

Influences of Spatial and Temporal Variation on Fish–Habitat Relationships Defined by Regression Quantiles

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Abstract.—We used regression quantiles to model potentially limiting relationships between the standing crop of cutthroat trout *Oncorhynchus clarki* and measures of stream channel morphology. Regression quantile models indicated that variation in fish density was inversely related to the width:depth ratio of streams but not to stream width or depth alone. The spatial and temporal stability of model predictions were examined across years and streams, respectively. Variation in fish density with width:depth ratio (10th–90th regression quantiles) modeled for streams sampled in 1993–1997 predicted the variation observed in 1998–1999, indicating similar habitat relationships across years. Both linear and nonlinear models described the limiting relationships well, the latter performing slightly better. Although estimated relationships were transferable in time, results were strongly dependent on the influence of spatial variation in fish density among streams. Density changes with width:depth ratio in a single stream were responsible for the significant ($P < 0.10$) negative slopes estimated for the higher quantiles (>80th). This suggests that stream-scale factors other than width:depth ratio play a more direct role in determining population density. Much of the variation in densities of cutthroat trout among streams was attributed to the occurrence of nonnative brook trout *Salvelinus fontinalis* (a possible competitor) or connectivity to migratory habitats. Regression quantiles can be useful for estimating the effects of limiting factors when ecological responses are highly variable, but our results indicate that spatiotemporal variability in the data should be explicitly considered. In this study, data from individual streams and stream-specific characteristics (e.g., the occurrence of nonnative species and habitat connectivity) strongly affected our interpretation of the relationship between width:depth ratio and fish density.

The history of habitat modeling to predict abundance or occurrence of stream fishes has shown that models often have low predictive ability, and those with high predictive ability have low transferability to different times or places (e.g., Fausch et al. 1988; Bozek and Rahel 1992; Leftwich et al. 1997). Habitat models that predict abundance often work only within narrowly defined temporal and spatial scales, whereas fish abundance, occurrence, and habitat conditions vary significantly in time and space (Matthews 1998). Density-dependent habitat selection (Bult et al. 1999), changes in habitat availability (Bozek and Rahel 1992), and interactions among habitat factors (Baltz et al. 1987) are common occurrences in the stream environment. Predictive habitat models that are applicable to a wide range of spatial and temporal scales will need to incorporate realistic assumptions for dealing with the wide range of variability

in habitat and populations consistently associated with stream fishes.

One common characteristic of fish–habitat relationships is unequal variation of abundance in relation to environmental factors (Terrell et al. 1996; Figure 1). Unequal variation is typically treated as undesirable noise in the application of standard statistical methods (e.g., analysis of variance [ANOVA]), and transformations (e.g., log transformations) are used to equalize variances so mean responses can be modeled to make valid statistical inferences. An alternative interpretation is that unequal variation in abundance reflects important biological processes and should be modeled explicitly. This view shifts the focus from mean responses to patterns of abundances that may be bounded by distinct upper or lower limits related to controls imposed by environmental conditions (Figure 1). There are many examples of bounded patterns of abundance in biology, including “constraint spaces” for animal abundance and body size relations (Brown 1995), and “factor-ceiling” (Thomson et al. 1996) or “wedge-shaped”

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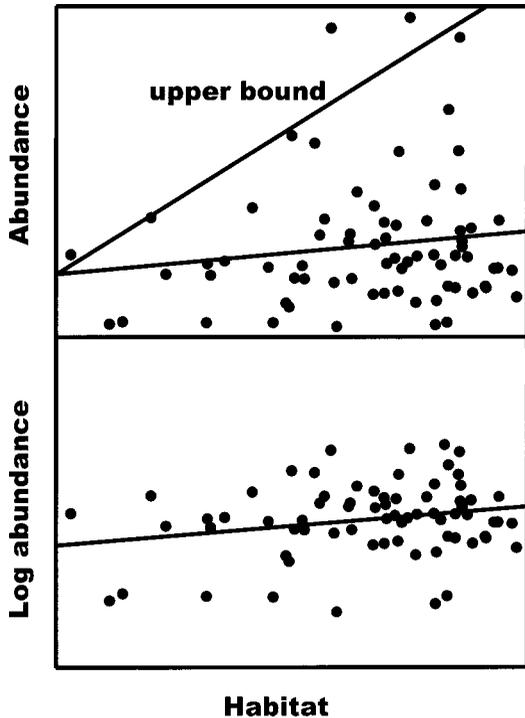


FIGURE 1.—Illustration of heterogeneous abundance in relation to habitat. The top panel illustrates a regression line fitted through the mean, along with a line representing a potential upper bound to the response of abundance to habitat. The bottom panel illustrates a regression line fitted through the mean with \log_{10} -transformed data.

(Terrell et al. 1996) habitat or environmental relationships. Applications of regression quantiles (Koenker and Bassett 1978) in ecology have modeled the edges or boundaries of such relationships (e.g., Terrell et al. 1996; Scharf et al. 1998; Cade et al. 1999).

The rationale for focusing on the boundaries of a response (e.g., abundance) distribution, rather than the mean, comes from the ecological concept of limiting factors (Cade et al. 1999). Many factors can potentially limit abundance of fish but not all will be operative at all times or places. For example, reductions in abundance due to disease, predation, or unsuitable temperatures may reduce the influence of spatial constraints (e.g., stream width) on population density. In some places, at some times, population density may be high enough for space to become a limiting factor. Thus, undefined causal relationships between potential limiting factors and abundance, occurrence, or some other biological response may result in pat-

terns of data with distinct upper or lower constraints.

Here, we apply regression quantiles to estimate relationships between habitat and standing crop (density, biomass) of populations of stream-living Lahontan cutthroat trout *Oncorhynchus clarki henshawi*. Cutthroat trout populations are notoriously variable (e.g., Benson 1960), and several researchers have expressed doubt about the ability of habitat models to define robust relationships (Platts and Nelson 1988; House 1995). Previous analyses of the data we present here using conventional regression methods were unable to detect relationships between mean standing crop of Lahontan cutthroat trout and specific habitat variables (Dunham 1996; Dunham and Vinyard 1997a). We analyzed data collected over a 7-year period in 6–13 streams to examine the spatial and temporal stability of relationships between standing crop of cutthroat trout and habitat. Habitat variables analyzed in this study included three simple measures of stream channel morphology: mean depth, mean wetted width, and width:depth ratio. Our interest was not in these variables per se, but rather in the spatial and temporal stability of regression quantile models, as revealed by the influence of observations from individual streams and years, respectively.

The motivation for application of regression quantiles is based on the theory of limiting factors (Cade et al. 1999), but like any method of analysis, regression quantiles can be used to define associations between any set of variables, even in the absence of a specific hypothesized mechanism (e.g., Dunham and Vinyard 1997a). Two of three variables used in this analysis (stream width and depth) could directly limit fish abundance. For example, standing crop of fish per unit length of stream may be expected to increase as stream width, and presumably space for territories, increases. Stream-living salmonids actively defend feeding territories, and space, as indexed by stream width, may be limiting (Grant et al. 1998). Alternatively, if greater depth provides increased habitat (e.g., pool) availability, there should be a positive response to mean depth. The ratio of stream width to depth is also a common measure of stream channel morphology and thought to be strongly tied to the integrity of stream channels (e.g., Beschta and Platts 1986; Myers and Swanson 1996). Width:depth ratio is commonly used in models of fish-habitat relationships (Fausch et al. 1988), although causal mechanisms associated with fish abundance have not been well defined. Although

it is useful to have some biological sense of potential limiting factors, associations revealed by regression quantiles do not in themselves necessarily indicate causal relationships.

Our primary objective in this study was to estimate the stability of modeled relationships between fish and habitat defined by regression quantiles in a spatially and temporally extensive data set. To examine temporal stability, we developed an initial set of models based on the first 5 years of data and compared the predictions to the last 2 years of data. We also examined spatial stability of model predictions by looking at the influences of observations from individual streams. In addition to the generic effects of space and time (Dunham and Vinyard 1997a; Wiley et al. 1997), we hypothesized that standing crop and habitat relationships may be affected by two specific characteristics of the study streams: presence of nonnative brook trout *Salvelinus fontinalis* and connectivity to migratory habitats. Connectivity may be important because cutthroat trout with access to downstream habitats may emigrate (Benson 1960; Northcote 1997), influencing the relationship of population density to limiting habitat factors at the scale of an individual stream (e.g., Benson 1960; McMahan and Tash 1988). Presence of nonnative brook trout may affect cutthroat trout density (Schroeter 1998; Dunham et al. 2000) and habitat relationships at a similar scale. We hypothesized that presence of brook trout and increased connectivity would result in reduced fish abundance and correspondingly reduce the potential limiting influences of stream channel morphology on standing crop.

Methods

Study Areas

Streams of the eastern Lahontan basin drain an area of approximately 7×10^4 km², covering most of northern Nevada and parts of southeast Oregon. The Lahontan basin is part of the Great Basin desert basin and range province (Grayson 1993). Detailed descriptions of stream habitats in the basin have been extensively reported elsewhere (e.g., Minshall et al. 1989; Jones et al. 1998). Lahontan cutthroat trout is the only salmonid native to the eastern Lahontan basin (La Rivers 1962). Other native fishes encountered in our study sites include speckled dace *Rhinichthys osculus*, Paiute sculpin *Cottus beldingi*, and Tahoe sucker *Catostomus tahoeensis* (Table 1). Of the 13 basin streams we studied, 10 supported isolated populations of Lahontan

TABLE 1.—Fish species occurrence (+) by stream in 13 streams in Nevada within the distribution of Lahontan cutthroat trout.

Stream ^a	Fish species				
	Lahontan cutthroat trout	Brook trout	Speckled dace	Paiute sculpin	Tahoe sucker
3MILE	+		+		
ABEL	+	+			
EMR	+			+	
FOREMAN	+		+		
FRAZER	+		+		+
GANCE	+		+	+	
INDIAN	+				
MOHAWK	+				
MRBC	+			+	
NFORK	+	+	+	+	
T	+		+	+	
TIERNEY	+	+			
WMR	+			+	

^a Stream name abbreviations are as follows: 3MILE = Threemile Creek, ABEL = Abel Creek, EMR = East Marys River, FOREMAN = Foreman Creek, Frazer = Frazer Creek, GANCE = Gance Creek, INDIAN = Indian Creek, MOHAWK = Mohawk Creek, MRBC = Marys River Basin Creek, NFORK = North Fork Humboldt River, T = T Creek, TIERNEY = Tierney Creek, and WMR = West Marys River.

cutthroat trout, 3 of which were functionally interconnected to each other and to downstream migratory habitats. Lahontan cutthroat trout co-occurred with nonnative brook trout in three of the isolated stream populations (Table 1).

Fish and Habitat Data

Population sampling.—To minimize differences due to within-season population changes, sampling was conducted over a 6–8 week period during low-flow conditions in summer and early fall (i.e., mid-July to early October, depending on the timing and magnitude of snowmelt and runoff). In each stream we sampled seven or more sites (25-m stream sections) spaced 300 m apart over a 2-km reach (Table 2). Sites with large beaver ponds were not sampled because of safety and logistical concerns. On rare occasions, sites had to be relocated due to beaver pond formation but were established as close as possible to previous sampling locations. During sampling, both upstream and downstream ends of each site were blocked with seines (4-mm mesh diameter) to prevent fish escape.

Fishes were captured by electrofishing (Coffelt models BP-2 and BP-4 backpack electrofishers) with three or more passes per segment (removal method; White 1982). In cases where no fish were captured or seen in the first two passes, a third

TABLE 2.—Number of sites sampled each year (1993–1997) in each of 13 Nevada streams examined for Lahontan cutthroat trout. Stream abbreviations are defined in Table 1.

Stream	1993	1994	1995	1996	1997	1998	1999
3MILE	0	0	0	7	20	7	7
ABEL	0	0	0	7	9	7	7
EMR	7	7	7	7	7	7	7
FOREMAN	7	7	7	0	15	7	7
FRAZER	7	7	7	7	10	7	7
GANCE	7	7	7	7	15	7	7
INDIAN	0	0	0	7	7	7	7
MOHAWK	0	0	0	7	13	7	7
MRBC	7	7	7	7	7	7	7
NFORK	0	0	0	7	15	7	7
T	0	7	7	7	16	7	7
TIERNEY	0	0	0	7	28	7	7
WMR	7	7	7	7	7	7	7

pass was not conducted. Fish abundance was estimated using a maximum likelihood procedure implemented by the program CAPTURE (White et al. 1982). When removal patterns failed to produce a population estimate, we used the total number of fish captured at a site as the estimate. This occurred in about 1% of all observations.

White et al. (1982) recommended minimum capture probabilities of at least 0.2 to obtain useful results with the removal method. Capture probabilities estimated by CAPTURE at sites averaged 78% over 1993–1999. This estimate is probably positively biased, but little is known of capture probabilities for removal estimates in relation to actual numbers of fish. Riley et al. (1993), who evaluated removal estimates for known numbers of parr of Atlantic salmon *Salmo salar* (75–115 mm fork length), found that capture probabilities generated by CAPTURE were overestimated by 11–24% in the smaller streams (7.2–9.9 m mean width) they studied. They also found population sizes were underestimated by 3.4–52.5%. Larger bias was associated with larger stream sizes. Our study streams were smaller (<6 m mean width; Figure 2) than the smallest of streams studied by Riley et al. (1993), but we cannot rule out the potential for negative bias in removal estimates.

Measurements recorded for each fish included standard length (mm) and mass (to the nearest 0.1 g). In rare cases when weights were not measured, length–weight regressions were used to estimate weights. If population estimates exceeded numbers of fish caught, weights of presumably uncaptured fish were estimated from the mean mass of fish captured at a site.

Stratification of fish samples.—In their review of

annual fluctuations in stream-living trout populations, Platts and Nelson (1988) identified Lahontan cutthroat trout (two populations studied) as one of the most numerically unstable of the five resident trout species they studied in 11 streams draining the Rocky Mountains and Great Basin. With regard to biomass (g/m^2), however, Lahontan cutthroat trout were among the most stable populations, which they attributed to the preponderance of young-of-year fish. Other studies in the region have similarly identified variability in recruitment as a major cause of fluctuations in stream-living trout populations (Benson 1960; Erman et al. 1988; Strange et al. 1992; Latterell et al. 1998).

We chose to focus our analysis on juvenile and adult trout (age ≥ 1 year) because (1) young-of-year fish are difficult to sample quantitatively with standard techniques, such as electrofishing (Bohlin et al. 1989); (2) emergence of young-of-year Lahontan cutthroat trout is highly variable spatially and among years, leading to further sampling difficulties (Dunham 1996); and (3) young-of-year fish may not have had enough time to disperse from natal habitats, possibly obscuring fish–habitat associations (Beard and Carline 1991). Juvenile and adult Lahontan cutthroat trout move freely within streams, as evidenced by their rapid recolonization of habitat following drought conditions (Dunham 1996). Therefore, habitat associations and assessments of spatial and temporal population variability may be most reliably determined with age-1 and older fish. Young-of-year Lahontan cutthroat trout were easily distinguished from older age-classes by length frequency distributions.

Measures of fish abundance.—We summarized biomass and population density in terms of grams or numbers of fish per meter length of stream, respectively. These measures often are reported in terms of stream surface area. In this analysis, stream width was accounted for by including it as a predictor in the regression models.

Habitat sampling.—Wetted channel width and depth were measured on transects situated perpendicular to the stream channel and spaced 2 m apart. Mean depth across the active channel was calculated from depth measurements taken at 25, 50, and 75% of the channel width, beginning from one bank (depth = 0; Overton et al. 1997). Wetted channel width at a transect was determined as described in Platts et al. (1983). Mean wetted width and depth within a site were used to estimate width:depth ratios.

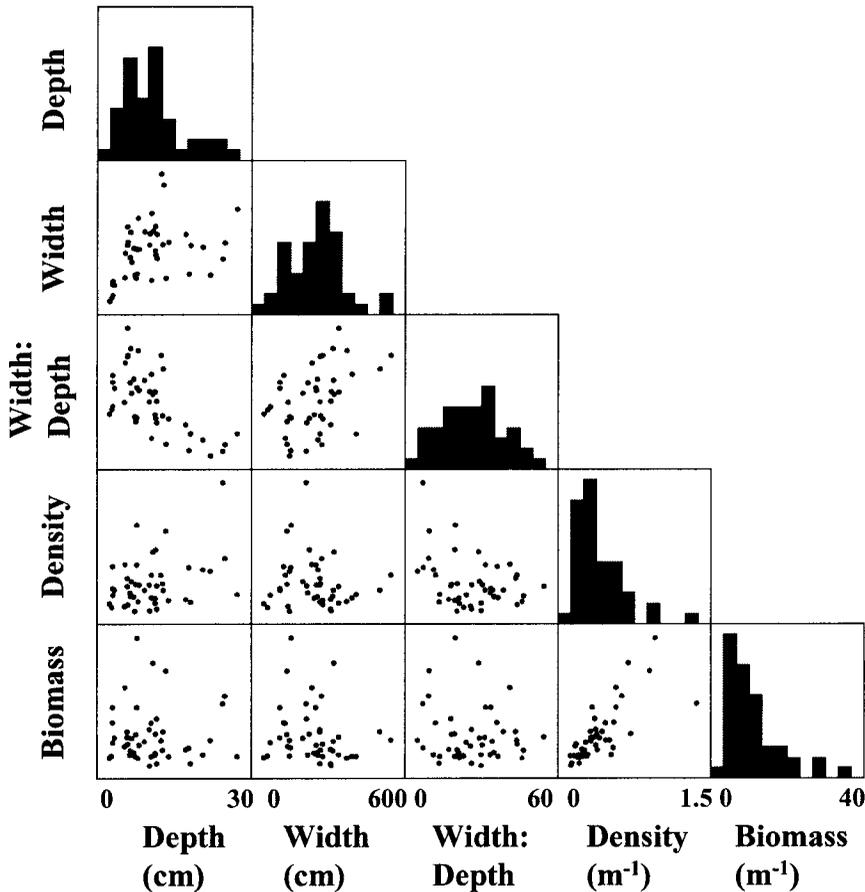


FIGURE 2.—Scatter-plot matrices for Lahontan cutthroat trout variables: depth (cm), stream width (cm), width:depth ratio, density per meter, and biomass (g/m) for 13 streams sampled in 1993–1997 in Nevada ($N = 45$).

Data Analysis

Analysis of fish–habitat relationships with regression quantiles.—From site samples we calculated mean values for density and biomass of Lahontan cutthroat trout per meter and for stream width (cm), depth (cm), and width:depth ratio for each stream and year. Data were aggregated for each stream and year because sites within streams may not be independent, and previous studies have shown stream-scale differences in standing crop are much greater than differences among sites within streams (Dunham and Vinyard 1997a). Temporal independence of standing crop in streams with longer time series (>4 years) was tested with a permutation variant of the Durbin–Watson test (Mielke 1991) for first-order autocorrelation. Scatter-plot matrices were examined for relations among variables for 1993–1997 data (Figure 2). Rates of change in mean density or biomass as functions of mean width, depth, and

width:depth ratios were estimated with regression quantiles (Cade et al. 1999; Koenker and Machado 1999) as linear and nonlinear ($y = \exp[\beta_0 + \beta_1 X_1 + \epsilon]$) functions for 1993–1997 observations.

Details of regression quantile modeling have been reported elsewhere (Terrell et al. 1996; Cade et al. 1999), so we provide only a brief outline of the method here. Regression quantiles estimate rates of change as a function of independent variables for all quantiles $[0, 1]$ of a distribution, rather than just focusing attention on changes in means. Homogeneous distributions (usual least-squares regression assumption) imply equal rates of change at all quantiles of the distribution and result in regression quantile estimates that are nearly parallel (equal slopes). Heterogeneous (wedge-shaped; Terrell et al. 1996; Figure 1) distributions imply unequal rates of change at different quantiles of the distribution and result in regression quantile slope estimates that are not

parallel (unequal slopes). For example, unequal variation of fish densities in relation to width:depth ratio is indicated in Figure 2. Visual inspection of the distribution of data points suggests the slope of a line tracking the upper bound of the relationship between width:depth ratio and density would be steeper than a line drawn through the center of the distribution.

Based on examination of scatter plots, we considered width:depth ratio to be our primary explanatory variable but considered adding additional variables (width or depth), based on results of quantile rank-score hypothesis tests and increases in coefficients of determination (Koenker and Machado 1999). Because regression quantiles are equivariant under monotonic transformations (Koenker and Portnoy 1996; Cade et al. 1999), estimates made in the linear logarithmic scale have the same statistical properties when back-transformed into their original nonlinear scale. We made use of this property when computing coefficients of determination (R^1) for linear and nonlinear regression quantiles. Note we refer to R^1 , and not R^2 , because regression quantiles minimize absolute, not squared deviations. Coefficients of determination for the nonlinear models were computed by back-transforming estimates to original scale by taking antilogs and obtaining the weighted sum of absolute deviations between observed and estimated trout per meter so that they could be compared with computed R^1 for the linear model.

The general formula for the regression quantile coefficient of determination is $R^1 = 1 - F(\tau)/R(\tau)$, where $F(\tau)$ is the weighted sum of absolute deviations minimized in estimating a full-parameter model ($\beta_0 + \beta_1$) and $R(\tau)$ is the weighted sum of absolute deviations minimized for estimating the reduced-parameter model (β_0) for any τ (Koenker and Machado 1999). We computed R^1 for 19 values of τ by increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$ and then plotted and compared them for the linear and nonlinear models. Confidence intervals (CI) on slope parameters were computed by inverting a quantile rank-score test for the same 19 values of τ (Koenker and Portnoy 1996; Cade et al. 1999; Koenker and Machado 1999). Conceptually, confidence intervals and R^1 can be computed for estimates of all possible values of τ . Confidence intervals for the 19 values of τ were sufficient to characterize sampling variation for the entire quantile process, which was plotted as a step function of slope estimates (ordinate) by τ (abscissa).

After having selected our best model form and

estimating regression quantiles for the 1993–1997 data, we applied these estimates to the 1998–99 data by constructing an 80% prediction interval (for an individual realization of new y) from the 10th and 90th regression quantiles (Zhou and Portnoy 1996) for the 1993–97 data. When appropriate, we combined the 1998–1999 data with the 1993–1997 data to provide revised estimates and confidence intervals.

Comparison of fish densities and habitat among streams.—We described patterns of variation in density and habitat among streams by using ANOVA and by explicitly modeling stream-group effects using regression quantiles. We predicted densities of Lahontan cutthroat trout should be reduced in streams with nonnative brook trout and in streams where juveniles may emigrate to downstream habitats (e.g., Benson 1960). Six streams fit into one of these categories. The remaining seven streams were isolated and supported only populations of Lahontan cutthroat trout and other (nonsalmonid) native fishes. Densities of Lahontan cutthroat trout in these two groups of streams were compared with a two-factor ANOVA to examine group and year (1993–1999) effects. Width:depth ratios were similarly compared. The effect of these two groupings of streams was examined in regression quantile models of trout density as a function of width:depth ratio. We did this by adding an indicator variable (0 = streams with brook trout or access to migratory habitats, 1 = isolated streams) and the interaction of this indicator variable with width:depth ratio ($y = \exp[\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2]$, where X_1 is width:depth and X_2 is the indicator variable for stream group). If the rank-score tests and confidence intervals suggested no differences in slopes ($\beta_3 = 0$), then a reduced model allowing only for separate intercepts ($y = \exp[\beta_0 + \beta_1 X_1 + \beta_2 X_2]$) was examined. This follows the usual protocol in analysis of covariance (ANCOVA) of testing for interactions among the continuous covariates and the categorical groupings before assuming the simpler model with unequal intercepts but common slopes.

Results

Scatter-plot matrices for 1993–1997 data (Figure 2) indicated that our dependent variables, density, and biomass had positive covariation; one outlying value was associated with very high density (1.17/m) but only moderate biomass (16.4 g/m). Width:depth ratios decreased with increasing depth but had little consistent relation with width (Figure 2). Biomass was not significantly related

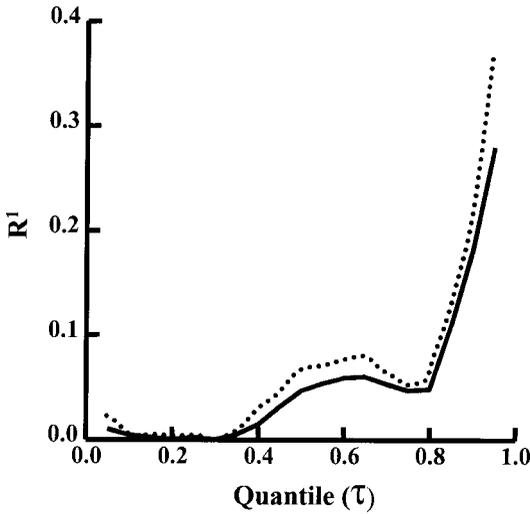


FIGURE 3.—Coefficients of determination (R^1) for linear ($y = \beta_0 + \beta_1 X_1 + \epsilon$; solid line) and nonlinear ($y = \exp[\beta_0 + \beta_1 X_1 + \epsilon]$; dotted line) regression quantiles for 19 values of τ , (i.e., increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$), where y is the average number of Lahontan cutthroat trout per meter and X_1 is average width:depth ratio. Lines plotted are linear interpolations between adjacent values of R^1 . Results are for data collected from 13 Nevada streams during 1993–1997.

to any of the potential independent variables, whereas density had a fairly well-defined wedge-shaped pattern (Terrell et al. 1996) of increasing variation with decreasing width:depth ratio that could be modeled with regression quantiles.

Both linear and nonlinear models indicated that the higher quantiles of Lahontan cutthroat trout densities increased with decreasing width:depth ratios at greater rates than lower quantiles. The nonlinear model fit the data better than the linear model (Figure 3) for all τ greater than 0.40, the greatest improvement in fit being at higher quantiles ($\tau > 0.90$). Addition of depth or width did not improve estimates at any quantile based on hypothesis tests ($P > 0.10$) or increased coefficients of determination. Rates of change in trout density with width:depth ratios were near zero for quantiles τ less than 0.40 and became progressively more negative with increasing τ (Figure 4). The regression quantile process for the nonlinear model indicated that rates of change in trout density also were near zero for quantiles τ less than 0.40 and fluctuated between -0.02 and -0.04 at higher quantiles (Figure 5).

To investigate the predictive power of our nonlinear model, we estimated a distribution-free 80% prediction interval based on the 10th and 90th re-

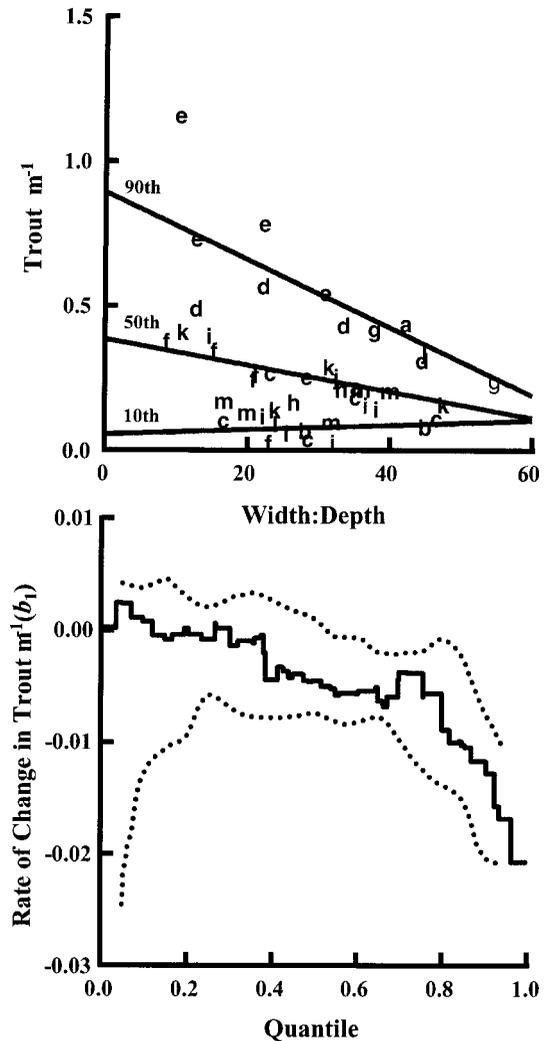


FIGURE 4.—Number of Lahontan cutthroat trout per meter by width:depth ratio and 0.10 (10th), 0.50 (50th), and 0.90 (90th) linear regression quantile estimates for 13 streams in the Lahontan basin of Nevada in 1993–1997 (upper graph). Streams are Threemile Creek (a), Abel Creek (b), East Marys River (c), Foreman Creek (d), Frazer Creek (e), Gance Creek (f), Indian Creek (g), Mohawk Creek (h), Marys River Basin Creek (i), North Fork Humboldt River (j), T Creek (k), Tierney Creek (l), and West Marys River (m). In the lower graph, estimated rates of change (b_1) for the linear model for all quantiles, $\tau [0, 1]$, are plotted as a step function (solid line); dotted lines represent the 90% confidence band formed by inverting quantile rank-score test at 19 values of τ (i.e., increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$).

gression quantile estimates for the 1993–1997 observations and determined where observations collected for the same streams in 1998 and 1999 fell relative to this 80% prediction interval. Twenty of

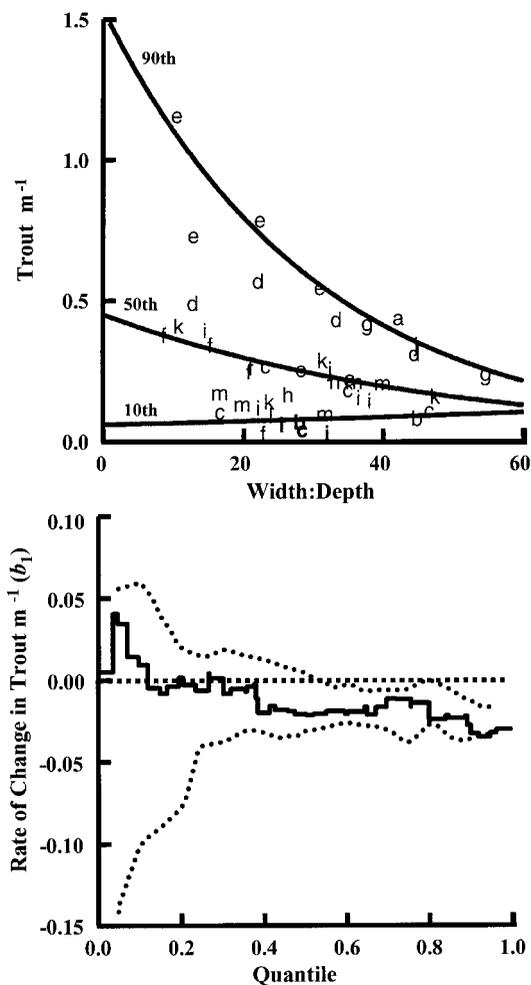


FIGURE 5.—Number of Lahontan cutthroat trout per meter by width:depth ratio and 0.10 (10th), 0.50 (50th), and 0.90 (90th) nonlinear regression quantile estimates for 13 streams in the Lahontan basin of Nevada in 1993–1997 (upper graph). In the lower graph, estimated rates of change (b_1) for the nonlinear model for all quantiles, τ [0, 1], are plotted as a step function (solid line); dotted lines represent the 90% confidence band formed by inverting quantile rank-score test at 19 values of τ (i.e., increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$).

26 (77%) new observations were contained within this interval, and those outside the interval also matched the overall pattern in the 1993–1997 data. The 80% prediction interval indicated that a doubling of variation in density, which was skewed towards higher values, occurred as width:depth ratio was reduced from 40 to 20.

When we combined the 1998 and 1999 data with the 1993–1997 data and estimated the regression quantiles for trout density as the nonlinear function

of width:depth ratio, we found a similar pattern for estimated rates of change for the combined data (Figure 6) and the 1993–1997 subset (Figure 5); some reduction in width of 90% CIs occurred, especially at lower quantiles (Figure 6). Estimated rates of change for the combined data differed from zero at quantiles greater than 0.70 (Figure 6), whereas with the 1993–1997 subset, the differences from zero were observed at quantiles greater than 0.55 (Figure 5). The increased number of observations ($N = 71$) for the combined data resulted in a 95th regression quantile estimate (Figure 6) that was similar to the 90th regression quantile estimate for the 1993–1997 observations (Figure 5). Temporal autocorrelation was not strong within a stream as indicated by the Durbin–Watson test for first-order autocorrelation on population trends (all $P > 0.31$).

Data points from individual streams were not randomly distributed with respect to the estimated quantiles (Figure 6). Cutthroat trout densities in Frazer, Foreman, Threemile, and Indian Creek were consistently near the estimated upper quantiles of rates of change associated with width:depth ratio. Examining scatter plots and estimated quantiles suggested that much of the negative rate of change in densities of cutthroat trout with width:depth ratio were driven by the high densities of fish in Frazer Creek (Figure 6). Indeed removal of the Frazer Creek observations resulted in regression quantile estimates that did not differ from zero ($P > 0.10$) for any quantile.

Densities of Lahontan cutthroat trout in isolated streams without nonnative brook trout were greater (mean = 0.40 fish/m) than densities in streams with either nonnative brook trout or access to migratory pathways (mean = 0.16 fish/m; $F_{1,57} = 33.27$, $P < 0.0001$). Mean density of the two groups was only weakly related to annual variability ($F_{6,57} = 1.74$, $P = 0.13$), and differences among groups were consistent among years (i.e., interaction term; $F_{6,57} = 0.53$, $P = 0.78$). Width:depth ratios were not different (mean difference = 1.7) among these groups of streams ($F_{1,57} = 1.22$, $P = 0.27$) but were different among years ($F_{6,57} = 11.21$, $P < 0.0001$). Year \times group interactions were not evident for width:depth ratios ($F_{1,57} = 0.33$, $P = 0.92$).

To explicitly examine the influence of stream-scale variation on regression quantile parameter estimates, we focused on the best-fitting nonlinear model. Our nonlinear regression quantile models that allowed for separate slopes and intercepts for the two groups of streams provided weak evidence

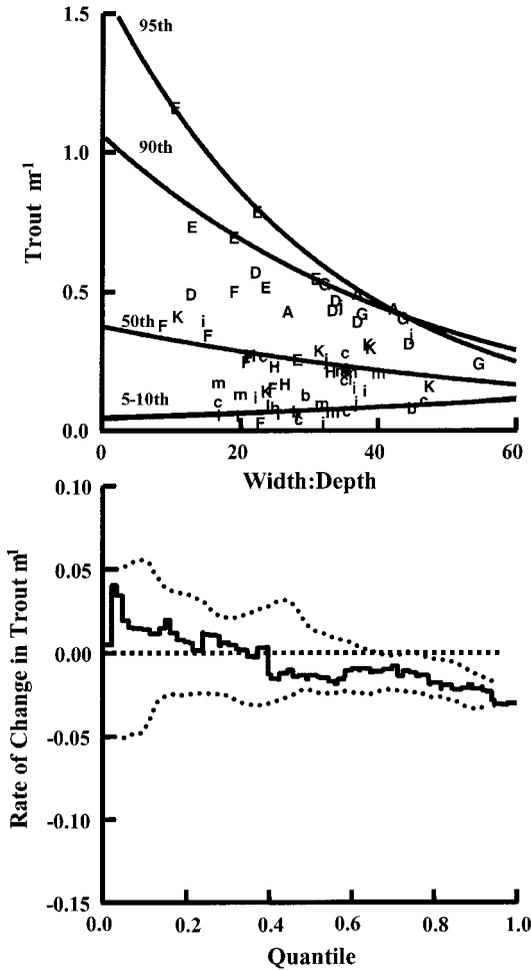


FIGURE 6.—Number of Lahontan cutthroat trout per meter by width:depth ratio and 0.05 (5th), 0.10 (10th), 0.50 (50th), 0.90 (90th), and 0.95 (95th) nonlinear regression quantile estimates for 13 streams in the Lahontan basin of Nevada in 1993–1999 (upper graph). Uppercase letters represent streams without brook trout or migratory pathways and lowercase letters streams with brook trout or migratory pathways. In the lower graph, estimated rates of change in numbers of Lahontan cutthroat trout per meter and width:depth ratio (b_1) for the nonlinear model for all quantiles, τ [0, 1], are plotted as a step function (solid line); dotted lines represent the 90% confidence band formed by inverting quantile rank-score test at 19 values of τ (i.e., increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$).

for the separate slopes; 90% CIs for estimated differences included zero for a wide range of quantiles (Figure 7). There was strong support for separate intercepts across all quantiles in the nonlinear model that allowed for separate intercepts for the two groups of streams (Figure 7). Streams without

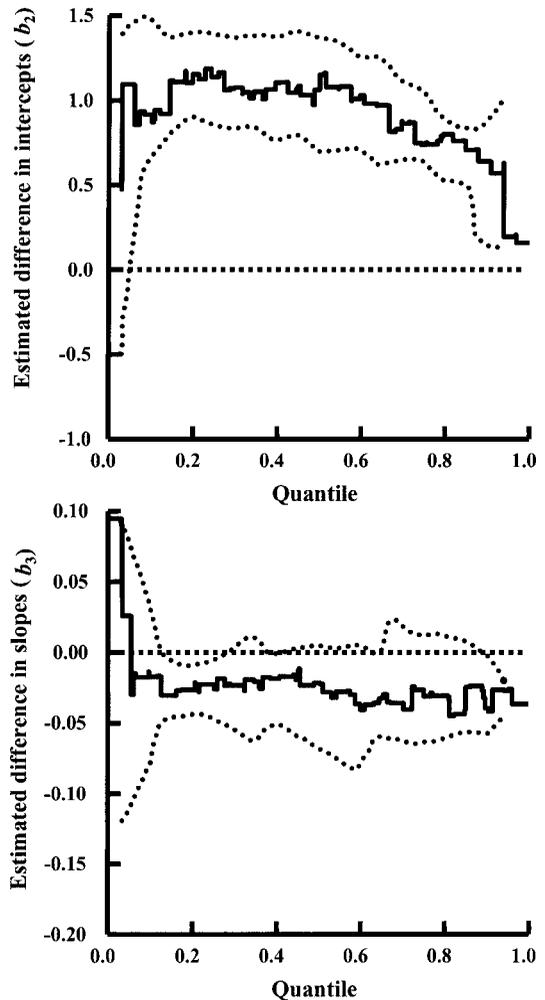


FIGURE 7.—In the upper graph, estimated differences in intercepts (b_2) between streams without brook trout or migratory pathways and those with brook trout or migratory pathways are shown for the nonlinear model of Lahontan cutthroat trout per meter by width:depth ratio, which allows for separate intercepts but common slopes for these groups. In the lower graph, the estimated difference in slope (b_3) between streams without brook trout or migratory pathways and those with brook trout or migratory pathways is shown for the nonlinear model, which allows for separate intercepts and slopes for these groups. Estimated differences in b_2 or b_3 are plotted (solid line) as a step function by all quantiles, τ [0, 1], and large dotted lines represent the 90% confidence band formed by inverting quantile rank-score test at 19 values of τ (i.e., increments of 0.05 from $\tau = 0.05$ to $\tau = 0.95$).

brook trout or access to migratory pathways had estimated intercepts that were 0.25–1.25 greater from lower to higher quantiles than streams with brook trout or those with access to migratory path-

ways. Expressed in the multiplicative form (non-linear model), this means that at any given width:depth ratio the lower quantiles of trout per meter were 3.5 ($\exp[1.25] = 3.49$) times greater and the higher quantiles were 1.3 ($\exp[0.25] = 1.28$) times greater for streams without brook trout or migratory pathways.

Discussion

Regression quantiles defined potentially limiting relationships between width:depth ratio and fish density. Other measures of channel morphology (mean depth and wetted channel width) did not appear to be related to density, and biomass was not significantly related to any habitat variable. Interpretation of the association between width:depth ratio and fish density is complicated by several factors, including (1) spatiotemporal variation in density, (2) effects of alternative limiting factors, and (3) selection of an appropriate final model. We focus our discussion on these three key issues.

Spatiotemporal Variability

Streams were not equally represented among the data points that defined the upper bounds of limiting relationships (Figure 6). In particular, data from four streams were consistently associated with higher regression quantiles. These four streams belonged to the group that represented populations in isolated habitats without nonnative brook trout. Density of cutthroat trout in this group of streams was greater on average and the quantiles conditioned on width:depth ratios were higher (but width:depth ratios did not vary among stream groups). Of particular concern for interpreting the meaning of our habitat models is the clustering of data from a single stream. The existence of a regression quantile model with a strong negative slope is due to the influence of data from Frazer Creek. Densities of fish in this stream were consistently among the highest we observed.

Temporal variation in density and habitat relationships was less obvious than spatial variation, at least in terms of model results for 1993–1997 data versus 1998–1999 conditions. Previous investigators (e.g., Platts and Nelson 1988; House 1995) suggested that high temporal variability in cutthroat trout populations may limit the utility of habitat models. By using regression quantiles, however, we were able to describe a potentially limiting relationship that was transferable across different years. We believe generalized models of limits are more likely to be transferable than at-

tempts to predict mean fish densities. Fausch et al. (1988) similarly recognized a precision-generality tradeoff in stream fish habitat models.

In terms of future sampling to develop limiting-factor models, our analysis suggests it would be most efficient to maximize the spatial representation of populations, rather than repeatedly sampling the same populations over time, at least in the case of relationships explored herein. The dominant influence of spatial variation on fish populations has been documented elsewhere in aquatic ecosystems (e.g., Matthews 1990; Rundle and Jackson 1996; Wiley et al. 1997). Temporal variation in population dynamics may be relevant in other contexts. For example, temporal variation was evident in analyses of self-thinning in some of the populations studied here (Dunham and Vinyard 1997b). In any case, the effects of both spatial and temporal variability should be initially examined, whenever possible, in the development of models that estimate the effects of limiting factors.

Effects of Alternative Limiting Factors

Stream-scale factors that may affect relative densities of fish, including connectivity to migratory habitats and occurrence of nonnative species, also may affect associations with potentially limiting habitat characteristics. As predicted, densities of fish in streams with these characteristics were consistently lower on average, and data from this group were rarely associated with higher regression quantiles (Figure 6). However, data from three of six populations in the group of isolated streams without nonnative trout (e.g., T, Gance, and Mohawk creeks) showed a similar pattern. In this latter trio of streams, alternative limiting factors could be at play.

Habitat variables analyzed in this study were among those commonly used in models of standing crop of fish in streams (Fausch et al. 1988). Because our primary objective in this study was to examine the influence of spatial and temporal variability on regression quantile models, our conclusions do not rest on any particular habitat variable. Nonetheless, it is interesting to note that stream width and depth did not show a limiting relationship with standing crop of fish. These variables are thought to have a direct and potentially limiting influence on fish populations. In contrast, width:depth ratio does not have an obvious direct connection to fish populations. However, it was the only variable significantly associated with standing crop. Connections between width:depth ratio and fish populations may result through a

number of indirect linkages associated with natural and human influences on stream channels and riparian habitats (Beschta and Platts 1986). Because increased width:depth ratios in small streams are often associated with habitat degradation (Beschta and Platts 1986; Myers and Swanson 1996; Clary 1999), a negative association between width:depth ratio and fish abundance is not unexpected.

The fact that observations from a single stream (Frazer Creek; Figure 6) were so influential on the overall relationship suggests that width:depth ratio is not the active limiting factor for cutthroat trout density in our sample of streams. Width:depth ratios within the range of those observed in Frazer Creek were commonly found in other streams (Figure 6), but fish densities in these streams were generally much lower. If other stream-scale factors were not important, we would expect high fish densities to occur with roughly equal frequency in all streams with similar width:depth ratios. This was not the case. Stream-scale factors other than width:depth ratio must therefore play a more direct role in determining population density. This analysis suggests that factors such as connectivity to migratory habitats and occurrence of nonnative species are potentially important for some streams in this data set, but other stream-related effects (Dunham and Vinyard 1997a) on fish density are difficult to specify.

Model Selection

Before the analysis, we had hypothesized several potential relationships between standing crop and stream channel morphology, presence of brook trout, and connectivity to migratory habitats. We used a wide range of regression quantiles and two different model forms (linear, nonlinear) to explore habitat relationships and evidence in support of our predictions. Our goal was not to select the best model from this analysis, but rather to examine the general form of the relationships and their stability across space and time. Formal methods for selection of alternative models and model averaging (see Burnham and Anderson 1998) are not adequately addressed for regression quantiles. Selecting models for regression quantiles is complex because model fit must be evaluated across a family of estimated quantiles rather than just for a single estimated function. Thus, it is difficult to evaluate the relative plausibility of alternative models based on different quantiles. Results of the analysis also varied among model forms (linear, nonlinear). Estimates of slope parameters changed dramatically for higher quantiles of the linear mod-

el (Figure 4), whereas slopes for the nonlinear model were relatively stable at higher quantiles (Figure 5). Both linear and nonlinear models fit the data well, however. The general pattern across all quantile estimates was similar indicating a potentially robust relationship not likely to be revealed with conventional methods of analysis, such as ordinary least-squares regression, or by limiting an analysis to a single quantile.

Conclusions

Regression quantiles have great promise for applications in ecology. In the statistical sense, regression quantiles may be useful because resulting models are robust to outlying data points, and are ideal for dealing with responses that exhibit heterogeneous variance in relation to predictor variables. In the biological sense, regression quantile models more accurately portray the concept of limiting factors. However, as our analysis indicates, application of regression quantiles to modeling habitat relationships must explicitly consider the spatial and temporal structure of the data, provided that structure can be defined. Furthermore, we found it was useful to examine a range of quantiles and model forms to understand potential relationships between habitat and standing crop of cutthroat trout (e.g., Figures 4, 5, 6).

In our data set, regression quantile models were robust in time, but not in space. Due to problems related to spatial variation in abundance, it was initially unclear whether our models reflected the limiting influence of width:depth ratio per se or influences on density due to other unmeasured factors operating at the scale of individual streams. By estimating and testing for the effects of two stream-scale factors (e.g., presence of brook trout and access to migratory habitats), we arrived at an interpretation of modeled relationships between density of cutthroat trout and width:depth ratio that was not as straightforward as the simple concept of limiting factors would suggest. Evaluation of spatial and temporal variation in abundance is critical because either may bias habitat associations (also see Ives and Klopfer 1997). This may not have been as evident if we had worked with a less spatially (or temporally) extensive series of data or if we had limited our analysis to a single quantile of the data distribution.

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References

- Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. *Transactions of the American Fisheries Society* 116:12–20.
- Beard, T. D., Jr., and R. F. Carline. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. *Transactions of the American Fisheries Society* 120:711–722.
- Benson, N. G. 1960. Factors influencing production of immature cutthroat trout in Arnica Creek, Yellowstone Park. *Transactions of the American Fisheries Society* 89:168–175.
- Beschta, R. L., and W. S. Platts. 1986. Significance and function of morphological features of small streams. *Water Resources Bulletin* 22:369–379.
- Bohlin, T., S. Hamrin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. Electrofishing-theory and practice with special emphasis on salmonids. *Hydrobiologia* 173:9–43.
- Bozek, M. A., and F. J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across sites and among years in Wyoming streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:552–564.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Bult, T. P., S. C. Riley, R. L. Haedrich, R. J. Gibson, and J. Heggenes. 1999. Density-dependent habitat selection by juvenile Atlantic salmon (*Salmo salar*) in experimental riverine habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1298–1306.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: an information-theoretic approach*. Springer-Verlag, New York.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323.
- Clary, W. P. 1999. Stream channel and vegetation responses to late spring cattle grazing. *Journal of Range Management* 52:218–227.
- Dunham, J., M. Rahn, R. Schroeter, and S. Breck. 2000. Diet selection by sympatric Lahontan cutthroat trout and brook trout: implications for species interactions. *Western North American Naturalist* 60:304–310.
- Dunham, J. B. 1996. *The population ecology of stream-living Lahontan cutthroat trout (Oncorhynchus clarki henshawi)*. Doctoral dissertation. University of Nevada, Reno.
- Dunham, J. B., and G. L. Vinyard. 1997a. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. *Transactions of the American Fisheries Society* 126:323–329.
- Dunham, J. B., and G. L. Vinyard. 1997b. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1025–1030.
- Erman, D. C., E. D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2195–2200.
- Fausch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables, 1950–85. U.S. Forest Service General Technical Report PNW-GTR-213.
- Grant, J. W. A., S. Ó. Steingrímsson, E. R. Keeley, and R. A. Cunjak. 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55(Supplement 1):181–190.
- Grayson, D. K. 1993. *The desert's past: a natural prehistory of the Great Basin*. Smithsonian Institution Press, Washington, D.C.
- House, R. 1995. Temporal variation in abundance of an isolated population of cutthroat trout in western Oregon, 1981–1991. *North American Journal of Fisheries Management* 15:33–41.
- Ives, A. R., and E. D. Klopfer. 1997. Spatial variation in abundance created by stochastic temporal variation. *Ecology* 78:1907–1913.
- Jones, K. K., J. M. Dambacher, B. G. Lovatt, A. G. Talabere, and W. Bowers. 1998. Status of Lahontan cutthroat trout in the Coyote Lake basin, southeast Oregon. *North American Journal of Fisheries Management* 18:308–317.
- Koenker, R., and G. Bassett. 1978. Regression quantiles. *Econometrica* 46:33–50.
- Koenker, R., and J. A. F. Machado. 1999. Goodness of fit and related inference processes for quantile regression. *Journal of the American Statistical Association* 94:1296–1310.
- Koenker, R., and S. Portnoy. 1996. *Quantile regression*. University of Illinois at Urbana-Champaign, College of Commerce and Business Administration,

- Office of Research Working Paper 97-100, Urbana-Champaign.
- La Rivers, I. 1962. Fishes and fisheries of Nevada. Nevada State Fish and Game Commission, Reno.
- Latterell, J. J., K. D. Fausch, C. Gowan, and S. C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. *Rivers* 6:240–250.
- Leftwich, K. N., P. L. Angermeier, and C. A. Dolloff. 1997. Factors influencing behavior and transferability of habitat models for a benthic stream fish. *Transactions of the American Fisheries Society* 126:725–734.
- Matthews, W. J. 1990. Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. *American Midland Naturalist* 124:31–45.
- Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.
- McMahon, T. E., and J. C. Tash. 1988. Experimental analysis of the role of emigration in population regulation of desert pupfish. *Ecology* 69:1871–1883.
- Mielke, P. W., Jr. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth-Science Reviews* 31:55–71.
- Minshall, G. W., S. E. Jensen, and W. S. Platts. 1989. The ecology of stream and riparian habitats of the Great Basin region: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.24).
- Myers, T. J., and S. Swanson. 1996. Long-term aquatic habitat restoration: Mahogany Creek, Nevada, as a case study. *Water Resources Bulletin* 32:241–252.
- Northcote, T. G. 1997. Potamodromy in Salmonidae—living and moving in the fast lane. *North American Journal of Fisheries Management* 17:1029–1045.
- Overton, K. O., S. P. Wollrab, B. C. Roberts, and M. A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. U.S. Forest Service General Technical Report INT-GTR-346.
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-138.
- Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. *North American Journal of Fisheries Management* 8:333–345.
- Riley, S. C., R. L. Haedrich, and R. J. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. *Journal of Freshwater Ecology* 8:97–101.
- Rundle, H. D., and D. A. Jackson. 1996. Spatial and temporal variation in littoral-zone fish communities: a new statistical approach. *Canadian Journal Fisheries Aquatic Sciences* 53:2167–2176.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460.
- Schroeter, R. E. 1998. Segregation of stream dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. University of Nevada, Reno.
- Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. *Environmental Biology of Fishes* 36:1–15.
- Terrell, J. W., B. S. Cade, J. Carpenter, and J. M. Thompson. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. *Transactions of the American Fisheries Society* 125:104–117.
- Thomson, J. D., G. Weiblen, B. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* 77:1698–1715.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. P. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.
- Wiley, M. J., S. L. Kohler, and P. W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. *Freshwater Biology* 37:133–148.
- Zhou, K. Q., and S. L. Portnoy. 1996. Direct use of regression quantiles to construct confidence sets in linear models. *Annals of Statistics* 24:287–306.