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Influences of Temperature and Environmental Variables on the Distribution of Bull Trout within Streams at the Southern Margin of Its Range

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Abstract.—The bull trout *Salvelinus confluentus* is believed to be among the most thermally sensitive species in coldwater habitats in western North America. We conducted a comprehensive field assessment of thermal habitat associations throughout the southern margin of the species' range. We developed models of thermal habitat associations using two data sets representing a geographically diverse range of sites and sampling methods. In both data sets, maximum temperature was strongly associated with the distribution of bull trout. In spite of the potential biases in these data sets, model predictions were similar. In both cases, the probability of the occurrence of bull trout exceeded 50% when the maximum daily temperature was less than 14–16°C, a result that is consistent with recent laboratory-based thermal tolerances. In one data set, we modeled the association between the distribution of bull trout and environmental variables, including temperature, instream cover, channel form, substrate, and the abundance of native and nonnative salmonid fishes. Only temperature was strongly associated with the distribution of bull trout. Our results and related studies of landscape habitat associations suggest that conservation efforts for bull trout would benefit from a focus on maintaining and restoring large and interconnected coldwater habitats.

In western North America, the bull trout *Salvelinus confluentus* is believed to be among the most thermally sensitive species in coldwater habitats (Rieman and McIntyre 1993; Buchanan and Gregory 1997; Haas 2001; Selong et al. 2001). The bull trout is listed as threatened under the U.S. Endangered Species Act and occupies a broad range across western North America (U.S. Fish and Wildlife Service 1999; Haas and McPhail 2001). Species with a narrow thermal ''niche'' (Magnuson et al. 1979) are most likely to be affected by alterations in water temperature regimes. In particular, species that are tied to coldwater habitats may be especially vulnerable to the increases in temperature that commonly result from human influences on such regimes (Poole and Berman 2001). Accordingly, issues regarding the sensitivity of bull trout to increases in temperature and that of temperature to human influences are of great interest to those involved in land management and species recovery efforts (Poole et al. 2001).

Information on the thermal tolerance of bull trout has come from a variety of indirect lines of evidence and localized studies in the field (e.g., Pratt 1992; Rieman and McIntyre 1993, 1995; Bonneau and Scarnecchia 1996; Buchanan and Gregory 1997; Dunham and Rieman 1999; Zurstadt 2000; Haas 2001; Gamett 2002) and laboratory (Selong et al. 2001). These studies provide insight into the thermal requirements of bull trout, but with the exception of analyses of climatic gradients (Rieman et al. 1997), a comprehensive analysis of the thermal habitat associations of bull trout in the field has not been conducted throughout the species' range. Of particular interest is the southern margin of the range, where temperature should be most important (e.g., Flebbe 1994). The present southern margin of this range is delineated by the Klamath basin in the west and the headwater tributaries to the upper Snake River downstream of Shoshone Falls in the east (Moyle 1976; Cavendar 1997).

Though temperature is widely reported to be important for bull trout, an understanding of the environmental requirements of this species is complicated by a variety of factors. The life cycle of the bull trout includes several stages (Rieman and McIntyre 1993), and conceivably each stage could have its own environmental requirements. For example, the thermal requirements for successful egg incubation appear to be very different from those for juvenile rearing (Buchanan and Gregory 1997). Bull trout also exhibit a broad array of life history strategies, including a variety of migratory behaviors. Individuals with different life histories (e.g.,

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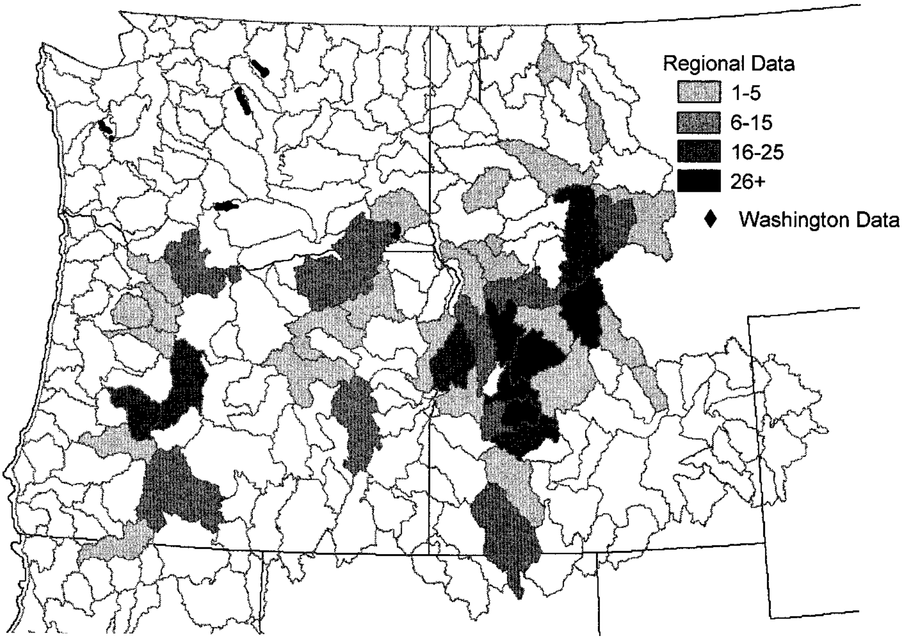

FIGURE 1.—Locations of sites sampled for stream temperature and the occurrence of small bull trout in the western United States. Regional data are for fourth-field watersheds (Rieman et al. 1997); Washington State data are from 109 sites in five streams. Shading indicates the number of observations per observation unit.

resident versus migratory) could respond differently to environmental conditions. Spatial and temporal variability may also be important (Dunham et al. 2002a) owing to the factors that modify the response of bull trout to temperature (Poole et al. 2001) and scale (Torgersen et al. 1999). Finally, the response of bull trout to environmental conditions can be measured for individuals or populations and for a variety of responses, including behavior, growth, survival, abundance, and distribution. The specific influence of temperature on these different responses may vary substantially (Poole et al. 2001).

Our primary interest was to examine the distribution of bull trout within streams by relating patterns of occurrence to a number of potentially important environmental variables, with a focus on maximum water temperatures and the fish distributions recorded during the warmest portion of the year. Temperatures during other portions of the year may also be important (e.g., Baxter and McPhail 1999). We considered only the distribution of smaller (<150-mm) bull trout representing resident (nonmigratory) individuals or juveniles that have yet to emigrate (Rieman and McIntyre 1993). Larger sizes may represent migratory individuals with less stable distributions, thus complicating attempts to develop habitat associations. The distribution of small bull trout is believed to represent areas within streams that are used for spawning and early rearing, which are critical to the persistence of populations (Dunham and Rieman 1999; Rieman and Dunham 2000; Dunham et al. 2002b).

Our objectives were to (1) determine whether temperature can predict the distribution of bull trout; (2) examine the generality of model predictions from different data sets; and (3) examine the influence of other environmental variables on the distribution of bull trout. We collected information on temperature and the distribution of small bull trout throughout the southern margin of the species' range within the United States, producing two different data sets (Figure 1). We used each data set to independently model the occurrence of small bull trout in relation to maximum water temperature and compared the results between them. In addition to temperature, we assessed the influences of other environmental conditions that could influence bull trout, including sediment size (especially the amount of fine sediment), cover (e.g., undercut banks and large wood), channel form (e.g., maximum depth, wetted width, and slope), and the presence of native and nonnative salmonids (Rieman and McIntyre 1993; Rich 1996; Dambacher and Jones 1997; Watson and Hillman

1997; Dunham and Rieman 1999; Hauer et al. 1999; Zurstadt 2000; Haas 2001).

Methods

Data Acquisition

Regional data set.—We assembled a database of 643 thermograph records from the entire current range of bull trout in the United States using data from our own surveys of bull trout and stream temperatures and data received from collaborating biologists in the region (Figure 1). Temperature records for the analysis of bull trout distributions in relation to maximum summer temperatures spanned the period 15 July–30 September. These dates were selected to encompass the period in which maximum water temperatures were expected to occur. We only used records generated with a consistent protocol (Rieman and Chandler 1999). The minimum requirement for temperature measurements was uniform sampling intervals of at least four instantaneous observations per day. Information on the occurrence of bull trout within 500 m of the site was also required for all records. All records were classified (present, absent, or unknown) for small (<150-mm) bull trout based on sampling by the biologists submitting the data. Only records with a definite presence or absence of small bull trout were used in this analysis. The final data set included 175 streams and 643 sites distributed throughout the western United States (Figure 1). The raw data are reported in Rieman and Chandler (1999). These and subsequent data (1999–2001) are available from the authors.

Washington State data set.—To ensure broad coverage of the stream habitat conditions experienced by bull trout in Washington State, we sampled five streams and 109 sites over a large geographic area (Figure 1). We selected streams from three general regions, namely, west of the Cascade Mountains, east of the Cascade Mountains, and the Blue Mountains (southeastern Washington). Final selection of study streams was based on workshops and consultations with over 100 local biologists familiar with these regions. Streams sampled for bull trout occurrence and temperature included the South Fork Skokomish River, Twisp River, Chiwawa River, Ahtanum Creek, and Tucannon River (Figure 1).

The locations of the sampling sites attempted to bracket the downstream distribution limits of small bull trout in each stream over the warmest time of year (15 July–15 September). Within each stream, 100-m-long sites were spaced 2 km apart in an upstream–downstream array. Site spacing varied occasionally due to logistical difficulties encountered in the field. The purpose of the 2-km spacing of the sites was to provide enough distance between sites to sample changing thermal conditions as a function of downstream changes in stream characteristics.

All fish sampling was conducted by means of single-pass night snorkeling (see Thurow 1994), which is among the most efficient methods for sampling bull trout (Thurow and Schill 1996; J. Peterson, USGS Georgia Cooperative Fish and Wildlife Research Unit, J. Dunham, P. Howell and R. Thurow, USDA Forest Service, and S. Bonar, USGS Arizona Cooperative Fish and Wildlife Unit, unpublished report). All bull trout were counted, and those less than 150 mm in total length were noted. Block nets were installed at the upper and lower unit boundaries to prevent fish movement into or out of the site during sampling. Block nets could not be held in some larger (wetted width, >5 m) streams. All sampling was conducted in late summer to early fall (15 July–15 September 2000), which is the warmest time of year.

The habitat information obtained at each site included the water temperature, amount of large wood, presence of undercut banks, channel slope, maximum depth, mean wetted width, and percentage cover of fine substrate. We sampled water temperatures at all sites with Tidbit temperature data loggers manufactured by Onset Computer Corporation. The data loggers were placed in polyvinyl chloride casings to protect them from physical damage. Data loggers were programmed and calibrated following manufacturer's instructions. Placement of the data loggers followed the methods outlined by Chandler et al. (in press). Temperatures were recorded every 30 min between 15 July and 15 September.

Large wood was defined as pieces of wood lying above or within the active channel that were at least 3 m long and 10 cm in diameter. Large wood was quantified both in terms of the total number of pieces and in terms of a wood classification modified from Moore et al. (1998; Table 1). Live pieces of wood (e.g., live trees) counted as large wood if they were within the active (wetted) channel (for wood counts) or bank-full channel (wood class rating) and leaning at an angle of 45° or less over or in the channel. We estimated channel slopes in the field with a hand level (Isaak et al. 1999). Channel widths and depths were measured using transects perpendicular to the stream channel (Platts et al. 1983; Overton et al. 1997). The per-

TABLE 1.—Large-wood classification ratings used in stream habitat surveys in Washington in 2000.

Rating	Description
1	Wood contributes little to stream habitat complexity, (consisting) mostly of small (10–30-cm, median-diameter), single pieces.
2	Wood consists of single pieces and small accumulations, providing cover and some complex habitat.
3	Medium (30–50-cm, median-diameter) and large (>50 cm, median-diameter) pieces of wood provide accumulations and debris jams, with good cover and complex habitat within the low-flow channel (during reduced stream discharge in mid to late summer and early fall, the low-flow channel is generally equivalent to the active channel).
4	Wood present as large single pieces, accumulations, and jams that provide good cover and complex habitat at all discharge levels.

cent of fine substrate (<6 mm) in a 1-m band of wetted stream channel parallel to each transect was also recorded. Transects were established at 10-m intervals within the 100-m sites.

Data Analysis

Development and cross validation of temperature models.—We used logistic regression (Allison 1999) to relate the occurrence of small bull trout to maximum daily temperature in both data sets. The patterns of occurrence in each data set were analyzed separately. Cross validations were performed both within and between data sets to evaluate model predictions (Olden and Jackson 2000). Within data sets, a leave-one-out cross validation was performed by sequentially omitting a single observation from the data set, fitting a model with the remaining observations, and using the model to predict occurrence for the omitted observation. This method allows the entire data set to be used as independent observations to evaluate model performance. Between data sets, we compared the predictions from models developed with one data set (regional or Washington State) with those from models developed from the other data set. Model predictions were classified as ''present'' when the predicted probability of occurrence equaled or exceeded 0.50. A probability cutoff of 0.50 is standard, but others could be used depending on the objectives (see Peterson and Dunham, in press). The frequency of the correct presence, absence, and overall (presence and absence) classification rates were summarized to evaluate model predictions.

Spatial variation and temperature associations.—As the data collected in Washington State in 2000 were from sites nested within streams, we tested for the influence of spatial variability both among sites within streams and among streams. To do this, we analyzed data from a subset of sites that could be spatially ordered along continuous lengths of stream. Variation among sites within a stream is important because such sites may not be truly independent, so that each observation does not contribute one degree of freedom to the analysis. Such spatial autocorrelation can result in inflated degrees of freedom and overestimation of the precision of model parameters and predictions (Legendre 1993). Within each stream, we ordered sites from upstream to downstream to test for the effects of spatial autocorrelation among sites. At a larger spatial scale, variation in the distribution patterns of bull trout among streams could obscure important patterns if not accounted for (Dunham and Vinyard 1997; Dunham et al. 2002a). We examined the effect of stream-scale variability on the associations between temperature and bull trout by treating the stream as a categorical or group variable in the analysis (Dunham and Vinyard 1997; Allison 1999).

Importance of other environmental variables in the Washington data set.—For the Washington data set, we also determined the importance of temperature relative to habitat variables and the occurrence of other fishes for predicting the distribution of small bull trout. We developed an a priori series of candidate models and used model selection procedures (Burnham and Anderson 2002) to evaluate the relative likelihood of each model given the data. Relative likelihoods were evaluated by means of Akaike's information criterion adjusted for overdispersion and small sample size (Burnham and Anderson 2002). Candidate models included the maximum temperature, the wood count or wood classification rating, the occurrence of other salmonids (rainbow trout *Oncorhynchus mykiss*, cutthroat trout *O. clarki*, and brook trout *S. fontinalis*), channel slope, undercut bank area, surface fines, stream size (wetted width and maximum depth), and all variables together.

Results

The maximum daily temperature for sites with small bull trout was 17.5°C and 26.2°C in the

TABLE 2.—Values of environmental variables at sites sampled for the occurrence of small bull trout in Washington in 2000. The mean value and range (minimum and maximum) for each variable are reported.

Variable	Small bull trout observed			Small bull trout not observed		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Maximum daily water temperature (°C)	14.1	10.8	17.5	17.0	9.4	25.8
Maximum depth (m)	1.15	0.46	3.00	0.93	0.31	6.00
Channel slope (%)	1.1	0	6.79	1.6	0	10.0
Mean width (m)	13.2	3.6	30.4	11.7	3.6	37.7
Undercut bank volume (m^3)	5.0	0	32.4	4.5	0	32.6
Mean surface fines (%)	10	0	33	16	1	74
Wood/m	0.16	0	2.12	0.08	0	0.26
Wood class rating	2.4	1	4	2.15	0	4
Brook trout density fish/m^2	0.001	0	0.02	0.0003	0	0.008
Rainbow–cutthroat trout density fish/m^2	0.02	0	0.16	0.03	0	0.12

Washington and regional data sets, respectively. The values of other environmental variables ranged widely among sites with and without small bull trout in Washington (Table 2). Maximum temperature consistently predicted the distribution of small bull trout. Parameter estimates for the Washington data set were similar to parameter estimates from the regional data set (Table 3). Overall error rates for the cross validations within and between models and data sets were similar (67–72%), but those for absence and presence were not (Table 4). Most notably, the regional model performed well in predicting the presence of bull trout with the Washington data set but poorly in predicting absence. Other cross-validated classification rates for presence and absence were similar and ranged from 64% to 77% (Table 4).

Spatial autocorrelation among sites was detected in the Washington data set, which indicates that the occurrence of bull trout at one site was not independent of the occurrence at adjacent sites. Differences among streams in the distribution of small bull trout in relation to maximum temperature were not important, however. The maximum temperatures associated with the distribution of bull trout within the five major study basins in Washington ranged from 14.1°C in the Twisp River to 17.5°C in Ahtanum Creek. The main effect of accounting for autocorrelation was wider confidence bounds for the parameter estimates (Table 3). Models that included summer maximum temperature were the most plausible in terms of explaining patterns of occurrence (Table 5). The global model was only half as likely as the model with summer maximum temperature alone (Table 5).

Discussion

Bull Trout Distribution and Temperature

The concordance in parameter estimates and cross validation both within and between data sets indicates a consistent relationship between temperature and the occurrence of small bull trout throughout the southern margin of the species' range. Model predictions with the regional data set produced slightly higher predicted probabilities of occurrence for bull trout at warmer (>12°C) maximum temperatures. This may be due to a larger sample size ($n = 643$) than for the Washington data set ($n = 109$). With a larger sample size, it should be more likely to observe bull trout in habitats with a low probability of use (e.g., warmer water). Alternatively, in some cases, the match be-

TABLE 3.—Logistic regression parameter estimates and confidence intervals for three models of bull trout occurrence in relation to maximum summer temperature. The Washington–spatial data set includes data from a spatially ordered set of sites sampled in Washington State in 2000. See text for descriptions of these data sets.

Data set	Parameter	Parameter estimated	95% Confidence interval
Washington	Intercept	5.47	(2.93, 8.49)
	Temperature	−0.38	(−0.58, −0.21)
Regional	Intercept	4.64	(3.74, 5.62)
	Temperature	−0.28	(−0.34, −0.23)
Washington–spatial	Intercept	7.91	(0.52, 15.31)
	Temperature	−0.52	(−0.98, −0.07)

TABLE 4.—Results of cross validations using the Washington (WA) and regional (REG) models (Table 3) to predict the presence or absence of small bull trout. The models were developed with data collected in Washington State in 2000 and a regional sample of existing data (Rieman and Chandler 1999, respectively). Cross validations within the models (i.e., WA → WA and REG → REG) were conducted by sequentially removing each observation from the data set, fitting the model with the remaining observations, and predicting the omitted observation. Cross validations between the models (i.e., WA → REG and REG → WA) were conducted by using a model developed with one data set to predict observations in the other. See text of descriptions of these data sets.

		Presence			Absence		
Cross validation	Overall accuracy	Correct	Incorrect	Percent correct	Correct	Incorrect	Percent correct
WA → WA	0.70	30	17	63.8	46	16	74.2
WA → REG	0.67	208	145	58.9	223	67	76.9
REG → WA	0.68	42	4	91.3	32	31	50.8
REG → REG	0.72	290	120	70.7	170	63	73.0

tween fish occurrence and ambient water temperature may not have been very accurate. Bull trout in some of the warmest sites may have been using localized thermal refugia that were not representative of temperatures in the well-mixed portion of the stream (Torgersen et al. 1999).

In spite of the broad similarity in patterns found in this study, predicting the occurrence of bull trout, particularly at ‘‘intermediate’’ temperatures, is uncertain. At the ends of the thermal continuum (<12°C and >25°C) bull trout responses to temperature are similar, as may be expected when the physiological and ecological effects of temperature are greatest. At intermediate temperatures, other factors could modify the thermal responses of bull trout. Local factors, such as environmental conditions or local adaptation, could modify these responses in some areas. Alternatively, smaller sample sizes and variability in sampling conditions (Peterson and Dunham, in press; Peterson et al., unpublished report) could explain the differences between the thermal responses of bull trout in local areas and the predictions of our models.

In comparing field studies of thermal habitat associations for bull trout it is also important to consider the life stage that is examined. Our choice to model the occurrence of small (<150-mm) fish was based on the assumption that they are present year-round (as would be the case, for instance, with juvenile and nonmigratory individuals). Larger bull trout are more likely to be migratory (Rieman and McIntyre 1993). Because bull trout migrations can be strongly tied to temperature (Rieman and McIntyre 1993), matching the occurrence of migratory individuals to temperatures recorded over a longer time period is more difficult. For example, Gamett (2002) modeled the occurrence of all size-classes of bull trout in relation to stream temperature, including some sites with only larger (>150-mm) fish. These fish may not have been present when temperatures were at a maximum (B. Gamett, U.S. Forest Service, personal communication), possibly accounting for bull trout occurrence being associated with slightly warmer water temperatures than found in this study.

The maximum temperatures associated with the distribution of bull trout were consistent with the results of laboratory studies of thermal tolerance.

TABLE 5.—Candidate models for the occurrence of bull trout at sites sampled in Washington in 2000. Models are listed in ascending order by relative likelihood, as indicated by Akaike's information criterion (AIC). To correct for overdispersion and small sample size, we used a modified version of AIC known as $QAIC_c$ (Burnham and Anderson 2002). Larger $\Delta QAIC_c$ weights indicate likely models.

Explanatory variable(s)	Number of parameters	$QAIC_c$	$\Delta QAIC_c$	$\Delta QAIC_c$ weight	% of maximum $\Delta QAIC_c$ weight
Temperature	2	86.05	0.00	0.66	100
Global model	11	87.39	1.35	0.33	50
Salmonids	3	96.37	10.33	0.00	0
Wood	3	96.73	10.69	0.00	0
Surface fines	2	97.10	11.06	0.00	0
Maximum depth	2	100.21	14.16	0.00	0
Channel slope	2	100.64	14.60	0.00	0
Wetted width	2	100.20	15.15	0.00	0
Undercut banks	2	101.80	15.75	0.00	0

Under laboratory conditions, mortality occurs in less than 24 h when bull trout are exposed to temperatures of 26°C or more (Selong et al. 2001). Bull trout can survive chronic exposure to temperatures up to 20°C for long periods of time, however. Selong et al. (2001) reported ultimate upper incipient lethal temperatures of 20.9°C and 23.5°C for 60-d and 7-d exposures, respectively. Our model predictions imply that although bull trout may be present at potentially lethal temperatures, the probability of occurrence is relatively low (e.g., <0.50) at maximum daily temperatures above approximately 14–16°C. The probability of occurrence does not become high (e.g., >0.75) until the maximum daily temperature declines to approximately 11–12°C. These patterns could reflect sublethal influences of temperature. Selong et al. (2001) found that the growth of bull trout on unlimited rations in the laboratory was maximized at 13.2°C. If rations are limited, the temperature at which maximum growth is realized can be shifted downward (T. McMahon, Montana State University, personal communication). More detailed field investigations of growth, behavior, and other responses are needed to better understand the sublethal responses of bull trout to temperature.

Bull Trout Distribution and Other Variables

Our results suggest that environmental variables other than temperature were not associated with the distribution of bull trout, a pattern reported in a similar study by Haas (2001). Possible reasons for this result are as follows: (1) small bull trout do not respond to these variables; (2) the variables were not measured with enough precision to detect effects; (3) the variables were not measured at appropriate scales; (4) the range of variation in the variables was not sufficient to detect effects; (5) there were habitat-related biases in sampling efficiency; and (6) environmental variables (other than temperature) that are important to bull trout were not measured in this study.

Given the range of environmental conditions believed to be important for bull trout (Rieman and McIntyre 1993) and salmonids in general (Bjornn and Reiser 1991), temperature is probably not the only factor that is important for determining the distribution of bull trout within streams. The importance of variables other than temperature was suggested by the moderate relative likelihood of the global model to predict the occurrence of bull trout (Table 5). Furthermore, temperature probably does not act independently of other environmental factors (Poole et al. 2001). Studies designed to specifically examine factors other than temperature per se would be valuable additions to this work.

Many environmental variables in streams are difficult to measure with a reasonable degree of repeatability or precision (Roper and Scarnecchia 1995; Roper et al. 2003). Lack of precision in the measurement of some of the variables in our study could have created noise in the data that prevented detection of habitat associations. In contrast to many environmental variables, water temperature is relatively simple to measure with high precision (Chandler et al., in press).

In this study, environmental variables were considered at the scale of 100-m sample sites. However, bull trout may select habitats at a spatial scale that is much smaller than this. For example, the sites in our study typically included several different habitat units (Frissell et al. 1986), such as pools, riffles, and runs. Bull trout may perceive and utilize habitats at this small scale, and aggregating information at the scale of an entire site may obscure such patterns. Alternatively, larger-scale characteristics of habitats may be more important, such as the characteristics of entire streams, watersheds, or ‘‘patches’’ of habitat (Dunham and Vinyard 1997; Rieman et al. 1997; Dunham and Rieman 1999; Torgersen et al. 1999; Dunham et al. 2002b).

For some environmental variables, the range of variation in the data was probably not sufficient to detect effects. For example, brook trout were uncommon and occurred at very low densities in the sites we sampled. However, nonnative brook trout have been implicated in the decline of bull trout in other areas (Rieman and McIntyre 1993; Leary et al. 1993; Gunckel 2001) where they may be more abundant. If we had included sites where brook trout were more abundant, we might have detected associations between brook and bull trout. Similarly, the range of variation in stream widths did not include very small ($<$2-m-wide) streams, where previous research suggests that the occurrence of bull trout is less likely (Dunham and Rieman 1999).

We cannot rule out the potential for habitat-related biases in sampling efficiency. Our surveys used night snorkeling, which is among the most efficient methods for detecting bull trout (Peterson et al., unpublished report). Nonetheless, fish may not have been detected under certain conditions. In particular, this might have been the case in sampling large streams on which the use of block nets was not possible. Studies of sampling efficiency

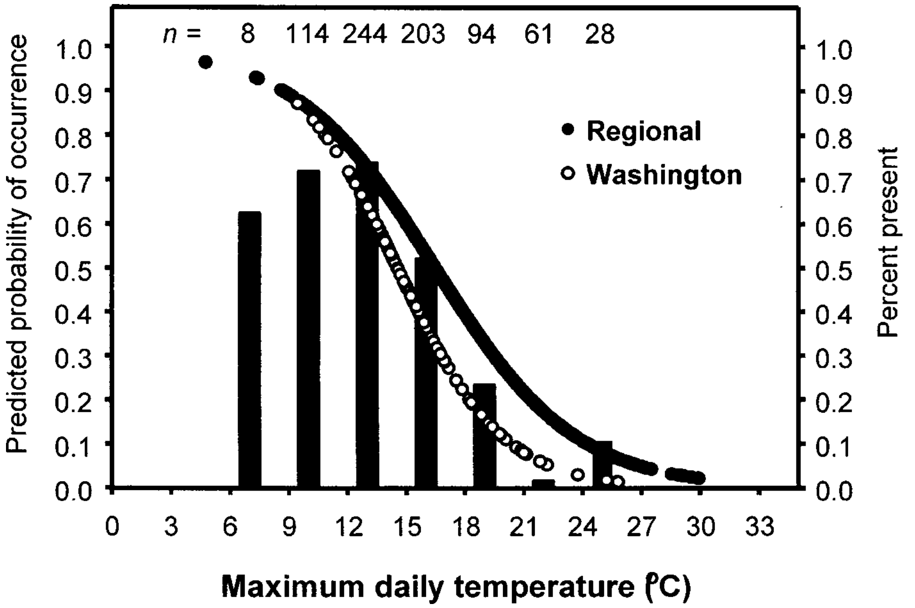

FIGURE 2.—Occurrence of small bull trout in relation to temperature. The left *y*-axis shows the predicted probability of occurrence in relation to maximum daily temperature for the regional and Washington 2000 data sets (indicated by circles). The right *y*-axis shows the percentage of sites (both data sets; $n = 752$ sites) where small bull trout were observed (indicated by bars). Bars are centered on 3°C bins with sample sizes indicated above each.

for bull trout (Peterson et al., unpublished report) indicate that temperature, stream size, cover, and channel slope can be important. The effect of temperature on sampling efficiency is positive. Bull trout are more likely to be active in the water column, and therefore observed, when water temperatures are higher. At colder (<10°C) temperatures, small bull trout may be concealed in the substrate (Thurow 1997).

Finally, we probably did not include all of the variables that are potentially important to bull trout in this study. Groundwater influence, for example (Baxter and McPhail 1999; Baxter and Hauer 1999), may be important for spawning site selection and potentially relevant to the distribution of small bull trout (Beard and Carline 1991). Factors affecting winter survival may also be key (Cunjak et al. 1998). Many variables are not easily quantified in broad-scale studies of fish distributions, and finer-scale studies of habitat relationships for small bull trout would be useful complements to this work (e.g., Baxter and Hauer 1999; Dunham and Rieman 1999; Torgersen et al. 1999).

Management Implications

Our results show that water temperature is important for small bull trout and that the effect of water temperature on the distribution of this species is relatively consistent across the southern margin of its range. Other environmental variables may also be important, but their effects were not obvious. Managers often question how cold water needs to be to support bull trout. The answer is not a single number, but rather a continuum of values associated with the expected probability of occurrence. Risk-averse strategies to protect this threatened species may adopt a more or less conservative approach to choosing an acceptable temperature for management purposes. For example, such an approach would entail protecting the full range of the habitats that bull trout might use (e.g., <26°C; Figure 2). Another approach would be to target restoration of water temperatures that bull trout are most likely to use (e.g., ≤12°C; Figure 2). The point estimates of the probability of occurrence from the models are not precise, and the uncertainty in model predictions could be an important consideration in choosing management criteria for temperature (Poole et al. 2001).

Maximum daily temperature is but one of a variety of summary measures or ‘‘metrics’’ that could be associated with the occurrence of bull trout or used for management criteria (others include the maximum temperature over a weekly or seasonal interval and the mean temperature over a daily, weekly, or seasonal interval). We used the maximum daily temperature because it is relatively easy to interpret and it provides relatively fine-scale information on thermal exposure. Looking at temperature in terms of means or multiday summaries could mask important information on exposure at finer scales. Detailed information on the biological importance of different kinds of thermal exposure (e.g., sublethal versus lethal and chronic versus acute) is lacking. Most measures of maximum temperature in streams supporting bull trout are highly correlated and therefore statistically redundant for predicting fish distributions.

Coldwater alone is not enough to support populations of bull trout, as is suggested by research linking the occurrence of local populations to the amount and distribution of potentially suitable thermal habitat on landscapes (e.g., Rieman and Dunham 2000; Dunham et al. 2002b). Our work shows that large, isolated, and undisturbed coldwater habitats are more likely to support local populations of bull trout. Conservation efforts to benefit bull trout would be more effective if existing areas with these characteristics were identified, along with areas where restoration could provide these conditions. Bull trout occupy a vast range in the western United States (Rieman et al. 1997), and current models predicting the distribution of suitable habitat are limited in extent. Further work is needed to provide useful landscape models for predicting stream temperature and the occurrence of local populations throughout the bull trout's range.

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