

Using Field Data to Estimate the Realized Thermal Niche of Aquatic Vertebrates

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Abstract.—The field-derived thermal niche of aquatic vertebrates is potentially useful in determining whether resource management plans are adequate to protect sensitive vertebrates. Our objective was to use field data to estimate the thermal niches of 16 species of aquatic vertebrates and to compare these values among five geographic regions in Oregon. Thermal niche values varied among regions; for example, the upper thermal limit for rainbow trout *Oncorhynchus mykiss* was 22.4°C in the Blue Mountains ecoregion and 16.9°C in the Cascades ecoregion. Nonmetric multidimensional scaling (NMS) analysis of aquatic vertebrate assemblages revealed that level-three ecoregions grouped vertebrate assemblages more cohesively than the third-order hydrologic unit code (basins). Analysis of similarities of Bray–Curtis distance measures supported NMS findings that the structures of aquatic vertebrate assemblages coincide more with ecoregions than with basins. The realized thermal niches calculated in this study are generally comparable to the maximum growth temperatures and upper thermal limits established by other field and laboratory techniques. This information is valuable for managers who devise water temperature criteria as well as fisheries ecologists interested in quantifying or delineating thermal habitat.

Vertebrate assemblages are commonly used to detect the impacts of human activity on aquatic resources (e.g., Fausch et al. 1990). Likewise, there is interest in the biological response of aquatic vertebrates to anthropogenic effects, such as global warming and deforestation. Thermal requirements of many fish and amphibians are largely unknown, even though such autecological information is pivotal in understanding a biological response to disturbance. Many laboratory studies have determined thermal limits and critical values of a limited number of species, but they are seldom placed in the context of natural conditions.

Thermal gradients are important determinants of species' distributions in aquatic habitats. Temperature may influence species through physiological processes (Coutant 1987) or by affecting species' interactions (Baltz et al. 1982; Reeves et al. 1987; Taniguchi et al. 1998). Animals compete for and partition habitats along temperature gradients. This process contributes directly to the fitness of the animal and delineates its thermal niche (Magnuson et al. 1979). Consequently, temperature may be treated as quantitatively as a consumable resource, such as food. Magnuson et al. (1979) quantified the fundamental thermal niche by examining the statistical distributions of temperatures select-

ed by species in a laboratory evaluation of their thermal preferences. By determining the thermal requirements of taxa based upon statistical analysis of field data, one can account for unique interactions with other variables in a particular locality.

Laboratory studies of temperature preference may not adequately reflect the thermal requirements of a species in nature. Aquatic vertebrates can shift thermal niches in response to the presence of competitors and have flexibility in thermal selection (Brandt et al. 1980). Social and biotic interactions resulting from the location of prey, predator avoidance, habitat availability, water depth, water velocity, intra- and interspecific competition, as well as genetic variability may account for a lack of conformity between laboratory preferenda and field distributions (Shrode et al. 1982). Since aquatic species are often not found at their laboratory preferenda in the field (Eaton et al. 1995), it is evident that thermoselection can be affected by other factors (Beitinger and Fitzpatrick 1979).

High temperature limits the distribution of salmonids and other species of concern; therefore, the demarcation of a thermal niche's upper limit is of great interest. Because human disturbances in Oregon streams are likely to raise temperatures rather than lower them (Sauter et al. 2001), except below bottom-spilling dams, the upper thermal limit is usually important to natural resource man-

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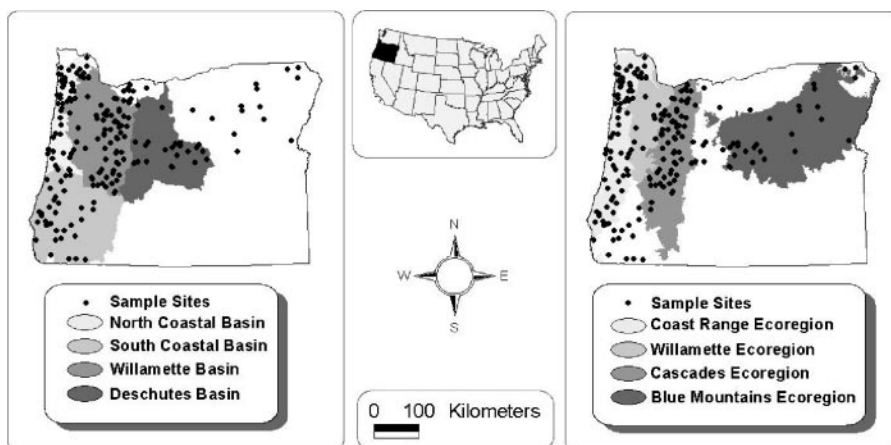


FIGURE 1.—Map of Oregon delineating the basins (left-hand panel) and ecoregions (right-hand panel) used to determine thermal niches, along with the locations of sample sites.

agers. The objective of this work was to utilize field-derived relative abundance and temperature data to estimate the thermal niches of aquatic vertebrates and compare these values among different geographic regions in Oregon. The thermal niche was calculated for 14 species in five geographic regions.

Study Area

A total of 199 sites on first- to third-order (Strahler 1964) wadable streams throughout Oregon were either chosen randomly or hand selected (Figure 1). Regionally, 48 sites were in the North Coastal basin (Watermolen 2002), 35 sites were in the South Coastal basin (Watermolen 2002), 72 sites were in the Coast Range ecoregion, 64 sites were in the Cascades ecoregion (Omernik 1987), and 23 sites were in the Blue Mountains ecoregion (Omernik 1987). The remaining 29 sites were included in the statewide analysis (all regions). Sites were partitioned into basin and ecoregion categories to investigate regional differences in species' thermal requirements. By ecoregion, the North Coastal basin consists of 98% Coast Range ecoregion and 2% Willamette Valley ecoregion. The South Coastal basin consists of 28% Coast Range ecoregion, 1% Willamette Valley ecoregion, 25% Cascades ecoregion, and 47% Klamath Mountains ecoregion.

Climate, geology, and habitat conditions vary across ecoregions. The Coast Range ecoregion has a maritime climate with high precipitation, mountains of low elevation, and highly productive coniferous forests that have historically been heavily managed for logging (Naiman et al. 2000). Abun-

dant lotic ecosystems support economically important species of Pacific salmon *Oncorhynchus* spp. in the Coast Range ecoregion. The Cascades ecoregion consists mainly of high-elevation mountains and alpine meadows with a moist, temperate climate. It contains extensive and highly productive coniferous forests that have historically been intensively logged. The Blue Mountains ecoregion is a complex of mountain ranges that are lower in elevation and drier than the Cascades ecoregion. Coniferous forests are less abundant than in the Cascades or Coast Range ecoregions. Logging and cattle grazing dominate land use in much of this ecoregion. The Klamath Mountains ecoregion includes the foothills and valleys of the Klamath and Siskiyou mountains. It is a mix of granitic, sedimentary, and metamorphic rocks, which is in contrast to the mostly volcanic rocks of the Cascades. It has a mild climate with long, dry summers and supports a mixed forest of conifers and hardwoods (Omernik 1987). Dominant land uses in the Klamath Mountains ecoregion are logging and agriculture.

Methods

To provide relative abundance data for species, aquatic vertebrate assemblages were sampled during the summer months (July through September) from 1998 to 2001 using single-pass electrofishing, a common method for sampling aquatic vertebrate assemblages for bioassessments (Lyons 1996; Lazorchak et al. 1998; Pusey et al. 1998). The aim of this method was to sample all habitat types proportionally within each reach. Reach length was 40 times the mean wetted channel width

(Lazorchak et al. 1998) and ranged from 150 to 500 m. The median value of the mean wetted channel width was 4.4 m (minimum, 0.6 m; maximum, 23.0 m). The median value of the mean channel thalweg depth (the deepest portion of the channel cross section) was 27 cm (minimum, 4 cm; maximum, 99 cm). Study reaches were shocked at higher voltages (500–900 V) than are typically utilized for single-species assessments. We identified fish and amphibians to the species level in the field and collected voucher specimens for verification in the laboratory.

Continuous temperature data were recorded at 30-min intervals by means of VEMCO temperature loggers. We deployed data loggers at study sites from late May to early July and removed them from September to October. The data loggers were placed in a well-mixed, shaded location to avoid thermal stratification or heating by direct solar radiation (ODEQ 1997). The temperature metric used for this study was the 7-d average of the daily maximum temperature for the 7-d period surrounding and including the sample date.

The species used for analyses were limited to obligate aquatic vertebrates that occurred at 5% or more of the sites. Lampreys were removed from the analysis due to inconsistent sampling effort for these species. We graphically compared species collection data to temperature to ensure adequate sampling coverage across the possible temperature ranges a species may inhabit.

Ordination.—We used nonmetric multidimensional scaling (NMS; Kruskal 1964; Mather 1976) to relate vertebrate assemblage patterns to the temperature gradient using PC-ORD software (McCune and Mefford 1999). Proportional abundance species' data were arcsine-square-root transformed to improve the normality of the data set (Zar 1999). Prior to performing the ordination analysis, we identified outlier sites in each region by calculating the average Bray–Curtis (Bray and Curtis 1957) distance of each site from every other site. We constructed a frequency distribution of these distances and flagged sites as outliers if they were greater than two standard deviations from the grand mean. We performed NMS ordinations with and without outliers. If the ordination without outliers resulted in a lower “stress” (i.e., departure from monotonicity in the plot of distance in the original dissimilarity matrix and distance in the reduced ordination space) solution than the original ordination, we considered the outliers inferential outliers (Tabachnik and Fidell 1996) and eliminated them from the data set. We used Bray–

Curtis distance to calculate the dissimilarity matrix (Bray and Curtis 1957) and sample units were assigned to random starting configurations for NMS using a random-number generator. The appropriate number of dimensions was determined when plots of final stress versus number of dimensions showed that a greater number of axes resulted in small reductions in stress. We calculated instability as the standard deviation in stress over the preceding 10 iterations. When instability reached a level of 0.00001, iterations were stopped and the solution was considered final. The stability of the solutions was also examined by plotting stress versus number of iterations.

When we plotted the final solution, we rotated the point cloud to maximize the correlation of temperature with the horizontal axis (Mather 1976). The strength of the relationship between the temperature values and the ordination scores was determined by calculating Pearson's correlation coefficient (r ; Clarke and Ainsworth 1993). Additionally, we calculated r for each species against the (previously rotated) horizontal axis, and the positions of species on the plot were compared to their abundances at a given site. Species were considered to have a strong relationship with temperature if greater than 10% ($r^2 > 0.1$) of the species' variance could be explained by the variance in temperature (Pan et al. 1996). Differences in species composition between the four basins and four ecoregions (Figure 1) were examined with a one-way analysis of similarity (ANOSIM) using the ANOSIM routine (PRIMER, version 5; Clarke 1993; see also Marchant et al. 2000). This routine tests the null hypothesis of no difference between groups of aquatic vertebrate community samples defined a priori using permutation or randomization methods on Bray–Curtis dissimilarity matrices (Clarke and Warwick 1994).

Weighted averaging.—We estimated thermal niche values using a weighted-average (WA) method with the CALIBRATE software (version 0.82; Juggins and ter Braak 1998). Aquatic vertebrate species with a temperature optimum closest to a given water temperature will tend to be the most abundant species (ter Braak and Barendregt 1986). An ecologically sound estimate of the center of a species' realized thermal niche is, therefore, the mean temperature for all the sites where a species is found weighted by the species' relative abundance. A species' realized niche width (RNW) is one standard deviation from the mean of the temperature weighted by the species' relative abundance (Birks et al. 1990). The WA estimate of a

species' realized niche center (RNC), or weighted mean, \hat{u}_k (Birks et al. 1990), is

$$\hat{u}_k = \frac{\sum_{i=1}^n y_{ik} x_i}{\sum_{i=1}^n y_{ik}}$$

where x = the environmental variable (temperature), x_i = the value of x in sample i , and y_{ik} = the abundance of k in sample i ($y_{ik} \leq 0$; $i = 1, \dots, n$ sites and $k = 1, \dots, m$ species).

Species RNW, or weighted standard deviation \hat{t}_k , is

$$\hat{t}_k = \left[\frac{\sum_{i=1}^n y_{ik} (x_i - \hat{u}_k)^2}{\sum_{i=1}^n y_{ik}} \right]^{1/2}$$

The CALIBRATE software corrected bias in the RNW value by adjusting for the estimated effective number of occurrences (Hill 1973). We calculated RNC and RNW separately for each of the five regions, as well as for all sites combined, to investigate the regional differences in species' thermal requirements and to explore the consequences of choosing different types of geographic boundaries (basin versus ecoregion).

We identified species' size-classes by examining aquatic vertebrate length data versus species' relative abundance for all sites and by visually determining length categories. We compared species' length categories to one another using a t -test (Zar 1999) to ascertain if the mean temperature of one length category was different from another. If length category mean temperatures were found to be significantly different ($P > 0.05$), they were treated as separate "species" in the WA and NMS analyses.

Results

Summer water temperatures ranged from 7.9°C to 28.6°C (median, 15.1°C) across all sites (Table 1). Temperatures tended to be warmest in the Blue Mountains ecoregion where the median temperature was 20.2°C and were progressively cooler from the South Coastal basin (median, 15.6°C) to the Coast Range ecoregion (median, 14.9°C) to the North Coastal basin (median, 14.8°C). The coolest median temperature was in the Cascades ecoregion (median, 13.0°C).

Sixteen species found across all regions were included in the WA analysis (Table 1). The Deschutes basin and the Willamette Valley ecoregion were not assessed as groups in the WA analysis because too few sites were sampled in those areas. Regionally, the greatest number of species was

assessed in the Coast Range ecoregion (10 species), followed by the North Coastal basin (8 species), the South Coastal basin and Cascades ecoregion (7 species each), and the Blue Mountains ecoregion (3 species). Four species were collected in the Blue Mountains ecoregion, but only three of these species were encountered in sufficient abundance to be included in the analysis. Brook trout, shorthead sculpin, longnose dace, and redbside shiners were not found in sufficient abundance to be included in the analysis of an individual region, but were numerous enough to be included in the analysis of all regions combined.

The distributions of relative abundance by temperature for some of the dominant taxa in the North and South Coastal basins and all basins combined are shown in Figure 2. All taxa included in the analysis had a wide array of relative abundances and occurred across a broad temperature range. We eliminated largescale suckers *Catostomus macrocheilus* and speckled dace in the North Coastal basin, largescale suckers and redbside shiners in the Coast Range ecoregion, longnose dace and shorthead sculpins in the Cascades ecoregion, and Paiute sculpins in the Blue Mountains ecoregion from the WA (RNC and RNW calculation) analysis because they failed to occur in an adequate number at a variety of sites. Taxa that were sampled adequately across a range of temperatures and relative abundance levels were assigned RNC and RNW values (Table 1).

The RNC and RNW values were estimated for 16 species across all areas combined (Figure 3). Tailed frog larvae and Pacific giant salamander larvae had the coolest RNCs, while redbside shiners, speckled dace, and bridgelip suckers had the warmest RNCs. The largest difference in RNC and RNW between regions was between the Cascades and Blue Mountains ecoregions. The RNW upper limit for rainbow trout was 22.4°C in the Blue Mountains and 16.9°C in the Cascades, a difference of 5.5°C. In the North Coastal basin, rainbow and cutthroat trout had a very similar RNC: 14.0°C for rainbow trout and 14.2°C for cutthroat trout. Interestingly, rainbow trout had a warmer RNC in the South Coastal basin (16.6°C) than in the North Coastal basin (14.0°C), while cutthroat trout RNCs were nearly the same at 14.3°C in both basins. The RNC and RNW values in the Coast Range ecoregion were similar to those in the North Coastal basin, but tended to be slightly warmer for some species. Generally, the RNC values for species found in multiple regions followed the trend in

TABLE 1.—Realized thermal niche values for species collected in each region. The upper limits of the realized thermal niches (RNWs) were calculated by adding one weighted SD to the realized thermal center (RNC; a weighted average). The number of sites where a species occurred and the unweighted minimum (min), median, and maximum (max) averages of the daily maximum temperature (°C) for the 7-d period surrounding the sample date are shown for each region and species.

Sites and species	Number of sites	Min	Median	Max	RNC	RNW (upper limit)
All sites combined						
All sites	199	7.9	15.1	28.6		
Tailed frog <i>Ascaphus truei</i> (larvae)	75	7.9	13.5	19.3	12.6	15.1
Pacific giant salamander <i>Dicamptodon ensatus</i>	100	7.9	14.2	20.2	13.0	15.2
Brook trout <i>Salvelinus fontinalis</i>	7	10.4	12.9	17.3	13.3	15.2
Cutthroat trout <i>Oncorhynchus clarkii</i>	122	9.2	14.5	23.7	13.9	16.4
Coho salmon <i>O. kisutch</i>	45	10.4	15.3	23.7	14.5	16.9
Shorthead sculpin <i>Cottus confusus</i>	10	9.2	14.3	22.9	14.5	17.5
Torrent sculpin <i>C. rhotheus</i>	29	10.4	15.4	19.8	15.8	18.4
Rainbow trout <i>O. mykiss</i>	113	10.0	16.2	28.6	16.0	19.7
Reticulate sculpin <i>C. perplexus</i>	74	9.7	15.5	25.8	16.1	19.1
Riffle sculpin <i>C. gulosus</i>	14	14.4	16.4	21.2	16.5	19.0
Paiute sculpin <i>C. beldingii</i>	19	10.0	16.4	22.9	16.6	20.5
Coastrange sculpin <i>C. aleuticus</i>	9	12.1	16.3	18.5	17.2	19.0
Longnose dace <i>Rhinichthys cataractae</i>	11	13.2	18.0	20.2	17.4	19.5
Redside shiner <i>Richardsonius balteatus</i>	11	16.6	21.1	25.8	21.1	23.7
Speckled dace <i>Rhinichthys osculus</i>	44	13.4	19.5	28.6	21.4	24.6
Bridgelip sucker <i>Catostomus columbianus</i>	13	16.2	22.5	25.7	21.9	23.8
North Coastal basin						
All North Coastal basin sites	48	10.4	14.8	21.2		
Pacific giant salamander	25	10.7	14.9	18.5	12.4	15.1
Coho salmon	27	10.4	14.7	18.9	14.0	15.9
Rainbow trout	32	10.4	14.9	21.2	14.0	16.0
Tailed frog larvae	18	11.3	14.5	17.0	14.1	16.1
Cutthroat trout	42	10.7	14.6	21.2	14.2	16.4
Torrent sculpin	13	13.0	13.5	18.6	14.7	16.8
Reticulate sculpin	37	10.4	14.9	21.2	15.5	17.7
Coastrange sculpin	6	12.1	15.3	17.7	15.9	18.1
South Coastal basin						
All South Coastal basin sites	35	12.6	15.6	23.7		
Pacific giant salamander	24	12.6	14.5	19.4	14.1	15.9
Cutthroat trout	19	12.6	14.5	23.7	14.3	15.8
Tailed frog larvae	13	12.7	14.8	18.5	15.3	17.6
Coho salmon	14	14.4	17.1	23.7	15.8	17.9
Rainbow trout	25	13.0	16.6	23.7	16.6	19.0
Reticulate sculpin	15	13.5	16.6	23.7	17.1	19.4
Speckled dace	9	16.3	18.2	23.7	19.2	21.5
Coast Range ecoregion						
All Coast Range ecoregion sites	72	10.4	14.9	23.7		
Pacific giant salamander	41	10.7	14.9	18.5	13.3	15.7
Cutthroat trout	59	10.7	14.5	23.7	14.2	16.2
Coho salmon	38	10.4	15.1	23.7	14.4	16.7
Torrent sculpin	14	10.4	13.6	18.6	14.6	16.9
Tailed frog larvae	24	11.3	14.6	18.5	14.7	16.9
Rainbow trout	49	10.4	15.3	23.7	14.9	17.6
Reticulate sculpin	48	10.4	15.0	23.7	15.7	18.0
Coastrange sculpin	8	12.1	16.0	18.5	16.9	19.0
Riffle sculpin	10	14.9	16.0	21.2	17.0	18.7
Speckled dace	10	14.9	18.2	23.7	19.1	21.8
Cascades ecoregion						
All Cascades ecoregion sites	64	7.9	13.0	20.2		
Tailed frog larvae	42	7.9	12.4	19.3	11.7	13.9
Pacific giant salamander	44	7.9	12.8	20.2	12.0	14.2
Reticulate sculpin	8	9.7	12.8	18.0	12.7	16.4
Cutthroat trout	44	9.2	13.5	19.3	12.9	15.2
Rainbow trout	22	10.0	14.3	20.2	14.3	16.9
Torrent sculpin	9	13.0	15.8	18.0	14.8	16.6
Paiute sculpin	12	10.0	15.9	20.2	15.2	18.3
Blue Mountains ecoregion						
All Blue Mountains ecoregion sites	23	11.2	20.2	25.7		
Rainbow trout	21	11.2	20.2	25.7	19.5	22.4
Speckled dace	17	16.2	22.3	25.7	21.6	24.5
Bridgelip sucker	11	16.2	22.5	25.7	22.0	23.8

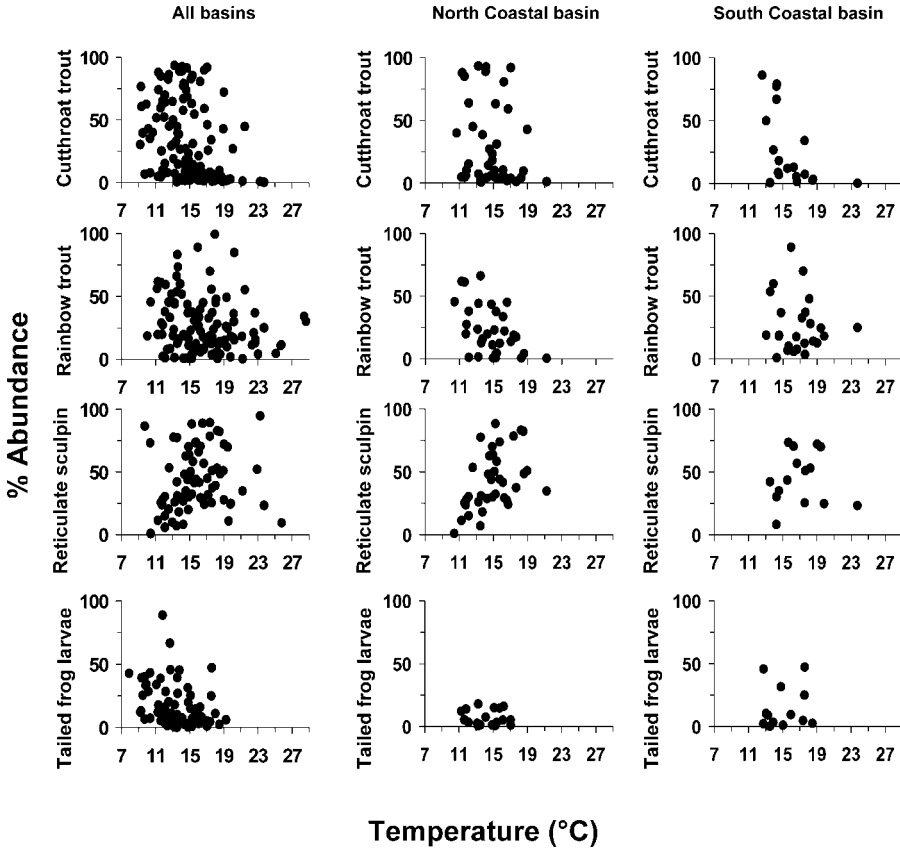


FIGURE 2.—Percent abundance versus temperature (average of the maximum temperature for the 7-d period that includes the sample date) of four aquatic vertebrate species collected in three Oregon study regions.

median temperatures from region to region (Table 1).

The strength of the relationship between NMS axis 1 and temperature is shown in Table 2, along with Pearson's correlation coefficients (r) for individual species against axis 1 and other ordination details. Temperature explained 43% of the variance in aquatic vertebrate distribution (r^2) among sites in all regions, 24% of the variance in the North Coastal basin, 43% of the variance in the South Coastal basin, 20% of the variance in the Coast Range ecoregion, 28% of the variance in the Cascades ecoregion, and 34% of the variance in the Blue Mountains ecoregion. Species distribution varied along axis 1 (water temperature axis) in all regions (Figure 4). Higher relative abundances of Pacific giant salamander larvae, for example, were strongly associated with colder temperatures. Conversely, higher relative abundance of speckled dace was associated with warmer temperatures. Species considered to have a strong re-

lationship to temperature ($r^2 > 0.1$) in all regions combined were cutthroat trout, Pacific giant salamander larvae, rainbow trout, speckled dace, and tailed frog larvae. Species that showed a strong relationship to temperature in the North Coastal basin were cutthroat trout, Pacific giant salamander larvae, reticulate sculpins, and riffle sculpins. In the South Coastal basin, all species showed a strong relationship to temperature. In the Coast Range ecoregion, cutthroat trout, reticulate sculpins, Pacific giant salamander larvae, speckled dace, and rainbow trout showed a strong relationship to temperature. In the Cascades ecoregion, cutthroat trout, Pacific giant salamander larvae, Paiute sculpins, rainbow trout, tailed frog larvae, and torrent sculpins showed a strong relationship to temperature. In the Blue Mountains ecoregion, bridgelip suckers, rainbow trout, and speckled dace showed a strong relationship to temperature (Table 2).

Visual inspection of the NMS ordination of spe-

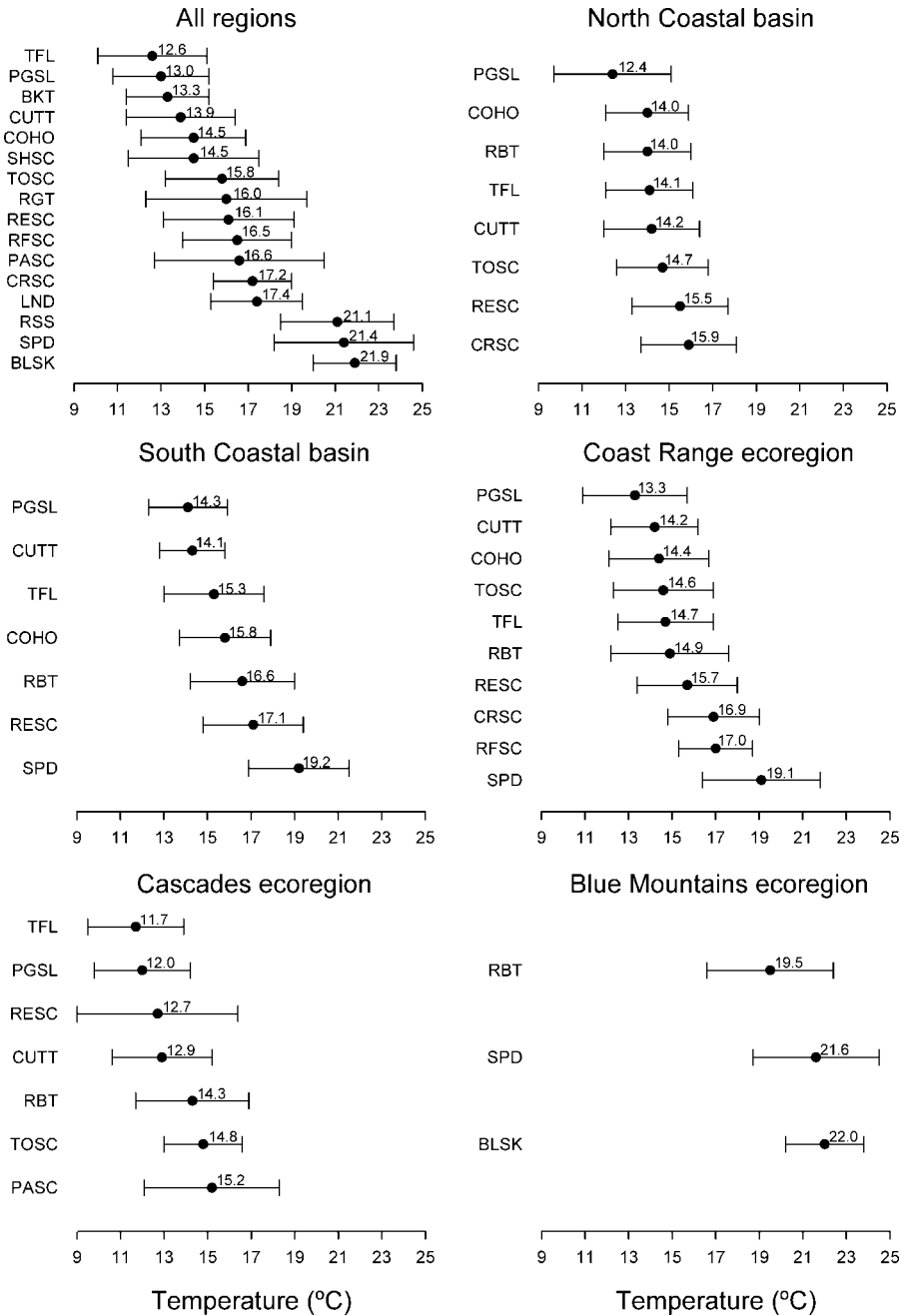


FIGURE 3.—Realized niche widths (horizontal lines) and realized niche centers (shaded ovals) for aquatic vertebrate species that were correlated with temperature ($r^2 > 0.1$) in each of the Oregon regions. Abbreviations are as follows: BLSK = bridgelip sucker; BKT = brook trout; COHO = coho salmon; CRSC = coastrange sculpin; CUTT = cutthroat trout; LND = longnose dace; PASC = Paiute sculpin; PGSL = Pacific giant salamander larvae; RBT = rainbow trout; RESC = reticulate sculpin; RFSC = riffle sculpin; RSS = reddsie shiner; SHSC = shorthead sculpin; SPD = speckled dace; TFL = tailed frog larvae; and TOSC = torrent sculpin.

TABLE 2.—Summary of nonmetric multidimensional scaling ordination information for regions. Fifty randomized Monte Carlo tests were run. Axis variance is the cumulative proportion of variance represented by each axis based on the r^2 between the distance in the rotated ordination space and the distance in the original space. Pearson correlation coefficients (r) are shown for temperature and for species relative abundance vis-à-vis axis 1 ordination scores (Figure 4).

Statistic or species	All regions	North Coastal basin	South Coastal basin	Coast Range ecoregion	Cascades ecoregion	Blue Mountains ecoregion
Number of dimensions	3	3	3	3	3	3
Monte Carlo test result (P)	0.02	0.02	0.02	0.02	0.02	0.04
Iterations	400	153	160	400	400	120
Final stress	14.7	9.5	9.6	12.0	12.6	5.7
Axis variance	0.809	0.936	0.898	0.910	0.887	0.966
Temperature	0.658	0.485	0.658	0.449	0.530	0.579
Relative abundance						
Bridgelip sucker	0.302					0.747
Brook trout	0.117					
Coastrange sculpin	0.128	0.137		0.252		
Coho salmon	0.237	0.176	0.428	0.245		
Cutthroat trout	-0.586	-0.704	-0.347	-0.861	-0.410	
Longnose dace	0.121				0.165	
Pacific giant salamander	-0.736	-0.365	-0.886	-0.565	-0.554	
Paiute sculpin	0.105				0.801	0.305
Rainbow trout	0.519	-0.052	0.569	0.364	0.632	-0.773
Redside shiner	0.221					
Reticulate sculpin	0.202	0.899	0.546	0.697	-0.080	
Riffle sculpin	0.198	0.403		0.294		
Shorthead sculpin	-0.063				-0.013	
Speckled dace	0.568		0.378	0.410		0.577
Tailed frog larvae	-0.518	-0.219	-0.397	0.205	-0.552	
Torrent sculpin	0.196	-0.115		0.178	0.356	

cies' relative abundance (Figure 5) revealed that ecoregions showed relatively distinct groupings, while basin groupings could be discerned but were somewhat less distinct. Willamette basin sites, in particular, were dispersed widely across the plot as were South Coastal basin sites. The Blue Mountains ecoregion sites and the Deschutes basin sites were the most cohesive groupings in both plots. Global ANOSIM results showed that there were significant differences ($P < 0.001$) among both ecoregions and basins. The global R -value was twice as large for ecoregions ($R = 0.402$) as it was for basins ($R = 0.201$). The R -statistic is a useful measure of the degree of separation of sites (Clarke 1993); R -values closer to one correspond to similarities across site groups being lower than those within site groups (i.e., R -values close to one are indicative of complete separation of the groups). The six pairwise ANOSIM tests among ecoregion groups and basin groups showed significant differences ($P \leq 0.05$ in all comparisons; Table 3). The higher R -value between the Blue Mountains ecoregion and the other ecoregions identified a greater degree of distinction than other between-group comparisons. The Coast Range and Willamette Valley ecoregions showed the least distinct comparison among ecoregions, but the R -value still indicated a substantial distinction between

groups. As with ecoregions, the higher R -value between the easternmost Deschutes basin and the other basins confirmed a considerable degree of distinction than other between-group comparisons. Conversely, the lower R -values shown in the pairwise comparisons of the North and South Coastal basins with the Willamette basin indicate relatively low within-group similarity relative to similarities between groups.

Our analysis revealed no differences among various life stages of the species we encountered for seven size-class comparisons.

Discussion

Delineation of the upper thermal limit for fish is relevant to temperature standards, land-use management plans, and determination of the habitat available to aquatic species. The distribution of coldwater fishes often reflects their inability to withstand high summer water temperatures (Eaton et al. 1995; Taniguchi et al. 1998); therefore, the upper limit of a species' thermal niche has special importance. Our temporal-sampling window occurred during the warmest time of the year, when the upper thermal limits of these organisms are of greatest interest. The RNC and RNW values calculated using the 7-d average maximum temperature are useful because they are comparable to

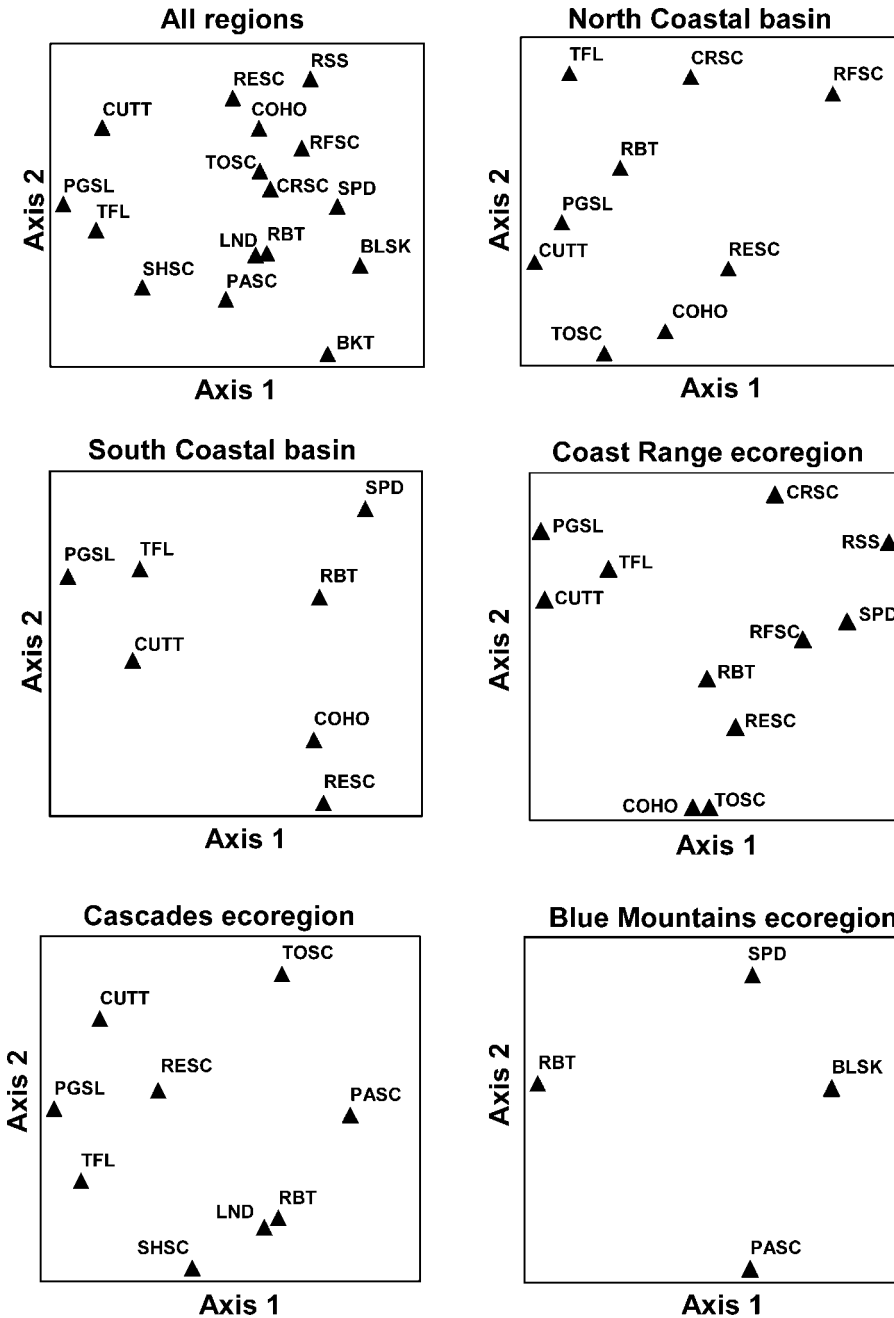


FIGURE 4.—Nonmetric multidimensional scaling species ordinations for each region in Oregon. Each plot was rotated such that axis 1 represents the strongest correlation with temperature. Triangles depict species' locations in ordination space. See the caption to Figure 3 for species abbreviations.

agency standards for maximum summer temperatures where average weekly maximum temperatures are the recommended criterion (Gamperl and Rodnick 2003). These criteria are often maximum temperatures not to be exceeded for a specified

time during the summer months and limit the allowable rate of temperature change or rise above ambient receiving water temperature. Development of water temperature criteria involves identifying limits that have both ecological and phys-

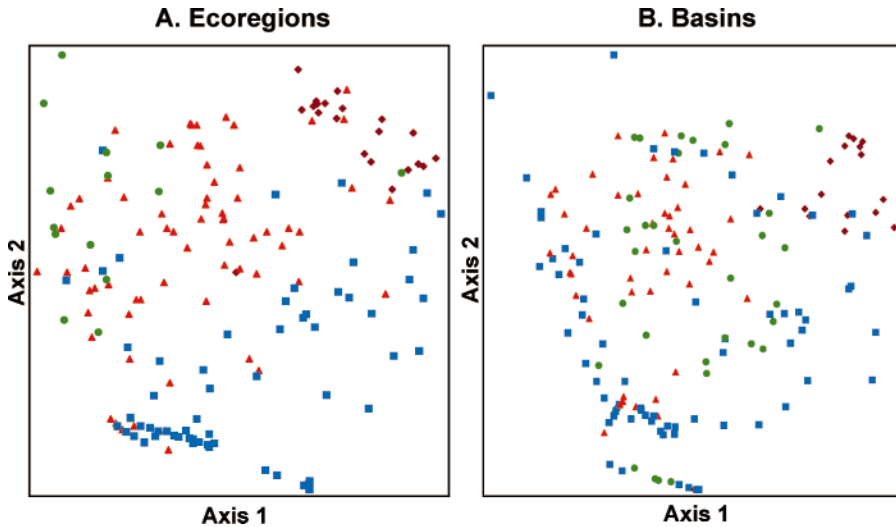


FIGURE 5.—Two-dimensional nonmetric multidimensional scaling (NMS) plot of study sites in Oregon based on the relative abundance (Bray–Curtis dissimilarity) of aquatic vertebrates by (A) ecoregion and (B) basin. Site symbols represent areas as follows: circles = the Willamette Valley ecoregion or South Coastal basin; squares = the Cascades ecoregion or Willamette basin; diamonds = the Blue Mountains ecoregion or Deschutes basin; and triangles = the Coast Range ecoregion or North Coastal basin. The NMS plot was rotated to maximize the distinction among groups in each panel.

iological significance for the species of concern (Brett 1971; NAS/NAE 1973). Estimation of the realized thermal niche of a species using weighted averaging will provide resource managers with guidance in setting relevant water temperature standards.

The realized thermal niches calculated in this study are comparable to the maximum growth temperatures and upper thermal limits from other field

TABLE 3.—*R*-values for pairwise analysis of similarity tests among four ecoregions and four basins in Oregon. Values indicate the extent to which between-region variability differs from within-region variability for species relative abundances. All values are significant (Bonferroni corrected $P \leq 0.05$).

Regions compared	<i>R</i>
Ecoregions	
Blue Mountains and Willamette Valley	0.743
Blue Mountains and Cascades	0.627
Blue Mountains and Coast Range	0.584
Cascades and Willamette Valley	0.484
Cascades and Coast Range	0.283
Coast Range and Willamette Valley	0.232
Basins	
Deschutes and North Coastal	0.722
Deschutes and Willamette	0.517
Deschutes and South Coastal	0.301
North Coastal and South Coastal	0.147
North Coastal and Willamette	0.093
South Coastal and Willamette	0.083

and laboratory studies. Table 4 compares temperature RNC and RNW upper limit values from this study to maximum growth temperatures and upper limits from the literature that were derived by various laboratory and field techniques for three salmonids. Nevertheless, the RNC gives different information than growth rate. It is an estimate of the center of a species' realized thermal niche as influenced by the local environment (Magnuson and DeStasio 1996). One may infer that at temperatures outside the limits of the RNW, fecundity is reduced until the local population is eliminated because recruitment falls below the critical threshold needed to maintain its competitiveness (Vannote and Sweeney 1980). Unsurprisingly, the experimental upper limits are higher than those determined by weighted averaging of field data. These are reflections of the fundamental and realized thermal niches for these species.

We recognize that there are substantial differences in the susceptibility of species to electrofishing. However, single-pass electrofishing has been used by others in our region to obtain relative abundance data (e.g., Van Sickle and Hughes 2000; Waite and Carpenter 2000). Our protocol of 40 wetted channel widths has been reported long enough for relative abundance estimates to stabilize (Angermeier and Smogor 1995). Study reaches were shocked at higher voltages to ensure that

TABLE 4.—Comparison of this study's realized niche center (RNC) and realized niche width (RNW) upper thermal limits and various values from the literature for juveniles of three salmonid species (all values °C). The experimental laboratory upper limits are from mortality tests. In the Fish and Temperature Database Matching System (FTDMS), fish presence data were matched temporally and spatially with weekly mean temperatures to derive composite thermal regimes; the 95th percentile of the maximum weekly mean temperature was then used as the upper thermal tolerance. Abbreviations are as follows: NC = North Coastal basin, SC = South Coastal basin, CR = Coast Range ecoregion, CA = Cascades ecoregion, and BM = Blue Mountains ecoregion.

Species	RNC	Maximum growth temperature	RNW upper limit	Experimental laboratory upper limit	FTDMS upper limit	EPA maximum
Coho salmon	14.5 (All)		16.9 (All)			
	14.0 (NC)	15 ^a (USDI 1970)	15.9 (NC)	25.0 ^b (Brett 1952)	23.4 (Eaton et al. 1995)	18, 24 (USEPA 1986)
	15.8 (SC)		17.9 (SC)	28.8 ^c (Becker and Genoway 1979)		
	14.4 (CR)		16.7 (CR)			
Cutthroat trout	13.9 (All)		16.4 (All)			
	14.2 (NC)		16.4 (NC)			
	14.3 (SC)	15 (Dwyer and Kramer 1975)	15.4 (SC)	25.7 ^d (Golden 1978)	23.2 (Eaton et al. 1995)	
	14.2 (CR)		16.2 (CR)			
Rainbow trout	12.9 (CA)		15.2 (CA)			
	16.0 (All)		19.7 (All)			
	14.0 (NC)		16.0 (NC)			
	16.6 (SC)	18.1 ^e (Eaton et al. 1995)	19.0 (SC)	26.6 ^f (Charlon et al. 1970)	24.0 (Eaton et al. 1995)	19, 24 (USEPA 1986)
	14.9 (CR)		17.6 (CR)	29.4 ^c (Gamperl and Rodnick 2003)		
	14.3 (CA)		16.9 (CA)			
	19.5 (BM)		22.4 (BM)			

^a Final thermal preferendum strongly related to the maximum growth temperature (Jobling 1981).

^b Upper lethal temperature at maximum acclimation temperature (time to 50% mortality, 6.3 d).

^c Determined by slowly raising the temperature until 50% mortality was achieved (acclimation temperature, 15°C).

^d Determined by slowly raising the temperature until 50% mortality was achieved (acclimation temperature, 23°C).

^e Calculated by fitting a second-degree polynomial trend line to experimental temperature-growth rate data collected by Hokanson (1977).

^f Upper thermal tolerance limit (acclimation temperature, 24°C; time to 50% mortality, 1 d).

organisms, such as sculpins, tailed frog larvae, and Pacific giant salamander larvae (that are more difficult to capture), were also collected. One factor that can cause differences in electrofishing efficiency is water conductivity (Zalewski and Cowx 1989; Hill and Willis 1994). Species that are less susceptible to electrofishing techniques may be captured more easily and appear to occur at a higher relative abundance at sites with higher conductivity. Our sites consisted of wadable first- to third-order streams, and water conductivity was consistently low (median, 63 $\mu\text{mhos/cm}$) with few exceptions.

Some of these results apply to only one life stage of some species, such as coho salmon smolts. Other species, such as rainbow trout and Pacific giant salamander larvae, were encountered at various life stages. Although our analysis revealed no differences among different life stages of the species we encountered, we feel that consideration of ontogenetic changes in thermal preference is worth-

while. It may be that differences in thermal requirements related to ontogenetic changes are difficult to detect with this type of sampling protocol (Angermeier and Smogor 1995). More work is necessary to address this topic.

Ordination of aquatic vertebrate assemblages in Oregon supports grouping them by ecoregion rather than by basin. Our goal was to minimize the variation in local and regional factors, such as habitat diversity, competition, predation, climate, dispersal patterns, and biogeographical history, in each group. Group membership was overlaid on the ordination of sites to give a graphical representation of the relationship among groups (Figure 5). Global ANOSIM results revealed significant differences in assemblage composition between all four groups of basins and ecoregions. The *R* statistics were much closer to one for ecoregions ($R = 0.402$) than for basins ($R = 0.201$), indicating a greater degree of cohesiveness among ecoregions. This is reflected in the degree of overlap

between groups in the NMS plots (Figure 5). The NMS was of sufficiently low stress to give a perceptible image of the group separations identified by the ANOSIM pairwise comparisons. The pairwise ANOSIM tests showed a pattern of distinctiveness between groups that was strongest on an apparently spatial gradient (Table 3). The higher R -values, which indicate more complete separation, were between more distantly separated (spatially) groups, such as the Blue Mountains ecoregion and the Willamette Valley ecoregion, while the lowest degree of separation (lower R -values) were between regions that were geographically close, such as the Coast Range ecoregion and the Willamette Valley ecoregion. Our results agree with Whittier et al. (1988) that ecoregions are more appropriate classifications for site categories than basins (see also Hughes et al. 1987). Although ecoregions seem to group aquatic vertebrate communities more effectively than basins in this study, regional history determines the assemblage composition of a particular location as strongly as the habitat type that is indicated by its ecoregion. The results of other studies caution against using autecological information from different ecosystems or regions (Whittier and Hughes 1998), and we argue that evaluations on a local level are worthwhile. The appropriate scale and extent of geographic categories, however, should be evaluated on a case-by-case basis (Strange 1998).

Since the underlying factors that structure aquatic vertebrate assemblages are thought to vary continuously, it makes sense that a more diverse region would provide a stronger gradient over which species composition changes. This is evidenced by a high correlation coefficient for all combined regions with temperature ($R = 0.658$; Table 2). The vertebrate assemblage in the South Coastal basin also showed a strong relationship to temperature ($R = 0.658$; Table 2). This relationship is only useful, however, if the geographic classification consists of a relatively cohesive faunal assemblage. It would be difficult to justify, for example, extrapolating RNC and RNW values within regions, where ecological data are sparsely or unevenly distributed, unless the important biotic and abiotic factors that drive faunal assemblages were relatively uniform.

Most of our sites were randomly selected with the intent of characterizing regional conditions. We feel that our sites accurately reflect the range of conditions available for aquatic vertebrates in this study within the constraints of the study design. Because ecoregions often have dominant

land-use characteristics (e.g., the Willamette Valley ecoregion is mainly agricultural, the Coast Range ecoregion is predominantly logging, etc.), the effect of "setting" may be depicted, to some degree, by grouping sites by ecoregion. However, if the region has an extensive history of persistent human disturbance, assemblages may correspond to ecoregion classifications only when land use differs significantly among ecoregions (Pan et al. 2000).

Although the relationship between temperature and aquatic vertebrate assemblages is well documented, we used NMS to identify the strength of the relationship between temperature and individual species and to determine its role in driving assemblage composition. Species may be considered to have a strong statistical relationship with temperature if greater than 10% of the variance in a species' relative abundance could be explained by the variance in temperature (Pan et al. 1996). In regions where temperature is shown to be an important factor in driving assemblage structure, temperature may play an important role in determining available habitat for a given species. Temperature explains 34% of the variance in the site ordination scores in the Blue Mountains ecoregion (Table 2). This strong relationship of the Blue Mountains vertebrate assemblage to temperature is likely due to the presence of rainbow trout; rainbow trout is the only species we encountered in this region that are associated with cool water temperatures (Figure 4; $r^2 = 0.60$). Because of the relative uniformity and distinctiveness of the Blue Mountains ecoregion, the strong statistical relationship of this species to temperature is an indicator of its importance to rainbow trout survival in this region. Therefore, its calculated RNW upper limit of 22.4°C should be given careful consideration. Other regions and species may be evaluated in the same way.

Temperature is a universal factor in the life history of fish and amphibians, but their distribution is a complex phenomenon that is subject to influence from an assortment of variables (Shrode et al. 1982). Intraspecific variation in thermal requirements among regions may be due to biotic factors such as competition, abiotic factors such as substrate and cover, and genetic differences between populations. Therefore, temperature in combination with other factors may confer the real ecological value of a species' thermal response (Reynolds 1977). It is evident that thermal niches calculated for each taxon are, to some degree, related to regional stream temperatures (Christie and

Smol 1993). Our results showed differences in thermal niches among some regions where median temperatures varied in a similar way. However, physiological responses of geographically separated populations are a factor of prevailing environmental temperatures. Laboratory tests on largemouth bass, for example, show the lowest temperature growth optima occur in fish from Ontario and the highest temperature growth optima occur in bass from Texas (Beitinger and Fitzpatrick 1979). Thus, it is reasonable that a species' thermal niche should vary with regional water temperatures.

An aquatic vertebrate's thermal niche, derived using field data, is ecologically relevant. There is clearly a need for consistent, quantitative data that respond to the question, Are there populational or geographical differences in the thermal requirements of a species? Resource policies should be region-specific; therefore, sound management decisions require detailed local information (Gift 1977) and priorities should be adjusted accordingly (Coutant 1987). Uses for quantitative regional data include developing biotic integrity indices (Fausch et al. 1984), determining the suitability of water bodies for protected species, and identifying environmental stressors in a system (Whittier and Hughes 1998). The thermal requirements of many fish and amphibians are poorly studied or unknown. A WA analysis may provide important measures of temperature requirements for poorly studied organisms, such as nongame endangered species, with negligible quantitative ecological information. With this field-based method, managers can determine the range of temperatures beyond which a species is unlikely to thrive.

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