

NOTES

Nonlinear Response of Trout Abundance to Summer Stream Temperatures across a Thermally Diverse Montane Landscape

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Abstract.—Stream temperature is a fundamental physical factor that affects the distribution and abundance of salmonids, but empirical inconsistencies exist regarding the nature of this relationship in wild populations. We sampled trout populations composed primarily of cutthroat trout *Oncorhynchus clarki* but also including brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* at 102 reaches on 24 first- to fourth-order streams across a thermally diverse montane landscape. Curves fit to scatterplots of density and biomass versus mean July–August stream temperatures suggested nonlinear, dome-shaped responses. Peaks occurred near mean stream temperatures of 12°C; x-intercepts were near 3°C and 21°C. We conclude that inconsistencies in previously reported temperature–abundance relationships for wild trout populations may have resulted from sampling only a subset of the thermal environments occupied by a species. Researchers analyzing this relationship should be cognizant of the range of temperatures studied and the expected form of the relationship over that range.

Temperature is a fundamental physical factor that strongly affects the distribution and abundance of stream salmonids (Railsback and Rose 1999; Poole et al. 2001). Temperature affects the physiological performance of individuals by influencing growth rates, scopes for activity, and food conversion efficiencies (Dwyer and Kramer 1975; Elliott 1976; Railsback and Rose 1999). The influence of temperature on physiological performance usually takes a nonlinear form in which performance increases with temperature until rising metabolic costs outstrip additional gains, at which point the relationship becomes negative (Wedemeyer and McLeay 1981). The functional

form of organismal relationships to strong environmental gradients has often been idealized as a symmetric Gaussian-, or bell-shaped, curve (Westman 1980). That many observed relationships do not conform to this view has resulted in alternative proposals (Austin 1976; Austin and Smith 1989). One alternative that may be pertinent for the temperature–trout relationship is an asymmetric response curve in which the performance metric peaks somewhere other than the center of the environmental range. Studies in controlled laboratory settings have shown relatively slow increases in rate processes (e.g., growth and feeding rates) with increasing temperature, followed by rapid decreases in these processes at warmer temperatures (Cherry et al. 1977; Brett and Groves 1979). Advantages in terms of growth rate and scope for activity may help explain why fish choose to live “close to chaos.”

Nonlinear relationships between stream temperature and trout performance have frequently been observed in laboratory settings, but how this relationship is expressed in wild populations is poorly understood, given the dearth of empirical examples. A common factor limiting earlier field work has been that sufficiently wide temperature ranges were not sampled, either because the range of stream temperatures available within a study area was limited or because sampling trout populations across a wide range of temperatures was not a primary study objective. Until recently, empirical support may also have been limited by a lack of data acquisition capabilities. However, the development of inexpensive and reliable digital thermographs has made the acquisition of stream temperature data less costly and more routine. Before this development, many broadscale studies used proxy variables such as elevation or air tem-

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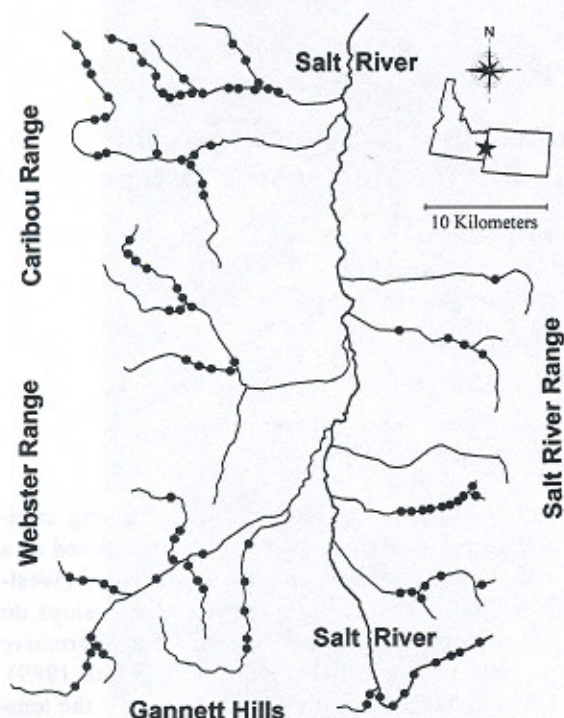


FIGURE 1.—Stream network in the Salt River watershed of western Wyoming and eastern Idaho. Trout populations were sampled at locations marked with circles.

perature of the study site, which are often weakly correlated to stream temperature in mountainous landscapes (Isaak and Hubert 2001) and may have partially obscured the temperature–trout relationship. In this note, we describe the response of trout abundance to stream temperature across a thermally diverse Rocky Mountain watershed. Implications of the observed response are discussed with regards to species-specific thermal preferences, habitat modeling, and climate change.

Methods

Study site.—Data were collected from the 2,150-km² Salt River watershed on the border between Idaho and Wyoming. This watershed is bordered by mountain ranges that differ markedly in morphology (Figure 1). On the east side of the watershed, the rugged Salt River Range rises to peak at elevations that exceed 3,300 m. The terrain in the Caribou and Webster ranges to the west and in the Gannett Hills to the south is less rugged, and elevations do not exceed 2,800 m. Valleys in upstream areas grade from constrained, with riparian floras dominated by conifers, to unconstrained in downstream areas, where riparian zones are composed of shrubs and grasses. The only trout

native to the watershed is cutthroat trout *Oncorhynchus clarki*, but brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* were introduced to the watershed during the middle of the 20th century.

The climate in the Salt River watershed is cold with humid winters. Mean annual air temperature on the Salt River valley floor is 3.5°C, the monthly averages ranging from -9.1°C in January to 16.7°C in July (Owenby and Ezell 1992). Climatic patterns, combined with the geomorphic diversity of the watershed, result in considerable variation in stream heating rates, and maximum summer temperatures ranging from 9.5°C to 25.0°C have been recorded in streams in this area (Isaak and Hubert 2001). Precipitation occurs as snow during cooler months and as rain during the remainder of the year. Hydrographs of streams are driven by snowmelt, with peak discharges in May and June followed by base flows from late July into March.

Data collection and analysis.—Trout were sampled at 102 reaches on 24 first- through fourth-order tributaries during 1996 and 1997 (Figure 1). Sampling began in early July, after discharge had peaked, and continued until mid-September. Sample reaches had average lengths of 180 m and were sampled at 50-m changes in elevation along the lengths of streams. Trout populations were sampled by using a backpack electrofisher (Model 15-C; Smith-Root, Vancouver, Washington) to conduct multiple removal efforts within reaches bounded by block nets (Zippin 1958). Each removal effort consisted of one upstream electrofishing pass, and passes were made until the confidence interval associated with the population estimate was less than 30% of the population estimate (average confidence interval width was 13%). Precision of population estimates was calculated in the field after the second and subsequent removal efforts by using a graph from MicroFish (Van Deventer and Platts 1989) in conjunction with rough estimates of population size and removal efficiency. Captured trout were identified to species, measured, and released outside the study reach. Additional details about sampling procedures are outlined in Isaak and Hubert (2000).

Population estimates for individual reaches were calculated with the maximum likelihood estimator in MicroFish (Van Deventer and Platts 1989). Age-0 trout were removed from consideration, based on the timing of their appearance in study streams and breaks in length-frequency histograms. Separate population estimates were calculated for trout of less than 135 mm total length (TL) and

those of 135 mm TL or more to reduce length-related differences in catchability that could decrease the accuracy of population estimates (Anderson 1995). Density estimates were obtained by combining population estimates for both length categories and dividing the total by the surface area of a reach. Biomass estimates were calculated by multiplying the population estimate for a length category by the mean weight of trout in that category, adding biomass estimates for both length categories, and dividing the total by the surface area of a reach.

Stream temperatures were recorded with digital thermographs (Model WTA32; Onset Computer Corp., Pocasset, Massachusetts) that were set to record a temperature every 30 min. We deployed the thermographs in sample reaches at opposite extremities of each study stream, placing them in streams during late June and leaving them in place until mid-September. For sample reaches that contained thermographs, we summarized the stream temperatures by calculating the mean temperature for the months of July and August. Mean temperatures for reaches without thermographs were interpolations based on stream-specific rates of temperature change, which we calculated by dividing the elevation difference between upstream and downstream thermographs into the difference in mean temperatures at these sites.

To test the accuracy of the method, we applied it to an independent data set collected from mountain streams in a region for which thermograph data were available at multiple sites ($n = 59$) between upstream and downstream thermographs. Linear regression analysis indicated a strong ($r^2 = 0.79$) and unbiased ($b_1 = 1.00$; 95% confidence interval = 0.863–1.137) relationship between temperatures predicted from thermograph endpoints and temperatures observed at intermediate sites (J. Dunham, Rocky Mountain Research Station, unpublished data). Therefore, although the interpolation of some stream temperatures may have added variation to the data set, this method appeared to provide relatively accurate estimates at reaches lacking thermographs.

Several models were used as possible representations of the relationship between trout abundance and stream temperature. The simplest model was a linear regression, but symmetric nonlinear responses were also modeled using a quadratic regression and a Gaussian curve, as follows:

$$Y = b_0 e^{-[(x-b_1)/b_2]^2}, \quad (1)$$

where Y = predicted abundance, x = mean stream temperature, b_0 = the amplitude parameter, b_1 = the location parameter, and b_2 = the scale parameter. A nonlinear asymmetric response was modeled by using a maxima function taken from Spain (1982):

$$Y = b_0 x e^{(b_1 x)}, \quad (2)$$

where Y = predicted abundance, x = mean stream temperature, and b_0 and b_1 are unknown parameters.

A \log_{10} transformation was applied to density and biomass values to minimize deviations from normality, and residual error assumptions were checked by using standard diagnostic tests in SAS (SAS Institute 1989). Constants were added to transformed values to eliminate negative values. Akaike's information criterion, adjusted for small sample size (Burnham and Anderson 1998), and R^2 values were calculated to facilitate model comparisons. Akaike's information criterion is superior to traditional measures of model fit (e.g., R^2) because it assesses how well data are represented by a model and penalizes for the number of parameters used, thereby highlighting parsimonious models.

Results

Fifty-seven of the 102 reaches sampled contained allopatric populations of cutthroat trout, one reach contained allopatric brown trout, and the remaining reaches contained sympatric associations of cutthroat trout and brown or brook trout. Biomass estimates ranged from 0.236 to 15.6 g/m² and density estimates ranged from 0.00143 to 0.562 fish/m². Mean July–August stream temperatures at sample reaches ranged from 5.6°C to 17.2°C. Allopatric cutthroat trout populations were found across the range of temperatures sampled (Figure 2). Sympatric populations of cutthroat trout and brown trout occurred in areas with mean temperatures greater than 9°C, whereas populations of cutthroat trout and brook trout occurred in areas colder than 9°C.

Scatterplots of trout abundance versus stream temperature suggested nonlinear, dome-shaped relationships (Figure 2). Statistical models described similar patterns, as the linear models yielded the poorest fits (Table 1). Nonlinear symmetric models (quadratic and Gaussian) provided similar data fits, and generally provided better representations of the data than the asymmetric nonlinear function. The curves associated with symmetric models peaked near mean stream temperatures of 12°C; predicted x -intercepts were near 3°C and 21°C.

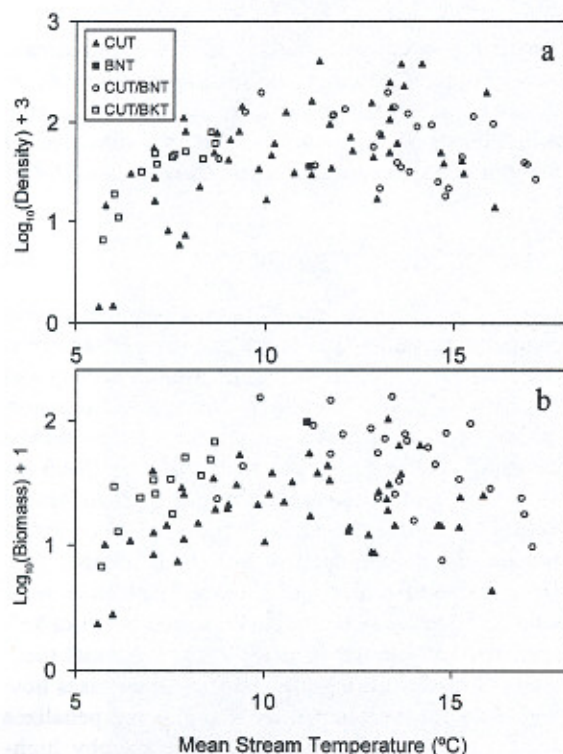


FIGURE 2.—Scatterplots of (A) trout density and (B) trout biomass versus stream temperature at 102 reaches in the Salt River watershed. Abbreviations are as follows: CUT = cutthroat trout, BNT = brown trout, and BKT = brook trout.

Discussion

Symmetric, nonlinear curves best represented trout population response to stream temperature. The apparent discrepancy between the patterns observed in our wild populations and the asymmetric responses of individuals in the laboratory (Cherry et al. 1977; Brett and Groves 1979) could be an artifact of comparisons made across biological scales or the imposition of additional constraints on wild populations. More specifically, in the uncontrolled environment of a stream, populations are regulated by multiple factors, many of which could alter the trout-temperature relationship. Evidence of this modification can be seen in other aspects of the relationships we documented. For example, peaks in curves for allopatric cutthroat trout populations occurred near 12°C, which is several degrees cooler than the temperature at which the scope for activity peaks in this species (Dwyer and Kramer 1975). Similarly, the upper lethal temperature for cutthroat trout has been reported as being near 24°C (Dickerson and Vinyard 1999; Johnstone and Rahel 2003), which is warmer than

the x -intercepts predicted from the relationships developed in this study. Similar discrepancies have been observed for growth rates of brown trout in the wild and in laboratory settings, that of the former being only 60–90% of the predicted maximum for a given temperature (Edwards et al. 1979). These discrepancies probably represent the costs of addressing environmental constraints associated with food limitations, competition, and reproduction and are often cast as the difference between fundamental and realized niches (Mueller-Dombois and Ellenberg 1974).

Despite the number of field studies that document linkages between trout populations and temperature, the functional forms of these relationships often appear to vary across the ranges of species (e.g., Rieman and McIntyre 1995; Saffel and Scarnecchia 1995). Most studies suggest a negative association (Platts and Nelson 1989; Li et al. 1994; Dunham et al. 2003), but this may reflect the preponderance of studies conducted near the southern margin of species ranges or the greater collection of data in accessible downstream areas, where stream temperatures are usually warmer. Although less common, examples of positive temperature associations also exist and typify data collected at high elevations, northern distributional extents, or locations where streams are heavily shaded (MacCrimmon and Campbell 1969; Scarnecchia and Bergersen 1987; Saffel and Scarnecchia 1995). Our results suggest these apparent discrepancies may be artifacts of truncated nonlinear responses, which appear as positive or negative associations—depending on which portion of the thermal range is sampled.

If wild trout populations exhibit a nonlinear response across a broad range of temperatures, the impact of climate warming may be context specific. Where warm stream temperatures are currently limiting, populations will be forced to retreat upstream and may become more fragmented (Rahel et al. 1996). Susceptibility to environmental and demographic stochasticity could increase, and local extirpations would be expected to become more common. The opposite may be true, however, where cold temperatures currently limit populations. In those areas, productivity gains may occur in habitats that are currently occupied, and the population range might expand into previously unoccupied areas (Milner and Bailey 1991). The management challenge in such a scenario will be to understand the thermal characteristics of a stream network, how these characteristics are like-

TABLE 1.—Summary of models describing potential relationships between stream temperature and trout abundance. Values in parentheses are SE estimates. Smaller Akaike information criterion (AIC_c) values indicate better model fits.

Response variable	Model	Parameter estimates			Significance	Error df	R^2	AIC_c
		b_0	b_1	b_2				
Trout density	Linear	1.13 (0.159)	0.0506 (0.0138)		<0.01	100	0.12	-165
	Quadratic	-1.72 (0.469)	0.615 (0.0895)	-0.0256 (0.00403)	<0.01	99	0.37	-198
	Gaussian	1.98 (0.0577)	12.0 (0.283)	7.89 (0.678)	<0.01	99	0.36	-196
	Maxima	0.338 (0.0321)	-0.0678 (0.00790)		<0.01	100	0.24	-180
Trout biomass	Linear	1.10 (0.129)	0.0287 (0.0111)		0.01	100	0.062	-209
	Quadratic	-0.99 (0.392)	0.442 (0.0748)	-0.0187 (0.00337)	<0.01	99	0.29	-235
	Gaussian	1.62 (0.0480)	11.8 (0.310)	8.54 (0.835)	<0.01	99	0.28	-234
	Maxima	0.313 (0.0282)	-0.0765 (0.00760)		<0.01	100	0.19	-223
Cutthroat trout density	Linear	0.665 (0.232)	0.0952 (0.0209)		<0.01	55	0.27	-85.1
	Quadratic	-2.24 (0.730)	0.685 (0.143)	-0.0277 (0.00667)	<0.01	54	0.45	-98.6
	Gaussian	2.03 (0.0804)	12.4 (0.486)	7.44 (0.936)	<0.01	54	0.44	-97.7
	Maxima	0.265 (0.0391)	-0.0455 (0.0124)		<0.01	55	0.34	-90.1
Cutthroat trout biomass	Linear	0.886 (0.160)	0.0370 (0.0144)		0.01	55	0.11	-127
	Quadratic	-1.31 (0.488)	0.483 (0.0959)	-0.0209 (0.00446)	<0.01	54	0.37	-145
	Gaussian	1.48 (0.0558)	11.6 (0.373)	7.74 (0.918)	<0.01	54	0.35	-143
	Maxima	0.267 (0.0335)	-0.0715 (0.0109)		<0.01	55	0.23	-135

ly to change, and what that change will mean for species of management concern.

Although stream temperature had a demonstrable effect on trout abundance across the Salt River watershed, considerable variation remained unexplained. This was not unexpected, given the simplicity of the models that were developed. Environmental characteristics related to community structure, stream hydrology, water chemistry, and physical habitat structure all impose on trout populations, but none of these factors were included as model predictors. Exclusion of these factors did not negate their effects, but translated them to departures from the mean response between temperature and trout abundance (Neter et al. 1989). Additionally, measurement errors associated with stream temperature or population estimates could have created additional variation. Despite these considerations, a temperature effect clearly remained discernable, which speaks to the importance of this factor in structuring salmonid populations across broad areas. Researchers including this variable in multivariate as-

essments should be cognizant of the range of temperatures studied and the expected form of the relationship over that range.

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