# A Comparison of Measures of Riverbed Form for Evaluating Distributions of Benthic Fishes

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*Abstract.*—A method to quantitatively characterize the bed forms of a large river and a preliminary test of the relationship between bed-form characteristics and catch per unit area of benthic fishes is presented. We used analog paper recordings of bathymetric data from the Missouri River and fish data collected from 1996 to 1998 at both the segment ($\sim 10^1$–$10^2$-km) and macrohabitat ($\sim 10^{-1}$–$10^0$-km) spatial scales. Bed-form traces were transformed to digital data with image analysis software. The slope, mean residual, and SD of the residuals of the regression of depth versus distance along the bottom, as well as mean depth, were estimated for each trace. These four metrics were compared with sinuosity, fractal dimension, critical scale, and maximum mean angle for the same traces. Mean depth and sinuosity differed among segments and macrohabitats. Fractal-based measures of the relative depth of bottom troughs (critical scale) and smoothness (maximum mean angle) differed among segments. Statistics-based measures of the relative depth of bottom troughs (mean residual) and smoothness (SD of the residuals) differed among macrohabitats. Sites with shovelnose sturgeon *Scaphirhynchus platorynchus* were shallower and smoother than sites without shovelnose sturgeon. When compared with sites without sicklefin chub *Macrhybopsis meeki,* sites with sicklefin chub were shallower, had shallower troughs, and sloped more out of the flow of the river. Sites with sturgeon chub *M. gelida* were shallower, had shallower troughs, and were smoother than sites without sturgeon chub. Sites with and without channel catfish *Ictalurus punctatus* did not differ for any bed-form variables measured. Nonzero shovelnose sturgeon density increased with depth, whereas nonzero sturgeon chub density decreased with depth. Indices of bed-form structure demonstrated potential for describing the distribution and abundance of Missouri River benthic fishes. The observed fish patterns, though limited, provide valuable direction for future research into the habitat preferences of these fishes.

A primary physical characteristic that defines a river is flow (Allan 1995). Flow and morphology determine the type and frequency of habitats available to fishes. Habitat that provides potential refugia from river current for bottom-dwelling or benthic fishes may consist of complex bottom relief associated with sedimentary bed form. Sedimentary bed form is defined as the longitudinal (i.e., parallel to flow) waves of bottom relief and is a function of velocity, particle size, flow depth, and the duration of the flow capable of moving a significant amount of sediment to reform the shape of the bed surface (Engelund and Fredsoe 1982; Middleton and Southard 1984; Southard and Boguchwal 1990). Deeper flows with higher velocities will form larger bed forms that have deeper troughs for a given sediment size if such flows persist long enough. Different bed topographies would result from the same flow for different sediment sizes. Bed form is essentially a record of recent past flows and varies both temporally and spatially. The potentially high energetic costs of maintaining position and moving upstream in a river influence fish habitat choice (Bunt et al. 1999;

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Guensch et al. 2001). Bottom relief becomes a potential refuge from flow and a means for minimizing energetic costs for fish (Gerstner 1998; Guensch et al. 2001). Therefore, the pattern of relief present as a result of past flows (i.e., sedimentary bed form) is one factor to which benthic fishes are likely to respond.

Spatial scale is an important consideration when describing how habitat, such as bed form, varies in rivers and streams (Frissell et al. 1986; Hawkins et al. 1993; Petts and Amoros 1996). Also, the importance of bed form to fishes may vary among species based on the strength of their association with the riverbed. Habitat characteristics vary among river sections, but they also vary among and within macrohabitat types (Hawkins et al. 1993). Quantitative metrics that can identify such differences are needed, particularly metrics that can determine differences in riverbed form at different spatial scales. Differences in bed form among sites may explain differences in fish abundance, particularly for a species like the shovelnose sturgeon *Scaphirhynchus platorynchus*, which lies and travels directly along the bottom. In contrast, channel catfish *Ictalurus punctatus* have benthic affinities but are generalists in their habitat use (Pflieger 1997). Similarly, smaller benthic species, such as sicklefin chub *Macrhybopsis meeki* and sturgeon chub *M. gelida*, might show differences between sites where the species is present versus absent for different parameters and might show patterns for the same parameters opposite those of larger species as a result of the spatial scale to which they respond.

As for most large rivers in the United States (Poff et al. 1997), modifications to the Missouri River ecosystem from impoundment and reservoir operation, channelization and channel maintenance, and flood control are extensive (Hesse 1987). Such alterations have major impacts on fish communities (Schlosser 1991; Gore and Shields 1995). Relating river channel morphologic characteristics with fish data is needed to develop insights into how the physical aspects of large rivers may affect fish distribution. To test this relationship, the characteristics of riverbed morphology must first be quantified. We developed a statistics-based approach to quantify large-river bed form, such that its longitudinal complexity is represented by a regression equation and the statistical moments about that equation (Beyer 1981), and we tested the approach on data from longitudinal traces of bottom topography collected along the Missouri River. We compared our approach to those

adapted from Schiemer et al. (2001) to characterize inshore retention zones and Nestler and Sutton (2000) to characterize large-river channel cross-sections when applied to longitudinal bed-form traces. Our objectives were to use data from the Missouri River to (1) develop statistics-based measures for describing the main-channel, sedimentary bed forms; (2) compare these statistics-based measures of bed form to sinuosity- and fractal-based measures in terms of their effectiveness at identifying differences among segments and macrohabitats; and (3) test the association of the measures from statistics-, sinuosity-, and fractal-based methods with the presence or absence of benthic fishes and, on a finer scale, nonzero fish densities.

## Methods

*Sample collection.*—Data used for this study were a subset of those collected during the Missouri River Benthic Fishes Study (MRBFS). The MRBFS was a systemwide cooperative effort designed to produce a baseline for evaluating how past and potential future alterations of the Missouri River might affect its fish community (Berry and Young 2001). The MRBFS included the warmwater, unimpounded main stem of the Missouri River from river kilometer (rkm) 3,217 above Fort Peck Reservoir, Montana, to its mouth in Missouri and included the lower 48 km of the Yellowstone River (Figure 1). The rivers were divided into segments based on geomorphic (e.g., large tributaries) or constructed features (e.g., dams; Figure 1). The MRBFS was based on a stratified random design that included 3 years of fish and habitat data collections (1996–1998) within 15 of 27 identified river segments, with six different macrohabitats sampled within each segment (Sappington et al. 1998). Bed-form data from the MRBFS were evaluated in this study at main-channel macrohabitat sites with recording fathometers (Lowrance model X-type graph recorders) at locations where drifting trammel nets and benthic trawls were used to collect fish (i.e., channel crossovers, outside bends, and inside bends). We selected for analysis a random subset of 217 of the approximately 2,300 Lowrance graph recorder paper traces collected. The predominant substrate for main-channel macrohabitats was sand (Galat et al. 2001); therefore, we restricted our analyses to bed-form shape and not substrate composition.

Longitudinal samples from 22.9-m-wide drifting trammel nets and 2-m-wide benthic trawls were collected (i.e., parallel to flow in a downstream direction), one after the other, to sample
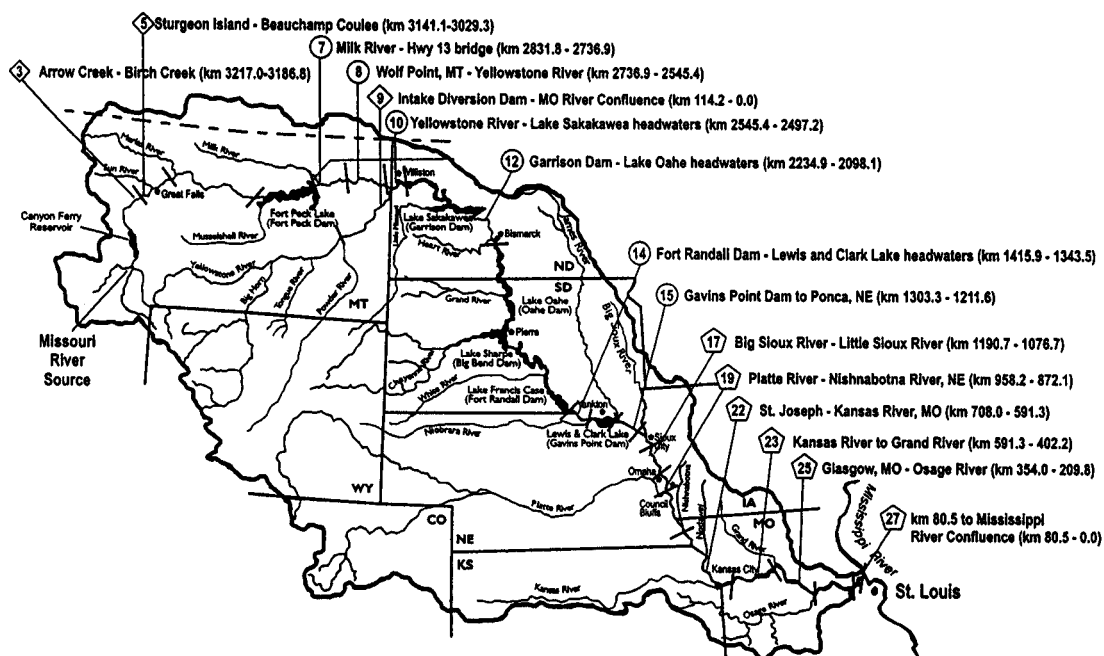
FIGURE 1.—Missouri River segments identified for data collection purposes in 1996–1998. Diamonds represent least-altered segments, circles represent interreservoir segments, and pentagons represent channelized segments.

large and small fishes from the same area. The longitudinal distance sampled for fish and bedform traces ranged from 75 to 300 m. The maximum longitudinal distance covered was 150 m in 1996 but increased to 300 m in 1997 and 1998. Bed-form data were collected along the same path as benthic trawl and drifting trammel net samples. The 75-m minimum sample length assured that the larger waveforms (i.e., those greater than 30.5 m), previously identified by Annambhotla et al. (1972) in the Missouri River, were included in a trace.

*Quantification of bed form.*—We scanned and rotated 180° each trace, then transformed it into a collection of x- and y-coordinates with OPTIMAS 6.1 image analysis software (Optimas Corporation 1996; Figure 2). Rotation of traces avoided negative depths (i.e., y) and simplified characterization of bed forms. Measurements from the Lowrance recorder were estimated to have a horizontal accuracy of 0.1 m or greater, with most between 0.5 and 1.0 m. Possible biases due to differences in length of river bottom covered or paper trace length were eliminated by estimating river bottom parameters from points taken every 1 mm along the river bottom. The number of x-values produced to represent a trace ranged from approximately 75,000 (i.e., 75 m of river bottom) to 300,000 (300 m of river bottom). Because parameter estimates

were based on overspecified data sets, they were considered the "true" values of each parameter.

*Statistics-based characterization of bed form.*—Our statistics-based approach incorporated standard statistical measures to describe the complexity of sedimentary bed form and the specific nature of that complexity. Four parameters were calculated from each trace to characterize the bottom traversed by fishing gears (Figure 2). First, mean depth was calculated. Second, overall orientation of a longitudinal section of river channel relative to direction of river flow was quantified from the slope of the regression of water depth with distance along that channel (i.e., depth slope). Depth slope provided a measure of general orientation of the bottom relative to flow over the sampled distance (i.e., a negative slope represents increasing depth with movement downstream). Third, the mean residual of the regression (i.e., first moment about the regression or depth residual) was used as a relative measure of average depth of individual bottom troughs. Depth residual was calculated by taking the mean of the absolute value of vertical distance between the regression line and the depth value at each of the 1-mm bottom distance values. Finally, the SD of the depth residuals of the regression (i.e., second moment about the regression, or depth SD of residuals) was used to produce

a



FLOW

b



Regression Line
Depth = 2.472 - 0.00735*distance

Mean Depth = 2.11 m
Depth Slope = - 0.00735 m
Mean Residual = 0.129653
Standard Deviation of Residual = 0.134
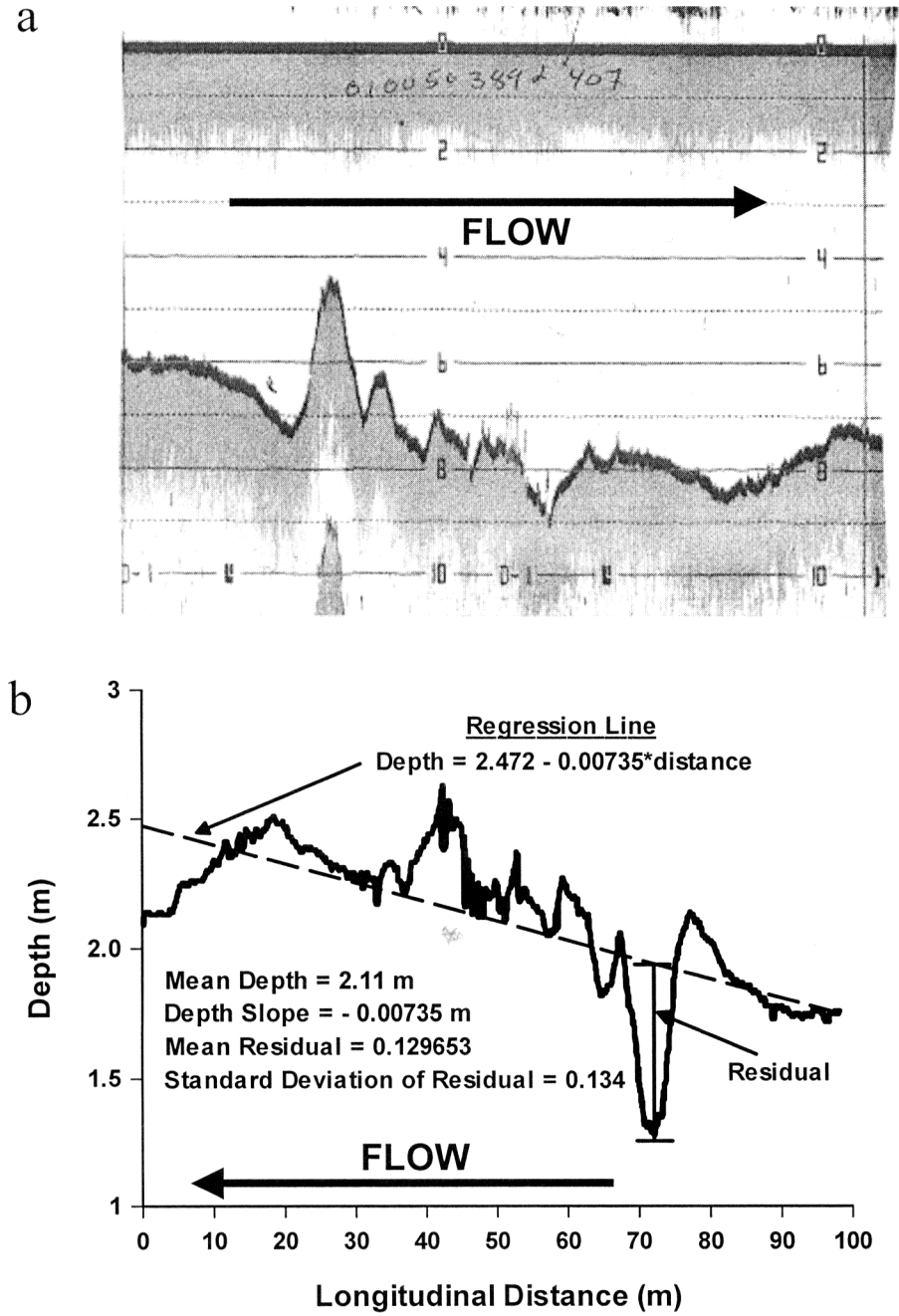
Residual

FLOW

Depth (m)

Longitudinal Distance (m)

FIGURE 2.—Example transformation to digital depth data and statistical analysis of a Missouri River bed-form paper trace collected in 1998. The trace was made in association with drifting trammel net and benthic trawl fish collections from a channel crossover in segment 5 above Fort Peck Reservoir (Figure 1). Panel (a) is the original Lowrance trace. Panel (b) is the resulting depth plot and statistical characterization of bottom trace after 180° rotation and use of OPTIMAS 6.1 image analysis software (Optimas Corporation 1996).
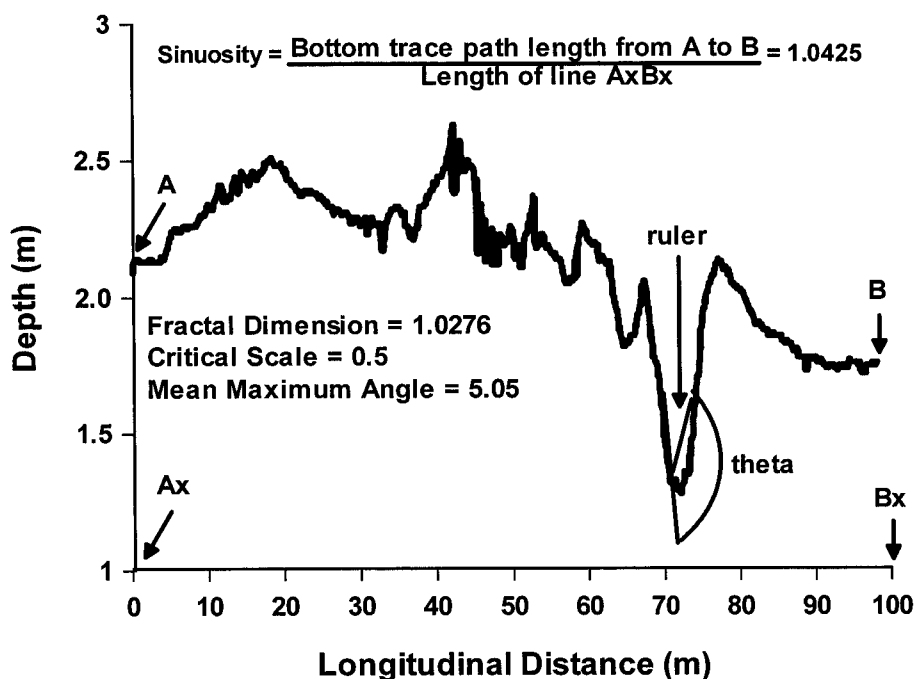
FIGURE 3.—Example sinuosity and fractal geometry of the Missouri River bed-form paper trace in Figure 2. The same ruler was used to estimate the fractal dimension and maximum mean angle. Theta is the angle used to estimate the maximum mean angle.

a measure of relative uniformity in troughs (i.e., bottom smoothness). The relative value, as opposed to actual value, of the mean and SD of the residuals results from all depth values being used, not just values that represented trough peaks or valleys.

Our statistical measures are similar to parameters previously used to describe longitudinal bed-form characteristics (e.g., Annambhotla et al. 1972; Shen and Cheong 1977) except that our measures are based on raw data as opposed to filtered data. Annambhotla et al. (1972) and Shen and Cheong (1977) used a "high-pass filter" on their data prior to analysis to remove long waveforms (i.e., those greater than 30.5 m). We analyzed raw data because long and short wavelengths in bed topography could be important to benthic fishes. Depth slope is a relative measure of the long waveform of a trace.

*Sinuosity-based characterization of bed form.*— Schiemer et al. (2001) calculated shoreline sinuosity by relating the length of the path between two points along the shoreline to the straight-line distance between those two points. Similarly, we defined bed-form sinuosity as the ratio of the measured length of the bottom contour, including all

peaks and valleys, and the straight-line distance covered along the bottom (Figure 3). Bed-form sinuosity was calculated as another relative measure of the smoothness of the bottom contour and incorporates patterns characterized by depth slope, depth residual, and depth SD of residuals into one value.

*Fractal-based characterization of bed form.*— Following Nestler and Sutton (2000), we calculated the fractal dimension, maximum mean angle (MMA), and critical scale for each bed-form trace. The fractal dimension was estimated with standard fractal analysis (Mandelbrot 1967). The angle measurement technique (AMT; Andrle 1994) was used to estimate MMA and critical scale.

The fractal dimension of a line, here the line that represents a bottom trace, is a noninteger greater than or equal to 1.0, and thus can be used to distinguish between traces with differing degrees of variation from a straight line. The higher the fractal value, the less straight a trace. The fractal dimension is similar to sinuosity in that it incorporates patterns characterized by depth slope, depth residual, and depth SD of residuals into one value.

The fractal dimension of a bed trace was deter-

mined as follows (Figure 3): First, a random start-ing point was selected along the trace within a single ruler (i.e., a straight line of a set length $\varepsilon$) distance of the left endpoint. Second, the trace was measured by sequentially moving the ruler to the right from the starting point until the length of the trace remaining could no longer accommodate the given ruler length. Each trace was measured 10 times with each length of ruler, where ruler lengths varied from 0.5 m to 37.5 m by steps of 0.5 m. We used 0.5 m as the minimum ruler length and increment based on our estimated accuracy of the fathometer. Third, the ruler path for a ruler length with the least sum of squared deviations from the trace was selected. Fourth, data for each ruler length was used to generate a Mandelbrodt–Richardson plot of $\log_e[N(\varepsilon)]$ by $\log_e(\varepsilon)$, where $N(\varepsilon)$ is the number of rulers of length $\varepsilon$ that fit along the trace. Fifth, fractal dimension was then approximated by the negative of the slope of the regression line through the points on the Mandelbrodt–Richardson plot (Barnsley 1988). This method is a correction of Nestler and Sutton's (2000) method, where the fractal dimension was defined as the negative slope of the plot of the length of the object when measured by a ruler of a given length (rather than the number of rulers of a given length that fit along the trace as done here) by the length of the ruler.

In Andrle's (1994) AMT, the focus is on the size of the angle produced by two adjacent rulers of the same length (Figure 3). As was the case for the fractal dimension, AMT required us to examine each trace at varying ruler lengths. The range of ruler lengths used here was the same as used in determination of the fractal dimension. In AMT, the MMA is the greatest mean angle that occurred among the rulers used to measure a trace, and crit-ical scale is the ruler length at which the MMA occurred. The MMA is a measure of bottom uni-formity or smoothness, while critical scale is a measure of average trough depth. For this method, we performed the following four steps: First, an initial point along the trace was chosen at random. Second, based on horizontal distance, we then identified the closest points on the trace upstream and downstream from the initial point that had a Euclidean distance of $\varepsilon$ from the initial point. Third, the supplement of the interior angle formed by these three points with the initial point as its vertex was then recorded (i.e., theta; see Figure 3). This process was done for 500 random starting points for each ruler length. Fourth, resulting angle measures were averaged for each ruler length.
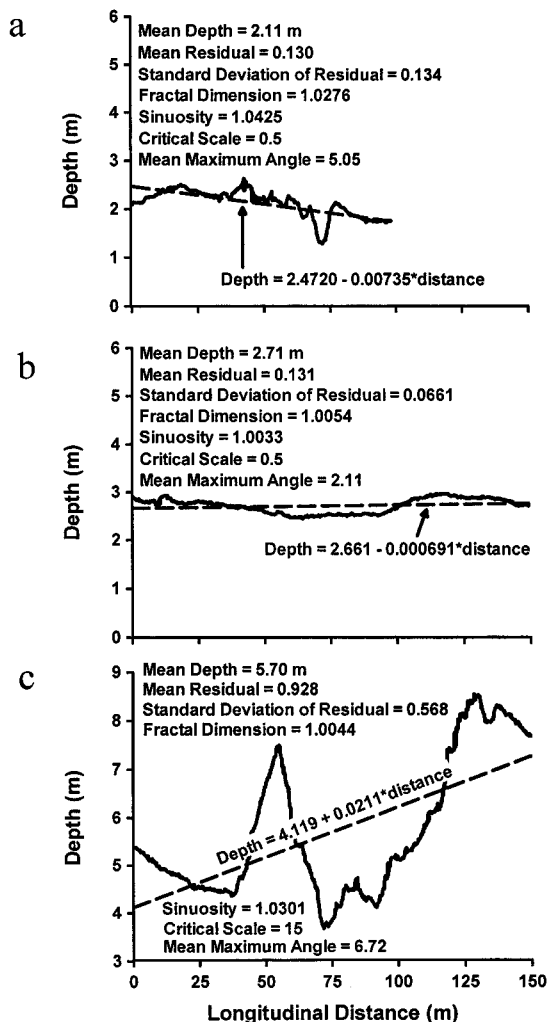


FIGURE 4.—Quantification of three example Missouri River bed-form paper traces collected from 1996 to 1998: **(a)** the trace from Figure 2, **(b)** a trace made in association with drifting trammel net and benthic trawl fish collections from an outside bend in segment 12 be-low Garrison Dam in 1997, and **(c)** a trace made in association with drifting trammel net and benthic trawl fish collections from an outside bend in segment 10 be-low the mouth of the Yellowstone River in 1996.

*Example bed-form quantifications.*—To demon-strate how different parameters vary among the three different methods used to characterize bed form, a range of bed-form examples and their as-sociated parameters are presented (Figure 4). A negative depth slope indicated a river bottom that was dropping out of the direct flow of the river (e.g., downstream edge of a sand bar) (Figure 4a), whereas a positive depth slope indicated a river

TABLE 1.—Species included in the Missouri River benthic fishes assemblage collected from 1996 to 1998.

| | | |
|---|---|---|
| Pallid sturgeon | Western silvery minnow | Flathead catfish |
| *Scaphirhynchus albus* | *Hybognathus argyritis* | *Pylodictis olivaris* |
| Shovelnose sturgeon | Plains minnow | Channel catfish |
| | *H. placitus* | |
| Common carp | Brassy minnow | Blue catfish |
| *Cyprinus carpio* | *H. hankinsoni* | *Ictalurus furcatus* |
| Flathead chub | Fathead minnow | Stonecat |
| *Platygobio gracilis* | *Pimephalus promelas* | *Noturus flavus* |
| Sicklefin chub | Blue sucker | Burbot |
| | *Cycleptus elongatus* | *Lota lota* |
| Sturgeon chub | Bigmouth buffalo | Sauger |
| | *Ictiobus cyprinellus* | *Stizostedion canadense* |
| Emerald shiner | Smallmouth buffalo | Walleye |
| *Notropis atherinoides* | *I. bubalus* | *S. vitreum* |
| Sand shiner | River carpsucker | Freshwater drum |
| *N. stramineus* | *Carpiodes carpio* | *Aplodinotus grunniens* |
| Shorthead redhorse | White sucker | |
| *Moxostoma macrolepidotum* | *Catostomus commersoni* | |

bottom sloping into the direct flow of the river (e.g., upstream edge of a sand bar) (Figure 4c). The mean residual and critical scale were less when a trace was composed of smaller troughs (Figure 4b) than when the troughs were larger (Figure 4c). A smoother, more uniform bottom (Figure 4b) had a lower depth SD of residuals, sinuosity, and MMA than a more variable bed form (Figures 4a, c). The fractal dimension was greatest for traces that had smaller and more variable troughs (Figure 4a).

*Statistical analysis.*—We used SAS/LAB software to identify transformations necessary to approximate normality and constant variance of each parameter for use in analysis of variance (ANOVA; SAS 1992). $Log_{10}$ transformation was used for MMA, depth residual, and depth SD of residuals. Other transformations included the square-root transformation of depth, the transformation of sinuosity as $1/(sinuosity)^2$, and the transformation of critical scale as $1/(critical scale)^{1.5}$. After transformations, only critical scale and sinuosity still violated constancy of variance and normality assumptions. Remaining violations of sinuosity, though significant, were more the result of our power to detect differences (i.e., large number of observations) than any extreme departures from parametric assumptions. For critical scale, the extreme number of small values meant no effective transformation could be found, and therefore these statistical results were considered the weakest. After transforming the data, we continued with parametric analyses of all transformed bed-form parameters because (1) the transformations were generally effective, (2) ANOVA is robust when assumption violations are not extreme (Snedecor and

Cochran 1980; Milliken and Johnson 1984; Neter et al. 1996), and (3) with equal or almost equal sample sizes, $F$-tests are effective even with heterogeneity of variance (Milliken and Johnson 1984).

Four parallel and complimentary analyses were conducted on the data. Three-way ANOVA (i.e., year, segment, and macrohabitat were the independent variables) tested the ability of the bed-form parameters (i.e., dependent variables) to identify differences among river segments and macrohabitats. We used type III sums of squares to get a conservative estimate of variance accounted for by a factor and its interactions, and thus a conservative test of significance. Our second and third analyses were designed to assess the relationship of the bed-form parameters to presence or absence of benthic fishes. One-way ANOVA was used to test mean differences in transformed bed-form parameters (i.e., dependent variables) between sites with and without fish (i.e., independent variable) individually for channel catfish, shovelnose sturgeon, sicklefin chub, and sturgeon chub, and for the entire group of 26 species of the Missouri River benthic fishes assemblage (Table 1). The four groups of parameters measured (i.e., independent variables were depth and sinuosity alone and statistics- and fractal-based parameters) were analyzed separately with logistic regression to test their ability to predict the presence and absence of fish (i.e., dependent variable) (SAS 1992). The fourth analysis was designed to look for more subtle (i.e., more microhabitat in nature) patterns in relationships between bed-form parameters (i.e., independent variables) and fish catch rates (i.e., dependent variable) than could be iden-

TABLE 2.—Three-way results of analysis of variance for each of eight transformed bed-form parameters measured for the Missouri River from 1996 to 1998 ($N = 217$ macrohabitat samples). $F$-values are shown with $P$-values in parentheses.

| Parameter | Year | Segment | Macrohabitat | Year × segment | Year × macrohabitat | Segment × macrohabitat |
|---|---|---|---|---|---|---|
| (Mean depth)$^{\frac{1}{2}}$ | 11.29 | 17.01 | 22.96 | 1.32 | 1.71 | 1.84 |
| | (<0.0001) | (<0.0001) | (<0.0001) | (0.1621) | (0.1505) | (0.0122) |
| Statistics-based parameters | | | | | | |
| Depth slope | 0.45 | 1.56 | 0.82 | 0.86 | 1.31 | 1.24 |
| | (0.6408) | (0.0985) | (0.4417) | (0.6566) | (0.2704) | (0.2129) |
| $Log_{10}$ (depth residual) | 0.93 | 1.22 | 6.81 | 1.45 | 1.62 | 1.66 |
| | (0.3969) | (0.2691) | (0.0015) | (0.0930) | (0.1726) | (0.0318) |
| $Log_{10}$ (depth SD of residual) | 0.96 | 1.51 | 6.94 | 1.56 | 1.69 | 1.59 |
| | (0.3857) | (0.1139) | (0.0013) | (0.0586) | (0.1548) | (0.0451) |
| (Sinuosity)$^{-2}$ | 3.63 | 2.75 | 3.89 | 1.47 | 1.64 | 0.76 |
| | (0.0290) | (0.0012) | (0.0226) | (0.0876) | (0.1667) | (0.8015) |
| Fractal-based parameters | | | | | | |
| Fractal dimension | 0.73 | 1.21 | 2.02 | 1.18 | 0.27 | 1.88 |
| | (0.4830) | (0.2774) | (0.1368) | (0.2722) | (0.8966) | (0.0096) |
| $Log_{10}$ (MMA$^a$) | 5.79 | 4.19 | 2.86 | 1.60 | 2.63 | 0.57 |
| | (0.0038) | (<0.0001) | (0.0608) | (0.0497) | (0.0369) | (0.9546) |
| (Critical scale)$^{-1.5}$ | 0.66 | 2.16 | 1.66 | 1.33 | 0.66 | 1.06 |
| | (0.5208) | (0.0122) | (0.1929) | (0.1553) | (0.6212) | (0.3998) |

$^a$ Maximum mean angle.

tified from presence/absence analyses. To accomplish this, we analyzed data from only sites where fish were collected. This allowed us to test for finer-scale relationships between bed-form parameters and fish catch rates because the influence of the many zero catch rates was eliminated. Any significant relationships found from these analyses would provide a better guide as to which parameters are more important to these fish within the macrohabitats where they are primarily found. To accomplish this goal, we used Spearman's rank correlation to test for relationships between bed-form parameters and nonzero catch rates based on untransformed data for the same individual species and the benthic fishes assemblage used in the analysis of the presence/absence data. Because only benthic fishes were considered, catch rates were based on catch per unit area (CPUA), or the total number of fish collected divided by bottom area sampled during each gear deployment (Wildhaber 1998). Area sampled was estimated by multiplying the width of the gear by distance sampled with the gear. The CPUA values used in the analyses were the average of the two gears.

Combined CPUA was considered valid for testing variations in fish density relative to bed-form variations despite potential differences in bias between gears and among bed-form types. First, the combination of the two gears was selected to help assure collection of all size-classes of fishes within and among species. The benthic trawl collected smaller size-classes and the drifting trammel net

larger size-classes. Second, only main-channel macrohabitat samples were analyzed, to assure comparisons were based on collections made with the same gears and methodologies. Third, extreme variations in bed form (Figure 4) occurred over relatively long distances (e.g., tens of meters), which should have allowed both fishing gears to remain in contact with the bottom through most of a sampling run for all bed-form types studied.

A Bonferroni-adjusted $P$-value of 0.00625 (i.e., $= 0.05/8$ bed-form parameters) was defined as a significant result to control for experimentwise error rate for each species of fish, and $P$-values between 0.00625 and 0.05 are reported here as marginally significant, yet acceptable for discussion due to the developmental nature of this study.

## Results

Some bed-form parameters differed significantly among segments and macrohabitats, whereas others differed significantly only among either segments or macrohabitats (Table 2). Depth and sinuosity differed among river segments and macrohabitats, although significance was marginal for sinuosity at the macrohabitat scale (Table 2). Maximum mean angle and critical scale differed among segments, but critical scale was marginally significant. Segments immediately below dams, the lower Yellowstone River, and the two segments on either side of the Kansas River confluence had lower MMA and therefore tended to be smoothest (Figure 5). Spatial patterns observed in sinuosity
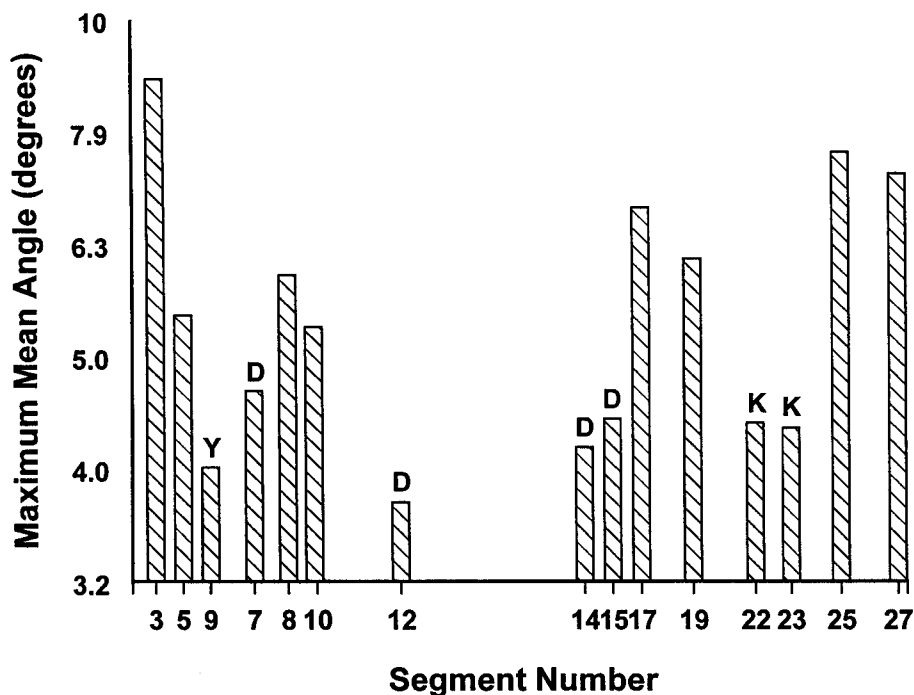
FIGURE 5.—Plot of maximum mean angle for each Missouri River segment as an estimate of bottom uniformity, based on data collected from 1996 to 1998. Segments are ordered from upstream to downstream based on the river kilometer midpoint for each segment, except for segment 9 (lower Yellowstone River [Y]). The letter D designates segments immediately below a dam, and K designates segments above and below the Kansas River.

were similar to those of the MMA. Depth residual and depth SD of residuals differed among macrohabitats. Inside bends had the shallowest troughs and an overall smoother structure than channel crossovers or outside bends, based on relative mean residual and mean SD of residuals (Figure 6). Depth, sinuosity, and MMA differed among years, but sinuosity was marginally significant. Fractal dimension and depth slope did not differ significantly among years, segments, or macrohabitats.

Various bed-form parameters differed between sites with and without fish (Table 3). Mean depth was shallower at sites with fish for the benthic fish assemblage as a group and each individual species, except for channel catfish and a marginally significant result for sicklefin chub. Sites with sicklefin chub had negative depth slopes (i.e., depth increased downstream) and sites without sicklefin chub had positive depth slopes, though marginally significant. Depth residual was smaller at sites with any benthic fish present and also at sites with sicklefin chub and sturgeon chub, though marginally significant for the benthic fish assemblage and sicklefin chub. Depth SD of residuals was lower

at sites with sturgeon chub than at sites without sturgeon chub, though marginally significant. Sinuosity was lower and MMA smaller at sites with shovelnose sturgeon. Fractal dimension and critical scale did not differ significantly between sites with and without fish in any comparisons. Bedform parameters that were predictive of the presence of a species in logistic regression analyses were the same as the parameters that were at least marginally significantly different between sites with and without a species, except for three instances (i.e., depth residual for the benthic fish assemblage and sturgeon chub, and depth SD of residuals for the sturgeon chub) (Table 3). Of these three instances, the sign of the logistic regression coefficient disagreed with observed mean differences for only depth SD of residuals for sturgeon chub.

The presence or absence of a given fish species explained less than 10% of the variability in bedform parameters (Table 3). Logistic regression models correctly predicted, at best, the presence of a species 62–72% of the time (62% for the shovelnose sturgeon sinuosity model, 64% for the shovelnose sturgeon fractal-based model, 67% for
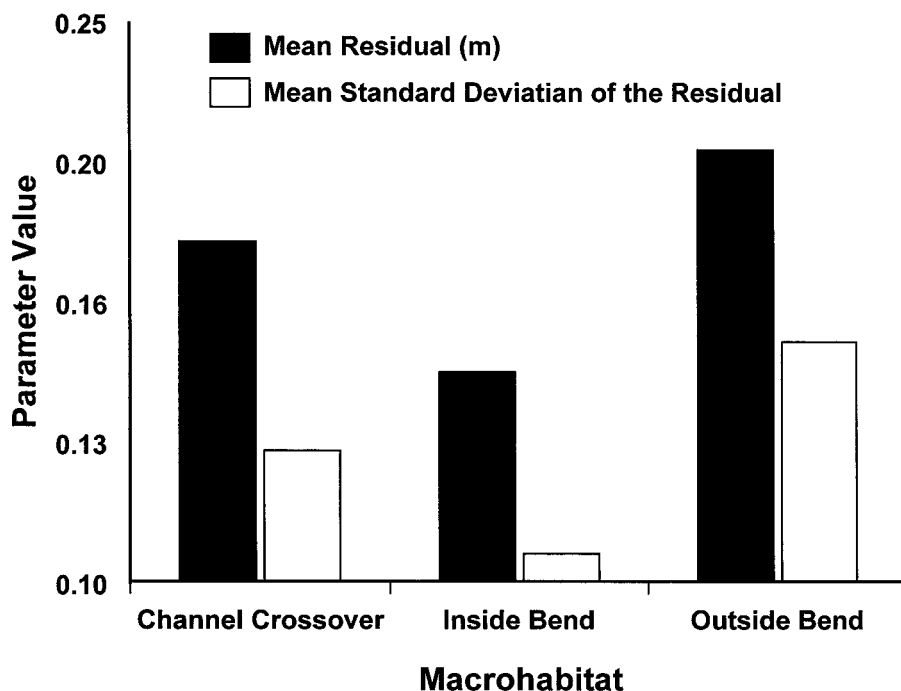
FIGURE 6.—Mean and SD of the residuals of the regression of depth against distance downstream in a riverbed trace for main-channel macrohabitats in the Missouri River, based on data collected from 1996 to 1998. The mean residual is a relative measure of trough depth, and the SD is a measure of the bottom smoothness of a macrohabitat.

the sicklefin chub statistics-based model, and 72% for the sturgeon chub depth model).

Only a few relationships were observed between nonzero CPUA and bed-form parameters for sites with a given fish species. Shovelnose sturgeon nonzero CPUA increased, whereas sturgeon chub nonzero CPUA decreased, with square root of mean depth (Table 4). No significant correlations were observed between nonzero CPUA of the benthic fishes assemblage as a group, sicklefin chub, or channel catfish and bed-form parameters. No bed-form parameter accounted for more than 18% of the variability observed in CPUA.

## Discussion

Our results demonstrate the utility of statistics-, sinuosity-, and fractal-based approaches for characterizing variation in large-river bed form. Also, we found some suggestive relationships between the resulting bed-form parameters and benthic fish densities in main-channel reaches of the Missouri River, although these were based on only a subset of MRBFS data. Values we observed for mean depth, depth slope, and depth residual were similar to those observed by Shen and Cheong (1977) in the Missouri River near Omaha, Nebraska. Over-

all, our statistics-based approach was able to identify differences among macrohabitats, but not segments, based on bed-form traces. The fractal-based approach identified differences among segments. However, sinuosity was the only measure of complexity or smoothness of a trace that identified differences among both segments and macrohabitats. Presence of fishes was related to sinuosity-based and fractal-based parameters for large species and statistics-based parameters for small species.

We found that measures of water depth and sinuosity of the statistics-, sinuosity-, and fractal-based parameters were able to distinguish among river segments and macrohabitats. Galat et al. (2001), using the entire set of MRBFS data, found that mean water depths increased longitudinally downstream among segments, with the shallowest waters found within segments in inside bends. Fractal-based measures of relative depth of troughs and bottom smoothness distinguished among segments but not macrohabitats. The observed increase in bed-form smoothness in segments below dams, as demonstrated by MMA, follows the known effect of dams in terms of downstream channel erosion (Poff et al. 1997). Statistics-based

measures of relative depth of troughs and bottom smoothness were able to distinguish among macrohabitats but not segments. Our observation that inside bends had the shallowest troughs and an overall smoother structure than either channel crossovers or outside bends is consistent with Galat et al.'s (2001) observation that inside bend macrohabitat had the lowest water velocities and greatest percentage of silt.

Further support for the potential usefulness of the methods described here is supplied by the relationships observed among fish densities and bed-form parameters. The patterns observed for mean depth fit the natural histories of the species used as examples (Lee et al. 1980; Cross and Collins 1995; Pflieger 1997). Excluding channel catfish, sites with fish were shallower than sites without fish. Our results indicate that shovelnose sturgeon, sicklefin chub, and sturgeon chub are associated more with the main-channel borders than the channel thalweg. However, the density of the relatively large shovelnose sturgeon increased with depth at sites where they were present, whereas the densities of the smaller sturgeon chub decreased with depth. Hence, sturgeon chub tended to occupy shallower waters of sites where present, whereas shovelnose sturgeon tended to occupy deeper waters of sites where present.

The bed-form parameters presented here provide measures of habitat complexity that should help in understanding fish distribution patterns not accounted for by depth alone. We found lower complexity or greater smoothness of the bottom at sites with fish than at sites without fish for shovelnose sturgeon and sturgeon chub. For both shovelnose sturgeon and sturgeon chub, their association with bed forms that have less relief and their body forms that facilitate use of higher flows (Allan 1995; Adams et al. 1997; Keenlyne 1997) suggest that these species may have less of a need for bed-form relief as a refuge from flow.

For sicklefin chub and sturgeon chub, shallower depth of troughs at sites with fish, based on mean residual, suggests limited importance of troughs as possible refugia. However, shallower troughs may provide these species with a partial refuge from direct contact with the main water flow while still allowing them to be opportunistic feeders of drifting food items, as has been demonstrated for Atlantic cod *Gadus morhua* (Gerstner 1998). The association of fish with larger substrate in rivers to more effectively drift feed has also been demonstrated (Hayes and Jowett 1994; Guensch et al. 2001). Furthermore, depth slope of sites with sicklefin chub was out of the flow, whereas sites without sicklefin chub sloped into the flow, indicating that sicklefin chub may use bottom relief as a refuge from flow at a scale above that of individual troughs. The more streamlined body of the sicklefin chub as compared with the sturgeon chub and shovelnose sturgeon suggests that sicklefin chub are not as directly associated with the bottom (Allan 1995). Sicklefin chub might gain more of an energetic benefit from flow refugia than these species. The channel catfish is more of a habitat generalist and more widely distributed than the other species tested (Lee et al. 1980; Cross and Collins 1995; Pflieger 1997), so it is not surprising that we found no relationships between bed-form parameters and channel catfish presence/absence or catch rates.

Although bed-form parameters were associated with patterns of fish presence and relative abundance, the ability of these parameters to identify factors affecting fish distribution may be limited and requires further investigation. For fish catch data, the primary factor related to both presence and absence of fish and nonzero fish densities was depth. Bed form may be important to benthic fish species; however, the strength of the observed results suggest that it is unlikely to be the primary factor accounting for fish distributions. Other factors (e.g., velocity, substrate composition, food availability, predation risk, temperature, etc.) may be more important than bed form, or it may be that bed form is just one of many factors used by a benthic fish for habitat selection. However, the results from our bed-form analyses are only suggestive, because they are based on a subsample of MRBFS data. Furthermore, we lack high-resolution velocity data to verify that observed relationships between bed form and fish numbers were a response to bed form as a flow refuge; such relationships have been observed by others (e.g., Hayes and Jowett 1994; Gerstner 1998; Guensch et al. 2001). Ultimately, the value of the relationships we observed between bed-form parameters and fish catch provide valuable direction for future research into the habitat preferences of these fishes.

If the patterns documented here hold up under further investigation, we recommend that managers wanting to examine the longitudinal variation of alluvial riverbeds first apply our statistics-based approach in concert with a sinuosity-based approach before a more complex fractal-based approach is attempted. The main advantage of our statistics-based approach is that the metrics

TABLE 3.—One-way analysis of variance (ANOVA) and logistic regression for the presence or absence of Missouri River benthic fish species collected from 1996 to 1998 ($N = 217$ macrohabitat samples). The one-way ANOVA tested mean differences between sites with and without a particular species for each of the bed-form parameters measured, based on transformed data (see text for transformations used); means are back transformed values. The logistic regression tested the ability of each of the groups of bed-form parameters to predict the presence of a species based on untransformed data. For each parameter, the first line shows the mean values with and without the species in question, the second line shows the percentage of variance accounted for and $P$-value from the ANOVA, and the third line shows the parameter estimate and $P$-value from the logistic regression.

| Parameter | Benthic fishes group | Channel catfish | Shovelnose sturgeon | Sicklefin chub |
|---|---|---|---|---|
| Mean depth (m) | 3.40; 4.65 | 3.83; 3.80 | 3.02; 4.22 | 3.10; 3.98 |
| | (9.1; <0.0001) | (0.0; 0.9190) | (8.9; <0.0001) | (3.4; 0.0065) |
| | [−0.32; <0.001] | [0.0081; 0.9122] | [−0.37; < 0.0001] | [−0.24; 0.0169] |
| Statistics-based parameters | | | | |
| Depth slope[a] | −3.14; −2.95 | −11.97; 0.98 | −8.77; −0.40 | −27.22; 2.38 |
| | (0.0; 0.9851) | (0.7; 0.2272) | (0.2; 0.4297) | (2.5; 0.0205) |
| | [2.82; 0.8845] | [−23.70; 0.2495] | [−17.32; 0.3953] | [−65.79; 0.0159] |
| Depth residual | 0.16; 0.19 | 0.17; 0.17 | 0.16; 0.18 | 0.14; 0.18 |
| | (1.9; 0.0414) | (0.1; 0.7244) | (0.9; 0.1637) | (2.1; 0.0312) |
| | [−3.58; 0.2635] | [−1.83; 0.5846] | [1.95; 0.5735] | [−9.74; 0.0456] |
| Depth SD of residual | 0.12; 0.14 | 0.12; 0.13 | 0.11; 0.13 | 0.11; 0.13 |
| | (1.5; 0.0749) | (0.0; 0.7927) | (1.0; 0.1478) | (1.3; 0.0955) |
| | [3.77; 0.4007] | [2.19; 0.6321] | [−3.71; 0.4491] | [9.49; 0.1145] |
| Sinuosity | 1.023; 1.024 | 1.021; 1.024 | 1.018; 1.026 | 1.020; 1.024 |
| | (0.2; 0.5449) | (0.8; 0.1937) | (3.5; 0.0056) | (0.7; 0.2133) |
| | [−3.28; 0.6282] | [−9.47; 0.2339] | [−26.19; 0.0092] | [−13.47; 0.2051] |
| Fractal-based parameters | | | | |
| Fractal dimension | 1.0045; 1.0036 | 1.0052; 1.0037 | 1.0048; 1.0038 | 1.0032; 1.0044 |
| | (0.2; 0.5328) | (0.5; 0.3208) | (0.2; 0.5158) | (0.2; 0.5145) |
| | [12.62; 0.3814] | [20.39; 0.1812] | [21.66; 0.1703] | [−8.40; 0.6459] |
| Maximum mean angle | 4.99; 5.60 | 4.77; 5.40 | 4.48; 5.57 | 4.87; 5.27 |
| | (1.3; 0.0925) | (1.5; 0.0718) | (4.6; 0.0015) | (0.04; 0.3509) |
| | [−0.062; 0.2289] | [−0.091; 0.1136] | [−0.20; 0.0021] | [−0.067; 0.3375] |
| Critical scale | 0.614; 0.614 | 0.616; 0.614 | 0.619; 0.612 | 0.622; 0.613 |
| | (0.0; 0.9924) | (0.0; 0.9487) | (0.0; 0.8045) | (0.0; 0.7964) |
| | [−0.0049; 0.9556] | [0.040; 0.6419] | [−0.0048; 0.9576] | [0.043; 0.6601] |

[a] Times $10^4$.

are more easily understood. Most fisheries managers have a general familiarity with regression but perhaps not with fractal geometry. Parameters for the statistics- and sinuosity-based approaches can be directly identified on the bottom trace. Fractal geometry is a more complex concept, and its results are harder to visually interpret. The sinuosity-based approach does not seem to be limited in its ability to differentiate bed forms at different scales. Our statistics-based approach does not seem to differentiate among bed forms at the segment scale and was effective at relating bed-form structure to only smaller benthic fish species. We found sinuosity was only related to large species of benthic fishes. Furthermore, sinuosity is based on only one measure that combines trough depth and relative smoothness, and thus it does not allow one to distinguish which factor contributes the most. The effectiveness of the fractal-based approach was limited to differentiating among bed forms only at the segment

scale and relating bed-form structure almost exclusively to large species of benthic fishes. The observation that fractals and sinuosity both tend to be influenced by large features (J. M. Nestler, U.S. Army Corps of Engineers Development Center, personal communications) helps to explain why all but one of the observed relationships of these parameters with fish catch occurred with large fish.

## Acknowledgments

TABLE 3.—Extended.

| Parameter | Sturgeon chub |
|---|---|
| Mean depth (m) | 2.80; 4.14 |
| | (9.6; <0.0001) |
| | [−0.43; <0.0001] |
| Statistics-based parameters | |
| Depth slope[a] | −4.91; −2.53 |
| | (0.0; 0.8405) |
| | [−1.69; 0.9471] |
| Depth residual | 0.14; 0.18 |
| | (3.9; 0.0035) |
| | [−5.25; 0.2168] |
| Depth SD of residual | 0.10; 0.13 |
| | (3.1; 0.0093) |
| | [3.80; 0.4958] |
| Sinuosity | 1.023; 1.023 |
| | (0.0; 0.9536) |
| | [−0.22; 0.9779] |
| Fractal-based parameters | |
| Fractal dimension | 1.0046; 1.0040 |
| | (0.0; 0.7563) |
| | [8.04; 0.6263] |
| Maximum mean angle | 4.90; 5.29 |
| | (0.4; 0.3264) |
| | [−0.050; 0.4160] |
| Critical scale | 0.621; 0.612 |
| | (0.0; 0.7938) |
| | [0.013; 0.8891] |

TABLE 4.—Spearman rank correlation coefficients (with P-values in parentheses) for bed-form parameters versus nonzero catch per unit area of Missouri River benthic fishes collected from 1996 to 1998. Asterisks indicate significant results at $P \leq 0.00625$ (i.e., Bonferroni $P = 0.05/8$ for each species). The number of macrohabitat samples in which a species was collected is given in brackets.

| Parameter | Benthic fishes [142] | Channel catfish [68] | Shovelnose sturgeon [70] | Sicklefin chub [40] | Sturgeon chub [50] |
|---|---|---|---|---|---|
| Mean depth | −0.163 | −0.061 | 0.421* | 0.151 | −0.390* |
| | (0.0533) | (0.6236) | (0.0003) | (0.3512) | (0.0051) |
| Depth slope | −0.047 | −0.054 | −0.116 | −0.180 | 0.033 |
| | (0.5763) | (0.6636) | (0.3394) | (0.2666) | (0.8190) |
| Depth residual | −0.145 | −0.132 | −0.015 | 0.051 | 0.051 |
| | (0.0858) | (0.2827) | (0.8996) | (0.7531) | (0.7232) |
| Depth SD of residual | −0.134 | −0.120 | −0.019 | −0.019 | 0.037 |
| | (0.1114) | (0.3308) | (0.8729) | (0.9065) | (0.7976) |
| Sinuosity | −0.080 | −0.035 | −0.001 | 0.155 | −0.174 |
| | (0.3458) | (0.7758) | (0.9932) | (0.3400) | (0.2269) |
| Fractal dimension | 0.084 | −0.021 | 0.074 | 0.188 | 0.047 |
| | (0.3226) | (0.8633) | (0.5410) | (0.2456) | (0.7483) |
| Maximum mean angle | −0.071 | 0.080 | 0.037 | 0.167 | −0.144 |
| | (0.4006) | (0.5192) | (0.7615) | (0.3024) | (0.3199) |
| Critical scale | −0.006 | −0.066 | 0.101 | −0.230 | −0.274 |
| | (0.9397) | (0.5922) | (0.4035) | (0.1528) | (0.0546) |

sightful review comments. Use of trade names in this paper is for informational purposes only and does not constitute an endorsement by the USGS.

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