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ARTICLE

Estimating Geographic Variation in Allometric Growth and Body Condition of Blue Suckers with Quantile Regression

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Abstract

Increasing our understanding of how environmental factors affect fish body condition and improving its utility as a metric of aquatic system health require reliable estimates of spatial variation in condition (weight at length). We used three statistical approaches that varied in how they accounted for heterogeneity in allometric growth to estimate differences in body condition of blue suckers *Cycleptus elongatus* across 19 large-river locations in the central USA. Quantile regression of an expanded allometric growth model provided the most comprehensive estimates, including variation in exponents within and among locations (range = 2.88–4.24). Blue suckers from more-southerly locations had the largest exponents. Mixed-effects mean regression of a similar expanded allometric growth model allowed exponents to vary among locations (range = 3.03–3.60). Mean relative weights compared across selected intervals of total length (TL = 510–594 and 594–692 mm) in a multiplicative model involved the implicit assumption that allometric exponents within and among locations were similar to the exponent (3.46) for the standard weight equation. Proportionate differences in the quantiles of weight at length for adult blue suckers (TL = 510, 594, 644, and 692 mm) compared with their average across locations ranged from 1.08 to 1.30 for southern locations (Texas, Mississippi) and from 0.84 to 1.00 for northern locations (Montana, North Dakota); proportionate differences for mean weight ranged from 1.13 to 1.17 and from 0.87 to 0.95, respectively, and those for mean relative weight ranged from 1.10 to 1.18 and from 0.86 to 0.98, respectively. Weights for fish at longer lengths varied by 600–700 g within a location and by as much as 2,000 g among southern and northern locations. Estimates for the Wabash River, Indiana (0.96–1.07 times the average; greatest increases for lower weights at shorter TLs), and for the Missouri River from Blair, Nebraska, to Sioux City, Iowa (0.90–1.00 times the average; greatest decreases for lower weights at longer TLs), were examined in detail to explain the additional information provided by quantile estimates.

The blue sucker *Cycleptus elongatus* is a benthic fish that is native to large rivers primarily in the Mississippi River basin; populations of the blue sucker are declining, and it is listed as a species of conservation concern in all 23 states where it occurs (Jelks et al. 2008). Construction of dams is considered detrimental to blue suckers (Pflieger 1997; Eitzmann et al. 2007; Jelks et al. 2008), and the species has been suggested as a potential indicator of overall aquatic system health (Hesse and Mestl 1993; Neely et al. 2008). Neely et al. (2008) developed a standard weight (W_s) equation from 46 populations of blue suckers across the species' geographic distribution, providing a potential foundation for using body condition of this species as an indicator of ecosystem health.

The key feature of any measure of body condition is that it should characterize weight adjusting for differences in size, which for fish is commonly expressed as some measure of length, such as total length (TL; Lleonart et al. 2000; Froese 2006; Pope and Kruse 2007; Peig and Green 2010). The W_s

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equation developed by Neely et al. (2008) for blue suckers used the empirical percentile method (Gerow et al. 2004, 2005) to estimate the 75th percentile of allometric growth of weight with length across the 46 blue sucker populations. Techniques for developing W_s equations have been constantly evolving (Murphy et al. 1991; Blackwell et al. 2000; Pope and Kruse 2007) since the original technique was first described by Wege and Anderson (1978). However, the approach to using W_s equations has remained essentially unchanged: the W_s equation is used to estimate W_s at a specified length, against which the observed weight (W) at that length is compared to estimate relative weight ($W_r = [W \div W_s] \times 100$; Wege and Anderson 1978).

Relative weight has been used for decades within its original context as a body condition index that could serve as a standard population-level goal for intensively managed sport fish populations, and W_r has evolved into a commonly used metric for describing the general health and well-being of fish populations (Murphy et al. 1991; Blackwell et al. 2000). Recently, there has been increased use of W_r for quantifying body condition of non-sport fishes (Bister et al. 2000; Didenko et al. 2004; Richter 2007; Rypel and Richter 2008; Ogle and Winfield 2009), such as the blue sucker. If body condition indices (e.g., W_r) of fish are to be used to characterize and interpret changes in the health of fish populations and associated aquatic systems, then knowledge about how best to estimate temporal and spatial variation in body condition indices is essential (Murphy et al. 1991; Porath et al. 2003; Pope and Kruse 2007).

Numerous concerns have been raised about using W_r for comparing and contrasting condition of fish across time and space or by environmental covariates (Cone 1989, 1990; Brenden et al. 2003; Cade et al. 2008; Gerow 2010). The most relevant concern is whether W_r can be compared reasonably if the groups of fish being compared do not share the same allometric growth of weight with length ($W = \beta_0 \mathrm{TL}^{\beta_1}$, where β_0 is the intercept and β_1 is the slope or exponent) as indicated by the W_s equation. There is abundant evidence of considerable variation in allometric growth exponents (β_1) among the populations (groups) of fish used for developing W_s equations for many species (Murphy et al. 1990; Brenden et al. 2003; Lai and Helser 2004; Hansen and Nate 2005; Ogle and Winfield 2009; Gerow 2010). Thus, it is reasonable to expect heterogeneous exponents for other fish populations that might be compared by use of W_r. Standard weight equations, including the one developed for blue suckers (Neely et al. 2008), are constructed by using various forms of averaging across potentially very different growth exponents to estimate a single allometric exponent. The issue with comparing W_r across groups of fish with different allometric exponents is similar to the issue of trying to conduct an analysis of covariance (ANCOVA) on weight–length relationships when the slopes in the linear model representation ($\log_{10} W$ as a function of $\log_{10}$TL) are not parallel among groups (locations, times, sexes, etc.). Averaging of the exponents (slopes) cannot be relied upon to provide a useful basis for comparison, except perhaps in limited circumstances. Gerow (2010) recently argued for estimating multiple W_s equations (e.g., for 25th, 50th, and 75th percentiles) to compute multiple values of W_r, a procedure that still implicitly invokes multiple forms of averaging exponents across fish within and among populations. Another weakness in Gerow's (2010) implementation and other implementations of the empirical percentile and regression line percentile methods (Gerow et al. 2004, 2005) is that the allometric growth relationship is not modeled for individual fish but rather is modeled for the averages of fish grouped by length intervals and population. Fundamentally, allometric growth is a property of an individual organism (Lleonart et al. 2000; Froese 2006), and statistical models based on measures for individual fish as replicates will better characterize this process.

Various statistical approaches for assessing fish body condition have circumvented issues with W_r by expanding the basic weight–length model to specifically allow for different allometric exponents among selected groupings of fish (Filbert and Hawkins 1995; Lai and Helser 2004; Cade et al. 2008; He et al. 2008). These statistical approaches share the explicit estimation of separate intercepts and slopes (exponents in the multiplicative allometric growth model) for selected groups of fish to account for heterogeneity in allometric growth among groups of fish or based on other potential predictors. Implicit in these approaches is the recognition that if slopes (exponents) are heterogeneous among groups of fish, then the interpretations of differences in body condition (weight differences adjusted for length) should not be based on differences at a single length (e.g., not as comparisons of intercept terms in an ANCOVA). Heterogeneity in allometric exponents in these expanded weight–length models is a form of statistical interaction implying that a reasonable interpretation of differences in weight adjusted for length requires evaluations at multiple levels of length in the allometric growth model. If the slopes (exponents) are homogeneous (parallel), then the group differences estimated at any single value of length (e.g., the intercept where $\log_{10}$length $= 0$) will apply to all other values of length. This simplification is not reasonable when slopes (exponents) are not homogeneous. Some comparative approaches used with W_r attempt to deal with the heterogeneous exponent issue by making comparisons for different intervals of length (Porath et al. 2003; Pope and Kruse 2007). This also is inadequate to account for biases if exponents are heterogeneous within the specified length intervals.

Statistical models that allow heterogeneous exponents among groups of fish can be estimated in either a fixed-effects or a mixed-effects parameterization of the linear model and in either a frequentist mode (Filbert and Hawkins 1995; Lai and Helser 2004; Cade et al. 2008) or a Bayesian mode (He et al. 2008). However, of the aforementioned approaches, only quantile regression (Cade et al. 2008) explicitly models the variation of exponents within groups of fish as a second source of heterogeneity in allometric exponents. The quantile regression approach of Cade et al. (2008) models the heterogeneity in exponents among groups of fish with fixed-effect interactions, allowing separate exponents among groups while also accounting

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for heterogeneity of variance in exponents within groups (i.e., by allowing all quantiles within groups to have different exponents). The Bayesian mixed-effects model of He et al. (2008) dealt with exponent variance heterogeneity within groups of lake trout *Salvelinus namaycush* and Chinook salmon *Oncorhynchus tshawytscha* by use of a weighted (inversely proportional to variance) analysis. However, similar to a weighted fixed-effects regression analysis, the weighted mixed-effects analysis of He et al. (2008) simply provides more-reasonable confidence interval (CI) estimates for exponents associated with the mean for a group of fish but without explicitly estimating different exponents for the quantiles associated with heterogeneity of variances within groups. Variation in allometric exponents within groups of fish may be as great as heterogeneity in exponents among groups of fish (Cade et al. 2008). A statistical model for fish body condition that incorporates within-group variation in exponents should provide additional insight into how fish populations are responding to changes in environmental variables.

We used blue sucker weight and length data compiled by Neely et al. (2008) to estimate and compare body condition across geographic locations in three ways: (1) with linear quantile regression (Cade et al. 2008), (2) with means from a linear mixed-effects model (Lai and Helser 2004), and (3) with mean W_r based on the Neely et al. (2008) W_s equation. These three statistical techniques vary in the degree to which they account for heterogeneity of allometric exponents: both within and among locations for the quantile regression model, among locations for the mixed-effects means model, and not at all for W_r. We describe how all three procedures detected a similar north–south gradient of increasing body condition for blue suckers, but we illustrate that statistical models allowing greater complexity of heterogeneity in allometric exponents provided greater insights on differences in body condition. We demonstrate additional useful interval summaries of weight at length from quantile regression that can aid in the interpretation of fish body condition across geographic locations not discussed by Cade et al. (2008). This comparison of multiple statistical estimates for quantifying spatial variation in body condition of blue suckers addresses Richter's (2007) call for additional evaluation of body condition in fishes outside of the traditional sport fish management paradigm.

TABLE 1. Nineteen geographic locations of blue suckers from the data used by Neely et al. (2008), the number of original populations combined into each location, the sample size of fish collected prior to 2008, and the sample size of fish collected in the Missouri River during 2008 (not used in analyses; R. = River, MO = Missouri, KS = Kansas, NE = Nebraska, IA = Iowa, SD = South Dakota, ND = North Dakota, MT = Montana, TN = Tennessee, OH = Ohio, TX = Texas, IN = Indiana, WI = Wisconsin).

Geographic location	Original populations	Pre-2008 *n*	2008 *n*
Lower Mississippi R.	2	108	
Missouri R. from Mississippi R., MO, to Osage R., MO	1	351	65
Missouri R. from Osage R. to Grand R., MO	2	319	67
Missouri R. from Kansas R., KS, to St. Joseph, MO	1	129	62
Missouri R. from St. Joseph, MO, to Nishnabotna R., NE	2	651	126
Missouri R. from Nishnabotna R. to Platte R., NE	1	1,956	389
Missouri R. from Platte R. to Blair, NE	1	1,242	287
Missouri R. from Blair, NE, to Sioux City, IA	1	1,279	241
Missouri R. from Sioux City, IA, to Ponca, NE	1	191	87
Missouri R. from Ponca, NE, to Gavins Point Dam, NE–SD	1	531	481
Missouri R., Lake Oahe, SD	5	155	
Missouri R., ND	2	312	
Missouri R., MT, and Yellowstone R.	7	169	59
Hatchie R., TN	2	63	
Kansas R., KS	1	173	
Ohio R., OH	1	96	
Rio Grande R. and Colorado R., TX	3	55	
Wabash R., IN	1	354	
Wisconsin R., WI	11	328	

METHODS

Blue sucker weight–length data.—Weights (W) and TLs for 8,462 blue suckers measured prior to 2008 from 46 populations in 14 states were compiled by Neely et al. (2008); we combined these populations into 19 geographic locations (Table 1; Figure 1) based on spatial proximity of sample locations in the same river system. Blue suckers were grouped into coherent geographic locations that maintained sufficient sample sizes (n > 50 fish; most n > 100 fish) within locations to permit a comprehensive quantile regression analysis. Total lengths ranged from 240 to 892 mm; the 5th, 25th, 50th, 75th, and 95th percentiles were 510, 594, 644, 692, and 765 mm, respectively.

Quantile regression models and analysis.—We used quantile regression to obtain estimates of the quantiles of weight as a function of TL without assuming a parametric form for the error distribution (Koenker and Bassett 1978; Cade and Noon 2003; Koenker 2005), thus allowing for heterogeneity in allometric exponents both within and among groups of fish (Cade et al.

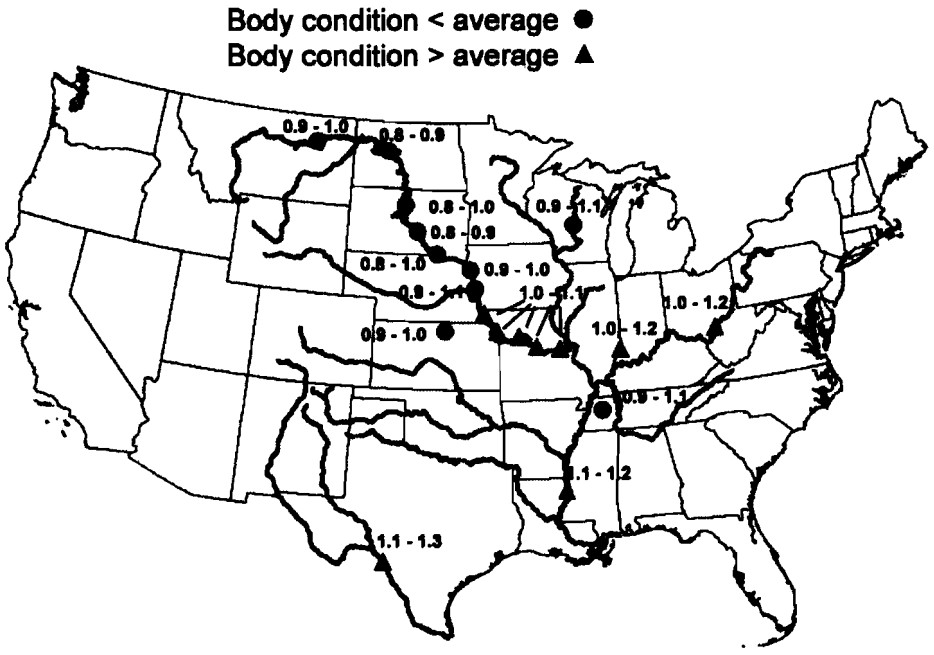

FIGURE 1. Approximate geographic locations of 19 blue sucker populations in the central USA. Numbers shown near symbols denote the range of proportionate differences (to the nearest tenth) from the average across the 19 locations for the 0.05–0.95 quantiles of adult weight at total lengths of 594, 644, and 692 mm. Symbols denote locations where the majority of the quantile distribution and means from the mixed-effects regression model of proportionate differences were less than 1 (red circles) or greater than 1 (blue triangles). [Figure available online in color.]

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2008). The essence of quantile regression is that the usual single mean function estimated in the linear model is replaced with a family of functions across all or a selected subset of quantiles on the interval 0–1. This provides a comprehensive view of how all parts of the distribution of the response variable (W) change conditional on predictor variables (TL and grouping variables). The quantile regression model of allometric growth expands on the scaled mass index approach of Peig and Green (2010) by allowing heterogeneity in exponents within and among groups.

We modified the expanded allometric model used by Cade et al. (2008) to estimate and compare body condition of blue suckers among 19 geographic locations. Intercept (β_0) and exponent (β_1) terms were averages across quantiles of the 19 locations, and the terms β_{0j} and β_{1j} were the proportionate differences in intercepts and exponents, respectively, from the average across locations by quantile (τ) for the $j = 1, \ldots, 18$ locations (i.e., the 19th location was obtained by subtraction),

$$Q_W(\tau|\mathrm{TL}, I_j) = \beta_0(\tau)\mathrm{TL}^{\beta_1(\tau)}10^{\beta_{0j}(\tau)I_j}\mathrm{TL}^{\beta_{1j}(\tau)I_j}, \quad (1)$$

where W is weight in grams, TL is in millimeters, and I_j are orthogonal contrasts that are coded as 1 if the location $j = 1, \ldots, 18$, as 0 if not, and as -1 if the 19th location ($\sum \beta_{0j}[\tau] = 0$, $\sum \beta_{1j}[\tau] = 0$). The model depicted in equation (1) was expressed as a linear model (equation 2) by applying $\log_{10}$ transformations, as is commonly done for most weight–length estimates in fisheries applications (Murphy et al. 1990):

$$Q_{\log_{10} W}(\tau|\log_{10}\mathrm{TL}, I_j) = \log_{10}\beta_0(\tau) + \beta_1(\tau)\log_{10}\mathrm{TL} + \beta_{0j}(\tau)I_j + \beta_{1j}(\tau)I_j\log_{10}\mathrm{TL}. \quad (2)$$

We also used an alternative parameterization of equation (2) by eliminating the β_0 and β_1 terms and using indicator variable coding, where I_j take the value of 1 if $j = 1, \ldots, 19$ locations and 0 if not such that estimates were obtained for the actual intercepts and exponents by location rather than as differences from the average across locations:

$$Q_{\log_{10} W}(\tau|\log_{10}\mathrm{TL}, I_j) = \beta_{0j}(\tau)I_j + \beta_{1j}(\tau)I_j\log_{10}\mathrm{TL}. \quad (3)$$

The quantile regression models (equations (2) and 3) allow the estimation of a wide variety of homogeneous and heterogeneous patterns of weight as a function of length (Cade et al. 2008). Because we anticipated heterogeneity in allometric exponents among blue sucker capture locations, we estimated changes in body condition by differences in the quantiles of weight and their CIs for adults at TLs of 510, 594, 644, and 692 mm, which were the 5th, 25th, 50th, and 75th percentiles, respectively, of lengths. The 25th to 75th percentiles of lengths were well represented

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at all locations and served as our primary measures to compare body condition among geographic locations. We also compared W at a TL of 510 mm at selected locations to examine how differences in body condition varied at a shorter length. These comparisons were done by rescaling TL by division ($\log_{10}\text{TL}_c = \log_{10}[\text{TL} \div \text{selected value}] = \log_{10}\text{TL} - \log_{10}[\text{selected value}]$) as described by Cade et al. (2008) such that intercept estimates on the rescaled TL data are now for the selected value of length rather than a $\log_{10}$TL equal to 0. Confidence intervals provided for $\beta_{0j}(\tau)$ in equation (2) on the rescaled data back-transformed by exponentiation are prediction intervals for location j weights $\div$ the average across weights at all locations given a TL equal to the specified value (i.e., where $\text{TL}_c = 1$). Similarly, CIs provided for $\beta_{0j}(\tau)$ in equation (3) on the rescaled data when back-transformed by exponentiation are then prediction intervals for location j weights given a TL equal to the specified value. The two alternative formulations of the 38-parameter model allowed us to examine intervals on proportionate differences in quantiles or actual quantiles of weight at any length. Back-transforming to the nonlinear allometric form provided valid quantile estimates in the original scale because the quantile estimators are equivariant to linear or nonlinear monotonic transformations of the dependent variable (i.e., $Q_{\log_{10} W}[\tau] = \log_{10} Q_W[\tau]$; Koenker 2005).

We used the linear quantile regression function rq(), available in quantreg version 4.46 for R version 2.10.1 (cran.r-project.org), to obtain model estimates, and we used the Powell sandwich kernel density option to estimate CIs on parameters (Koenker 2005: 80–81). The Powell sandwich kernel density estimator of CIs was used rather than the rank-score test inversion approach used by Cade et al. (2008) because the large sample sizes in the blue sucker models required excessive computing time for the rank-score test inversion approach. In some of the limited comparisons we made, the blue sucker model CIs yielded by the Powell sandwich kernel density estimator were similar to the CIs produced by the rank-score test inversion approach with weighting for heterogeneous errors (Koenker and Machado 1999; Cade et al. 2006). Because of large sample sizes, we estimated quantiles by increments of 0.01 from 0.05 to 0.95 (i.e., 91 estimates) rather than obtaining all possible estimates on the interval $\tau \in [0.05, 0.95]$. Graphs of parameter estimates and 95% CIs were made for $\tau = \{0.05, 0.06, \ldots, 0.94, 0.95\}$, and estimated functions were graphed for a subset of $\tau = \{0.05, 0.25, 0.50, 0.75, 0.95\}$ to provide a comprehensive description of changes in quantiles of weight as a function of length. Confidence intervals provide their stated coverage level pointwise by quantile. Example command scripts for conducting quantile regression analyses in quantreg are provided in Appendix A (in the online version of this paper).

Mixed-effects mean regression model.—We estimated mean weight–length regression models allowing for separate intercepts and exponents among locations by using a linear mixed-effects model similar to that used by Lai and Helser (2004),

$$E[\log_{10} W] = \log_{10} \beta_0 + \beta_1 \log_{10} \text{TL} + \log_{10} \alpha_{0j} + \alpha_{1j} \log_{10} \text{TL} + \varepsilon, \quad (4)$$

where β_0 and β_1 are the fixed-effect intercept and exponent for an average location; $\log_{10}\alpha_{0j}$ and α_{1j} are random deviations of the intercepts and exponents for the $j = 1, \ldots, 19$ locations ($\log_{10}\alpha_0 \sim \text{N}(0, \sigma_0^2)$, $\alpha_1 \sim \text{N}(0, \sigma_1^2)$, with correlation ρ_{12} between $\log_{10}\alpha_0$ and α_1); and $\varepsilon \sim \text{N}(0, \sigma_e^2\mathbf{U})$. We used a weighted analysis to account for variances in $\log_{10}W$ increasing with $\log_{10}$TL, where variance weights in the diagonal matrix $\mathbf{U}$ were inversely proportional to $\log_{10}$TL. We used a similar approach of rescaling at TLs of 510, 594, 644, and 692 mm, as was done for the quantile regression model, to examine differences in body condition of blue suckers by comparing mean weights at selected lengths across locations. Here, the exponentiated estimates of $\log_{10}\alpha_{0j}$ (and their CIs) are the estimated proportionate differences in mean weight for the jth location $\div$ mean weight for an average location given a TL equal to a specified value. We estimated mixed-effects models using the lmer() function in lme4 version 0.999375–32 for R software.

Relative weight analysis.—We used the linear W_s equation ($\log_{10}W_s = -6.301 + 3.456 \cdot \log_{10}\text{TL}$) from Neely et al. (2008) to estimate W_s and to compute W_r for blue suckers obtained prior to 2008. Because W_r is simply the proportionate difference between W and W_s (i.e., $W_r = W \div W_s$; the multiplication by 100 being superfluous), we used $\log_{10}W_r = \log_{10}W - \log_{10}W_s$ to compare proportionate differences in mean W_r among the 19 locations by using fixed-effects analysis of variance. We compared W_r for fish in two TL intervals (510–594 and 594–692 mm) so that these comparisons could be related to those obtained from quantile regression and mixed-effects mean regression models for TLs of 510, 594, 644, and 692 mm. Sample sizes in these length intervals were always more than adequate for comparisons of means among groups. Differences in means and their CIs were back-transformed by exponentiation. Because the $\log_{10}W_r$ values are residuals, these comparisons of W_r were similar to testing for group differences in an ANCOVA that (1) assumes that the W_s equation holds for all groups and (2) completely adjusts for allometric growth for the lengths used in the analysis.

RESULTS

Quantile Regression Estimates of Blue Sucker Body Condition

The average of the quantile regression exponents across all 19 locations varied by $\pm$ 0.05 around 3.45 for τ of 0.05–0.95 (Figure 2), similar to the exponent of 3.456 from the W_s equation for blue suckers. However, allometric exponents varied from 2.88 to 4.24 across quantiles for the 19 individual

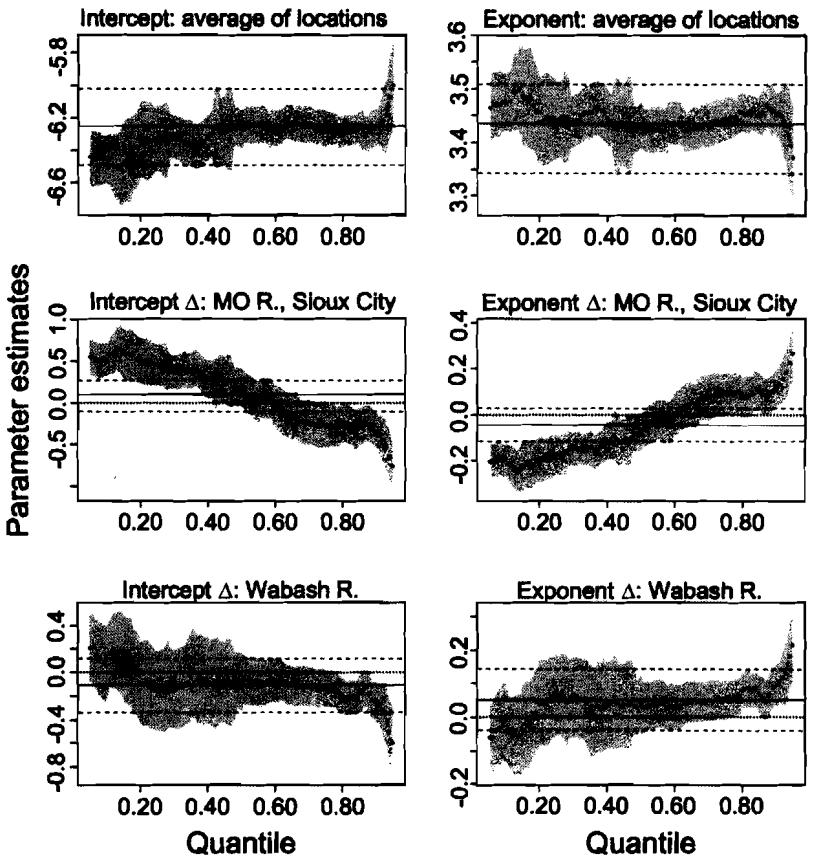

FIGURE 2. Estimates (black dots) and 95% confidence intervals (CIs; gray bands) at quantiles of 0.05–0.95 for 6 of the 38 parameters in the quantile regression model (equation 2) of blue sucker weights conditional on total length. Estimates for the Missouri River from Blair, Nebraska, to Sioux City, Iowa, and for the Wabash River, Indiana, are differences (Δ) in intercepts and exponents from the average across the 19 central U.S. locations (Figure 1). Solid blue lines and dashed blue lines are the comparable mean estimates and 95% CIs, respectively, from the mixed-effects mean regression model (equation 4). Estimates for the remaining 32 parameters are presented in Figure B.1 (Appendix B online). [Figure available online in color.]

geographic locations; rivers in Texas had the largest exponents at lower quantiles, and Lake Oahe on the Missouri River, South Dakota, had the smallest exponents at all quantiles. Proportionate differences in weights with respect to the average across locations for adult blue suckers at TLs of 594, 644, and 692 mm for equation (2) ranged from 1.08 to 1.30 for southern locations (the lower Mississippi River and Texas rivers) and from 0.84 to 1.00 for northern locations (Lake Oahe; the Missouri River in North Dakota–Montana; and the Missouri River from Ponca, Nebraska, to Gavins Point Dam, Nebraska–South Dakota; Figure 1). This indicates as much as a 55% greater weight at length ($1.55 = 1.30 \div 0.84$) between locations. Most locations with fish in above-average body condition were at the more southerly latitudes; the less-than-average body condition of blue suckers in the Hatchie River, Tennessee, was the notable exception (Figure 1). The well-sampled section of the Missouri River from its confluence with the Mississippi River upstream to Gavins Point Dam (Table 1) reflected a gradient of proportionate differences from 1.02–1.11 downstream to 0.83–0.92 upstream (Figure 1); weight at length was as much as 34% greater in the southern, downstream locations.

Estimates from equation (2) for all locations are provided in Figure B.1 (Appendix B in the online version of this paper), but here we illustrate details for a range of differences found by examining estimates by quantile for the Missouri River from Blair, Nebraska, to Sioux City, Iowa, and for the Wabash River, Indiana (Figures 2, 3, and 4). Exponents for the Wabash River exceeded the average across populations by 0.10 at upper quantiles but differed little at lower quantiles (Figure 2), indicating heterogeneity in allometric exponents. Heterogeneity in exponents (Figure 2) or proportionate differences in weight (Figure 4) are indicated by quantile estimates and confidence bands that deviate from a constant horizontal band. Graphs of quantile estimates, weight, and length for fish in the Wabash River substantiated the greater allometric growth relative to the average across locations (Figure 3), consistent with the differences in exponents (Figure 2). Heterogeneity in proportionate differences in quantiles of weights for Wabash River blue sucker

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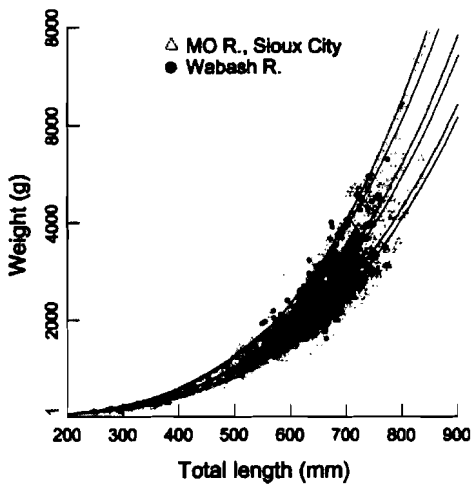

FIGURE 3. Estimates at quantiles of 0.05 (lower three lines), 0.50 (middle three lines), and 0.95 (upper three lines) for blue sucker weights conditional on total length based on data for the Missouri River from Blair, Nebraska, to Sioux City, Iowa (orange dashed lines), and for the Wabash River, Indiana (gray lines). Thin black lines are the comparable quantile estimates averaged across the 19 central U.S. locations included in the quantile regression model (equation 2). Symbols represent the weights and lengths for fish from the Missouri River (open orange triangles) and Wabash River (gray shaded circles) locations. [Figure available online in color.]

adults with respect to the average across locations was evident at all lengths examined but decreased with increasing length. When TL was 510 mm, weights of adults were 1.07 times the average (hereafter, "× avg.") at lower quantiles and 0.96 × avg. at higher quantiles (Figure 4). As TL increased to 692 mm, weights varied from around 1.05 × avg. at lower quantiles to around 1.02 × avg. at higher quantiles (Figure 4). Thus, the greatest differences in weight at length for adults in the Wabash River compared with the rangewide average were for fish that weighed less (lower quantiles) at shorter TLs, although most weights at length were greater than average except for the heaviest fish at shorter lengths.

Allometric exponents for the Missouri River from Blair to Sioux City were as much as 0.20 less at lower quantiles and 0.10 greater at higher quantiles than the average across locations, indicating substantial heterogeneity in exponents (Figure 2). Graphs of quantile estimates, weight, and length for fish from this location indicated that most quantiles of allometric growth were less than the average across locations (Figure 3). Heterogeneity in proportionate differences in quantiles of weights for adults in this Missouri River segment relative to the average across locations was evident at all lengths examined but increased with increasing length. At a TL of 510 mm, weights of adults were 0.96 × avg. at lower quantiles and were around 0.93 × avg. at higher quantiles (Figure 4). As TL increased to 692 mm, blue sucker weights were 0.90 × avg. at lower quantiles and approached 1.00 × avg. at the highest quantiles (Figure 4). Thus, the lowest weights at length for adults in this Missouri River segment compared with the rangewide average were for fish that weighed less (lower quantiles) at longer TLs, and all but the heaviest fish (highest quantiles) at length weighed less than average.

Estimated weights by quantile based on equation (3) that correspond to proportionate differences estimated from equation (2) also are depicted in Figure 4 (right column of panels) for adult blue suckers from the two locations. Fish from the Wabash River had substantially greater weights at lower quantiles compared with fish sampled in the Missouri River from Blair to Sioux City (Figure 3). Blue suckers with the lowest weights at length (lower quantiles) were as much as 17% heavier ($1.166 = 1.05 \div 0.90$) in the Wabash River than in the Missouri River segment. Thus, the Wabash River fish that were in less-than-average condition (lower quantiles) exhibited substantially better condition than the Missouri River (Blair to Sioux City) fish that were in less-than-average condition, whereas differences between the two locations were less for fish in better-than-average condition (higher quantiles; Figure 4).

We can also summarize the distributional differences of weight at length by estimating prediction and tolerance intervals. Point estimates of weight at a given length for the 0.05 and 0.95 quantiles (Figure 4) form a 90% prediction interval ($0.95 - 0.05 = 0.90$) for weight of a single new fish at that length. For example, at a TL of 594 mm, the 90% prediction interval was 1,368–2,152 g for the Missouri River from Blair to Sioux City and was 1,562–2,246 g for the Wabash River. Lower 95% CI endpoints of 0.05 quantiles and upper 95% CI endpoints of 0.95 quantiles (Figure 4) can be used to form 95% tolerance intervals for 90% of fish at that length (or, equivalently, for all future observations of fish). At a TL of 594 mm, the 95% tolerance interval on 90% of fish at that length was 1,350–2,194 g for the Missouri River segment and was 1,521–2,304 g for the Wabash River. Tolerance intervals are longer because their probability content is at least 95% for any number of fish, whereas the prediction intervals are an average statement for a single fish (Vardeman 1992).

The prediction and tolerance intervals above provide distributional summaries that can be used to establish relevant intervals of weight to associate with new observations of fish described only by TL measurements. However, we might also be interested in characterizing the percentiles for a new observation of a fish for which both weight and TL have been measured, comparable to how W_r is often used (Cade et al. 2008). As an example, consider a blue sucker with a W of 3,000 g and a TL of 692 mm (Figure 5). The W_r of this individual would be 0.918 ($W_r = 10^{\log_{10}[3{,}000]-[-6.301+3.456\times\log_{10}\{692\}]}$), indicating a weight that is 8% less than the standard 75th-percentile weight. If this adult is from the Wabash River, then the weight at length is consistent with the 23rd to 36th percentiles based on intersection with 95% CIs for quantiles of weight at length (Figure 5). If this fish is from the Missouri River (Blair to Sioux City), then the weight at length is consistent with the 63rd to 70th percentiles. If this fish is from a location other than the 19 locations used in our analyses, what interval of percentiles should apply to

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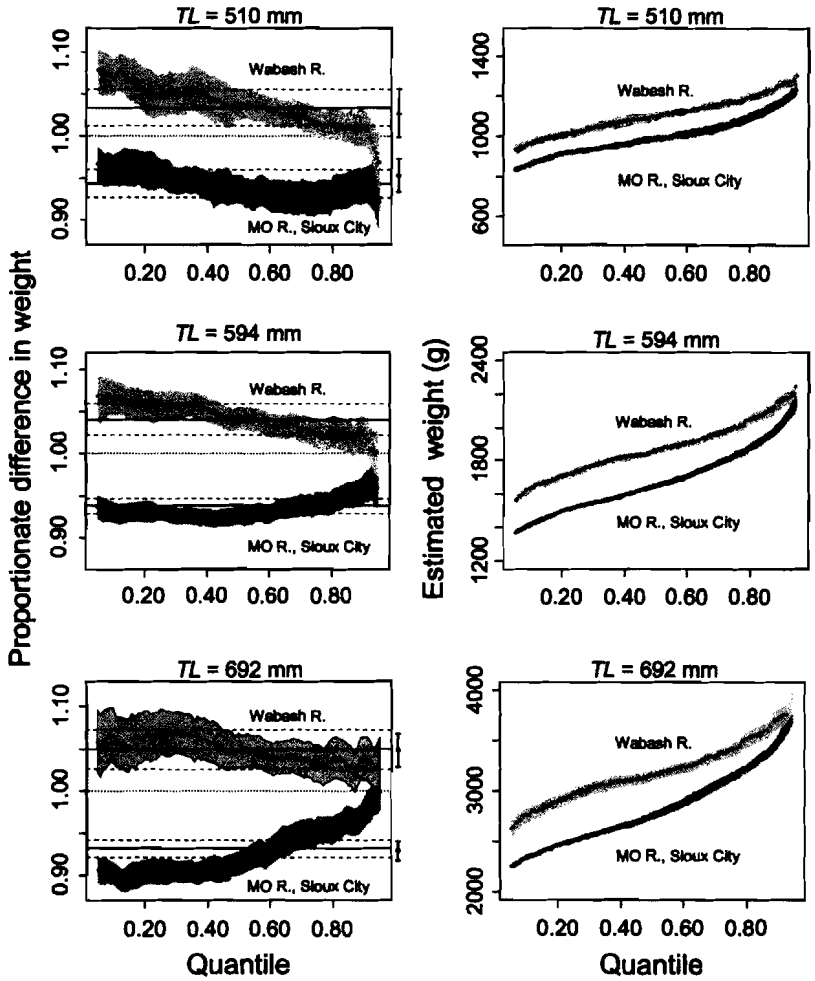

FIGURE 4. Estimated proportionate differences (black dots) at quantiles of 0.05–0.95 for weight at a total length (TL) of 510, 594, or 692 mm for adult blue suckers in the Missouri River from Blair, Nebraska, to Sioux City, Iowa (orange bands = 95% confidence intervals [CIs]), and in the Wabash River, Indiana (gray bands = 95% CIs), with respect to the average across the 19 central U.S. locations (left column of panels). Solid blue lines are estimates from the mixed-effects mean regression model (equation 4), and dashed blue lines are 95% CIs on those estimates. Solid circles at the right edge of the quantile panels are proportionate differences (±95% CIs) in relative weight for a TL interval of 510–594 mm (top left panel) or 594–692 mm (bottom left panel). The right column of panels depicts the estimated 0.05–0.95 quantiles of weight and corresponding 95% CIs for the same lengths from the alternative quantile regression model (equation 3). [Figure available online in color.]

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reasonably reflect the uncertainty? It is tempting to consider the interval of 44th to 52nd percentiles around the point estimate of the 49th percentile, associated with the intersection of W = 3,000 g and the confidence band for the averages of quantiles across the 19 locations, as a relevant interval to characterize this uncertainty for a fish from another location. Such an approach would be consistent with the use of W_s equations and W_r, which average across all sampled locations. However, this interval is associated with averages across all locations and is not a relevant interval for describing uncertainty in percentiles of weight at length for a single fish from a single unspecified location. A more realistic interval about this point estimate would be the 5th to 95th percentiles obtained by intersecting the W of 3,000 g and the most extreme weight-at-length distributions for this TL (692 mm), which are associated with Lake Oahe and the lower Mississippi River (Figure 5). Thus, this weight at length for an individual fish could be associated with any interval of percentiles between the 5th and 95th percentiles if we assume that the estimated variation in distributions of weight at a TL of 692 mm among the 19 sampled locations is representative of all locations.

Mixed-Effects Mean Regression Estimates of Blue Sucker Body Condition

Estimates for mean weight as a function of length from the mixed-effects mean regression model (equation 4) had exponents and proportionate differences in weight at TLs of 510, 594, 644, and 692 mm that were intermediate in value compared with

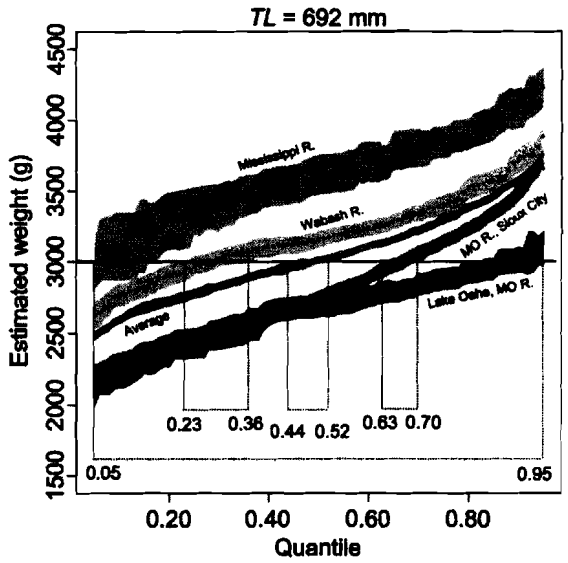

FIGURE 5. Estimates at quantiles of 0.05–0.95 for weight at a total length (TL) of 692 mm for adult blue suckers: Missouri River from Blair, Nebraska, to Sioux City, Iowa (orange band = 95% confidence interval [CI]); Wabash River, Indiana (gray band = 95% CI); the average across the 19 central U.S. locations (light-blue band = 95% CI); lower Mississippi River (magenta band = 95% CI); and Lake Oahe on the Missouri River (green band = 95% CI). Confidence bands for all other locations not shown here are contained between those for the lower Mississippi River and Lake Oahe. Solid black line represents a blue sucker with an observed weight (W) of 3,000 g at a TL of 692 mm. Intervals indicated by dotted lines represent percentiles consistent with a W of 3,000 g for the Wabash River (0.23–0.36), the average across locations (0.44–0.52), or the Missouri River segment (0.63–0.70). The interval from 0.05 to 0.95 represents the interval at this TL across distributions for all locations. [Figure available online in color.]

the lowest and highest estimates across quantiles for a location. The estimated exponent for mean weight as a function of length for an average location was 3.426 (95% CI = 3.34–3.51), but exponents were as low as 3.033 for Lake Oahe and as high as 3.597 for the Missouri River from Sioux City to Ponca. Proportionate differences in mean weight with respect to the average across locations for adults at TLs of 510, 594, 644, and 692 mm for equation (4) ranged from 1.13 to 1.17 for Texas rivers and the lower Mississippi River and ranged from 0.87 to 0.95 for Lake Oahe, the Missouri River in North Dakota–Montana, and the Missouri River from Ponca to Gavins Point Dam.

Details on differences in exponents and proportionate differences in mean weight for adult blue suckers from the Missouri River (Blair to Sioux City) and Wabash River locations are provided for comparison with quantile estimates reported above. Fish in the Wabash River had mean weights that were 1.033 × avg. (95% CI = 1.01–1.06) at a TL of 510 mm, 1.041 × avg. (95% CI = 1.02–1.06) at 594 mm, and 1.050 × avg. (95% CI = 1.03–1.07) at 692 mm (Figure 4). These mean weight estimates are clearly intermediate in value to those provided by the quantile estimates, and the differences in quantile estimates and mean weights increased with increasing heterogeneity at shorter lengths (Figure 4). Confidence intervals on the estimated differences in intercepts and exponents for mean weights indicated no difference from the average population and reflected differences found across the central 60% of the quantile distribution (Figure 2). Greater differences found in the tails of the distribution for τ less than 0.20 and greater than 0.80 were not reflected in the mean estimates. Fish in the Missouri River segment had mean weights that were 0.943 × avg. (95% CI = 0.93–0.96) at a TL of 510 mm, 0.938 × avg. (95% CI = 0.93–0.95) at 594 mm, and 0.932 × avg. (95% CI = 0.92–0.94) at 692 mm (Figure 4). Confidence intervals on estimated differences in intercepts and exponents for mean weights indicated no difference from the average location but clearly failed to discern greater differences estimated at lower and higher quantiles (Figure 2). Proportionate differences in mean weights and their CIs for these two locations were clearly intermediate in value when compared with quantile estimates, indicating that the mean did not reflect heterogeneous differences associated with fish in both greater-than-average (higher quantiles) and less-than-average (lower quantiles) body condition (Figure 4). Greater disparity between the quantile and mean regression estimates occurred for the Missouri River segment, where heterogeneity in allometric exponents across quantiles was greater (Figure 2).

Relative Weight Estimates of Blue Sucker Body Condition

Comparison of blue sucker $\log_{10} W_r$ among locations by use of fixed-effects analysis of variance indicated that proportionate differences in mean W_r ranged from 1.10 to 1.11 × avg. for adults with TLs of 510–594 mm and ranged from 1.17 to 1.18 × avg. for adults with TLs of 594–692 mm in the lower Mississippi River and the Texas rivers. Proportionate differences in mean W_r were 0.88–0.98 × avg. at 510–594 mm and were 0.86–0.87 × avg. at 594–692 mm in the Missouri River, North Dakota, and the Missouri River from Ponca to Gavins Point Dam. For the 510–594-mm TL interval, proportionate differences in mean W_r differed from the proportionate differences in mean weight from the mixed-effects regression by 0.85–1.23 and exhibited r-values of 0.87–0.91 across locations. For the 594–692-mm interval, proportionate differences in mean W_r differed from the proportionate differences in mean weight from the mixed-effects regression by 0.93–1.10 and had r-values of 0.98–0.99 across locations. Thus, mean W_r followed a pattern of lesser proportionate differences in northern locations relative to southern locations, similar to the pattern found for the mean and quantile regression models.

Mean values of W_r for blue suckers from the Missouri River (Blair to Sioux City) were 0.953 × avg. (95% CI = 0.93–0.97) for the 510–594-mm TL interval and 0.929 × avg. (95% CI = 0.92–0.94) for the 594–692-mm TL interval. There was greater departure between the proportionate differences in means estimated by W_r compared with the mixed-effects regression model for the 510–594-mm interval than for the 594–692-mm interval (Figure 4). Similar to the mean regression model estimates, proportionate differences in mean W_r did not reflect minimal

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reductions (approaching 1.0) estimated for higher quantiles of fish with greater-than-average body condition at longer lengths. Mean W_r values for fish from the Wabash River were 1.026 × avg. (95% CI = 1.00–1.06) for the 510–594-mm interval and were 1.049 × avg. (95% CI = 1.03–1.07) for the 594–692-mm interval. Again, there was greater departure between the proportionate differences in means estimated by W_r compared with the mixed-effects regression model for the 510–594-mm interval than for the 594–692-mm interval (Figure 4), and mean W_r estimates failed to reflect the greater weight differences for fish in lower-than-average body condition (lower quantiles), especially at shorter lengths.

The patterns of departure of W_r can be explained by examining scatter plots of W_r for the 594–692-mm TL interval with respect to the W_s equation and quantile estimates all divided by W_s (Figure 6). Heterogeneity in remaining allometric growth was indicated by quantile estimates for the Missouri River (Blair to Sioux City) and Wabash River that were not parallel to the quantile estimates averaged across locations or to the W_s equation. Although the lack of parallelism in slopes appears to be slight when plotted on the $\log_{10}$ scale (Figure 6), the differences when exponentiated were more substantial, as indicated above. The heterogeneity remaining in the quantile estimates for the Missouri River segment exhibited a classic pattern of variance increasing with the predictor TL such that lower quantiles had decreasing slope and upper quantiles had increasing slope. The heterogeneity in the Wabash River was most pronounced in the increasing slopes of upper quantiles. The proportionate differences in W_r assumed that there was no remaining allometric change in W with TL within either of the TL intervals (510–594 or 594–692 mm) that were used to group the values.

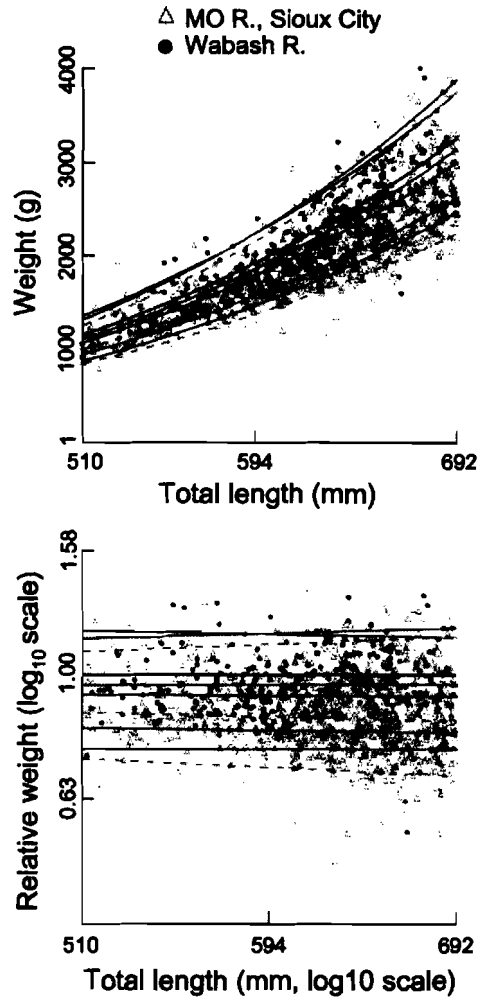

FIGURE 6. Top panel presents estimates at quantiles of 0.05 (lower three lines), 0.50 (middle three lines), and 0.95 (upper three lines) for blue sucker weights conditional on total length (TL) for the Missouri River from Blair, Nebraska, to Sioux City, Iowa (orange dashed lines), and for the Wabash River, Indiana (gray lines), based on a TL interval of 510–692 mm. Thin black lines are the comparable quantile estimates averaged across the 19 central U.S. locations included in the quantile regression model (equation 2). The solid red line represents the exponentiated standard weight (W_s) equation ($\log_{10}W_s = -6.301 + 3.456 \cdot \log_{10}\text{TL}$). Symbols represent the weights and lengths for fish from the Missouri River (open orange triangles) and Wabash River (gray shaded circles) locations. The bottom panel has the same observations and model estimates transformed to the $\log_{10}$(relative weight) scale by rescaling $\log_{10}$(weight), $\log_{10}$(TL), quantile estimates, and the W_s equation (now a horizontal function at 1.0; red line) by the W_s equation. Some of the quantile estimates are not parallel to either the horizontal W_s equation line or the averaged quantiles across locations, thus indicating the remaining heterogeneity in allometric growth for the two locations. [Figure available online in color.]

DISCUSSION

There clearly was substantial variation in the exponents of allometric growth that impacted variation in body condition of adult blue suckers among locations in the major drainages of the central USA. The differences in allometric exponents within and among locations (from less than 3 to over 4) were associated with weights at longer TLs (e.g., 692 mm) that varied by 700–800 g among adults (central 90th percentiles) within a location and by as much as 2,000 g among locations. Although the use of W_r to characterize body condition involved averaging across all allometric exponent differences, proportionate differences in W_r still followed the trend of decreasing body condition with increasing latitude, which was found by the mean and quantile regression models of allometric growth. The trend of decreasing body condition with increasing latitude could be related to physiological growth tolerances and water temperature but requires further investigation. A similar latitudinal gradient for growth rates of blue suckers has been noted by others (Bednarski and Scarnecchia 2006; Eitzmann et al. 2007) and has been suggested more generally for fishes of the Missouri River (Braaten and Guy 2002).

We observed some convergence in weight distributions at length for the highest quantiles, which represent fish in greater-than-average body condition, such as the blue suckers in the Wabash River and in the Missouri River from Blair to Sioux City (Figure 4). If this convergence at the highest quantiles

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of weight at length represents convergence to some maximum physiological limit on the weight obtainable for blue suckers, then it is reasonable to expect heterogeneous distributions of weights at length because some of the collected fish may be near a physiological weight limit imposed by length, whereas others will be below the weight limit for a variety of reasons. This length-imposed limit to weight suggests that similar statistical issues associated with modeling limiting factors (discussed by Cade and Noon 2003) apply to understanding the biological or environmental factors associated with differences in weight–length relationships.

Based on the present study, the work of Cade et al. (2008), and studies describing the development and applications of W_s equations (Murphy et al. 1990; Brenden et al. 2003; Lai and Helser 2004; Hansen and Nate 2005; Ogle and Winfield 2009; Gerow 2010), we believe that heterogeneity in allometric exponents should be considered the norm when evaluating fish body condition. The amount of information on variation in body condition provided by quantile estimates will always be as much as or more than that provided by mean estimates, and the amount of information provided by both of these expanded allometric models will always be as much as or more than that provided by analyses of W_r. Mean allometric models can be considered averages across the quantiles; thus, when there is substantial heterogeneity among quantiles within a location, the mean will average out the greater and lesser proportionate changes in the distribution of fish weight at length. Although we estimated our mean regressions as mixed-effects models, we could have reasonably estimated them as fixed-effects models also, which would have yielded similar behavior with respect to the quantile estimates.

Some of the differences among locations might reflect inconsistent time frames for sampling blue suckers with respect to seasons. The data set of Neely et al. (2008) lacked information to determine differences or similarities in the season of sampling. Pope and Willis (1996) have suggested that comparisons of condition are best made across similar seasons. To the extent that the sampling of blue suckers might have been inconsistent across seasons, especially with regard to prespawning versus postspawning periods, we might expect some differences in allometric exponents and body condition. In some of the limited temporal analyses we conducted, we found substantial annual variation in blue sucker body condition for three of four locations examined on the Missouri River based on fish samples obtained during the same season in 2008 and prior to 2008. Thus, while some location differences could reflect unknown, inconsistent sampling across seasons, it also is likely that there are substantial annual differences in blue sucker body condition within the same location during the same season. As with any other species, detailed comparisons of body condition for the blue sucker would benefit from being able to control for seasonal differences, either by limiting sampling to a common season or by including season as another predictor in the model. However, it is doubtful that controlling for seasonal or annual variation in weight–length relationships will eliminate the heterogeneity in allometric growth exponents we observed for blue suckers. Obtaining biologically relevant information (e.g., water temperature, water chemistry, hydrology, etc.) that can be incorporated into these quantile regression models as predictor variables to identify statistical associations is a logical next step to determining specific causes for changes in body condition and relating them to environmental changes.

Estimates of proportionate differences provided by W_r are similar to those provided by mean allometric regression models when allometric exponents are (1) relatively homogeneous among the groups of fish being compared and (2) similar to the exponent in the W_s equation. However, there is no a priori reason to expect those conditions. Verifying that the conditions have been met requires detailed allometric modeling similar to our regression analyses. Shifting to a percentile other than the 75th percentile to define W_s equations, as has been recently suggested by Gerow (2010), will not alter the reliance of W_r on a single allometric exponent. Regardless of the percentile selected, W_r only provides reasonable estimates of proportionate differences in body condition when there is homogeneity of exponents within and among the groups of fish being compared. All percentiles will yield equivalent proportionate differences because W_r based on different percentiles would only shift by a constant across all groups when there is homogeneity of exponents.

Our reasonably successful use of W_r to quantify a similar north–south gradient of increasing body condition was predicated on comparing mean W_r in a multiplicative model by using logarithmic transformations, something that seems to be rarely done in W_r comparisons (Brenden et al. 2003; Pope and Kruse 2007). Multiplicative comparisons of mean W_r are justified because W_r values are simply a form of residual from an allometric relationship estimated in the log–log transformed scale. Our comparisons of W_r for the central interval of lengths (25th to 75th percentiles) were made because we knew that substantial sample sizes were available for each geographic location, thus facilitating powerful statistical comparisons of mean W_r. The effect of heterogeneity in allometric exponents was minimized at these central values of length. At more-extreme lengths (e.g., the 5th percentile, which was used for some of our analyses), heterogeneity of allometric exponents has more-pronounced effects on the disparities between proportionate differences in mean W_r compared with mean allometric regression model estimates.

We note that our CI estimates for proportionate differences in W_r were the typical naïve estimates that do not incorporate the sampling variability associated with estimating the W_s equation. Brenden et al. (2003) proposed some alternative approaches for incorporating this sampling variability into SEs for W_r estimates. However, a complication that has not been well addressed in the procedures developed by Brenden et al. (2003) is that estimates of allometric growth for computing W_s equations by using either the empirical percentile method or regression line percentile method are really based on

relationships where the means for groups of fish are statistical replicates, and thus these relationships are fundamentally misleading when applied to evaluate sampling variation in the W_r of individual fish. Regardless of the percentile used to estimate W_s equations via either the empirical percentile or regression line percentile method (Gerow 2010), the sampling variability of the allometric model estimates has been attenuated by not using individual fish as statistical replicates. Rather than trying to solve these issues for W_r, our analyses demonstrate that one can always obtain better to comparable estimates with fewer statistical complications by estimating quantiles or means from an expanded allometric growth model on individual fish.

Our approach of estimating proportionate differences or actual weight distributions at a specified length or percentiles associated with a specific combination of weight and length from the quantile regression analyses (as in Figure 5) provides a general alternative to using W_s equations and W_r for characterizing the body condition of individual fish. Any of the extensive weight–length data sets that have been compiled to estimate W_s equations for various fish species (e.g., Bister et al. 2000; Gerow et al. 2005) might profitably be reanalyzed with appropriate quantile regression models. Look-up charts, graphs, or computer computations could then be derived to evaluate proportionate differences in weight at length relative to average percentiles across populations, individual locations, or regional groupings of populations as desired. Investigators would then have a basis for comparing small numbers of individual fish to percentile distributions of weight at length from more-extensive data sets. We emphasize that the groups of fish against which weight-at-length comparisons need to be made are likely to vary greatly among studies, and thus no universal standard should be specified. The present study and the study by Cade et al. (2008) demonstrate that research investigations evaluating fisheries management with larger samples of fish can readily expand the quantile regression model of allometric growth to include the covariates that are necessary to interpret relevant effects. A focus on percentiles of weight at length for fish is consistent with the use of percentiles in evaluating human growth (Wei et al. 2006).

Both the quantile regression and mean regression models of allometric growth have the advantage of being able to obtain estimates and CIs for actual weights at any specified length as well as proportionate differences in weights among groups of fish—something that is not directly obtained from using W_r. However, when exponentiating the mean estimates and their CIs from $\log_{10}$ transformed models back to the original scale of weight in grams, it is important to adjust for the back-transformation bias by using a procedure such as the nonparametric smearing estimate of Duan (1983). Quantile regression avoids this back-transformation bias issue. Quantile regression also provides distribution-free estimates of prediction intervals for the weight of a single new fish at a specified length and tolerance intervals for weights for a proportion of fish at that length (equivalent to a prediction interval for any number of new fish). Prediction and tolerance intervals also can be estimated from weighted mean regression models based on the assumed normal distribution (Vardeman 1992), but they are more sensitive to violations of the parametric error distribution assumptions than are CIs on the mean regression parameter estimates.

A complication from modeling heterogeneity in exponents with either quantile or mean allometric regression models is that differences in body condition must be examined at multiple lengths. Body condition is an expression of weight at length, but when we allow heterogeneous allometric exponents within and among groups of fish, comparisons of weight at length must be performed at multiple lengths to be informative. We only used four lengths in our evaluation of adult blue sucker body condition to quantify large-scale geographic variation while minimizing the amount of material presented; however, there is nothing to prohibit the use of more lengths for a more-detailed examination. Investigators that attempt to use body condition as an expression of concepts such as fish community health or aquatic habitat quality or as a predictor of community trophic structure or community productivity (as discussed by Richter 2007) should not limit themselves to evaluating weights at the lengths used in the present paper. The choice of how many and which lengths to use should be driven by the pertinent scientific or management questions.

In addition to the development of statistical models that include environmental covariates related to changes in body condition, the same form of allometric growth model can be expanded further to incorporate ideal growth data wherein the lengths and weights of individual fish are recorded for multiple years within the same seasons. Fisheries applications typically lack information on the long-term trajectory of allometric growth of individual fish. However, estimates of the quantiles of allometric growth or the residuals from mean allometric growth based on a large number of fish measured within a single year are essentially projections that are interpreted as if the functional trajectories will continue to other lengths at other years within similar seasons for an individual fish (Lleonart et al. 2000). This assumption can be challenged and models can be refined by obtaining measurements on individual fish that are weighed at multiple lengths as they grow. These temporal trajectories can be accommodated in quantile regression or mean regression models by including information on weight at prior time points as additional predictors in a longitudinal growth model (e.g., as was done with human growth by Wei et al. 2006). Although data on growth of individual fish may not be available, we prefer a consistent modeling approach that permits incorporating this longitudinal growth information when it is available. Ultimately, an understanding of how fish body condition is related to physiological differences that affect subsequent growth, survival, and reproduction requires linkages to individual fish.

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