sufficient space to support viable population sizes (Harig et al. 2000; Hilderbrand and Kershner 2000), and adequate refugia from wildfire and other stochastic events (Propst et al. 1992). Several studies have recommended management actions that extend the downstream distribution of existing populations where possible (MFWP 1999; Hilderbrand and Kershner 2000). Increases in habitat area increase the diversity of available habitat types, support larger population sizes, and increase population resilience to stochastic disturbance (Moyle and Yoshiyama 1994; Harig et al. 2000; Hilderbrand and Kershner 2000). Our results indicate that access to lower elevation habitats may be necessary to ensure that growing conditions are sufficient to maintain the long-term viability of cutthroat trout populations. In this regard, our results are consistent with recommendations that translocation sites be located relatively low within stream networks (MFWP 1999; Harig et al. 2000; Hilderbrand and Kershner 2000).

Stream temperature data acquisition can be expensive and time-consuming, especially in headwater habitats. Since water temperature ranges are directly connected to species-specific growth rates in fish, spatially explicit stream temperature models, such as the one developed here, can be linked to models of fish growth to evaluate habitat suitability for a particular fish species across broad geographic areas. We view this study as a framework for future linkages between thermal modeling and fisheries biology that will help water quality regulators and fishery professionals refine water temperature criteria to support coldwater fish. Our study complements a growing body of studies demonstrating the importance of stream temperature to westslope cutthroat trout (Feldmuth and

Eriksen 1978; Mullan et al. 1992; Shepard et al. 1998). The results of this study should help fish managers prioritize conservation efforts for westslope cutthroat trout by predicting habitat suitability at potential reintroduction or population expansion sites.

Acknowledgments

The Montana Department of Fish, Wildlife, and Parks; Montana Trout Foundation; and the Montana Cooperative Fishery Research Unit at Montana State University–Bozeman helped fund this study. Pat Clancey, Brad Lehrman, Adam Sanhow, David Barnes, Paul Hutchinson, and Doug Rider assisted in collecting field data. We are grateful to Beth Bear of Montana State University for use of preliminary information on the thermal requirements of westslope cutthroat trout and Peter Baker of Stillwater Sciences for statistical advice. Comments by Carol Griswold, Daniel Goodman, Thomas McMahon, and three anonymous reviewers greatly improved the final manuscript.

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