

## QUANTILE REGRESSION REVEALS HIDDEN BIAS AND UNCERTAINTY IN HABITAT MODELS

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**Abstract.** We simulated the effects of missing information on statistical distributions of animal response that covaried with measured predictors of habitat to evaluate the utility and performance of quantile regression for providing more useful intervals of uncertainty in habitat relationships. These procedures were evaluated for conditions in which heterogeneity and hidden bias were induced by confounding with missing variables associated with other important processes, a problem common in statistical modeling of ecological phenomena. Simulations for a large ( $N = 10\,000$ ) finite population representing grid locations on a landscape demonstrated various forms of hidden bias that might occur when the effect of a measured habitat variable on some animal was confounded with the effect of another unmeasured variable. Quantile ( $0 \leq \tau \leq 1$ ) regression parameters for linear models that excluded the important, unmeasured variable revealed bias relative to parameters from the generating model. Depending on whether interactions of the measured and unmeasured variables were negative (interference interactions) or positive (facilitation interactions) in simulations without spatial structuring, either upper ( $\tau > 0.5$ ) or lower ( $\tau < 0.5$ ) quantile regression parameters were less biased than mean rate parameters. Heterogeneous, nonlinear response patterns occurred with correlations between the measured and unmeasured variables. When the unmeasured variable was spatially structured, variation in parameters across quantiles associated with heterogeneous effects of the habitat variable was reduced by modeling the spatial trend surface as a cubic polynomial of location coordinates, but substantial hidden bias remained. Sampling ( $n = 20\text{--}300$ ) simulations demonstrated that regression quantile estimates and confidence intervals constructed by inverting weighted rank score tests provided valid coverage of these parameters. Local forms of quantile weighting were required for obtaining correct Type I error rates and confidence interval coverage. Quantile regression was used to estimate effects of physical habitat resources on a bivalve (*Macomona liliana*) in the spatially structured landscape on a sandflat in a New Zealand harbor. Confidence intervals around predicted 0.10 and 0.90 quantiles were used to estimate sampling intervals containing 80% of the variation in densities in relation to bed elevation. Spatially structured variation in bivalve counts estimated by a cubic polynomial trend surface remained after accounting for the nonlinear effects of bed elevation, indicating the existence of important spatially structured processes that were not adequately represented by the measured habitat variables.

**Key words:** bivalves; habitat; hidden bias; limiting factors; quantile regression; rank score tests; spatial trend.

### INTRODUCTION

The relationship between an organism and its habitat is of theoretical interest in ecology because it is fundamentally tied to questions about distribution and abundance (Wiens 1989, Huston 2002). Understanding habitat relationships also is important for natural resource management because environmental regulations in the United States (e.g., National Environmental Policy Act, Fish and Wildlife Coordination Act, National

Forest Management Act) and other countries often necessitate consideration of animal habitat requirements in land use planning. Theoretical and management applications have led to the development of numerous mathematical and statistical models for quantifying the relationship between an organism and the resources provided by its habitat (Morrison et al. 1998, Stauffer 2002). The reliability of quantitative predictions from animal habitat models has been questioned, however, because factors other than the resources provided by habitat may limit populations (Rotenberry 1986, Fausch et al. 1988, Terrell et al. 1996, Terrell and Carpenter 1997). Typically, not all factors that limit pop-

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ulations are measured and included in habitat models, either due to logistical constraints or because they are unknown. As a consequence, statistical predictions of responses to changes in habitat often lack the generality to be considered reliable statements of outcomes likely to occur at other times or places than those originally sampled. This hinders both the development of general theory related to resource selection and the utility of models for predicting outcomes of alternative management or conservation actions.

The distribution and abundance of any species is constrained by biophysical factors (e.g., climate, soil productivity), habitat resources (e.g., vegetation providing food and cover), and interspecific (e.g., competition and predation) and intraspecific (e.g., density-dependent behavioral responses) biotic interactions (Morrison 2001, Huston 2002, O'Connor 2002). A species will be locally abundant when none of the factors are limiting over some relevant interval of time and space. When any single factor is limiting, the species will be constrained to lower abundance than expected when all factors are permissive. If the factor that is limiting differs among sample locations and times and is unmeasured at some sample locations, then the species response may exhibit heterogeneous variation across levels of the measured factors simply because they were not limiting at all times or locations sampled (Van Horne and Wiens 1991, Kaiser et al. 1994, Cade et al. 1999, Huston 2002). Heterogeneity then is a logical consequence of having incomplete information on the interactions among the multiple biotic and abiotic factors that affect growth, survival, and reproduction of the organism. Any important factor that is not explicitly included as a parameter in a statistical model is implicitly included as part of the error distribution. When those unmeasured factors interact with the measured factors, the error distribution will be heterogeneous with respect to the variables included in the model. This creates a form of hidden bias (*sensu* Rosenbaum 1991, 1995, 1999), where effects attributed to the measured habitat variables are confounded with effects due to other unmeasured variables associated with other processes.

Statistical distributions that are heterogeneous with respect to variables observed on some focal process have created interpretation issues for a variety of phenomena in addition to resource selection, e.g., density-dependent competition in plants (Cade and Guo 2000), plant productivity vs. diversity (Huston et al. 2000, Grace 2001, Huston and McBride 2002, Schmid 2002), resource–consumer interactions (Clark et al. 2003), and regional vs. local community organization (Angermeier and Winston 1998). Recently, quantile regression has been used to estimate parameters for heterogeneous responses to limiting factors, where rates of change (slopes) cannot be the same for all parts of the distribution by definition (Terrell et al. 1996, Cade et al. 1999, Cade and Noon 2003). Viewing resources as con-

straints on organisms rather than as correlates suggests that changes near the maximum response better represent effects when the measured factors (e.g., habitat) are the active limiting constraint (Kaiser et al. 1994, Terrell et al. 1996, Thomson et al. 1996, Cade et al. 1999, Huston 2002, O'Connor 2002, Cade and Noon 2003). This is predicated on an assumption that unmeasured processes should only reduce responses relative to the focal process (Kaiser et al. 1994, Terrell et al. 1996, Cade et al. 1999, Cade and Guo 2000). However, other forms of interaction among measured and unmeasured variables can generate heterogeneous distributions, and estimated changes in the entire response distribution should more completely characterize relationships in the presence of hidden bias.

Our objectives were fourfold. First, we further explored patterns of heterogeneity and hidden bias revealed with quantile regression by expanding the simulation examples of Cade et al. (1999) and Huston (2002) to include large, finite populations and additional relationships between measured and unmeasured variables. Second, we demonstrated how effects of unmeasured limiting factors that were spatially structured could be accounted for by incorporating spatial trend surfaces (Borcard et al. 1992, Lichstein et al. 2002) in quantile regression models. Third, the statistical performance of quantile rank score tests were evaluated for unweighted and weighted estimates for large, finite populations in simulations in which unmeasured variables hidden in the error term induced complex forms of heterogeneity. Finally, we used quantile regression to model bivalve abundance in relation to physical habitat and spatial trend on a tidal sandflat in a New Zealand harbor, data previously analyzed by Legendre et al. (1997). In this example application we demonstrated approaches for selecting among candidate models using the Akaike Information Criterion, estimating weighted parameters and confidence intervals, and estimating tolerance intervals for a proportion of the population. Our ultimate objective is to encourage estimation and interpretation of more relevant statistical intervals to characterize the real uncertainty in modeled relationships between organisms and their habitat resources.

#### LINEAR QUANTILE REGRESSION MODELS

Linear models  $y = \beta_0 X_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p + \varepsilon$  used with quantile regression include those where the errors  $\varepsilon$  may be independent and identically distributed (iid) or independent but not identically distributed (inid), e.g.,  $(\gamma_0 + \gamma_1 X_1)\varepsilon$ ;  $X_0$  is a column of ones for an intercept and  $X_1$  to  $X_p$  are continuous or categorical indicator variables. The quantile regression parameterization of the linear model,  $Q_y(\tau|X) = \beta_0(\tau)X_0 + \beta_1(\tau)X_1 + \beta_2(\tau)X_2 + \dots + \beta_p(\tau)X_p$ , transfers the effect of the error distribution  $\varepsilon$  to parameters for a family of quantiles indexed by  $\tau$  ( $0 \leq \tau \leq 1$ ), where  $\beta_p(\tau) = \beta_p + F_\varepsilon^{-1}(\tau)$  and  $F_\varepsilon^{-1}$  is the inverse of the cumulative distribution of the errors. If the errors are

TABLE 1. Parameters used in quantile regression simulations for generating finite populations of  $N = 10\,000$  from the model  $y = \theta_0 X_0 + \theta_1 X_1 + \theta_2 X_2 + \theta_3 X_1 X_2 + \varepsilon$ .

Model	$\theta_0$	$\theta_1$	$\theta_2$	$\theta_3$	$r(X_1, X_2)$	$X_2$ spatially structured?
Additive	1.0	0.41	0.005	0.0000	0.00	no
Interference	1.0	0.41	0.000	-0.0001	0.00	no
Facilitation	1.0	0.01	0.000	0.0001	0.00	no
Interference	1.0	0.41	0.000	-0.0001	0.56	no
Interference	1.0	0.41	0.000	-0.0001	0.92	no
Interference	1.0	0.41	0.000	-0.0001	0.00	yes

Note:  $X_1 = \text{uniform}[0, 50]$ ;  $X_2 = \text{uniform}[0, 4000]$  for  $r(X_1, X_2) = 0$ ,  $X_2 = 1200 + 32.0X_1 + \text{uniform}[-1200, 1200]$  for  $r(X_1, X_2) = 0.56$ ,  $X_2 = 600 + 56.0X_1 + \text{uniform}[-600, 600]$  for  $r(X_1, X_2) = 0.92$ , or spatially structured as  $X_2 = 2000 + 4.5\text{LONG} + 7.5\text{LAT} + 0.1\text{LONG}^2 - 0.2\text{LAT}^2 + 0.005\text{LONG}^3 + \text{uniform}(-900, 900)$ , with LONG and LAT coordinates  $[-50, 50]$ ; and  $\varepsilon$  was lognormal (median = 0,  $\sigma = 0.75$ ) or uniform  $[-0.50, 0.50]$ .

homogeneous (iid), then slopes are identical for all quantiles ( $\beta_p(\tau) = \beta_p$ ,  $p > 0$ ) although the intercepts  $\beta_0(\tau)$  differ. Otherwise, if the errors are heterogeneous (inid), then slopes for some or all quantiles may differ for one or more independent variables. Additional technical details are in Cade et al. (1999) and Koenker and Hallock (2001) and an extensive primer on quantile regression is provided by Cade and Noon (2003).

Confidence intervals for parameter estimates in quantile regression can be constructed by several procedures but commonly are based on inverting the quantile rank score test because of their ease of computation and because they were found to be little affected by error heterogeneity (Koenker 1994). Conceptually, the quantile rank score test can be considered a sign test extended to any quantile and the linear model as it is based on the signs of the residuals from a null model with constrained parameters. Recent evaluations (Koenker and Machado 1999, Cade 2003) suggest that weighted versions of the quantile rank score test are required to provide valid confidence interval coverage for models with heterogeneous errors. Weighted quantile regression models are constructed by multiplying weights ( $w$ ) by the dependent and independent variables,  $Q_{wy}(\tau|X) = w\beta_0(\tau)X_0 + w\beta_1(\tau)X_1 + w\beta_2(\tau)X_2 + \dots + w\beta_p(\tau)X_p$ . Appropriate weights are proportional to the density of the errors evaluated at a selected quantile  $\tau$  and can be estimated by a variety of techniques (Koenker and Machado 1999, Cade and Noon 2003). The weighted estimates are consistent, like their unweighted counterparts, but have reduced sampling variation.

#### QUANTILE REGRESSION SIMULATIONS WITH UNMEASURED VARIABLES

##### *Design and methods*

Because the effects of important unmeasured variables are implicitly incorporated into the error term of a statistical model, quantile regression is a useful approach for exploring hidden bias as changes in the error distribution are revealed by changes in  $\beta_p(\tau)$ . To explore patterns of heterogeneity due to missing infor-

mation on some important limiting factor, we generated large, finite populations of  $N = 10\,000$  from a two-variable linear model with interaction,  $y = \theta_0 X_0 + \theta_1 X_1 + \theta_2 X_2 + \theta_3 X_1 X_2 + \varepsilon$ . Errors were iid lognormal to create asymmetric or iid uniform to create symmetric distributions. By varying the correlation between  $X_1$  and  $X_2$  and direction and size of interaction effects due to  $\theta_3$  (Table 1), it was possible to simulate a range of linear, nonlinear, homogeneous, and heterogeneous distribution patterns associated with an estimating model that lacked an important variable. Spatial structuring was explored by relating the unmeasured limiting factor  $X_2$  to latitude (LAT) and longitude (LONG) coordinates for the center of 10 000 square blocks on a  $100 \times 100$  grid (Table 1). We used a homogeneous cubic polynomial spatial trend surface model (Borcard et al. 1992, Legendre et al. 1997) to yield an  $R^2 = 0.426$  with the least-squares regression estimate of the mean spatial trend surface (Appendix A). The large, finite population can be thought of as 10 000 100-ha blocks occurring on a landscape of  $100 \times 100$  km extent. Simulation data were generated with random number functions in S-Plus 2000 (Insightful Corporation, Seattle, Washington, USA), and quantile regression models were estimated with S-Plus scripts available in *Ecological Archives* E080-001 or with the Blossom statistical package (*available online*).<sup>6</sup>

The  $\tau$ th regression quantile of the generating model was  $Q_y(\tau|X_0, X_1, X_2, X_1 X_2) = \theta_0(\tau)X_0 + \theta_1 X_1 + \theta_2 X_2 + \theta_3 X_1 X_2$ , where  $\theta_0(\tau) = \theta_0 + F_\varepsilon^{-1}(\tau)$ . This was a homoscedastic linear regression model where all parameters other than the intercept ( $\theta_0$ ) are the same for all quantiles  $\tau$ , i.e., parallel hyperplanes (Cade et al. 1999). The  $\tau$ th regression quantile of the estimating model where the effect of the unmeasured covariate  $X_2$  was not directly estimable was  $Q_y(\tau|X_0, X_1) = \beta_0(\tau)X_0 + \beta_1(\tau)X_1$ . In the estimating model both the intercept  $\beta_0(\tau)$  and slope  $\beta_1(\tau)$  for the measured covariate might vary with quantile  $\tau$  because the modified error term  $\varepsilon' = \varepsilon + \theta_2 X_2 + \theta_3 X_1 X_2$  included a mix of the additive random

<sup>6</sup> (<http://www.fort.usgs.gov/products/software/blossom.asp>)

component and a multiplicative component that was a function of the measured covariate  $X_1$ . We compared regression quantile parameters  $\beta_0(\tau)$  and  $\beta_1(\tau)$  from the estimating model with parameters  $\theta_0(\tau)$  and  $\theta_1$  from the generating model for the finite populations to examine differences due to different interaction effects and correlations with the unmeasured variable ( $X_2$ ). By using parameters for the population of  $N = 10\,000$  with the estimating model, our interpretations of hidden bias were not affected by sampling variation of estimates.

*Additive, no interaction*

We first simulated from an additive ( $\theta_3 = 0$ ) generating model (Table 1) to demonstrate why the heterogeneous constraint patterns investigated by Terrell et al. (1996), Cade et al. (1999), and Huston (2002) imply that there must be more than just additive effects between the measured and unmeasured processes generating the data. When the estimating model  $y = \beta_0 X_0 + \beta_1 X_1 + \varepsilon'$  was used because  $X_2$  was unmeasured, all the unexplained variation in the modified error term  $\varepsilon' = \varepsilon + \theta_2 X_2$  was additive. This caused differences between quantiles of the intercept parameters  $\beta_0(\tau)$  in the estimating  $Q_y(\tau|X_0, X_1) = \beta_0(\tau)X_0 + \beta_1(\tau)X_1$  and generating  $\theta_0(\tau)$  models but negligible differences between the slope parameters  $\beta_1(\tau)$  and  $\theta_1$  (Fig. 1). The estimating model had homogeneous variances like the generating model with bias in intercepts and little bias in slopes. Thus, rates of change in  $X_1$  based on sample estimates for any quantile or the mean would be similar in repeated random sampling. The slightly chaotic fluctuation in parameter values at the highest quantiles ( $\tau > 0.99$ ) for this and other simulations were due to generating the finite population as a sample from an error distribution that assumes infinite population size.

*Multiplicative interference interaction*

A multiplicative interference interaction ( $\theta_3 < 0.0$ ) generating model (Table 1) produced an increasing variance pattern similar to those discussed by Terrell et al. (1996), Thomson et al. (1996), Cade et al. (1999), and Huston (2002). There was little bias in the intercept  $\beta_0(\tau)$  but large bias in the slope  $\beta_1(\tau)$  parameter across quantiles of the estimating model relative to the generating model parameters  $\theta_0(\tau)$  and  $\theta_1$ , respectively (Fig. 1). Bias of  $\beta_1(\tau)$  relative to  $\theta_1$  was less with increasing quantile ( $\tau \rightarrow 1$ ). This is easy to explain by recognizing that the modified error distribution ( $\varepsilon' = \varepsilon + -0.0001X_1X_2$ ) was multiplicative with respect to  $X_1$ , and higher quantiles occurred when  $-0.0001X_1X_2$  approached its maximum as  $X_2$  approached its minimum of zero. Lower quantiles occurred when  $-0.0001X_1X_2$  approached its minimum as  $X_2$  approached its maximum of 4000. The lognormal error distribution resulted in a distribution in which  $\beta_1(\tau)$  did not converge with  $\theta_1$  at highest quantiles. However, when this example was simulated with a uniform error distribution,  $\beta_1(\tau)$  converged with  $\theta_1$  at the highest

quantiles. The lesson is that we can never be sure of the magnitude of bias when important variables are unmeasured since in applications we will never know the exact distributional form of the generating process. However, we can be confident that estimates for upper quantiles are less biased than those for lower quantiles or for the mean when the assumption of interference interactions with unmeasured variables is reasonable.

*Multiplicative facilitation interaction*

A multiplicative facilitation interaction ( $\theta_3 > 0.0$ ) generating model (Table 1) yielded an increasing variance pattern similar to the previous example for the interference interaction except that now  $\beta_1(\tau)$  at lower quantiles ( $\tau \rightarrow 0$ ) were less biased relative to  $\theta_1$  (Fig. 1). The explanation again is that the modified error distribution ( $\varepsilon' = \varepsilon + 0.0001X_1X_2$ ) is multiplicative with respect to  $X_1$ , but now higher quantiles occurred when  $0.0001X_1X_2$  approached its maximum as  $X_2$  approached its maximum of 4000. Lower quantiles occurred when  $0.0001X_1X_2$  approached its minimum as  $X_2$  approached its minimum of 0. This simulation coupled with the previous one demonstrated that the type of interaction (+ for facilitation or - for interference) between the measured variables and unmeasured processes determines whether lower or upper quantiles provide less biased estimates for the measured effects.

*Multiplicative interference interaction and correlation*

Nonlinear, increasing variance patterns were simulated by a slightly more complicated interference interaction model with varying degrees of correlation ( $r$ ) between the measured habitat variable  $X_1$  and the unmeasured variable  $X_2$  (Table 1). Here the obvious nonlinear response required an estimating model with a quadratic polynomial of  $X_1$ ,  $y = \beta_0 X_0 + \beta_1 X_1 + \beta_2 X_1^2 + \varepsilon'$  (Fig. 2). Stronger heterogeneity with less nonlinearity was evident for  $r(X_1, X_2) = 0.56$  and more homogeneity with stronger nonlinearity for  $r(X_1, X_2) = 0.92$ . Nonlinearity occurred because the correlation structure implied that some of the effect of  $X_2$  was linearly related to  $X_1$ , and, thus, their interaction in the modified error term  $\varepsilon' = \varepsilon + -0.0001X_1X_2$  was partly explained by the quadratic term  $X_1^2$ . The stronger the correlation between the measured  $X_1$  and unmeasured  $X_2$ , the more  $X_1^2$  captured the interaction effect in the modified error term  $\varepsilon'$ , increasing the nonlinearity ( $|\beta(\tau)|$ ) and decreasing the heterogeneity indexed by changes in  $\beta_1(\tau)$ . Depending on whether the signs of the interaction ( $\theta_3$ ) and correlation ( $r$ ) coefficients were similar ( $+\theta_3, +r$ , and  $-\theta_3, -r$ ) or dissimilar ( $+\theta_3, -r$ , and  $-\theta_3, +r$ ), nonlinear functions curved upwards or downwards, respectively. The lesson is that correlation between measured and unmeasured variables can result in nonlinear response relationships; the stronger the correlation the greater the nonlinearity and less heterogeneous the response. This also suggested that some

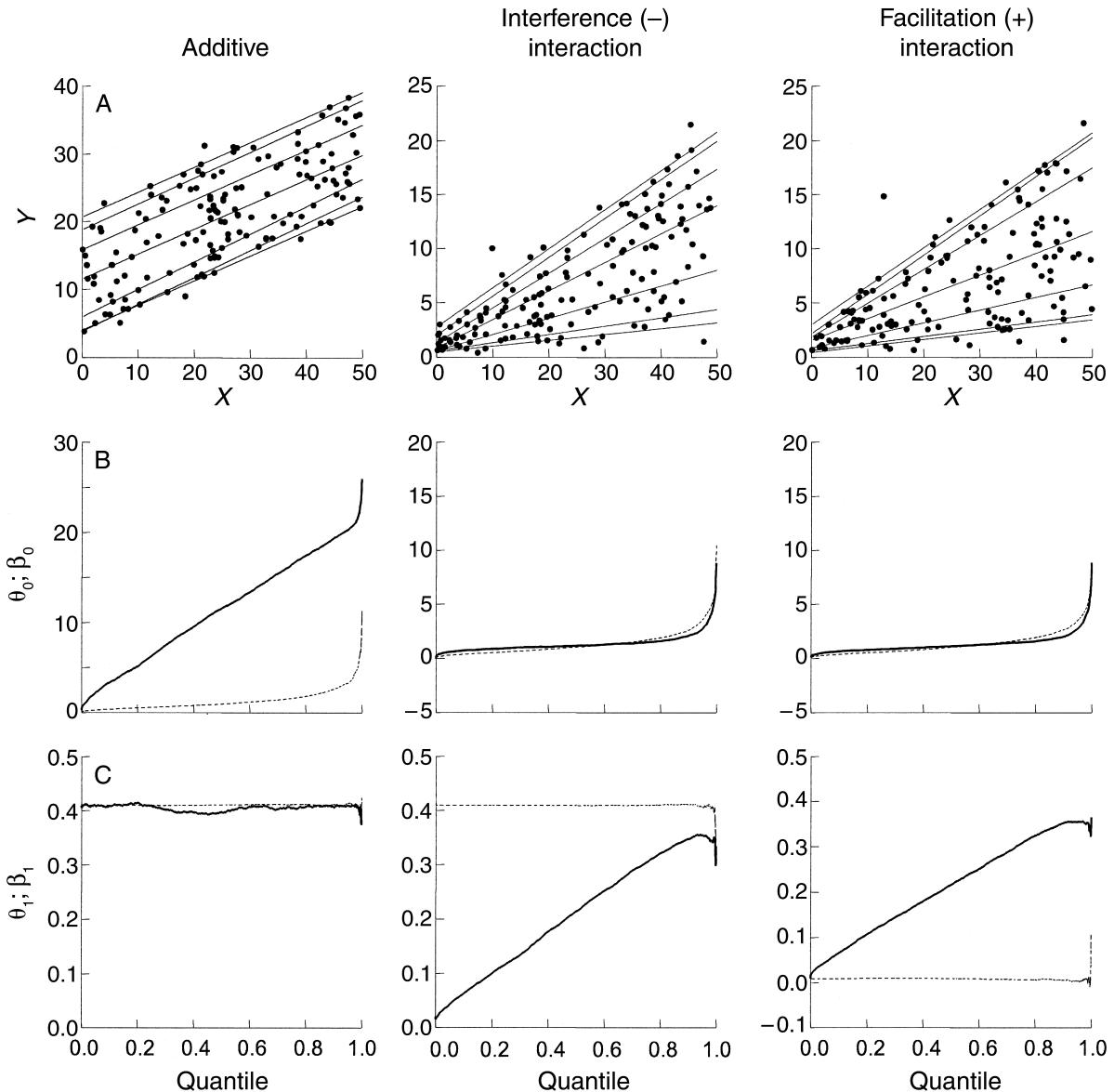


FIG. 1. (A) Samples ( $n = 150$ ) from the  $N = 10\,000$  population of grid cells from the generating model  $y = \theta_0 X_0 + \theta_1 X_1 + \theta_2 X_2 + \theta_3 X_1 X_2 + \varepsilon$  for additive, interference interaction (-), and facilitation interaction (+) models, with  $\varepsilon$  lognormally distributed (parameters in Table 1). Lines plotted are for selected regression quantile estimates ( $\tau \in \{0.95, 0.90, 0.75, 0.50, 0.25, 0.10, 0.05\}$ ) when the estimating model is  $y = \beta_0(\tau)X_0 + \beta_1(\tau)X_1 + \varepsilon'$  because  $X_2$  was not measured. (B) The deviation between  $\beta_0(\tau)$  and  $\theta_0(\tau)$  and (C) the deviation between  $\beta_1(\tau)$  and  $\theta_1(\tau)$  by quantiles for the finite population ( $\theta$ 's have dashed lines, and  $\beta$ 's have solid lines).

surrogate variable that was strongly correlated with the unmeasured variables might help account for some of the variation in the modeled relationships.

#### *Multiplicative interference interaction and spatial correlation*

The spatial coordinates of sample locations are a potential set of surrogate variables for unmeasured processes that are spatially structured. An interference interaction model was simulated with no correlation between measured and unmeasured variables but with the

unmeasured variable related to latitudinal and longitudinal coordinates (Table 1). The estimating model  $y = \beta_0 X_0 + \beta_1 X_1 + (\beta_2 X_1 \times \text{LAT}) + (\beta_3 X_1 \times \text{LONG}) + (\beta_4 X_1 \times \text{LAT}^2) + (\beta_5 X_1 \times \text{LONG}^2) + (\beta_6 X_1 \times \text{LONG}^3) + \varepsilon'$  had relatively homogeneous parameters  $\beta_2(\tau)$ – $\beta_6(\tau)$  across quantiles for the interactions of the measured habitat variable with the spatial trend surface, consistent with the homogeneous variation in the spatially structured unmeasured variable (Fig. 3). Variation in  $\beta_1(\tau)$  across quantiles was evident for the measured habitat variable with less bias relative to  $\theta_1$  at

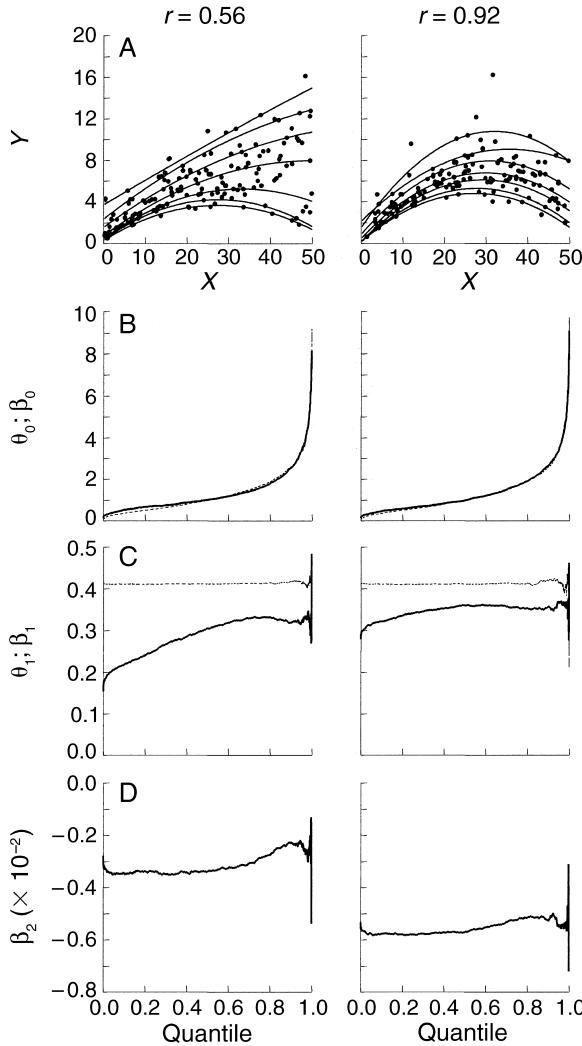


FIG. 2. (A) A sample ( $n = 150$ ) from the  $N = 10\,000$  population of grid cells from the generating model  $y = \theta_0 X_0 + \theta_1 X_1 + \theta_2 X_2 + \theta_3 X_1 X_2 + \varepsilon$  for interference interaction,  $\varepsilon$  lognormally distributed, and where  $r(X_1, X_2) = 0.56$  and  $0.92$  between measured and unmeasured variables (parameters in Table 1). Lines plotted are for selected regression quantile estimates when the estimating model is  $y = \beta_0(\tau)X_0 + \beta_1(\tau)X_1 + \beta_2(\tau)X_1^2 + \varepsilon'$  because  $X_2$  was not measured. Panels B–D show: (B)  $\beta_0(\tau)$  and  $\theta_0(\tau)$  deviating slightly for some quantiles ( $\tau$ ) of the finite population ( $\theta$ 's have dashed lines and  $\beta$ 's have solid lines); (C)  $\beta_1(\tau)$  and  $\theta_1(\tau)$  deviating less for higher quantiles and less for  $r(X_1, X_2) = 0.92$ ; and (D)  $\beta_2(\tau)$  across quantiles, with more negative estimates for  $r(X_1, X_2) = 0.92$  indicating greater nonlinearity; multiply the y-axis scale numbers in (D) by  $10^{-2}$  for actual values.

higher quantiles. Notice by comparing  $\beta_1(\tau)$  in Fig. 3, where some of the effect of the unmeasured variable was accounted for by the spatial trend, with  $\beta_1(\tau)$  in Fig. 1, where it was not, that variation and average bias across quantiles was less for the spatial model although bias at higher quantiles was slightly greater. Stronger spatial structuring of the unmeasured variable ( $X_2$ ) produced less variation in  $\beta_1(\tau)$  across quantiles and less

bias relative to  $\theta_1$ . However, the amount of variance explained ( $R^2 = 0.426$ ) with the spatial trend surface simulated in Fig. 3 was typical of the better results achieved in ecological investigations (e.g., Legendre et al. 1997). The lesson is that considerable heterogeneity and bias in parameters associated with effects of measured processes likely will remain even after accounting for effects of unmeasured processes by modeling their spatial structure with a trend surface.

PERFORMANCE OF QUANTILE RANK SCORE TESTS FOR MODELS WITH HIDDEN BIAS

Type I error rates for quantile rank score tests commonly used for constructing confidence intervals for

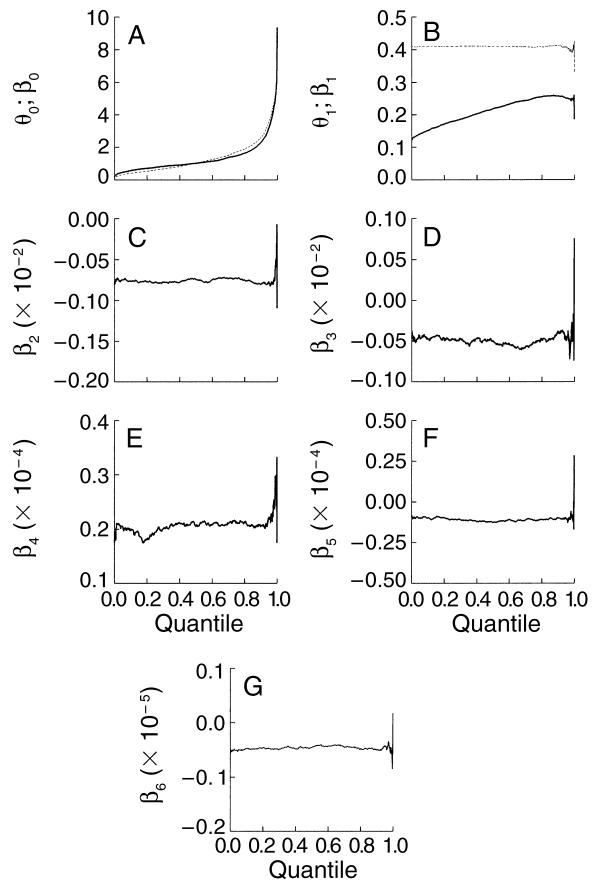


FIG. 3. Parameters for the  $N = 10\,000$  population of grid cells from the interference interaction generating model ( $\theta$ 's have dashed lines) as in Fig. 1 but with  $X_2$  spatially structured (parameters in Table 1); and for the estimating model  $y = \beta_0(\tau)X_0 + \beta_1(\tau)X_1 + [\beta_2(\tau)X_1 \times \text{LAT}] + [\beta_3(\tau)X_1 \times \text{LONG}] + [\beta_4(\tau)X_1 \times \text{LAT}^2] + [\beta_5(\tau)X_1 \times \text{LONG}^2] + [\beta_6(\tau)X_1 \times \text{LONG}^3] + \varepsilon'$  ( $\beta$ 's have solid lines) used because  $X_2$  was not measured: (A)  $\beta_0(\tau)$  and  $\theta_0(\tau)$  deviating slightly for some quantiles ( $\tau$ ); (B)  $\beta_1(\tau)$  and  $\theta_1(\tau)$  deviating less for higher quantiles; (C)–(G) relatively homogeneous effects of  $\beta_2(\tau)$ ,  $\beta_3(\tau)$ ,  $\beta_4(\tau)$ ,  $\beta_5(\tau)$ , and  $\beta_6(\tau)$  across quantiles for the interactions with the cubic polynomial spatial trend. For panels (C)–(G), y-axis scale numbers must be multiplied by the factor given in the y-axis label to obtain actual values.

$\beta_0(\tau)$  and  $\beta_1(\tau)$  were simulated for a range of sample sizes ( $n = 20, 30, 60, 90, 150,$  and  $300$ ) and quantiles ( $\tau = \{0.01, 0.05, 0.10, 0.25, 0.50, 0.75, 0.90, 0.95, 0.99\}$ ) by repeatedly sampling from the finite population of  $N = 10\,000$  generated by the interference interaction model (Table 1). Weighted quantile estimates were required to maintain correct Type I error rates and confidence interval coverage. Because the heterogeneity induced by the confounding between measured variables and important unmeasured variables was not a simple location/scale form, weights were estimated for the selected quantiles based on a local interval (bandwidth) of quantiles (Koenker and Machado 1999, Cade and Noon 2003). Power to detect the homogeneous spatial trend surface model in Fig. 3 indicated  $>80\%$  power for  $\alpha = 0.05$  was achieved for unweighted estimates of  $\beta_2(\tau) - \beta_6(\tau)$  for  $\tau = 0.05 - 0.90$  when  $n \geq 150$ . Details on methods and results of simulations are in Appendix B.

#### EXAMPLE APPLICATION

##### Methods

Legendre et al. (1997) and Legendre and Legendre (1998:745–746) evaluated the contributions of spatial trend, physical habitat variables, and biotic interactions to bivalve distribution and abundance in a New Zealand harbor. Physical habitat variables included sediment characteristics, bed elevation, and hydrodynamic measures likely to affect larval deposition, transport of juveniles, food supply, and feeding behavior. There were many strong correlations among the physical habitat variables considered. Biotic interactions considered adult–juvenile interactions by adding abundance of bivalves in different size classes to the models. Effects of a spatial trend surface, abundance of competitors, and habitat conditions were partitioned by considering nested sets of models in a linear least-squares regression (Legendre et al. 1997), following procedures of Borcard et al. (1992). We explored relationships for one species, *Macomona liliana*, using similar procedures but estimated with quantile regression. We present comprehensive analyses for the 22–23 January 1994 counts of  $>15$ -mm *Macomona*, adult size class, in  $0.25\text{-m}^2$  quadrats randomly located within 200 grid cells on a  $250 \times 500$  m area on the sandflat of Wiroa Island, Manukau Harbor, New Zealand (Fig. 4). The data used are provided in the Supplement. A condensed summary of results for *Macomona* in size class 0.5–2.5 mm are in Cade (2003).

We followed similar steps in modeling bivalve counts as used by Legendre et al. (1997) but made several adjustments because regression quantile estimates were used to account for heterogeneity and because we had a slightly different philosophy regarding model selection. Bivalve counts were not normalized by taking logarithms as done by Legendre et al. (1997). When selecting polynomial terms to include in the final

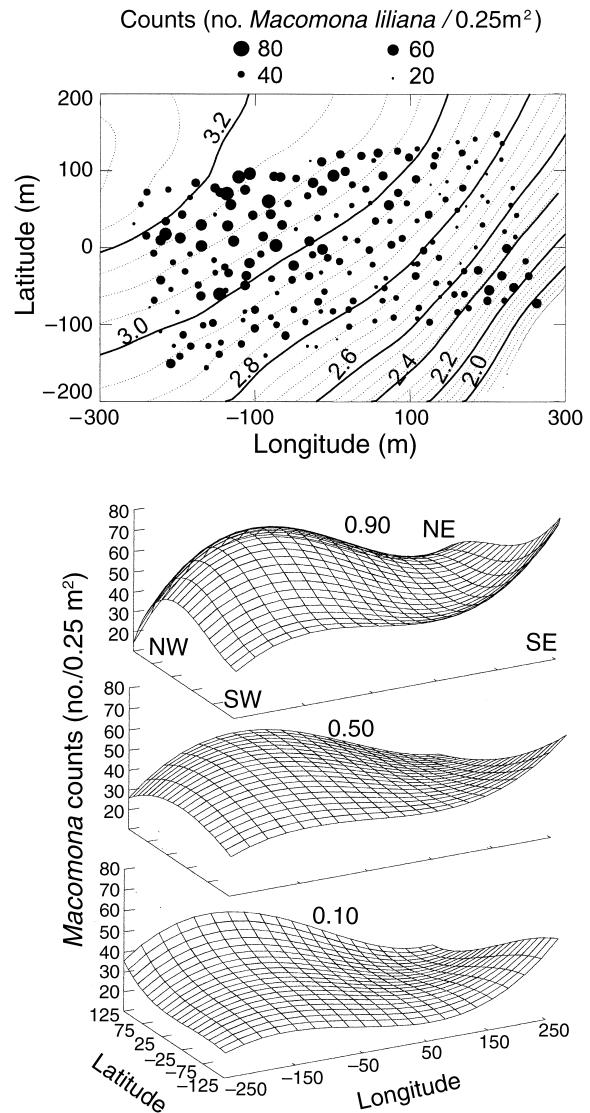


FIG. 4. Counts of  $>15$ -mm *Macomona liliana* in  $0.25\text{-m}^2$  quadrats ( $n = 200$ ), 22–23 January 1994, by location and bed elevation (meters above chart datum) contours on a  $250 \times 500$  m area of sandflat at Wiroa Island, Manukau Harbor, New Zealand (data from Legendre et al. [1997]). Counts are proportional to the size of the circle. Cubic polynomial spatial trend surfaces are for the 0.90, 0.50, and 0.10 regression quantiles of counts. Latitude (LAT) and longitude (LONG) were centered to mean zero. The view is from the southwest corner of the site.

spatial trend surface model, we considered models with all linear terms; all linear and quadratic terms; and all linear, quadratic, and cubic terms; this resulted in comparisons of three spatial trend models. We did not eliminate any individual monomial term from the set of linear, quadratic, or cubic polynomial terms as done by Legendre et al. (1997).

We used  $R^1(\tau)$  coefficients of determination (Koenker and Machado 1999) to compare fits of different regression quantile models across  $\tau = 0.05 - 0.95$  by in-

crements of 0.05. However,  $R^1(\tau)$ , like  $R^2$  from least-squares regression, cannot decrease with increasing number of parameters and, thus, it was desirable to have a statistic that adjusts for inclusion of additional parameters relative to sample size. Therefore, we selected among models using a small-sample-size-corrected version of the Akaike Information Criterion ( $AIC_c$ ) developed by Hurvich and Tsai (1990) for the 0.50 regression quantile (i.e., least absolute deviation regression) and extended to other quantiles;  $AIC_c(\tau) = 2n \times \ln(\text{SAF}(\tau)/n) + 2p(n/(n-p-1))$ , where  $\text{SAF}(\tau)$  was the weighted sum of absolute deviations minimized in estimating the  $\tau$ th quantile regression with  $p$  parameters (including one for estimating  $\sigma$ ). Appendix C describes computations for  $R^1(\tau)$  and  $AIC_c(\tau)$  and their justification. We computed differences ( $\Delta AIC_c(\tau)$ ) between  $AIC_c(\tau)$  for more complex models and the simplest model with just a constant ( $\beta_0$ ) to facilitate comparisons among models in a fashion comparable to using coefficients of determination.

The modeling steps Legendre et al. (1997) and we followed were (1) select an appropriate polynomial spatial trend surface model for bivalve counts; (2) select an appropriate model for bivalve counts as a function of the physical environmental variables; and (3) test whether the spatial trend surface explained a significant fraction of additional variation given that the physical environmental variables were already in the model. The two steps based on abundance of competitors were not required for the adult (>15 mm) *Macomona* (Legendre et al. 1997). Legendre et al. (1997) fit a spatial trend surface model first to determine whether there was any spatial structuring at the scale of the study plot associated with effects of ecological processes. However, we also considered the spatial trend surface as a potential surrogate for effects of unmeasured processes to be included in models after having accounted for effects associated with the measured variables.

#### *Spatial trend surface*

The cubic polynomial explained the greatest proportion of variation in counts of adult *Macomona* across  $\tau = 0.05$ – $0.95$  and was the preferred trend surface model based on  $R^1(\tau)$  coefficients of determination and  $AIC_c(\tau)$  (Fig. 5). Trend surfaces plotted for the 0.90, 0.50, and 0.10 quantiles had wavy variation along the northwest to southeast axis similar to the least-squares regression surface estimated by Legendre et al. (1997), but the divergence of the quantile surfaces towards the northwest was indicative of greater variation in counts (Fig. 4). The regression quantile estimates established that variation in abundance and not just mean abundance of adult *Macomona* had a spatial trend on the Wiroa sandflat. Substantially more variation was explained for higher than lower quantiles of the trend surface as indicated by  $R^1(\tau)$  coefficients of determination (Fig. 5).

#### *Physical habitat*

Legendre et al. (1997) found that only two physical habitat variables explained any of the variation in mean counts (log transformed) of adult *Macomona*, bed elevation (in meters) and percentage of time the plot was covered by >20 cm of water during spring tide. These also were the only physical habitat variables that we found explained any of the variation in quantiles of adult *Macomona*. However, these two variables were near perfectly linearly correlated ( $r = -0.999$ ) because bed elevation has a direct, physical relation to water depth during high tides. We therefore chose to use only bed elevation in the physical habitat model. Legendre et al. (1997) used a cubic polynomial of bed elevation to model the nonlinear response of large *Macomona* counts (Fig. 6). We initially considered this model too but also examined a simpler quadratic polynomial and compared models based on  $R^1(\tau)$  and  $AIC_c(\tau)$ . There was very little improvement in coefficients of determination by going to the cubic compared to the quadratic polynomial (Fig. 5). Differences in  $\Delta AIC_c(\tau)$  supported use of the cubic polynomial of bed elevation only for 0.80–0.85 quantiles. An examination of the cubic polynomial model of bed elevation suggested that regression quantile fits that were better with the cubic term were greatly influenced by the outlying minimum elevation value of 1.95 m. Removing this influential value and estimating quadratic and cubic polynomial models and associated fit and model selection statistics again indicated even less support for including the cubic bed elevation term.

The nonlinear response of large *Macomona* to bed elevation (Fig. 6) indicated increasing abundance at lower and higher bed elevations and increasing variation in abundance at higher elevations (Fig. 4). Rank score tests indicated that the joint effect of the linear and quadratic terms differed from zero for  $\tau > 0.10$  ( $P < 0.05$ ) but not for  $\tau \leq 0.10$  ( $P > 0.15$ ). Because bed elevation was near-perfectly negatively correlated with percentage of time the location was covered by >20 cm of water at spring flood tide, this relationship indicated that higher counts of adult *Macomona* occurred at locations that were flooded for shorter and longer periods of time. This was inconsistent with the Legendre et al. (1997) interpretation that adult *Macomona* abundance was structured by food availability determined by the amount of time a location was exposed to tidal flooding.

Although heterogeneity in abundance across bed elevation was not extreme, we constructed weighted regression quantile estimates for  $\tau = 0.05$ – $0.95$  by increments of 0.05, where weights were estimated separately for each individual quantile with a variant of the bandwidth approach used by Koenker and Machado (1999). Details of this approach to constructing local quantile weights are in Appendix D. Weighted estimates for the quadratic polynomial terms of bed ele-

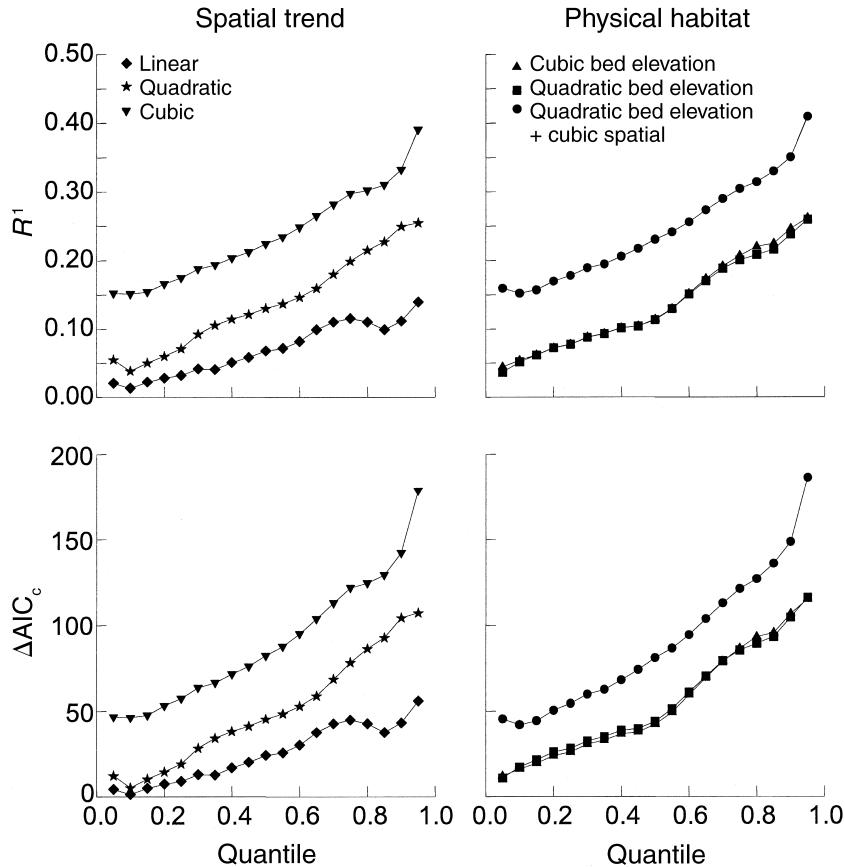


FIG. 5.  $R^1(\tau)$  coefficients of determination and differences in Akaike Information Criteria [ $\Delta AIC_c(\tau)$ ] for linear, quadratic, and cubic polynomial spatial trend surfaces and for quadratic and cubic functions of bed elevation (in meters) and quadratic function of bed elevation plus cubic spatial trend for  $\tau = 0.05$ – $0.95$  (by increments of 0.05) regression quantiles of  $>15$ -mm *Macomona liliana* counts in 0.25-m<sup>2</sup> quadrats ( $n = 200$ ), 22–23 January 1994, on the sandflat of Wiroa Island, Manukau Harbor, New Zealand (data from Legendre et al. [1997]). All  $\Delta AIC_c(\tau)$  were computed by subtracting the  $AIC_c(\tau)$  for the model with just an intercept ( $\beta_0$ ) from the  $AIC_c(\tau)$  for more complex models.

vation followed a similar pattern of changes with quantiles as the unweighted estimates, although weighted estimates smoothed over a little detail because they were only done for 19 increments of  $\tau$  between 0.05 and 0.95 (Fig. 7). The 90% confidence intervals for the weighted estimates were slightly narrower than those for the unweighted estimates at most higher quantiles. The overall pattern and inference for weighted estimates did not differ substantially from those for unweighted estimates, consistent with the moderate amount of heterogeneity in adult *Macomona* counts across bed elevation (Fig. 6).

Simultaneous 80% prediction intervals on 80% of adult *Macomona* densities indicated more than a doubling in interval lengths from 22–44 to 27–85 per 0.25 m<sup>2</sup> as bed elevation increased from 2.7 to 3.2 m (Fig. 6). Lower intervals that extended below zero counts (nonsensical) for bed elevations  $\leq 2.5$  m and upper intervals exceeding 100 for bed elevations  $\leq 2.2$  m were unreliable. The wide intervals were due to fewer observations at lowest bed elevations. This band of in-

tervals was estimated by constructing simultaneous confidence intervals for the 0.10 and 0.90 regression quantile estimates at 25 values of bed elevation between 2.10 and 3.30 m. The simultaneous prediction intervals emulated the Working-Hotelling simultaneous confidence intervals (Neter et al. 1996:234) for intercept estimates  $b_0(\tau)$  with the origin of bed elevation shifted to the 25 values selected for prediction. Two-sided intervals were constructed by inverting the weighted quantile rank score test with an  $\alpha = 0.0316 = 1 - [\text{prob } F((3 \times F(0.80, 3, 197)), 1, 197)]$ , using the upper part of the confidence interval for  $b_0(0.90)$  and the lower part of the confidence interval for  $b_0(0.10)$ . The interval band displayed in Fig. 6 was, thus, a statement about the central 80% of adult *Macomona* densities that would be expected to occur with respect to bed elevation in 80% of repeated random samples, i.e., a tolerance band. Slight irregularities in the simultaneous confidence intervals should not be overinterpreted as they were likely due to the vagaries of interpolating between discrete probabilities associ-

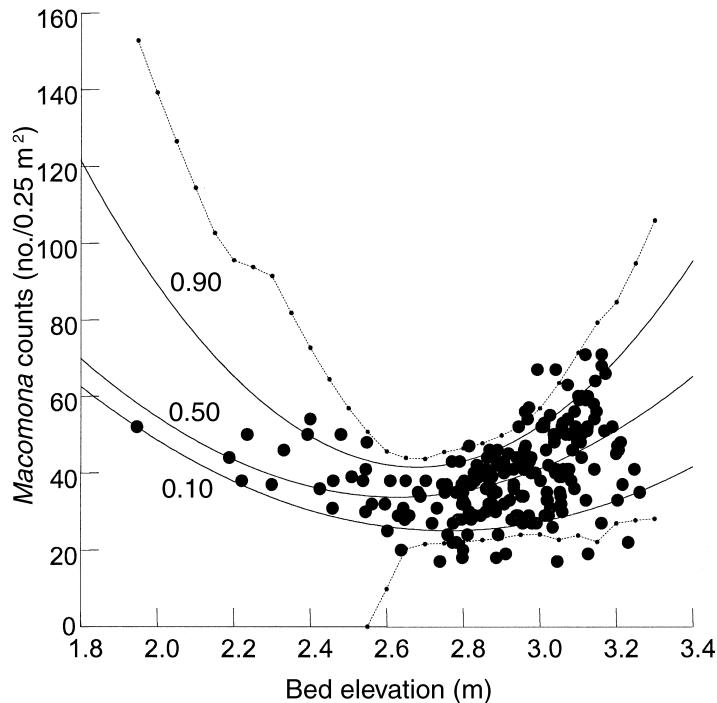


FIG. 6. Counts of >15-mm *Macomona liliana* in 0.25-m<sup>2</sup> quadrats ( $n = 200$ ), 22–23 January 1994, on the sandflat of Wiroa Island, Manukau Harbor, New Zealand, by bed elevation (in meters). Solid lines are 0.90, 0.50, and 0.10 regression quantile estimates of *Macomona* counts as a quadratic function of bed elevation. Lines with small dots connect upper and lower Working-Hotelling 80% simultaneous confidence intervals for predicted 0.90 (upper) and 0.10 (lower) regression quantiles at 28 selected values of bed elevation.

ated with the rank score test statistics (Cade 2003). Use of a more stringent confidence level such as 90% required smaller individual  $\alpha$ 's that resulted in intervals with greater irregularities.

#### *Physical habitat plus spatial trend*

Adding the cubic polynomial spatial trend surface to the model indicated that there was additional variation in adult *Macomona* abundance that was spatially structured after accounting for effects of bed elevation (Fig. 5). Changes in  $\Delta\text{AIC}_c(\tau)$  clearly supported the model with bed elevation and the spatial trend surface over the model with just bed elevation (Fig. 5). Sampling distributions for most quantiles ( $0.20 < \tau < 0.85$ ) indicated the joint effects of the polynomial spatial coefficients differed from zero (rank score  $T$ ,  $P < 0.05$ ) after accounting for bed elevation but did not differ (rank score  $T$ ,  $P > 0.10$ ) from zero for lower ( $\tau \leq 0.20$ ) and higher ( $\tau \geq 0.85$ ) quantiles. Because bed elevation itself was spatially structured along the northwest to southeast axis (Fig. 4), estimated effects of bed elevation after adjusting for spatial trend were attenuated, reversed in sign, and did not differ from zero (Fig. 8). Only unweighted estimates were used with this model, as the previous analysis on bed elevation suggested effects of heterogeneity were not sufficient for weighted confidence intervals to differ substantially from unweighted ones.

The model including bed elevation and spatial trend indicated similar wavy variation in adult *Macomona* abundance from the northwest to southeast as estimated by the spatial trend surface alone, except that some of

the variation in the northwest corner was reduced (compare Figs. 4 and 8). However, the spatial trend surface model explained nearly as much variation as the model that included bed elevation and spatial trend (Fig. 5). Because increases in adult *Macomona* abundance above and below 2.6–2.8 m bed elevation followed the dominant spatial trend from the northwest to southeast (Fig. 4), the effects of bed elevation and the spatial trend surface were partially confounded and probably should not both be included for an interpretable model.

#### DISCUSSION

Our example simulations demonstrated how heterogeneous and nonlinear relations in habitat models can easily arise from confounding with some important but unmeasured processes. More complicated arguments are not required to explain why heterogeneity and nonlinearities are so common in statistical models of animal responses to their habitat resources. Although the dimensions of the measured habitat variables ( $X_1$ ) and the unmeasured limiting factors ( $X_2$ ) were kept to single variables for simulation purposes, it is reasonable to extend interpretation of these simulation results to greater dimensions by thinking of  $X_1$  and  $X_2$  as being the composite additive effect of more than two variables. Our simulations focused on confounding with unmeasured variables not related to habitat resources. It also is reasonable to extend the results and interpretations to situations in which confounding occurs with some important habitat resources that were not measured and included in the model used for estimation.

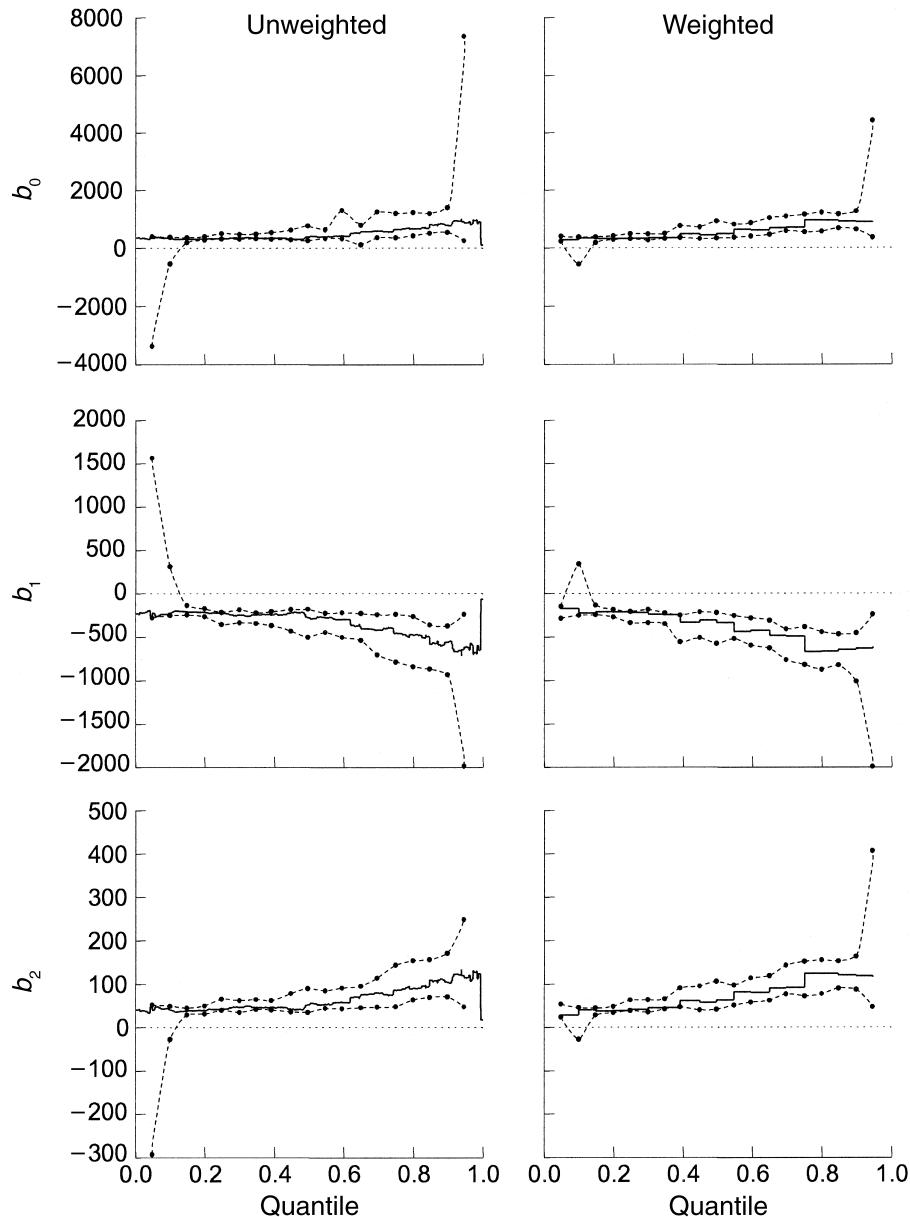


FIG. 7. Estimates for intercept [ $b_0(\tau)$ ], linear [ $b_1(\tau)$ ], and quadratic [ $b_2(\tau)$ ] terms for regression quantiles of >15-mm *Macomona liliana* counts in 0.25-m<sup>2</sup> quadrats ( $n = 200$ ), 22–23 January 1994, on the sandflat of Wiroa Island, Manukau Harbor, New Zealand, as a quadratic function of bed elevation (in meters) for both unweighted and weighted models. Solid lines are step functions of parameter estimates by quantiles ( $\tau$ ), all for unweighted estimates and for  $\tau = 0.05$ –0.95 by increments of 0.05 for weighted estimates. Dashed lines connect pointwise 90% confidence intervals based on inverting the  $T$  rank score tests for  $\tau = 0.05$ –0.95 by increments of 0.05.

The philosophy embodied in our simulations reflects a view that most ecological relations have an appearance of randomness not because they are inherently random but because we are always estimating them with incomplete information (Regan et al. 2002). As long as random variation induced by missing information is small and homogeneous, conventional regression estimation procedures (e.g., least squares) may provide useful, reasonable estimates of conditional re-

lationships. When missing information is for processes of substantial importance to an organism, it is reasonable to expect large, heterogeneous random variation and estimates with hidden bias. While all organisms are dependent on some suite of resources obtained from their habitat, at many times and locations other factors may actually exert more influence on organism growth, survival, reproduction, and dispersal, causing a perceived disconnection between the organism response

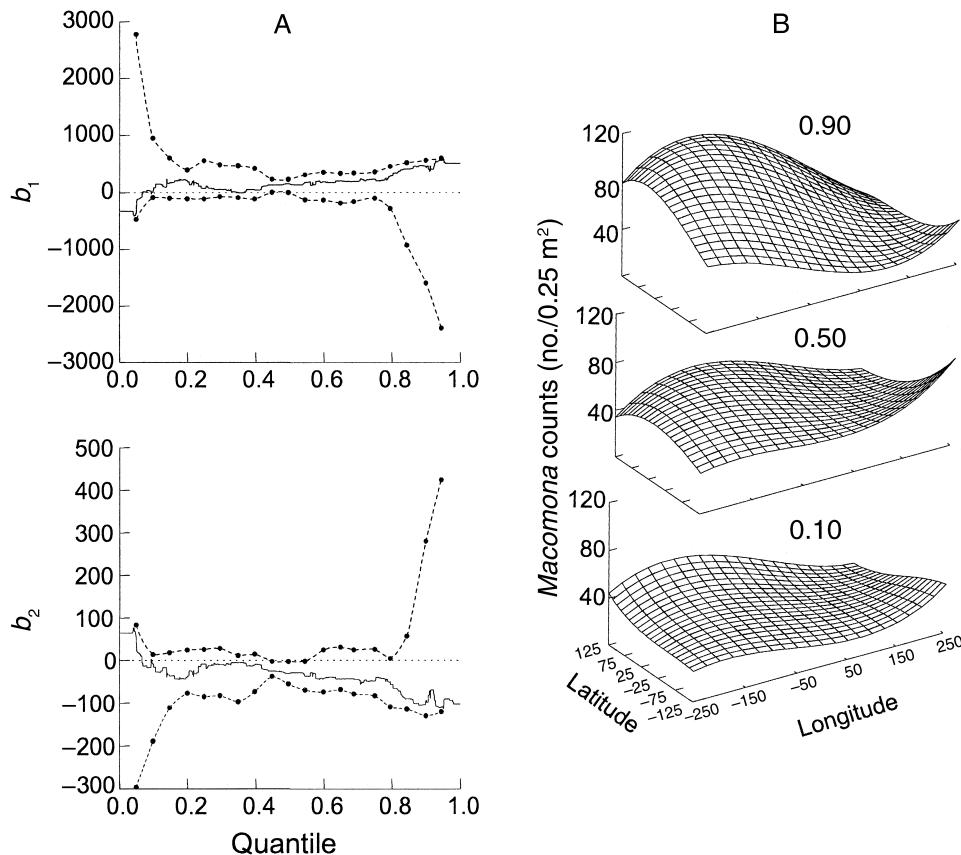


FIG. 8. (A) Estimates for linear [ $b_1(\tau)$ ] and quadratic [ $b_2(\tau)$ ] terms for regression quantiles of  $>15$ -mm *Macomona liliana* counts in  $0.25\text{-m}^2$  quadrats ( $n = 200$ ), 22–23 January 1994, on the sandflat of Wiroa Island, Manukau Harbor, New Zealand, as a quadratic function of bed elevation (in meters) after adjusting for the cubic polynomial spatial trend surface. Solid lines are step functions of parameter estimates by quantiles ( $\tau$ ), and dashed lines connect pointwise 90% confidence intervals based on inverting the  $T$  rank score tests for  $\tau = 0.05\text{--}0.95$  by increments of 0.05. (B) The 0.90, 0.50, and 0.10 cubic polynomial spatial trend surfaces after adjusting for the quadratic function of bed elevation at the mean value of 2.9 m. The view is from the southwest.

and the requisite habitat resources. Garshelis (2000) and Morrison (2001) both have argued for improving our knowledge of animal habitat relations by focusing modeling efforts on more specifically defined resources and relating them to demographic parameters such as survival and reproductive rates that ultimately contribute to differences in abundance. These are reasonable suggestions. But neither a more focused definition of what constitutes a habitat resource nor measuring alternative demographic parameters will eliminate issues of hidden bias due to confounding between measured habitat factors and unmeasured ones associated with other processes.

Inference procedures based on rank scores for weighted regression quantile estimates provided valid intervals reflecting the sampling distribution of parameter estimates for the measured habitat processes, but the parameters for the estimating model clearly were biased relative to those generating the responses. In applications, the degree of hidden bias will be greater or lesser for different quantiles depending on the non-

estimable interaction effects and unknown error distributions. If it is possible to rule out certain types of interaction effects (e.g., facilitation) with unmeasured processes, then we might profitably focus estimation and inference procedures for quantile regression at one end of the probability distribution (e.g., upper quantiles). While interference interactions may be more common in ecological systems, facilitation interactions have been suggested for some processes, e.g., transgressive over-yielding where plant biomass is greater when a nitrogen-fixing legume and a  $C_4$  grass are grown together than when either species is grown separately (Huston and McBride 2002). Facilitation interactions are more difficult to articulate for animal habitat relationships but may exist. Deciding whether interference or facilitation interaction is a more reasonable assumption requires knowledge obtained from sources other than the data being analyzed. In the absence of such knowledge, it would appear prudent to obtain estimates and confidence intervals across the entire in-

terval of quantiles that provide reliable estimates (e.g.,  $\tau = 0.05-0.95$ ).

We encourage the use of prediction intervals, and especially simultaneous prediction intervals or tolerance intervals, as a strong antidote to overzealous expectations that any habitat model can provide precise predictions. Prediction and tolerance intervals provide confidence statements related to individual or a proportion of individual observational units (Vardeman 1992). These were areal plots in our simulations and example application as in most habitat models. It is unreasonable to expect habitat models to provide very precise predictions for any individual area when they exclude many other important processes, which we often barely understand or know how to measure. The uncertainty associated with multiple unmeasured processes will likely increase as we increase the spatial and temporal extent of our sampling. Thus, the conundrum of developing useful habitat models is that generality requires extensive sampling in time and space, but doing this almost ensures that many other unmeasured processes will be limiting at some locations and times. However, this does not imply that useful predictions are impossible with habitat models, especially for management or conservation purposes. Predictions made by characterizing intervals of response with procedures such as those presented here are useful measures of uncertainty when we expect population responses to vary greatly across different locations (or time) even if they have similar habitat resources. Prediction and tolerance intervals provide measures of sampling variation for individual units that actually can be observed and on which management or conservation actions can be implemented. Improving predictions from habitat models requires understanding the contexts in which habitat models fail or succeed as predictors of population change by considering contingencies across individual units of area on landscapes.

Our simulation results demonstrated that heterogeneity that arises due to confounding between measured and unmeasured variables often will not be a simple location-scale form. In this situation, weighted regression quantile estimates and rank score tests require estimating weights that are based on changes in a local interval of quantiles around a specific quantile rather than globally applied across all quantiles. We used a minor modification of bandwidth estimation procedures developed by Hall and Sheather (1988) as extended to regression quantiles by Koenker and Machado (1999). Although adequate, there clearly is room for improvement in these procedures, including automating their computation in the necessary software.

Our use of  $\Delta AIC_c$  for model selection with the bivalve data extended Hurvich and Tsai (1990) procedures for median regression ( $\tau = 0.5$ ) to other quantiles. The fact that some large  $\Delta AIC_c$  between models at high and low quantiles were associated with sampling distributions of parameter estimates that did not differ

from zero was a little disconcerting. This may reflect a fundamental difference between  $AIC_c$  and hypothesis tests, the former being inductive and the latter deductive inference, or that we extended estimates and inferences too far into the extreme quantiles for them to be reliable. Machado (1993) discussed extension of the Schwarz information criterion (SIC) to robust  $M$  estimates, including median regression, for linear models. The SIC increases more rapidly with additional parameters than  $AIC_c$  and, thus, will generally lead to selection of lower dimension models. Additional research on application of information criteria to regression quantile model selection is clearly warranted.

Use of cubic polynomials of location coordinates to estimate spatial trend surfaces provided a reasonable method for modeling larger scale spatial gradients of responses (Legendre et al. 1997) that are of most interest for models of animal response to habitat. Spatial trend surfaces provided an indication of spatial variation in organism response that would suggest effects of some relevant ecological processes (Legendre et al. 1997) and provided a method for accounting for some of the variation due to unmeasured processes that were spatially structured. Other methods for fitting flexible quantile response surfaces to location coordinates such as piecewise linear or cubic splines are possible and may offer advantages in some situations (Koenker et al. 1994, He and Ng 1999).

It is important to remember that gradients in space offer no ecological interpretation per se (Legendre et al. 1997). It is possible to defeat the entire purpose of developing general habitat relationships by over-reliance on modeling spatial structure. Consider the models of adult *Macomona* as a function of bed elevation and spatial structure. There was more variation in adult *Macomona* abundance explained by the spatial trend surface alone than by the nonlinear bed elevation model. A parsimonious model that explained most variation with fewest parameters would be the cubic spatial trend surface model. Yet this model of bivalve counts based on spatial gradients on one sandflat has little chance of generalizing to other locations because it includes no information on ecological processes. The cubic spatial trend does suggest that spatially structured processes are operating within the scale of the sampled  $250 \times 500$  m area (Legendre et al. 1997). There is greater potential for generalizing the bed elevation relationship to other locations to the extent that bed elevation is related to hydrodynamic processes affecting settlement, feeding, and survival of bivalves. Similarly, models that include indicator variables allowing for different habitat relationships for different geographic locations (e.g., Dunham and Vinyard 1997), although justified from a statistical standpoint, may actually defeat our desire to develop general habitat relationships. Quantile regression allows contextual differences associated with different geographic locations to be expressed through different rates of change for different

quantiles of one probability model (e.g., Dunham et al. 2002).

Although our focus in this article is on applications and interpretations of quantile regression for estimating animal habitat relationships, it should be apparent that heterogeneous distributions associated with many other ecological phenomena could benefit from similar analyses. The inference tools and interpretations of linear quantile regression have been developed sufficiently that routine analyses are now possible. We expect that quantile regression estimates for intervals of responses might prove enlightening for some controversial ecological debates such as whether plant productivity is a function of diversity (Grace 1999, Huston et al. 2000, Huston and McBride 2002, Schmid 2002).

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#### LITERATURE CITED

- Angermeier, P. L., and M. R. Winston. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* **79**:911–927.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73**:1045–1055.
- Cade, B. S. 2003. Quantile regression models of animal habitat relationships. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Cade, B. S., and Q. Guo. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos* **91**:245–254.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* **1**:412–420.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* **80**:311–323.
- Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003. Coexistence: how to identify trophic trade-offs. *Ecology* **84**:17–31.
- Dunham, J. B., B. S. Cade, and J. W. Terrell. 2002. Influences of spatial and temporal variation on fish–habitat relationships defined by regression quantiles. *Transactions of the American Fisheries Society* **131**:86–98.
- Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. *Transactions of the American Fisheries Society* **126**:323–329.
- Fausch, K. D., C. L. Hawks, 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.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology*. Columbia University Press, New York, New York, USA.
- Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution, and Systematics* **2**:1–28.
- Grace, J. B. 2001. Difficulties with estimating and interpreting species pools and the implications for understanding patterns of diversity. *Folia Geobotanica* **36**:71–38.
- Hall, P., and S. Sheather. 1988. On the distribution of a studentized quantile. *Journal of the Royal Statistical Society, Series B* **50**:381–391.
- He, X., and P. Ng. 1999. Quantile splines with several covariates. *Journal of Statistical Planning and Inference* **75**:343–352.
- Hurvich, C. M., and C.-L. Tsai. 1990. Model selection for least absolute deviations regression in small samples. *Statistics and Probability Letters* **9**:259–265.
- Huston, M. A. 2002. Introductory essay: critical issues for improving predictions. Pages 7–21 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hafler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covelo, California, USA.
- Huston, M. A., L. W. Aarssen, M. P. Austin, B. S. Cade, J. D. Fridley, E. Garnier, J. P. Grime, J. Hodgson, W. K. Lauenroth, K. Thompson, J. H. Vandermeer, and D. A. Wardle. 2000. No consistent effect of plant diversity on productivity. *Science* **289**(5483):1255.
- Huston, M. A., and A. C. McBride. 2002. Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. Pages 47–60 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, New York, New York, USA.
- Kaiser, M. S., P. L. Speckman, and J. R. Jones. 1994. Statistical models for limiting nutrient relations in inland waters. *Journal of the American Statistical Association* **89**:410–423.
- Koenker, R. 1994. Confidence intervals for regression quantiles. Pages 349–359 in P. Mandl and H. Hušková, editors. *Asymptotic statistics. Proceedings of the Fifth Prague Symposium*. Physica-Verlag, Heidelberg, Germany.
- Koenker, R., and K. F. Hallock. 2001. Quantile regression. *Journal of Economic Perspectives* **15**:143–156.
- 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., P. Ng, and S. Portnoy. 1994. Quantile smoothing splines. *Biometrika* **81**:673–680.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English edition. Elsevier Science, Amsterdam, The Netherlands.
- Legendre, P., et al. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99–128.
- Lichstein, J. W., T. R. Simons, S. A. Shriener, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* **72**:445–463.
- Machado, J. A. F. 1993. Robust model selection and *M*-estimation. *Econometric Theory* **9**:478–493.
- Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management* **65**:613–623.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. *Wildlife habitat-relationships: concepts and applications*. Second edition. University of Wisconsin Press, Madison, Wisconsin, USA.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*. Irwin, Chicago, Illinois, USA.
- O'Connor, R. J. 2002. The conceptual basis of species distribution modeling: time for a paradigm shift? Pages 25–33 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hafler, M. G. Raphael, W. A. Wall, and F. B. Samson,

- editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California, USA.
- Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* **12**:618–628.
- Rosenbaum, P. R. 1991. Discussing hidden bias in observational studies. *Annals of Internal Medicine* **115**:901–905.
- Rosenbaum, P. R. 1995. Quantiles in nonrandom samples and observational studies. *Journal of the American Statistical Association* **90**:1424–1431.
- Rosenbaum, P. R. 1999. Reduced sensitivity to hidden bias at upper quantiles in observational studies with dilated treatment effects. *Biometrics* **55**:560–564.
- Rotenberry, J. T. 1986. Habitat relationships of shrubsteppe birds: even “good” models cannot predict the future. Pages 217–221 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Schmid, B. 2002. The species richness-productivity controversy. *Trends in Ecology and Evolution* **17**:113–114.
- Stauffer, D. F. 2002. Linking populations and habitats: where have we been? Where are we going? Pages 53–61 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covelo, California, USA.
- Terrell, J. W., B. S. Cade, J. Carpenter, and J. M. Thompson. 1996. Modeling stream fish habitat limitations from wedged-shaped patterns of variation in standing stock. *Transactions of the American Fisheries Society* **125**:104–117.
- Terrell, J. W., and J. Carpenter. 1997. Selected habitat suitability index model evaluations. U.S. Department of Interior, Geological Survey, Information and Technology Report USGS/BRD/ITR-1997-0005.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* **77**:1698–1715.
- Van Horne, B., and J. A. Wiens. 1991. Forest bird habitat suitability models and the development of general habitat models. U.S. Department of Interior, Fish and Wildlife Service, Fish and Wildlife Research Report Number 8.
- Vardeman, S. B. 1992. What about the other intervals? *American Statistician* **46**:193–197.
- Wiens, J. A. 1989. *The ecology of bird communities*. Volume 1. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.

#### APPENDIX A

A figure presenting the cubic polynomial trend surface used in simulations to generate the values of  $X_2$ , an unmeasured nonhabitat variable, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-041-A1.

#### APPENDIX B

The performance of regression quantile rank score tests for models with hidden bias is available in ESA's Electronic Data Archive: *Ecological Archives* E086-041-A2.

#### APPENDIX C

Model selection criteria are available in ESA's Electronic Data Archive: *Ecological Archives* E086-041-A3.

#### APPENDIX D

The method used for estimating local quantile weights is available in ESA's Electronic Data Archive: *Ecological Archives* E086-041-A4.

#### SUPPLEMENT

Bivalve data (Legendre et al. 1997) used for example application are available in ESA's Electronic Data Archive: *Ecological Archives* E086-041-S1.