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Large-Scale Factors Associated with Sicklefin Chub Distribution in the Missouri and Lower Yellowstone Rivers

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Abstract.—The conservation and management of imperiled fishes requires information on the factors influencing their distribution. The sicklefin chub *Macrhybopsis meeki* is an imperiled, small-bodied, riverine fish largely restricted to the main-stem Missouri, lower Yellowstone, and middle Mississippi rivers. We tested the association of sicklefin chub presence/absence with physical habitat, temperature, turbidity, flow, and piscivore abundance between July and October 1996–1997 at a riverscape spatial scale encompassing about 48–192-km-long segments over nearly 2,000 km of the Missouri and lower Yellowstone rivers. Four of the 64 variables examined were significantly associated with sicklefin chub presence/absence: distance to upstream impoundment, flow constancy (a measure of flow variability), mean turbidity, and percent of total annual flow occurring in August. The frequency of occurrence of sicklefin chub was highest when study segments were over 301 km downstream from an impoundment, flow constancy was 0.56 or lower (indicating variable flow), mean summer–early autumn turbidity was 80 nephelometric turbidity units or greater, and less than 10% of total annual flow occurred in August. Two complimentary models were developed from these results: a univariate model containing only a distance-to-upstream-impoundment term, and a multiple model that included mean turbidity and August flow. Models were evaluated for accuracy with an independent data set from 1998. The univariate model was a more accurate predictor of sicklefin chub presence/absence in 1998, with correct predictions in 79% of the 14 segments sampled, compared with 69% for the multiple model. These results demonstrate, at a riverscape spatial scale, the importance of maintaining or restoring long, free-flowing reaches containing a natural range of variability in seasonal low flows and turbidity to conserve a small-bodied, obligate-riverine fish.

North American prairie rivers have been extensively altered over the past 150 years (Rabeni 1996). River alterations include construction of dams and impoundments, channelization, and introduction of nonnative fishes. Dams, in particular, exert pervasive effects by altering flow regimes, reducing base flows, fragmenting fish populations and habitat, and modifying temperature and turbidity (Rosenberg et al. 2000). Concurrent with these alterations have been the decline and imperilment of many native prairie fishes (Miller et al. 1989; Rabeni 1996; Ricciardi and Rasmussen 1999). Virtually all large rivers in the semiarid and arid portions of the United States have undergone these changes, including the Arkansas, Canadian, and Platte rivers (Fausch and Bestgen 1997), the Colorado River (Schmidt et al. 1998; Minckley et al. 2003), the Rio Grande River (Molles et al. 1998), and the Missouri River (Hesse et al. 1989).

The Missouri River is the longest river in the United States (3,768 km), and extensive modifications have resulted in imperilment of its fluvial-dependent native fish community (Galat and Zweimüller 2001; Galat et al., in press). The lower one-third of the river has been channelized to support navigation, and much of the floodplain is isolated from the river by levees (Galat et al. 1998). These modifications have altered channel geomorphology and reduced in-channel and floodplain habitat diversity by decreasing the area and number of sand bars, islands, side channels, and off-channel habitats. Reduced main-channel width and sinu-

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osity have increased water depth and velocity (Pflieger and Grace 1987; Hesse et al. 1989; Galat et al. 1996). Six large dams constructed between 1937 and 1963 impounded the middle one-third of the river. Impoundment has altered natural thermal and hydrologic regimes and has reduced sediment load and turbidity (Hesse et al. 1989; Galat and Lipkin 2000). Nonnative, piscivorous fishes (e.g., Chinook salmon *Oncorhynchus tshawytscha*, walleye *Sander vitreus* [formerly *Stizostedion vitreum*], and smallmouth bass *Micropterus dolomieu*) are stocked into main-stem reservoirs and coldwater, low-turbidity reaches below dams for recreational fishing (Hesse et al. 1989). These large-scale modifications have collectively been implicated in the decline of many native Missouri River fishes (Pflieger and Grace 1987; National Research Council 2002). However, quantitative associations between alterations and declines of native riverine fishes at the spatial scale of an entire river, or "riverscape" (Fausch et al. 2002), are uncommon.

One imperiled, obligate-riverine species is the sicklefin chub *Macrhybopsis meeki*, a small-bodied fish primarily found in the main-stem Missouri River, the lower Yellowstone River, and the middle Mississippi River from the Missouri River's confluence to the Ohio River's confluence (Pflieger 1997). This species has developed unique adaptations to promote existence in highly turbid waters, including external taste buds on the dorsal and pectoral fins, abundant lateral line neuromasts, and numerous sensory papillae in the gular region and within the buccal cavity (Moore 1950; Davis and Miller 1967; Reno 1969). The sicklefin chub is classified as globally rare (G3, Natural Heritage Network 2002) and is listed as imperiled by seven of the eight states situated along the main-stem Missouri River (Galat et al., in press). Until recently, this species was also a candidate for federal listing due to a 50% decline in its historical range (USOFR 2001).

Identification of habitat requirements and species interactions is a fundamental step in imperiled species' conservation, management, and recovery (Rahel et al. 1999). Thus, quantitative associations between sicklefin chub distribution and large-scale alterations in physical habitat, water quality, flow regime, and piscivorous fish abundance along the Missouri River may help explain the species' imperiled status and aid conservation and recovery. Our objectives were to: (1) identify the selected large-scale physical habitat, water temperature, turbidity, flow regime, and predation variables that are most associated with sicklefin chub presence/absence (P/A) in Missouri River segments; (2) describe sicklefin chub habitat use relative to these variables with frequency-of-use histograms; (3) develop a multiple-variable model that best predicts sicklefin chub P/A; and (4) test model accuracy with an independent data set.

Methods

Sampling design.—Sicklefin chub P/A and concurrent physical measurements were obtained from field collections conducted by the Missouri River Benthic Fishes Consortium (Berry and Young 2001). We adopted a hierarchical spatial sampling design that included segments, macrohabitats, and sites and conducted standardized fish and physical variable sampling over 1,851 km of the Missouri River and 114 km of the lower Yellowstone River (Galat et al. 2001). The Missouri River portion of the study area encompasses nearly 60% of the entire length of the warmwater main stem, exclusive of reservoirs.

Twenty-seven segments were identified in riverine portions of the Missouri and lower Yellowstone rivers (Figure 1). Segments were identified based on changes in hydrogeomorphic features (e.g., tributaries, floodplain width) and constructed features (e.g., dams and channelization). A subset of 17 segments (length range: 16.1–191.6 km) that included the full compliment of segment-scale lotic conditions (e.g., variable turbidities, discharges, channel patterns) was sampled in 1996 (Galat et al. 2001). Low fish catches prompted increased sampling effort in 1997 (detailed below), necessitating a reduction in the number of segments sampled to 14 (length range: 48.3–191.6 km; Figure 1). Segments were sampled from approximately mid-July through mid-October, when river stage was typically low and stable.

To ensure that the diversity of abiotic conditions present was sampled, segments were partitioned into six macrohabitats: channel crossover, outside bend, inside bend, nonconnected secondary channel (i.e., secondary channels with only a downstream connection), connected secondary channel (i.e., flowing-water channels), and tributary mouth (see Galat et al. 2001 for detailed macrohabitat descriptions). Abiotic conditions were particularly complex within some macrohabitats, and these diverse conditions were captured by further partitioning into mesohabitats. Connected secondary channels were subclassified as deep or shallow, tributary mouths were subclassified as large or small, and inside bends were subclassified as chan-

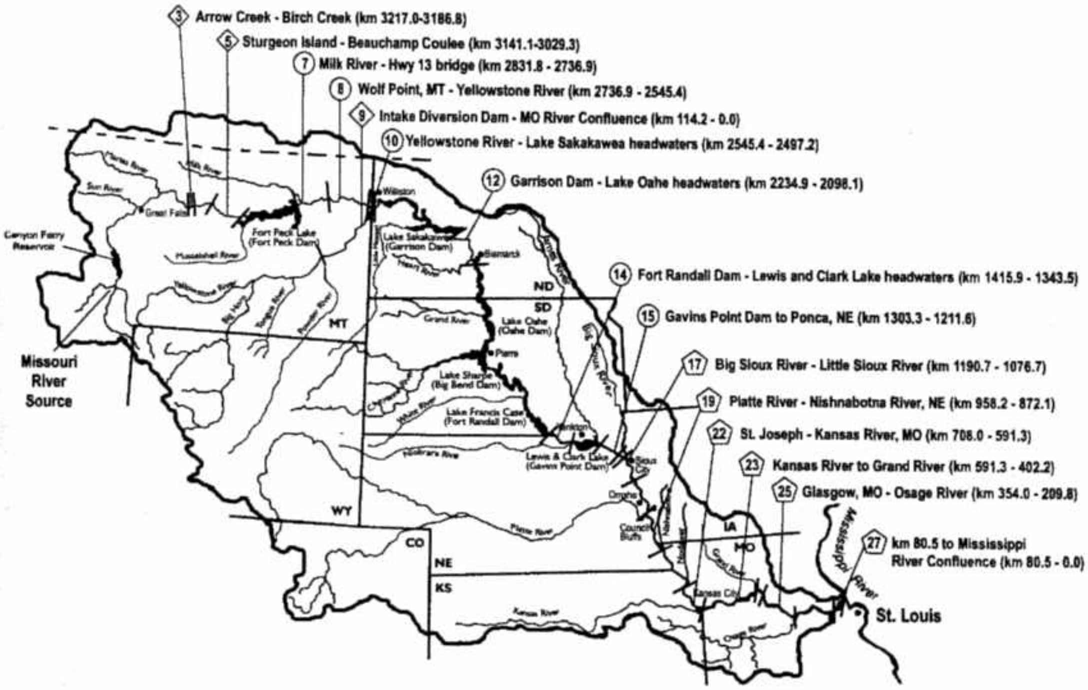

FIGURE 1.—Approximate locations of Missouri River and lower Yellowstone River study segments. Diamonds represent least-altered segments, circles represent inter-reservoir segments, and pentagons represent channelized segments. Segments 5–10, 12, 14, 15, 17–19, 21–23, 25, and 27 were sampled in 1996. Segments 5, 7–10, 12, 14, 15, 17, 19, 22, 23, 25, and 27 were sampled in 1997 and 1998.

nel border, sand bars, steep shorelines, or pools (Galat et al. 2001).

Five replicates of each macrohabitat type, if present, were randomly sampled in each segment in 1996. Within-segment sampling was increased in 1997 by sampling five replicates of both macro- and mesohabitats if present. For example, two inside-bend channel border mesohabitats and three inside-bend sandbar mesohabitats constituted five inside-bend macrohabitat replicates in 1996, whereas five of each mesohabitat type were sampled in 1997 (i.e., five channel borders, five sand bars, five steep shorelines, and five pools). Sites were replicated sampling locations for fishes and environmental variables within each macro- or mesohabitat replicate. Number of site replicates per macro- or mesohabitat varied from two to three, depending on the fish collection gears deployed (Galat et al. 2001).

Sicklefin chub were sampled over the entire study area by use of standardized gears and by following standardized collection methods (Sappington et al. 1998). Shallow-water (i.e., ≤1.2 m) sites were sampled with a bag seine (10.7 m long × 1.8 m high; 5-mm mesh; 1.8-m × 1.8-m × 1.8-m center bag), and deeper sites were sampled with a benthic trawl (2 m wide × 0.5 m high; 3.2-mm inner-mesh net).

Variables.—Presence/absence of sicklefin chub in a segment was the dependent variable used in our analyses because our objective was to identify important predictors of habitable conditions (Allen and Hoekstra 1992) at spatial scales greater than 10 km, not to examine factors affecting the relative abundance of fish at smaller spatial scales (i.e., macro- or mesohabitats).

We tested 64 independent variables within six broad categories for significant associations with sicklefin chub P/A in river segments (Table 1). These variables reflected modifications to Missouri River physical features (e.g., geomorphology, flow, turbidity, temperature) and biota (potential predation by introduced piscivores). See Dieterman (2000) for detailed descriptions of each independent variable and their measurement.

Statistical analyses.—Univariate and multiple logistic regression models were developed to identify a subset of the total number of measured variables that best predicted sicklefin chub P/A in segments. Development of logistic models fol-

TABLE 1.—Segment-scale variables grouped under broad categories (number of variables per category in parentheses) that were tested with logistic regression for association with sicklefin chub presence/absence in Missouri River and lower Yellowstone River study segments, 1996–1998. Variables with an asterisk were determined at the time of fish sampling; others were obtained from existing sources. See Dieterman (2000) and listed references for these data sources and for further descriptions of variables.

Category	Variables
Physical habitat (16)	Channel width, sandbar density, island density, sandbar and island density, channel sinuosity, channel pattern, channel width-to-length ratio, channel slope, floodplain width, deep connected secondary channel density, nonconnected secondary channel density, small tributary mouth density, large tributary mouth density, river bend density, macrohabitat diversity, distance to upstream impoundment
Water temperature* (5)	Mean water temperature, minimum water temperature, maximum water temperature, range of water temperatures, coefficient of variation of water temperature
Turbidity* (3)	Mean turbidity, minimum turbidity, maximum turbidity
Interannual flow statistics (4; Colwell 1974)	Constancy, contingency, predictability, constancy/predictability ratio
Intraannual flow statistics (31; Richter et al. 1996; Haines et al. 1988)	Coefficient of variation (CV = 100 · SD/mean) of daily mean flows within each month, percent of total annual flow in each month, CVs of 1-d , 3-d, 7-d, 30-d, and 90-d flows for each year, day of the year of the 1-d annual minimum flow, and day of the year of the 1-d annual maximum flow
Piscivore abundance* (4)	Catch per unit effort (CPUE) of all piscivores collected in bag-seine samples, (no. fish/haul), CPUE of all piscivores collected in stationary gill nets (no./1,000 h), CPUE of introduced or commonly stocked sight-feeding piscivores in bag-seine samples (no./haul), and CPUE of introduced or commonly stocked sight-feeding piscivores in stationary gill nets (no./1,000 h)

lowed guidelines in Hosmer and Lemeshow (1989). Individual physical habitat, temperature, turbidity, flow regime, and piscivore variables significantly associated with sicklefin chub P/A were first identified with univariate logistic regression models. Variables not significantly associated with sicklefin chub P/A in univariate models were culled. Frequency-of-use histograms were then developed to illustrate habitat-use relationships between sicklefin chub P/A and significant variables identified with the univariate logistic regressions. Spearman's rank correlations (r_s) were then used prior to multiple logistic model development to reduce problems of collinearity and further cull variables (e.g., Watson and Hillman 1997). Correlations were used to identify a final list of variables that were most highly correlated with sicklefin chub P/A but not significantly correlated with each other. Correlations were considered important if they were significant ($P \leq 0.05$) and demonstrated strong relationships (generally $r_s > 0.40$). Multiple logistic models were then developed by manually entering and removing various combinations of variables until the best models, based on significance and fit, were achieved. Interaction terms of main effects selected in the final model were also evaluated.

Models were evaluated for significance by use of a log-likelihood test ($-2 \log L$) for the overall model, a log-likelihood ratio test, and the Wald chi-square statistic (Hosmer and Lemeshow 1989; Menard 1995). Model fit was examined with the adjusted coefficient of determination (R^2) (Hosmer and Lemeshow 1989; Menard 1995; SAS Institute, Inc. 1995), which can be interpreted as the traditional proportion of variation explained (Nagelkerke 1991). Models were developed with the Statistical Analysis System (SAS Institute, Inc. 1995), and acceptance levels were adjusted by the sequential Bonferroni correction for multiple tests (Holm 1979; Rice 1989), thereby maintaining experimentwise error rates at the 0.05 level. This technique was applied to the P-value associated with the log-likelihood test for significance of the overall model.

Spatial independence of observations was assessed with spatial autocorrelation (Griffith 1987; Legendre and Fortin 1989). For purposes of this study, we assumed that spatial autocorrelation existed if the proportion of sites with a sicklefin chub present within a segment could be partly predicted by the proportion of sites with a sicklefin chub present in adjoining segments (Legendre 1993). Spatial autocorrelation was assessed with Geary's c coefficient (Legendre and Fortin 1989). Coefficients were tested for significance (i.e., $c \neq 0$, $\alpha = 0.05$) following methods described by Griffith (1987). The sequential Bonferroni technique was again used to correct for multiple tests of Geary's c coefficient.

Model accuracy was tested with an independent data set (Olden et al. 2002). Sicklefin chub and physical habitat, temperature, turbidity, flow regime, and piscivore variables were sampled in 1998 in the same manner as in 1997. The 1998 data were input into the logistic model developed from the 1996–1997 data to predict the probability of sicklefin chub presence in 1998. Because logistic regression rarely predicts absolute presence (i.e., model predicted probability rarely equals 1.0), we considered sicklefin chub to be present in a segment if model predicted probabilities exceeded 0.58 (i.e., the a priori probability of species prevalence in the 1996–1997 data set used to develop the model). The a priori probability of species prevalence to determine P/A helps reduce the effects of chance predictions (Olden et al. 2002). Actual presence was then assessed with 1998 field data. Predicted P/A was compared to observed P/A with a classification table and chi-square test (SAS Institute, Inc. 1995). The classification table summarized the percentages of correctly and incorrectly classified presences and absences. A significant chi-square test ($P \leq 0.05$) meant that predicted values were associated with observed values, indicating an accurate model.

Results

Sicklefin chub were present in 11 of 17 segments in 1996, 8 of 14 segments in 1997, and 7 of 14 segments in 1998. They were collected in segments 5, 8–10, 22, 25, and 27 (Figure 1) in all three years and in segments 15 and 19 in 1996 exclusively. Sicklefin chub were present in segment 23 in 1996 and 1997, but not in 1998. They were also present in segment 21 in 1996, but this segment was not sampled in 1997 or 1998. Spatial independence, as assessed with Geary's c coefficient, generally indicated positive spatial autocorrelation. However, no coefficient differed significantly from zero following corrections for multiple tests, indicating that sicklefin chub presence in a given segment was independent of sicklefin chub presence in adjoining segments.

Four of 64 segment-scale variables were significantly associated with sicklefin chub P/A in univariate logistic regressions following correction for multiple tests. The four significant variables were (1) distance to upstream impoundment ($-2 \log L = 21.544$, $P = 0.0001$), (2) flow constancy ($-2 \log L = 23.005$, $P = 0.0004$), (3) mean segment turbidity ($-2 \log L = 29.106$, $P = 0.0005$), and (4) percent of annual flow occurring in August ($-2 \log L = 26.074$, $P = 0.0008$). The frequency of occurrence of sicklefin chub was highest when (1) segments were over 301 km downstream from an impoundment, (2) flow constancy was 0.56 or less, indicating an association with segments having more variable flow regimes, (3) mean summer–early autumn turbidity was 80 nephelometric turbidity units [NTU] or higher, and (4) the amount of total annual flow in August was lower than 10% (Figure 2).

The distance to upstream impoundment was the first variable retained for multiple logistic model development because it exhibited the strongest correlation ($r_s = 0.70$) with sicklefin chub P/A (Table 2) and had the most significant association with P/A among the univariate logistic regressions. Mean turbidity, percent of annual flow in August, and flow constancy were significantly correlated ($P \leq 0.05$) with distance to upstream impoundment and therefore were not considered further in development of the first multiple logistic model. Thus, the first segment-scale model, termed model A, only included distance to upstream impoundment. However, distance to upstream impoundment is unlikely a causal factor affecting distribution of fishes; in other words, a fish is not influenced by distance to a dam, but by one or more of the environmental conditions the dam represents. Additionally, distance to upstream impoundment on a great river like the Missouri River provides little in terms of practical management alternatives. Therefore, we developed a second model (model B) by omitting distance to upstream impoundment. Model B included mean turbidity and percent of annual flow in August; these variables were retained over flow constancy because they were more strongly correlated with sicklefin chub P/A and were not correlated with each other (Table 2).

The relative importance of multiple variables was best described by models A and B (Table 3). Model A provided a good fit to the data ($R^2 = 0.64$). Removal of the August flow term significantly altered model B (log-likelihood ratio test comparing models with and without the August flow term: $-2 \log L = 15.013$, $P < 0.001$), indicating that the two-term model was best. Model B also provided a good fit to these data ($R^2 = 0.76$), but the model was not significantly improved by an interaction term. In summary, sicklefin chub in the Missouri River were predicted to be present most often in segments far downstream from reservoirs, where flow constancy was low, turbidity during midsummer–early autumn was

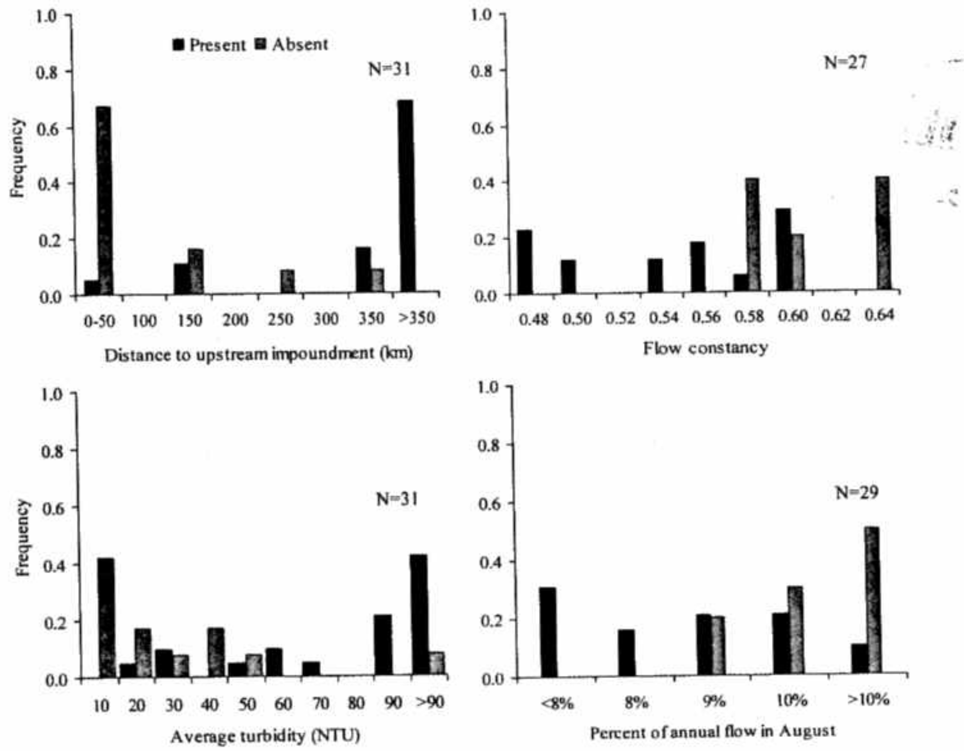

FIGURE 2.—Relative frequency of sicklefin chub presence and absence in relation to distance to upstream impoundment, flow constancy (range from 0 to 1.0, with 1.0 being the most constant), average turbidity in nephelometric turbidity units (NTUs), and percent of annual flow in August for Missouri River and lower Yellowstone River study segments sampled in late summer to early autumn 1996 and 1997.

high, and the percent of annual flow in August was low.

Model A was more accurate than model B at predicting sicklefin chub P/A. Model A accurately predicted sicklefin chub P/A in 79% of the 14 Missouri River segments sampled in 1998 (Table 4), whereas model B predicted 69% of 13 segments accurately. Model A incorrectly predicted two of eight segments (25%) to have sicklefin chub present when none were collected, whereas model B incorrectly predicted 4 of 11 segments (36%) to have sicklefin chub present (Table 4). Predicted P/A of sicklefin chub in segments in 1998 was significantly associated with observed P/A for model A (χ^2 = 4.67, df = 1, P = 0.031). The predicted P/A of sicklefin chub for model B was not significantly associated with observed probabilities (χ^2 = 2.75, df = 1, P = 0.097).

Discussion

Our results provide a robust quantitative association between the contemporary pattern of reduced distribution for a small-bodied, obligate-fluvial minnow and large-scale geomorphic and

TABLE 2.—Spearman's rank-order correlation matrix for significant segment-scale variables following univariate logistic regressions. Data were obtained from the Missouri and lower Yellowstone rivers in 1996 and 1997. Values presented are correlation coefficients (r_s), with probabilities that coefficients differ from zero in parentheses. Variables in the leftmost column are ranked [from most to least correlated] with sicklefin chub presence/absence.

Variable	Sicklefin chub	Distance to impoundment	Mean turbidity	August flow
Distance to impoundment	0.70 (<0.001)			
Mean turbidity	0.65 (<0.001)	0.70 (<0.001)		
August flow	−0.55 (0.002)	−0.65 (<0.001)	−0.15 (0.412)	
Flow constancy	−0.53 (0.004)	−0.84 (<0.001)	−0.68 (<0.001)	0.46 (0.014)

TABLE 3.—Logistic regression models used to predict the occurrence of sicklefin chub in selected Missouri and lower Yellowstone river segments based on data collected in 1996 and 1997. Distance to upstream impoundment in model A is measured in kilometers from the upstream-most segment boundary to the impoundment. Mean turbidity (nephelometric turbidity units) in model B is based on measurements made from mid-July through mid-October. The $-2\log$-likelihood ($-2\log L$) statistic tests the significance of the overall model, and the Wald χ^2-statistic tests the significance of the individual coefficients. The odds ratio is the multiplicative factor by which the odds of a segment's having a sicklefin chub change when the independent variable increases by one unit.

Model and term	Coefficient	SE	Wald χ^2	$P > \chi^2$	Odds ratio	$-2\log L$ Value	$-2\log L$ χ^2	P
Model A								
Constant	−1.6215	0.7345	4.87	0.0273		21.544	19.837	0.0001
Distance to upstream impoundment	0.0096	0.0036	7.06	0.0079	1.010			
Model B								
Constant	11.2617	5.8291	3.73	0.0534		14.093	23.270	0.0001
Mean turbidity	0.0496	0.0222	5.00	0.0253	1.051			
Percent of annual flow in August	−1.3990	0.6540	4.57	0.0324	0.247			

flow features over much of the channel riverscape. The distance to impoundment integrates many biophysical factors that reservoirs are known to affect, including sediment loads, dissolved oxygen levels, invertebrate and ichthyoplankton drift, and flow regime (Ward and Stanford 1983; Dynesius and Nilsson 1994; Rosenberg et al. 2000; Bunn and Arthington 2002). Flow constancy, August flow, and turbidity were factors our analysis isolated as likely mechanisms through which dams influence longitudinal distribution of sicklefin chub in the Missouri River. Moreover, they represent realistic variables that can be managed within a context of reservoir operations, rather than strictly requiring dam removal (Hart et al. 2002). Fausch et al. (2002) emphasized identification of factors that managers can effectively change when conducting large-scale studies on riverscapes. Schmidt et al. (1998) referred to operational changes that could be made to dams to accomplish re-regulation of flow releases that provide more natural flows and sediment transport.

The most plausible effect of low August flow (river stage) is its positive influence on availability of nursery habitat for age-0 sicklefin chub. Humphries et al. (1999), in their low-flow recruitment hypothesis, argued that successful spawning and recruitment of some species of riverine fishes occur when and where low flows provide slow-flowing, edge habitats with high densities of small prey. Most sicklefin chub catches in the lower Missouri River have occurred along shorelines associated with sand bars, and most fish were likely age-0 juveniles, as lengths ranged from 19 to 40 mm

TABLE 4.—Accuracy of segment-scale logistic regression models developed from 1996–1997 data for predicting sicklefin chub presence/absence in Missouri and lower Yellowstone river segments in 1998.

Model and prediction	Proportion of segments	Percentage of segments
Model A (distance to upstream impoundment)		
Correct predictions		
Predicted presence in segment where sicklefin chub were collected	6/8	75%
Predicted absence in segment where sicklefin chub were not collected	5/6	83%
Incorrect predictions		
Predicted presence in segment where sicklefin chub were not collected	2/8	25%
Predicted absence in segment where sicklefin chub were collected	1/6	17%
Overall correct classification by model A	11/14	79%
Model B (mean turbidity and percent August flow)		
Correct predictions		
Predicted presence in segment where sicklefin chub were collected	7/11	64%
Predicted absence in segment where sicklefin chub were not collected	2/2	100%
Incorrect predictions		
Predicted presence in segment where sicklefin chub were not collected	4/11	36%
Predicted absence in segment where sicklefin chub were collected	0/2	0%
Overall correct classification by model B	9/13	69%

total length (Gelwicks et al. 1996; Grady and Milligan 1998). Sicklefin chub have rarely been collected in reservoirs (Werdon 1993; Hesse 1994), backwaters (Fisher 1999), or inundated floodplains (Galat, unpublished data), thus corroborating the species' life history classification as an obligate-fluvial specialist. These findings imply that shallow, riverine shorelines provide critical nursery habitat for sicklefin chub. Shorelines with gradually sloping banks are important nursery habitats for many obligate-riverine fishes because they provide reduced current velocity, shallow water depths, greater light penetration, higher water temperatures, and increased primary production (Schiemer et al. 1995; Scheidegger and Bain 1995; Humphries and Lake 2000). Over 90% of the shallow-water, low-velocity sandbar habitat was eliminated following channelization of the lower Missouri River. Reservoir operations create seasonal flow inversions (i.e., high flows during historically low-water periods and vice versa) and produce high August flows that inundate most of the few remaining sand bars, thus eliminating them as fish nursery habitat (Galat and Lipkin 2000; U.S. Fish and Wildlife Service 2001; National Research Council 2002). Shallow-water shorelines are also reduced below reservoirs because dams discharge sediment-free water, which contributes to downstream channel degradation and incision (Hesse et al. 1989; Patton and Hubert 1993).

Many native fishes adapted to the turbid waters and fluctuating flow regimes of prairie and desert rivers have declined throughout the central and western United States in conjunction with widespread damming and with the proliferation of fishes adapted to clearer waters and more stable flow regimes (Rabeni 1996; Pringle et al. 2000; Minckley et al. 2003; Schultz et al. 2003). Our results demonstrated that sicklefin chub were less likely to be present in Missouri River segments with high flow constancy and lower midsummer–early autumn turbidity, thereby reinforcing these prior observations. Bonner and Wilde (2002) tested a competitive mechanism for these faunal changes and found that elevated turbidity reduced prey consumption by three visually feeding cyprinids, whereas three other species adapted to turbid rivers were less affected. Many turbid-water fishes, including sicklefin chub, have elaborate sensory adaptations that promote foraging in turbid waters. These fishes possess numerous internal and external taste buds, enlarged vagal brain lobes, and abundant lateral line neuromasts, but have poorly developed visual senses, as indicated by reduced eye diameter and optic brain lobe size (Moore 1950; Davis and Miller 1967; Reno 1969). Water clarity increases following main-stem impoundment of the Missouri River led to increased numbers of pelagic planktivores such as gizzard shad *Dorosoma cepedianum* and sight-feeding fishes such as emerald shiners *Notropis atherinoides* and red shiners *Cyprinella lutrensis* (Pflieger and Grace 1987). Such fishes may now compete with sicklefin chub in low-turbidity segments of the Missouri River.

Although model B suggests more specific mechanisms influencing sicklefin chub distribution than does model A, model B was less accurate at predicting sicklefin chub P/A in 1998. All incorrect predictions from model B were due to the model's difficulty in predicting sicklefin chub presence (Table 4). However, model B never incorrectly predicted sicklefin chub absence. This result means that sicklefin chub were always absent from segments predicted to have inadequate August flows and turbidity, whereas segments predicted to have suitable August flows and turbidity sometimes had sicklefin chub present but sometimes did not. Clearly, August flows and turbidity affected sicklefin chub P/A, but they were not the only factors. Additional variables that we did not evaluate may preclude sicklefin chub presence in some segments (Table 4). Therefore, model B appears to be biologically meaningful but may not be as comprehensive as model A.

Model A is probably integrating more factors influencing sicklefin chub distribution in the Missouri River than flow constancy, August flow, and midsummer–early autumn turbidity. We postulate that dams are affecting the early life history of sicklefin chub in a manner similar to other Great Plains fishes belonging to the guild of pelagic broadcast spawners (Fausch and Bestgen 1997; Luttrell et al. 1999). This guild, whose members produce nonadhesive, semibuoyant, drifting eggs, includes the congeneric speckled chub *Macrhybopsis aestivalis* (Fausch and Bestgen 1997). Pelagic broadcast spawners require long segments of unimpounded river to successfully reproduce, because eggs and larvae drift during development (Platania and Altenbach 1998). Eggs and larvae that drift into reservoirs before larvae are able to move horizontally are believed to perish due to lack of resources or due to predation (Fausch and Bestgen 1997; Platania and Altenbach 1998). Although sicklefin chub egg type and spawning behavior have not been described, fish species within the same genus typically share fundamental reproductive strategies (Johnston and Page 1992; Johnston 1999). Also, sicklefin chub × speckled chub hybrids have been collected (Pflieger et al. 1999), further supporting the notion of similar reproductive strategies.

Bonner and Wilde (2000) proposed a minimum distance of 200–300 km between impoundments to provide adequate distances of free-flowing reaches for egg and larval development of pelagic, broadcast-spawning fishes in Great Plains rivers. The results of our model A, which predicted sicklefin chub presence to be highest in segments over 301 km downstream from an impoundment, is remarkably similar to their conclusion. Unfortunately, only 42 free-flowing rivers longer than 200 km remain in the contiguous 48 states, and only five of these rivers exist in the Great Plains region (Benke 1990). Although the Missouri River is not one of them, it does have three reaches that are free-flowing for over 300 km: above Fort Peck Lake, Montana; between Fort Peck Dam and Lake Sakakawea, North Dakota; and downstream from Gavins Point Dam, South Dakota (Galat and Lipkin 2000). Our analysis of factors influencing sicklefin chub distribution along the Missouri and lower Yellowstone rivers reinforces the importance of retaining existing free-flowing riverine stretches over 300 km long and their associated natural seasonal flow and sediment dynamics. Moreover, conservation and recovery efforts for pelagic-spawning, riverine fishes will likely be most successful when applied at a large spatial scale within the riverscape.

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