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[Article]

Fish Assemblage Relationships with Physical Habitat in Wadeable Iowa Streams

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Abstract.—Fish assemblages play a key role in stream ecosystems and are influenced by physical habitat. We analyzed fish assemblages and physical habitat at 93 randomly selected sites on second- through fifth-order wadeable Iowa streams to explore fish assemblage relationships with reach-scale physical habitat in this agriculturally dominated landscape. Sites were sampled using DC electrofishing and the wadeable streams physical habitat protocol of the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program. In all, 82 species were collected, with species richness at sites averaging 14. Over 80% of the sites had fish assemblages rated as fair (53%) or poor (32%) based on a fish index of biotic integrity (FIBI). Ordination separated sites from the two major river drainages along an axis of impairment, with sites in the Missouri River drainage exhibiting lower FIBI scores than sites in the Mississippi River drainage. Physical habitat at most sites exhibited fine substrates, eroding banks, and low-gradient, nonmeandering channel and was dominated by glides. Thirty physical habitat variables describing channel morphology, channel cross section and bank morphology, fish cover, human disturbance, large woody debris, relative bed stability, residual pool, riparian vegetation, and substrate differed significantly between sites with FIBI scores rated as poor and those with FIBI scores rated as good or excellent. Eighteen physical habitat variables were significant predictors of fish assemblage metrics and FIBI in multiple linear regression models, with adjusted R^2 values ranging from 0.12 to 0.58. Seventy percent of the model coefficients reflected substrate (40%), residual pool (21%), and fish cover (9%) variables. Fish assemblages in wadeable Iowa streams are strongly associated with the quality of physical habitat. Thus, understanding and addressing the determinants of physical habitat are crucial for managing streams in Iowa and other agricultural regions.

Fish assemblages play a key role in stream ecosystems through herbivory, planktivory, insectivory, and piscivory (Allan 1995; Matthews 1998). These trophic interactions have been shown to affect stream community composition directly by reducing prey abundances and indirectly through competitive release. Fish can act to alter stream nutrient cycling by herbivory or through translocation of nutrients via consumption and subsequent excretion. Fish also act to modify their physical surroundings. Bioturbation by stream fish can have direct and indirect effects on other stream inhabitants by altering critical habitats through removal of fine sediments from spawning beds, construction of gravel-mound redds, grazing of algae and macrophytes, or suspension of fine sediments while foraging.

Fish assemblages also play a crucial role in the assessment of stream health (Simon 1999). Fish can be easily captured and measured and have been used as indicators of environmental health since the 1800s (Davis 1995). Fish are normally present in even the smallest streams, and the general public can more easily relate to statements about fish than to statements about other taxonomic groups of stream biota (Karr 1981). Fish assemblages are good response indicators because they integrate the effects of multiple stressors (Karr et al. 1986), can persist and recover from natural disturbances, and can reflect both current and long-term environmental effects (Barbour et al. 1999). Development of multimetric indices, such as the index of biotic integrity (IBI; Karr 1981; Fausch et al. 1984; Wilton 2004), and establishment of biological criteria

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(Lyons 1992; Yoder and Rankin 1995; Wilton 2004) have enabled use of fish assemblages as indicators of stream health.

Physical habitat is an important determinant of the condition of stream fish assemblages (Hughes et al. 2006). Physical habitat characteristics, such as current velocity (Poff and Allan 1995), water temperature (Wang et al. 2003), coarse particulate organic matter and woody debris (Gregory et al. 1991), depth and cover (Schlosser 1982; Berkman and Rabeni 1987), appropriate substrates for spawning (Berkman and Rabeni 1987), and relative bed stability (Kaufmann and Hughes 2006), have all been shown to influence fish assemblages. Fish species diversity has been shown to increase as habitat diversity increases (Gorman and Karr 1978). Habitat alterations that reduce complexity (Paragamian 1987; Shields et al. 1994; Lau et al. 2006) or decrease the stability of environmental conditions (Poff and Allan 1995; Lammert and Allan 1999; Diana et al. 2006) have been shown to reduce fish diversity and abundance. Modification of physical habitat can lead to brief or long-lasting changes in the composition of stream fish assemblages depending on the severity of the disturbance (Reice et al. 1990).

Streams in Iowa and other midwestern states have been profoundly altered due to pervasive agricultural land use (Menzel 1983; Karr et al. 1985; Waters 1995; Heitke et al. 2006). In the mid-19th century, Iowa was transformed from prairie and wetlands that absorbed water to cultivated fields and pastures, which accelerated drainage and reduced water storage (Bogue 1963; Menzel 1983). This hydrologic change occurred through extensive conversion of native land cover to row crops, draining of wetland soils, ditching, and channelization, which caused an increase in peak flows and a decrease in base flow (Campell et al. 1972). An estimated 4,800 km of stream channel in Iowa were lost to channelization (Bulkley 1975). As peak flows increased, so did the streams' power or ability to erode and carry sediment. The resulting channel erosion and incision led to decreased substrate heterogeneity and an increase in dominance of sand and silt (Menzel 1983). The amount of cover for fish was reduced as the increased stream power removed aquatic macrophytes and as increased sedimentation covered coarse substrates (Menzel 1983). Channelization removed woody debris and reduced habitat complexity. In western Iowa, severe erosion and incision resulting from channelization and agricultural land use necessitated construction of over 400 grade control structures immediately downstream from bridges, which in turn have impeded fish passage and altered upstream fish assemblages (Litvan et al. 2008a, 2008b). These direct and indirect effects of agriculture have been shown to reduce species diversity and abundance in streams in Iowa (Paragamian 1987; Heitke et al. 2006) and other midwestern states (Karr et al. 1985; Roth et al. 1996; Allan et al. 1997; Wang et al. 1997).

The overall goal of this study was to explore fish assemblage relationships with reach-scale physical habitat in wadeable Iowa streams. Our specific objectives were to (1) quantify and characterize the fish assemblages, including biotic integrity, in an unbiased sample of wadeable, second- through fifth-order Iowa streams representing all major river drainages and ecoregions, (2) quantify and characterize reach-scale physical habitat conditions at fish collection locations, (3) identify physical habitat variables that are significantly associated with fish assemblage characteristics, and (4) quantify, describe, and interpret fish assemblage relationships with physical habitat. Our study was part of two nationwide U.S. Environmental Protection Agency (USEPA) programs: the Environmental Monitoring and Assessment Program (EMAP; Whittier and Paulsen 1992) and the Wadeable Streams Assessment (WSA) program (USEPA 2006).

Study Area

Site Selection

Stream locations were selected by the USEPA Office of Research and Development using the systematic stratified random selection procedure developed for EMAP and the WSA program (Stevens and Olsen 1999). Stream segments were defined as lengths of stream extending from a downstream confluence to the next upstream confluence. All second- and higher-order stream segments on the U.S. Geological Survey's 1:100,000-scale River Reach 3 (USGS 1999) map coverage of Iowa, with the exceptions of the Mississippi and Missouri rivers, were eligible for selection. Segments were selected at random, stratified by stream order. Specific site locations along selected segments were in turn selected randomly, and these locations were the center of sampling reaches. If greater than 60% of a reach to be sampled was judged to be nonwadeable, the site was excluded.

Ecoregions of Iowa

Iowa contains four ecoregions (Figure 1) as described by McMahon et al. (2001). The largest ecoregion is the Western Corn Belt Plains, characterized by smooth to irregular plains and low hills, 69–89 cm of annual precipitation, and native tallgrass prairies and oak (*Quercus* spp.) and hickory (*Carya* spp.) forests that are largely converted to row crop agriculture. The Western Corn Belt Plains ecoregion is divided into seven subregions (Griffith et al. 1994). The Northwest Iowa Loess Prairies subregion has the

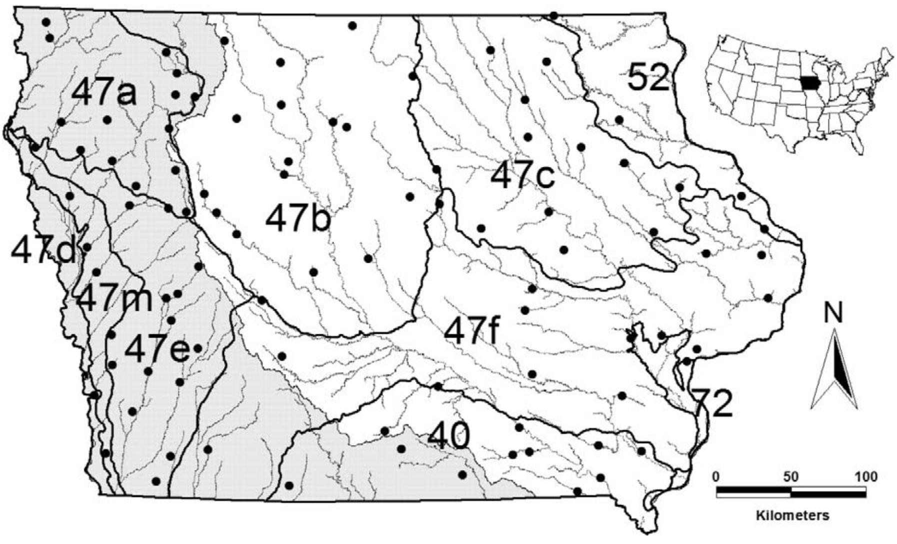

FIGURE 1.—Locations of the 93 sites sampled and analyzed for fish assemblage and physical habitat in wadeable Iowa streams. Ecoregions of Iowa are Central Irregular Plains (40), Western Corn Belt Plains (47; includes subregion 47a = Northwest Iowa Loess Prairies, 47b = Des Moines Lobe, 47c = Iowan Surface, 47d = Missouri Alluvial Plain, 47e = Loess Hills and Steeply Rolling Prairies, 47f = Southern Iowa Rolling Loess Prairies, 47m = Western Loess Hills), Paleozoic Plateau (52), and Interior River Lowland (72). Shaded area indicates land in the Missouri River drainage; unshaded area indicates land that drains to the Mississippi River.

highest elevation and the lowest average precipitation in the state. In north-central Iowa, the Des Moines Lobe subregion has loamy soils and a poorly developed stream network. Most of this subregion has been converted from wet prairie to intensive row crop agriculture with substantial subsurface drainage. The Iowan Surface subregion transitions from the limestone bedrock of the Paleozoic Plateau to the glacial landforms of the Des Moines Lobe. Stream gradients in the Iowan Surface subregion are generally low, but groundwater from limestone aquifers contributes significantly to some streams. In the Missouri Alluvial Plain subregion, most streams are channelized and wetlands have been drained for row crop agriculture. The Western Loess Hills subregion and the Loess Hills and Steeply Rolling Prairies subregion are characterized by thick deposits of loess soils, greater topographic relief than that in neighboring subregions, and significant amounts of rangeland, pasture, and deciduous forest. Streams in the Western Loess Hills subregion are particularly prone to erosion because of the higher gradients and light and friable soils. The Southern Iowa Rolling Loess Prairies subregion is characterized by moderate topographic relief and loess soils.

The Central Irregular Plains ecoregion in far southern Iowa is topographically more irregular than most of the Western Corn Belt Plains. This ecoregion is characterized by irregular plains and low hills, 76–89 cm of annual precipitation, and native tallgrass prairies and oak and hickory forests that are converted to a mixture of row crop agriculture and pasture, with significant deciduous forests occupying riparian zones and areas of highest topographic relief.

The Paleozoic Plateau ecoregion in northeast Iowa, referred to as the "Driftless Area" due to its lack of recent glaciations, differs sharply from the other ecoregions in Iowa. This ecoregion is characterized by significant topographic relief, 81–86 cm of annual precipitation, and native maple (*Acer* spp.) and basswood (*Tilia* spp.) forests that are converted to a mixture of row crops, pastures, and riparian forests. Due to the topographic relief, relatively thin soils, and shallow and often exposed limestone bedrock, streams in this ecoregion are entrenched in forested, shady valleys; have cooler and more stable temperatures from groundwater input and higher shading; have higher gradients; and have coarser substrates than other ecoregions.

The Interior River Lowland ecoregion, lying primarily to the south and east of Iowa in the Mississippi, Illinois, Missouri, Ohio, and Wabash River valleys, occupies a small portion of southeast Iowa along the Mississippi River and lower Iowa and Cedar rivers. In Iowa, this ecoregion is characterized by relatively flat alluvial floodplains, annual precipitation of 86–91 cm, native prairies and oak and hickory forests that are converted to row crop agriculture, and forests present along riparian corridors and steeper valley slopes.

Methods

Fish assemblages.—Fish assemblages were sampled following the Iowa Department of Natural Resources wadeable streams bioassessment protocol (Wilton 2004). Fish assemblages were sampled in reaches using single-pass upstream electrofishing with either a DC tow barge or single or dual pulsed-DC backpack electrofishers (Simonson and Lyons 1995; Yoder and Smith 1999). Reaches were centered on the X-point and isolated with block nets to prevent escape. The reach length for streams with a mean width of less than 12 m was 30 times the mean width. The reach length for streams with a mean width greater than 12 m was 20 times the mean width, with a maximum length of 400 m. An effort was made to sample all accessible macrohabitats in the reach and collect all stunned fish. All fish collected were identified to species, counted, examined for external physical abnormalities, and released alive.

We calculated 12 metrics that have been shown to indicate fish assemblage health in Iowa streams (Wilton 2004). The 12 metrics include (1) number of native fish species, (2) number of sucker species, (3) number of sensitive fish species, (4) number of benthic invertivore species, (5) percent abundance of the three dominant fish species, (6) percentage of fish as benthic invertivores, (7) percentage of fish as omnivores, (8) percentage of fish as top carnivores, (9) percentage of fish as simple lithophilous spawners, (10) fish assemblage tolerance index, (11) adjusted catch per unit effort, and (12) percentage of fish with deformities, erosions, lesions, or tumors (DELTs). These metrics are similar to those included in the original IBI of Karr et al. (1986). All metrics are assumed to have a positive relationship with fish assemblage health except percent abundance of the three dominant fish species, percentage of fish as omnivores, fish assemblage tolerance index, and percent DELTs, which are assumed to have negative relationships with biological integrity. The 12 metrics were combined to generate a fish IBI (FIBI) score with a range of 0–100, where a score of 71–100 is excellent, 51–70 is good, 26–50 is fair, and 0–25 is poor (Wilton 2004).

Physical habitat.—Physical habitat was sampled following the USEPA EMAP wadeable streams physical habitat protocol (Peck et al. 2006), with data reduction and metric calculation as described by Kaufmann et al. (1999). This protocol generated 342 variables of reach-scale physical habitat in 11 categories, including channel morphology, channel cross section and bank morphology, fish cover, flow, human disturbance, large woody debris, relative bed stability, residual pools, riparian vegetation, sinuosity and slope, and substrate composition. Sampling occurred over a reach length that was 40 times the mean stream width and centered on the selected X-point. Eleven cross-sectional transects were evenly spaced at four times the mean wetted stream width along the reach. To characterize channel and riparian condition, measurements of cross section dimensions were taken at each transect. These measurements included wetted channel width, bank-full width, bank-full height, height of channel incision, undercut bank distance, and depths at five points: left bank, 25% width, mid-channel, 75% width, and right bank. Bank-full channel is defined as the channel that is filled by moderate-sized flood events that typically occur every 1–2 years. These events normally do not spill over into the floodplain but can be estimated by the location of a slope change on the bank, the point where water would begin to overflow the banks. Flows at bank-full stage are considered to control the channel dimensions in most stream channels. The angle of the bank was measured from the water's edge with a clinometer. Measurements of channel slope and bearing were taken by back-sighting to the previous transect using a clinometer and compass. Canopy density was measured with a convex Lemmon spherical crown densiometer at each bank while facing the bank and from the mid-channel facing upstream, downstream, and each bank.

Along each cross-sectional transect, estimates of substrate size and embeddedness were recorded at the same locations where depths were measured. Substrates were estimated with a modified Wolman pebble count. Embeddedness is an estimate of the lack of interstitial spaces between the substrate particles in a 10-cm radius around the sampled particle. Additional estimates of substrate size were taken halfway between transects at the same five channel locations (left bank, 25% width, mid-channel, 75% width, and right bank) for a total of 105 particles throughout the entire reach. Size was estimated into one of 13 size-classes from fines to bedrock. Relative bed substrate stability was estimated as a ratio of the observed mean substrate particle diameter to the critical diameter at bank-full flow, which is the largest particle diameter that would be mobile during a bank-full flow event.

Riparian vegetation at each transect was classified visually within a 10-m^2 area centered on transects and extending 10 m from each bank. Cover was classified as absent, sparse ($<$10%), moderate (10–40%), heavy (40–75%), or very heavy ($>$75%). Vegetation was further classified into three height categories (canopy: $>$5.0 m; mid-layer: 0.5–5.0 m; ground cover: $<$0.5 m) and classified by type (deciduous, coniferous, shrubs, grasses, and barren).

Instream cover at each transect was classified visually within an area extending 5 m upstream and 5 m downstream along the transect. Cover categories included filamentous algae, macrophytes, large woody debris, small woody debris, live trees, roots, overhanging vegetation, undercut bank, boulders, and other. Proximity of human disturbances was recorded at each transect as (1) on the bank, (2) within 10 m of the bank, or (3) beyond 10 m from the bank but visible from the stream.

Thalweg profile was derived by measuring maximum depth along the channel at 10 or 15 evenly spaced intervals between the 11 transects, creating 100 or 150 individual measurements along the entire reach. In streams with a mean width less than 1.5 m, the interval was decreased to capture the heterogeneity of the habitat by taking 15 measurements. In streams that had a mean width greater than 1.5 m, 10 intervals were used between transects. At each interval, maximum depth was measured, habitat was classified by water flow characteristics (e.g., pool, glide, riffle, or rapid), pool-forming features were identified, and the presence of soft and small sediments was recorded. Thalweg profiles were used to estimate residual pool characteristics. A residual pool was defined as an area that would contain water even at zero discharge due to the damming effect of its downstream riffle crest. The residual pool longitudinal profile of the reach was used to calculate reach aggregate volumes and residual pool summary variables. Depositional sediment bars, islands, side channels, backwaters and anthropogenic disturbances (e.g., field drain pipes) were also recorded as the thalweg profile was mapped between transects. All pieces of large woody debris were counted between transects and were categorized by length, diameter, and presence in the wetted channel or bank-full channel.

Stream discharge was estimated using the velocity area method at a single transect close to the center of each reach that had relatively uniform depth, substrate, and flow. Transects were divided into 15 or more cells such that cells were less than 1 m in width. Velocity was measured with a Marsh-McBirney flowmeter at 60% water column depth in each cell. The sum of all cell products (width $\times$ depth $\times$ velocity) was used to estimate stream discharge (m^3/s) for the reach.

Data analysis.—Fish assemblage characteristics were analyzed for association with the 342 reach-scale physical habitat variables. We used a five-step variable selection process to test for association with the fish assemblages and create models to predict fish assemblage metrics and FIBI. The five steps included (1) nonmetric multidimensional scaling (NMDS) ordinations, (2) fitting physical habitat variables as vectors to the ordinations and testing for significance, (3) rank-sum tests of the physical habitat variables between sites with FIBI scores of 25 or lower (poor) and sites with scores greater than 50 (good or excellent), (4) removal of redundant variables, and (5) multiple linear regressions to identify physical habitat variables that are significant predictors of fish assemblage metrics and FIBI.

We created three separate NMDS ordinations based on species abundance, species presence or absence, and fish assemblage metrics. The NMDS method is a nonlinear ordination used to graphically represent the similarity in species composition in multiple dimensions. Sites with similar assemblages plot close together, and sites with dissimilar assemblages plot far apart. The NMDS is unconstrained by environmental variables, so the ordination of sites is driven only by species composition. Unconstrained ordinations are more appropriate for investigating relationships with a large suite of environmental variables (P. Dixon, Iowa State University, personal communication). Environmental variables can then be fit to the ordination as regressed vectors to identify or test for associated environmental gradients. The ordination of species abundance was based on a matrix of pairwise similarities between sites generated using Bray–Curtis distance coefficients (Legendre and Legendre 1998). Species abundances were quantified as number per 100 m of stream. The presence–absence ordination was generated from a matrix of pairwise similarities between sites using Jaccard distance coefficients (Legendre and Legendre 1998). The ordination of fish assemblage metrics was generated from a matrix of pairwise similarities between sites using Canberra distance coefficients (Legendre and Legendre 1998). We chose not to remove any species from the analyses because we reasoned that uncommon or rare species are sampled less frequently because they are responding to environmental conditions and are thus important in detecting environmental changes (Cao et al. 1998).

All physical habitat variables were fit to the ordination as vectors. Vectors indicate the direction of most significant change, which can be interpreted as the direction of an environmental gradient. The length of the vector is proportional to the strength of the correlation between the ordination and the physical habitat variable. This can be interpreted as the strength of the environmental gradient. Tests for significance of these correlations were run using Monte Carlo permutation tests. The R^2 value was considered significant if it was greater than the 95th percentile of 1,000 randomly permuted correlations. Variables that were significantly correlated with the ordination were retained. The NMDS ordination was created using the metaMDS function, permutation tests were performed using the envfit function, and surface fitting was performed with the ordisurf function in the Vegan package (Oksanen et al. 2007) for R software (R Development Core Team 2006).

The physical habitat variables that were significantly correlated with at least one ordination were then evaluated using Wilcoxon rank-sum tests. Variables were tested for their ability to distinguish between sites with poor FIBI scores ($\leq$25) and sites with good or excellent scores ($>$50). Variables that significantly ($P \leq 0.05$) distinguished between sites based on FIBI scores were retained. These retained variables were then assessed for redundancy. Groups of highly correlated variables were considered redundant and reduced to one variable (Pearson's product-moment correlation coefficient $r > 0.75$). Variables that have been previously shown to influence biotic condition, variables with high correlation values with the NMDS ordinations, and composite variables were retained from groups of correlated variables. Rank-sum tests and correlation analyses were performed in the Statistical Analysis System (SAS; SAS Institute 1996).

Stepwise multiple linear regression was used to identify statistically significant predictors of fish assemblage metrics and FIBI from the retained set of physical habitat variables. Forward stepwise variable selection was used, in which the first variable chosen produced the single-variable model with the highest r^2 and subsequent variables were chosen to maximize the improvement in R^2 while maintaining significance of all previously included variables. The significance level for inclusion of predictor variables was 0.05. Regression models were checked for overly influential observations, and residual plots were examined to evaluate assumptions of linearity and equal variance. Multiple linear regression analysis was performed in SAS (SAS Institute 1996) using PROC REG and the STEPWISE variable selection procedure.

Results

Site Selection

Of the 106 total sites sampled, 93 were retained for further analysis (Figure 1; Rowe 2007). Ten sites were omitted because they were dominated by coldwater species. Coldwater streams are very limited in Iowa, are subject to intensive salmonid stocking and management, and support fish assemblages that are more appropriately evaluated with an IBI specifically designed for coldwater assemblages (Lyons et al. 1996; Mundahl and Simon 1999). Furthermore, assemblages at these 10 sites differ from the majority of assemblages in response to temperature rather than physical habitat, which was the focus of our analysis. Three additional sites were omitted because no fish were captured and severe pollution was suspected. The remaining 93 sites represented all four ecoregions of Iowa and the seven subregions within the Western Corn Belt Plains ecoregion (Figure 1).

Fish Assemblages

We collected 43,737 fish from 82 species (Table 1). Species richness at sites ranged from 1 to 35, with a mean of 14. Total catch at sites ranged from 14 to 1,835 fish, with an average catch of 186 fish/100 m. The bluntnose minnow had the highest total catch, followed by the creek chub, central stoneroller, sand shiner, and bigmouth shiner. Creek chub occurred at the most sites, followed by the bigmouth shiner, sand shiner, bluntnose minnow, green sunfish, johnny darter, and white sucker. Three nonnative species were sampled: common carp, goldfish, and brown trout. Common carp were frequently sampled, occurring at 37% of the sites, whereas only a single goldfish and a single brown trout were sampled.

Tolerance index, a measure of the proportion of intermediate and tolerant species (possible range = 0–10), averaged 7.2 (observed range = 3–10). A tolerance index value of 10 describes an assemblage dominated by fish that are tolerant of environmental degradation. The average FIBI score at sites was 34; the lowest score was 1 and the highest was 90. Six sites (6%) were scored as excellent (FIBI $>$ 70), eight sites (9%) were scored as good (FIBI = 51–70), 49 sites (53%) were scored as fair (FIBI = 26–50), and 30 sites (32%) were scored as poor (FIBI $\leq$ 25).

The NMDS ordinations of species abundance, species presence–absence, and FIBI metrics were evaluated at two and three dimensions. There was only a small improvement in stress values between ordinations with two or three dimensions, so all analyses were performed in two dimensions to simplify graphical presentation. Stress values ranged between 15.1 for the ordination of FIBI metrics and 21.7 for the ordination of species abundance. All three types of ordination (species abundance, species presence–absence, and FIBI metrics) revealed equivalent patterns of similarity among sites. Therefore, we will present only the ordination of species abundance, which retains the most information and has the clearest patterns.

The NMDS ordination of sites by species abundance showed good separation of sites, with a tendency for sites in the major river drainages to show some separation (Figure 2). There was some clustering of sites by ecoregion. For example, the Paleozoic Plateau sites grouped to the far left and the Interior River Lowland sites grouped near the top. However, there

TABLE 1.—Fish species collected from 93 second- through fifth-order wadeable Iowa streams. Species are listed in descending order of percent occurrence at sites.

Species	Species code	Occurrence (%)	Total number caught
Creek chub *Semotilus atromaculatus*	CKCB	86	3,687
Bigmouth shiner *Notropis dorsalis*	BMSN	80	3,492
Sand shiner *Notropis stramineus*	SNSN	77	4,104
Bluntnose minnow *Pimephales notatus*	BNMW	66	4,365
Green sunfish *Lepomis cyanellus*	GNSF	65	1,520
Johnny darter *Etheostoma nigrum*	JYDR	61	1,473
White sucker *Catostomus commersonii*	WTSK	59	2,072
Fathead minnow *Pimephales promelas*	FHMW	53	1,872
Central stoneroller *Campostoma anomalum*	CNSR	48	3,033
Bluegill *Lepomis macrochirus*	BLGL	43	484
Common shiner *Luxilus cornutus*	CMSN	43	2,916
Common carp *Cyprinus carpio*	CARP	38	224
Stonecat *Noturus flavus*	STCT	38	162
Red shiner *Cyprinella lutrensis*	RDSN	37	2,087
Suckermouth minnow *Phenacobius mirabilis*	SMMW	34	344
Eastern blacknose dace *Rhinichthys atratulus*	BNDC	32	1,937
Spotfin shiner *Cyprinella spiloptera*	SFSN	30	2,015
Channel catfish *Ictalurus punctatus*	CNCF	28	779
Largemouth bass *Micropterus salmoides*	LMBS	27	190
Brassy minnow *Hybognathus hankinsoni*	BSMW	26	812
Shorthead redhorse *Moxostoma macrolepidotum*	SHRH	26	206
Quillback *Carpiodes cyprinus*	QLBK	24	185
Hornyhead chub *Nocomis biguttatus*	HHCB	23	721
Northern hog sucker *Hypentelium nigricans*	NHSK	23	368
Black bullhead *Ameiurus melas*	BKBH	22	47
Yellow bullhead *Ameiurus natalis*	YLBH	22	94
Fantail darter *Etheostoma flabellare*	FTDR	20	716
River carpsucker *Carpiodes carpio*	RVCS	20	206
Golden redhorse *Moxostoma erythrurum*	GDRH	19	550
Orangespotted sunfish *Lepomis humilis*	OSSF	16	132
Blackside darter *Percina maculata*	BSDR	15	42
Smallmouth bass *Micropterus dolomieu*	SMBS	14	179
Southern redbelly dace *Phoxinus erythrogaster*	SRBD	13	341
Gizzard shad *Dorosoma cepedianum*	GZSD	12	1,056
Slenderhead darter *Percina phoxocephala*	SHDR	10	109
Bullhead minnow *Pimephales vigilax*	BHMW	9	52
Banded darter *Etheostoma zonale*	BDDR	8	254
Black crappie *Pomoxis nigromaculatus*	BKCP	8	18
Brook stickleback *Culaea inconstans*	BKSB	8	48
Flathead catfish *Pylodictis olivaris*	FHCF	8	39
Highfin carpsucker *Carpiodes velifer*	HFCS	8	34
Rosyface shiner *Notropis rubellus*	RYSN	8	59
American brook lamprey *Lampetra appendix*	ABLP	7	37
Emerald shiner *Notropis atherinoides*	ERSN	7	115
Freshwater drum *Aplodinotus grunniens*	FWDM	7	20
Northern pike *Esox lucius*	NTPK	7	11
Flathead chub *Platygobio gracilis*	FHCB	5	29
Goldeye *Hiodon alosoides*	GDEY	4	4
Shortnose gar *Lepisosteus platostomus*	SNGR	4	16
White crappie *Pomoxis annularis*	WTCP	4	8
Bigmouth buffalo *Ictiobus cyprinellus*	BMBF	3	11
Mud darter *Etheostoma asprigene*	MDDR	3	13
Rainbow darter *Etheostoma caeruleum*	RBDR	3	50
Rock bass *Ambloplites rupestris*	RKBS	3	25
Slender madtom *Noturus exilis*	SDMT	3	27
Tadpole madtom *Noturus gyrinus*	TPMT	3	13
Walleye *Sander vitreus*	WLYE	3	5
White bass *Morone chrysops*	WTBS	3	8
Black redhorse *Moxostoma duquesnei*	BKRH	2	91
Blackstripe topminnow *Fundulus notatus*	BTTM	2	5
Golden shiner *Notemigonus crysoleucas*	GDSN	2	7
Iowa darter *Etheostoma exile*	IODR	2	7
Longnose dace *Rhinichthys cataractae*	LNDC	2	18
Largescale stoneroller *Campostoma oligolepis*	LSSR	2	26
Plains minnow *Hybognathus placitus*	PNMW	2	4
Silver chub *Macrhybopsis storeriana*	SVCB	2	21
Mississippi silvery minnow *Hybognathus nuchalis*	SVMW	2	64
Brook silverside *Labidesthes sicculus*	BKSS	1	1

TABLE 1.—Continued.

Species	Species code	Occurrence (%)	Total number caught
Brown trout *Salmo trutta*	BNTT	1	1
Central mudminnow *Umbra limi*	CMMW	1	5
Freckled madtom *Noturus nocturnus*	FKMT	1	1
Goldfish *Carassius auratus*	GDFH	1	1
Grass (redfin) pickerel *Esox americanus*	GSPK	1	4
Gravel chub *Erimystax x-punctatus*	GVCB	1	17
Logperch *Percina caprodes*	LGPH	1	2
Orangethroat darter *Etheostoma spectabile*	OTDR	1	25
Pumpkinseed *Lepomis gibbosus*	PNSD	1	2
Redfin shiner *Lythrurus umbratilis*	RFSN	1	1
Sauger *Sander canadensis*	SGER	1	1
Smallmouth buffalo *Ictiobus bubalus*	SMBF	1	11
Silver redhorse *Moxostoma anisurum*	SVRH	1	3
Warmouth *Lepomis gulosus*	WRMH	1	3

was significant interspersion of sites from different ecoregions, suggesting that ecoregional differences explain little of the variation within the ordination.

We fit flexible surfaces to the ordination to explore relationships with stream health (FIBI score) and stream size (stream order) and to facilitate interpretation (Figure 3). The surface describing stream health showed a gradient in which FIBI increased from the bottom right toward the upper left corner. The stream order surface showed a gradient of increasing stream

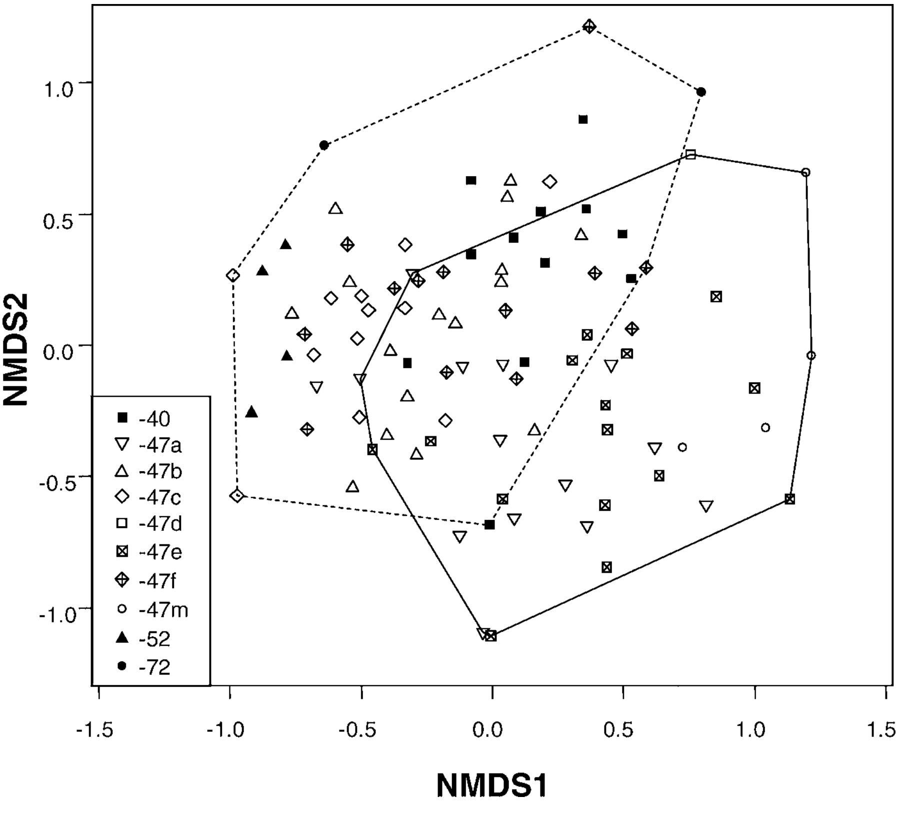

FIGURE 2.—Nonmetric multidimensional scaling (NMDS) ordination based on fish species abundance in 93 sites on wadeable Iowa streams. Polygon hulls outline sites within the Mississippi River drainage (dashed border) or Missouri River drainage (solid border). Key at lower left indicates ecoregion or subregion (defined in Figure 1 and described in text).

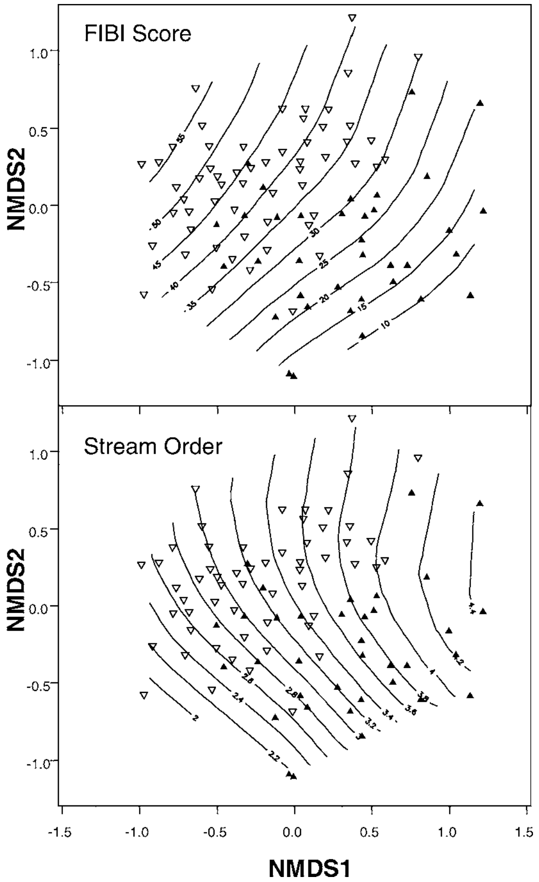

FIGURE 3.—Nonmetric multidimensional scaling (NMDS) ordination based on fish species abundance in 93 sites and relationships with the fish index of biotic integrity (FIBI) and stream order of wadeable Iowa streams. Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites in the Mississippi River drainage. The ordination is fitted with two flexible surfaces; the top shows a gradient of FIBI score ($r^2 = 0.43$), and the bottom shows a gradient of stream order ($r^2 = 0.39$).

size from the bottom left to the upper right. The R^2 values for correlations between the ordination and the surfaces indicated that these factors explained a large amount of the variation in the ordination: 43% for the FIBI surface and 39% for the stream order surface.

Figure 4 is the same ordination shown in Figure 2 but with species superimposed as weighted average positions based on site abundances. This technique facilitates interpretation of the ordination and is an alternative to labeling axes with species that account for strong effects on axis scores. Species that occur in smaller streams, such as the brook stickleback, fathead minnow, johnny darter, and southern redbelly dace, plot to the bottom left (compare with Figure 3). Species commonly found in larger streams and rivers, such as the walleye, white bass, gizzard shad, and freshwater drum, plot in the upper right. Species that are sensitive to environmental degradation, such as the northern pike, black redhorse, gravel chub, and smallmouth bass, tend to plot in the upper left. Species that are ubiquitous in Iowa, such as the sand shiner, yellow bullhead, suckermouth minnow, and green sunfish, are plotted near the origin.

Physical Habitat

Over 35,200 m of stream channel were sampled, and sites encompassed a variety of physical habitat conditions. Watershed size varied from 5.2 to 2,146.1 km^2, with a mean of 332.5 km^2. Twenty-five sites (27% of the total) were second order, 28 (30%) were third order, 30 (32%) were fourth order, and 10 (11%) were fifth order. The mean stream width varied from 1 to 37 m, with an overall mean of 10 m. The mean stream depth varied from 10.4 to 125.5 cm, with an overall mean of 47.8 cm. The wetted width : depth ratio had a range of 3.3–84.0 and a mean of 26.0. Sites were typically dominated by small substrates and eroding banks. The percentage of sand and fine sediments combined ranged from 44.2% to 99.0%, with a mean of 78.6%. Samples from sites in the Paleozoic Plateau ecoregion and the three northern subregions of the Western Corn Belt Plains (Northwest Iowa Loess Prairies, Des Moines Lobe, and Iowan Surface) had greater amounts of gravel and coarse substrates and smaller amounts of sand and fine substrate than samples from the Central Irregular Plains, the Interior River Lowland, and the southern subregions of the Western Corn Belt Plains (Figure 5). Sites also differed when grouped by major drainage basin. Samples from sites within the Missouri River drainage had more hardpan and fines and less cobble and bedrock than samples from sites in the Mississippi River drainage. The height of channel incision ranged from 0.5 to 10.4 m, with an average of 3.1 m. Sites in the Missouri River drainage were on average 1.2 m more incised than sites in the Mississippi River drainage ($P = 0.002$). Statewide, most sites were low gradient, nonmeandering, and dominated by glide habitat. Channel slope varied from 0.0% to 1.6%, with a mean of 0.2%. Only seven sites had slopes that were greater than 0.5%. The reach-scale sinuosity varied from 1.0 to 4.2, with an average of 1.2. Percent glide habitat varied from 0% to 100%, with a mean of 70.2%.

Relationships between Fish Assemblages and Reach-Scale Physical Habitat

Permutation tests identified 211 physical habitat variables as significantly correlated ($P < 0.05$) with at

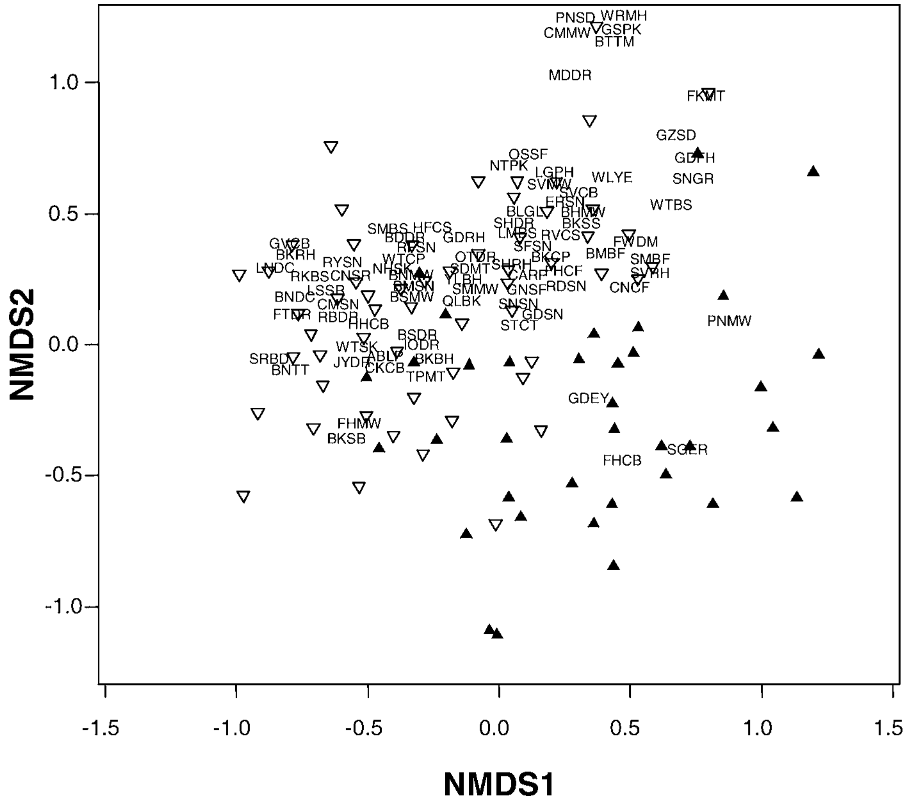

FIGURE 4.—Nonmetric multidimensional scaling (NMDS) ordination based on fish species abundance in 93 sites on wadeable Iowa streams and centroids of fish species distributions. Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites located in the Mississippi River drainage. The four-letter species codes (defined in Table 1) are plotted as a weighted average of species abundance by site. Some species locations were adjusted slightly for clarity.

least one of the three ordinations (Rowe 2007). One-hundred ninety-two variables were significantly correlated with the species abundance ordination, 206 variables were significantly correlated with the species presence–absence ordination, and 173 variables were significantly correlated with the FIBI metric ordination. Among the 211 variables that were significantly correlated with at least one of the NMDS ordinations, each of the 11 categories of physical habitat was represented by at least one variable.

Wilcoxon rank-sum tests identified 94 variables that were significantly different ($P < 0.05$) between sites with FIBI scores greater than 50 and sites with FIBI scores of 25 or less (Rowe 2007). Sixty-four variables were removed because they were strongly correlated ($r > 0.75$) with other variables in the same category. The remaining 30 variables in nine categories were considered to be potentially important determinants of fish assemblage characteristics and were retained for further analysis (Table 2). Variables expressing channel morphology, including standard deviation of thalweg depth, mean width : depth ratio, and percent riffle, were greater at sites with FIBI scores exceeding 50, whereas pool head length with sediment smaller than 16 mm in diameter and percent glide were greater at sites with FIBI scores of 25 or less. Variables expressing channel cross section and bank morphology, including standard deviation of bank-full width and mean bank-full width : depth ratio, were greater at sites with FIBI scores higher than 50, whereas mean bank angle and mean channel incision height were greater at sites with FIBI scores less than or equal to 25. All variables expressing fish cover, including areal proportion of boulders, percent large cover types, areal proportion of all natural cover types, and areal proportion of large cover types, were greater at sites with FIBI scores exceeding 50. A variable that expresses a form of human disturbance, row crops near the bank, was greater at sites with FIBI scores of 25 or less. All variables expressing large woody debris

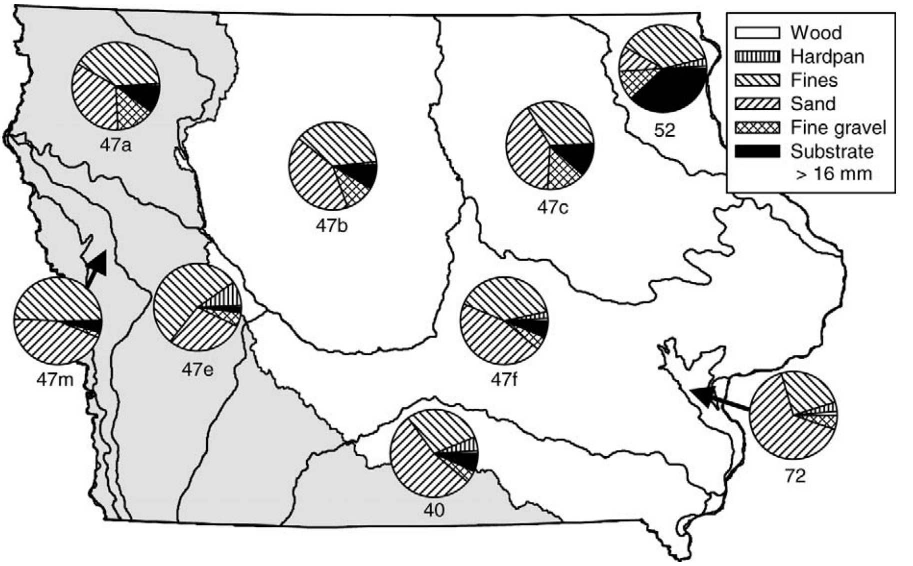

FIGURE 5.—Mean percent substrate composition of sampled reaches at 93 sites on wadeable Iowa streams, presented by region (defined in Figure 1). Subregion 47d was omitted because it contained only one site. Shaded area indicates land in the Missouri River drainage; unshaded area indicates land that drains to the Mississippi River.

were greater at sites with FIBI scores higher than 50. A variable expressing relative substrate stability, the $\log_{10}$ transformed ratio of mean observed substrate diameter to estimated critical substrate diameter at bank-full flow, was greater at sites with FIBI scores over 50. All variables expressing residual pool dimensions were greater at sites with FIBI scores exceeding 50. One variable that represented riparian vegetation—canopy cover—was greater at sites with FIBI scores higher than 50; another such variable—mid-layer herbaceous vegetation—was greater at sites with FIBI scores of 25 or less. Substrate variables, including the $\log_{10}$ transformed 84th-percentile diameter class, percent fine gravel, and percent coarse substrate (>16 mm in diameter), were greater at sites with FIBI scores over 50, whereas percent fine sediments and percent sand plus fine sediments were greater at sites with FIBI scores less than or equal to 25.

Twelve multiple linear regression models were constructed to predict fish assemblage metrics and FIBI (Table 3). The physical habitat predictors included 18 variables representing nine categories. Two example relationships of a fish assemblage metric and FIBI with their most strongly related physical habitat predictors are shown in Figure 6. Seventy percent of the model coefficients shown in Table 3 reflected substrate (40%), residual pool (21%), or fish cover (9%) variables. The model for number of native species explained 57% of the variation and included mean residual width (+, positive relationship), percent fine gravel (+), fish cover (+), and canopy cover (+). The model for FIBI explained 50% of the variation and included coarse substrate (+), mean residual width (+), percent fine gravel (+), and channel incision height (−, negative relationship). The other 10 models explained an average of 35% of the variation (Table 3).

The 18 physical habitat variables identified as predictors of FIBI and fish assemblage metrics (Table 3) were plotted as vectors on the ordination of fish species abundance (Figure 7). Groups of vectors aligned along both axes. High percentages of fine and coarse gravel, boulders, and large fish cover features aligned opposite of channel incision height and percent sand and fine sediment along NMDS axis 1. Several variables describing channel and bank morphology, large woody debris, relative bed stability, and residual pool aligned with NMDS axis 2 and opposite the vectors expressing riparian row crops and percent fine sediment.

Cover, substrate, relative bed stability, channel incision height, and human disturbance variables were associated with major drainages and FIBI (compare Figure 2 with Figures 3, 7). Large fish cover features, coarse substrate, and relatively stable substrates characterized Mississippi River basin sites with higher FIBI scores, whereas sand and fine substrates, greater channel incision height, and row crops near the bank characterized Missouri River basin sites with lower FIBI scores.

TABLE 2.—The 30 physical habitat variables significantly correlated with at least one ordination and significantly different between sites with good or excellent (>50) and poor (≤25) fish index of biotic integrity (FIBI) scores in wadeable Iowa streams. Variable names are as in Kaufmann et al. (1999) and Peck et al. (2006).

Variable	Description	Mean	SD	Mean for FIBI >50	Mean for FIBI ≤25
	Channel Morphology				
PCTUSED	Pool head length with sediment < 16 mm in diameter (%)	92.37	16.86	80.55	97.08
SDDEPTH	Standard deviation of thalweg depth (cm)	16.78	9.86	19.25	13.56
XWD_RAT	Mean width : depth ratio	26.02	19.13	32.23	20.78
PCT_GL	Glide (%)	70.25	25.54	59.44	75.29
PCT_RI	Riffle (%)	8.06	9.87	15.75	8.18
	Channel Cross Section and Bank Morphology				
XBKA	Mean bank angle (degrees)	38.04	10.74	31.54	40.72
SDBKF_W	Standard deviation of bank-full width (m)	2.39	2.04	3.27	1.46
XINC_H	Mean channel incision height (m)	3.11	1.66	2.21	3.80
BFWD_RAT	Mean bank-full width : depth ratio	9.81	4.86	12.39	7.80
	Fish Cover				
XFC_RCK	Boulders (areal proportion)	0.02	0.05	0.07	0.01
PFC_BIG	Large woody debris, boulder, undercut bank, or artificial structure presence (% reach)	0.59	0.27	0.70	0.51
XFC_NAT	All natural fish cover types (areal proportion)	0.19	0.13	0.24	0.15
XFC_BIG	Large woody debris, boulder, undercut bank, or artificial structure (areal proportion)	0.07	0.06	0.12	0.04
	Human Disturbance				
W1H_CROP	Row crop (proximity-weighted presence)	0.46	0.32	0.30	0.59
	Large Woody Debris				
C2DM100	Above bank-full channel: in size-classes of small, medium, large, and extra large (pieces/100 m)	0.44	1.04	0.48	0.21
C1TM100	Total number : all sizes (pieces/100 m)	9.36	12.04	15.40	7.43
V1TM100	Total volume : all sizes (m^3/100 m)	4.13	5.70	5.63	2.60
RCHDMDLL	Above channel, medium diameter, long length (number)	0.08	0.27	0.21	0.00
	Relative Bed Stability				
LRBS_BW6	$\log_{10}$(mean observed substrate diameter/estimated substrate critical diameter at bankfull flow)	−1.71	0.61	−1.29	−1.79
	Residual Pool				
RPGT50	Residual pools > 50 cm deep (number)	1.35	1.36	1.86	0.83
RPMXDEP	Maximum residual depth (cm)	69.84	44.97	75.49	56.52
RPXWID	Mean residual width of reach (m)	3.05	2.18	3.93	1.93
RPV100R	Residual pool volume (m^3/100-m reach)	39.03	50.42	44.92	18.45
	Riparian Vegetation				
XMH	Midlayer herbaceous vegetation cover	0.33	0.22	0.24	0.41
XC	Canopy cover	0.26	0.27	0.37	0.21
	Substrate				
LSUB_D84	84th-percentile $\log_{10}$(diameter) class (mm)	0.51	1.41	1.41	0.40
PCT_FN	Fines: <0.06 mm (%)	39.63	23.21	27.85	46.21
PCT_SAFN	Sand and fines: <2 mm (%)	78.65	14.63	60.57	81.98
PCT_GF	Fine gravel: 2–16 mm (%)	8.61	8.11	14.90	6.47
PCT_BIGR	Coarse gravel and larger: >16 mm (%)	8.95	10.78	22.27	4.47

Discussion

Fish assemblages in wadeable Iowa streams are associated with physical habitat characteristics. We identified 30 physical habitat variables that were significantly related to fish assemblage composition and significantly different between sites judged as poor based on FIBI score and sites judged as good or excellent. Eighteen of these variables were included in multiple regression models predicting fish assemblage metrics and FIBI. Several of the models explained over half of the variation in fish assemblage metrics and FIBI. These relationships are strong evidence that stream fish assemblages are influenced by physical habitat quality. Furthermore, we believe this supports use of physical habitat in conjunction with biological indicators for assessment of wadeable streams in Iowa.

Previous research suggests that physical habitat influences stream fish at three scales: reaches, mesohabitats, and microhabitats (Frissell et al. 1986). Ten of the 18 variables we identified as predictors of fish

TABLE 3.—Multiple linear regression models of fish assemblage metrics and fish index of biotic integrity (FIBI) based on physical habitat variables (defined in Table 2) in wadeable Iowa streams (adj. = adjusted; RMSE = residual mean square error). Models were created with stepwise multiple regression. Variables are listed in order of inclusion in models.

Metric	Model Adj. R^2	Model RMSE	Variable	Coefficient	P
Number of native species	0.57	4.48	Intercept	2.077	0.1146
			RPXWID	1.735	<0.0001
			PCT_GF	0.248	<0.0001
			PFC_BIG	4.155	0.0222
			XC	4.483	0.0492
Number of sucker species	0.54	1.38	Intercept	−0.624	0.0389
			RPXWID	0.503	<0.0001
			PCT_GF	0.061	0.0010
			PCT_BIGR	0.039	0.0049
			RCHDMDLL	1.530	0.0083
Number of sensitive species	0.39	1.94	Intercept	−1.276	0.0038
			PCT_BIGR	0.071	0.0003
			RPXWID	0.248	0.0385
			PCT_GF	0.102	0.0002
			XC	2.281	0.0216
Number of benthic invertivore species	0.58	1.38	Intercept	3.713	0.0050
			RPXWID	0.809	<0.0001
			PCT_SAFN	−0.051	0.0002
			PFC_BIG	1.582	0.0326
Percent abundance of top-3 abundant species	0.28	13.26	Intercept	65.363	<0.0001
			PCT_FN	0.243	0.0002
			PCT_BIGR	−0.376	0.0054
			RCHDMDLL	−13.061	0.0158
Percent abundance of benthic invertivores	0.18	10.96	Intercept	5.577	0.0003
			PCT_BIGR	0.491	<0.0001
Percent abundance of omnivores	0.26	15.74	Intercept	40.910	<0.0001
			PCT_GF	−0.860	0.0002
			RPMXDEP	0.245	0.0002
			LRBS_BW6	8.742	0.0041
			RPV100R	−0.159	0.0069
			PCT_BIGR	−0.466	0.0089
			XFC_RCK	73.565	0.0468
Percent abundance of top carnivores	0.36	5.79	Intercept	−12.759	<0.0001
			XWD_RAT	0.131	0.0038
			LRBS_BW6	−3.690	0.0004
			W1H_CROP	6.118	0.0029
			SDBKF_W	0.846	0.0255
Percent abundance of simple lithophilous spawners	0.48	4.62	Intercept	10.584	0.0026
			RPXWID	2.855	<0.0001
			XFC_RCK	31.977	0.0031
			RCHDMDLL	5.249	0.0073
			PCT_SAFN	−0.102	0.0064
			SDDEPTH	−0.265	0.0007
			BFWD_RAT	−0.518	0.0082
Tolerance index	0.31	1.16	Intercept	8.492	<0.0001
			PCT_BIGR	−0.049	<0.0001
			RPXWID	−0.166	0.0041
			PCT_GF	−0.041	0.0078
Adjusted catch per unit effort	0.12	35.10	Intercept	103.480	<0.0001
			PCT_SAFN	−0.908	0.0005
FIBI	0.50	13.45	Intercept	21.361	<0.0001
			PCT_BIGR	0.825	<0.0001
			RPXWID	2.773	<0.0001
			PCT_GF	0.482	0.0093
			XINC_H	−2.204	0.0156

assemblage metrics and FIBI were measured at—and presumably operate at—the reach or mesohabitat scale. These variables represent channel morphology, channel cross section and bank morphology, residual pool, and riparian characteristics. The remaining eight variables express substrate composition or cover for fish; these are microhabitat-scale elements that relate to feeding, reproduction, and predator or current avoidance.

Half of the habitat predictor variables, including mean residual width of reach, maximum residual depth, residual pool volume per 100 m, standard deviation of thalweg depth, standard deviation of bank-full width,

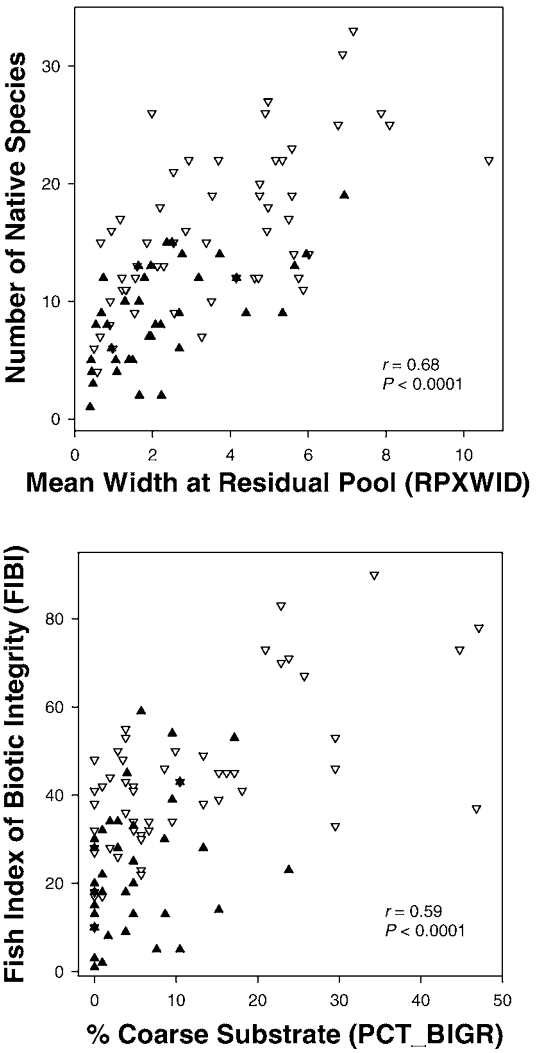

FIGURE 6.—Example relationships of a fish assemblage metric (upper panel) and the fish index of biotic integrity (FIBI; lower panel) with their most strongly related physical habitat predictors in wadeable Iowa streams. Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites located in the Mississippi River drainage. Physical habitat variable codes in parentheses correspond to descriptions in Table 2.

mean width : depth ratio, mean bank-full width : depth ratio, mean channel incision height, and row crops near the bank, express the availability, heterogeneity, or quality of fish habitat at the reach scale. All of these habitat variables exhibited relationships with fish assemblage metrics and FIBI that were consistent with previous research. Several studies have demonstrated a relationship between the number of fish species and the diversity of habitats available, implying that a reduction in habitat diversity would lead to a reduction in the number of species (Gorman and Karr 1978). Shields et al. (1994) found that incised streams in northwest Mississippi had reduced species richness and smaller fish relative to a nonincised reference site. Infante et al. (2006) showed that streams in Michigan's Lower Peninsula with decreased depth at low flow and increased incision had reduced fish species richness and biomass. In an earlier study of Iowa streams, loss of habitat diversity from channelization reduced game fish abundances and total fish abundances but did not reduce species richness (Paragamian 1987). Loss of habitat diversity also reduced invertebrate drift density in channelized reaches of Iowa streams (Zimmer 1976).

Channel incision results in loss of fish diversity and abundance through alteration of channel form, flow, and reduced connection with the floodplain. If sediment transport exceeds input, the result is a negative sediment budget leading to streambed erosion, which initially involves downcutting and then widening of the stream channel (Schumm 1977). This process embeds coarse substrates in fine sediments, buries riffles, fills pools, and ultimately results in an unstable, homogenous stream bottom with little variation in depth and habitat diversity. As pools fill with sediment and eventually disappear, they no longer provide refuge at low flow, forcing fish to inhabit shallower areas with increasing temperature and decreasing dissolved oxygen (Smale and Rabeni 1995). At high flows, incised channels have reduced frictional resistance, which increases current velocity, bed shear stress (Kaufmann et al. 2008), and hydraulic stress on biota and leads to further erosion (Infante et al. 2006). Incision isolates the channel from the floodplain, preventing fish from accessing preferred spawning and rearing habitats and from entering low-velocity refugia during periods of high discharge (Kwak 1988; Turner et al. 1994).

Riparian vegetation affects stream biota by supplying large woody debris and cover and influencing instream temperature, bank stability, and primary production (Gregory et al. 1991). Ten of the variables distinguishing between sites with poor FIBI scores and those with good or excellent FIBI scores and four of the significant predictor variables described large woody debris, cover, and riparian vegetation; all exhibited relationships with FIBI and fish assemblage metrics that were consistent with previous research. Large woody debris serves as cover for fish, collection areas for particulate organic matter, and colonization sites for macroinvertebrates (Angermeier and Karr 1984) and can help to trap sediment and influence channel morphology and diversity (Gurnell et al. 2002; Wallerstein and Thorne 2004). All four woody debris

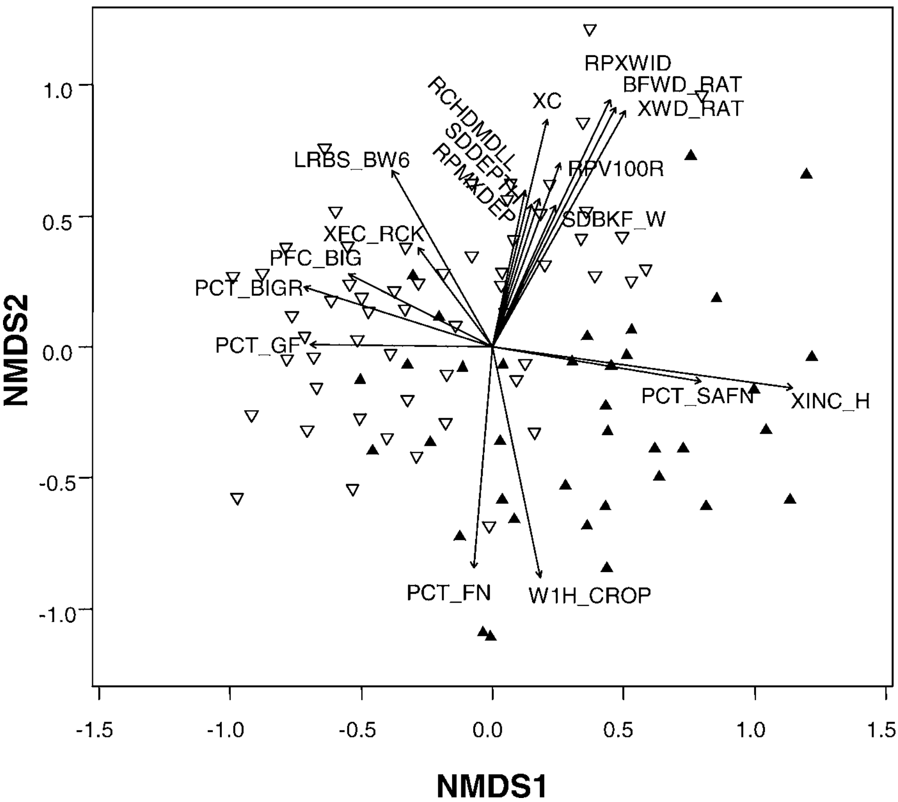

FIGURE 7.—Nonmetric multidimensional scaling (NMDS) ordination based on fish species abundance in 93 sites on wadeable Iowa streams and relationships with physical habitat variables (codes defined in Table 2). Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites located in the Mississippi River drainage. Physical habitat variables that were significant predictors of fish assemblage metrics and the fish index of biotic integrity are plotted as vectors. Vector arrow indicates the direction of the most significant change, and length of arrow is proportional to the strength of correlation with the ordination.

variables that distinguished between sites with poor FIBI scores and sites with good or excellent FIBI scores had lower values at the sites with poor FIBI scores. Medium-diameter, long pieces of woody debris found above bank-full height were negatively correlated with the percent contribution of the top-three most abundant fish species, which in turn is negatively related to FIBI and stream health (Wilton 2004). Although Heitke et al. (2006) found no significant relationship between large woody debris and fish assemblages in Iowa streams, our study, which employed a more robust sampling design and had a much larger sample size, corroborated other studies suggesting that large woody debris is beneficial to fish assemblages in midwestern streams (Stauffer et al. 2000; Talmage et al. 2002). Vegetation stabilizes banks primarily through the development of a dense matrix of roots that holds soils and reduces their susceptibility to erosion. Vegetation naturally armors the stream bank and acts to physically prevent or reduce bank erosion (Zaimes et al. 2004). Riparian forest buffers also reduce sediment input from row crop fields by up to 90% (Lee et al. 2000, 2003). The absence of riparian vegetation exposes the channel to direct sunlight and elevates daytime temperatures (Wang et al. 2003). In our study, canopy cover was nearly twice as extensive at sites with FIBI scores greater than 50 than at sites with FIBI scores of 25 or less.

Excessive fine substrates have been associated with reduced fish diversity in upper midwestern streams (Waters 1995; Nerbonne and Vondracek 2001; Talmage et al. 2002; Diana et al. 2006; Heitke et al. 2006) and have been shown specifically to reduce the abundance of benthic invertivores, herbivores, and simple lithophilous spawners (Berkman and Rabeni 1987). All of the substrate variables distinguishing between sites with poor FIBI scores and those with good or excellent FIBI scores and all of the significant predictor variables representing substrate in our study showed relationships that were consistent with previous research.

Fish cover describes elements of the stream that provide refuge from predators and high current velocity. Cover also serves to retain particulate organic matter, provide colonizing sites for macroinvertebrates, and increase channel stability and hydraulic roughness. Heitke et al. (2006) showed a positive relationship between rock and total cover abundance with FIBI score in Iowa streams. Wang et al. (1998) showed a positive relationship between percent instream cover and fish IBI in low-gradient Wisconsin streams. In our study, all of the fish cover variables distinguishing between sites with poor FIBI scores and sites with good or excellent FIBI scores and the two significant predictor variables reflecting fish cover showed relationships that were consistent with previous research.

With their tendency toward higher FIBI scores, sites in the Mississippi River drainage were characterized as somewhat less impaired than sites in the Missouri River drainage. There are two possible explanations for this difference. First, streams in the Missouri River drainage could simply be more impaired than streams in the Mississippi River drainage. Second, the FIBI as currently calibrated could fail to account for natural differences between the Mississippi and Missouri River drainages. We favor the first explanation, but we acknowledge that some adjustment in how the FIBI is applied to the two major drainages might be desirable. Percentage of coarse substrates, fish cover, and bed stability all were greater at sites in the Mississippi River drainage. Sites in the Missouri River drainage generally had higher percentages of fine substrates, more incised channels, and greater proximity to row crop agriculture. Higher percentages of fine substrates in the Missouri River drainage in Iowa are probably related to the highly erosive and friable nature of the loess soils that dominate the ecoregions associated with this drainage. In addition, we found greater percentages of coarse substrates in the northern regions than in the southern regions; this reflects the more recent glaciation and thinner deposits of loess soils in northern Iowa than in southern Iowa (Menzel 1987). The combination of erodible loess soils, lack of coarse substrate, and high percentage of row crop agriculture in the riparian zone interact to increase erosion and impair fish assemblages in the Missouri River drainage.

The Missouri River drainage has a less-diverse fish assemblage than the Mississippi River drainage, and the FIBI corrected for this difference in calibrating the richness metrics (Wilton 2004). However, functional metrics, such as percentage of lithophilous spawners, may be inappropriate for the Missouri River drainage. Only two species of lithophilous spawners, the shorthead redhorse and suckermouth minnow, commonly occur in the Missouri River drainage. Metrics that account for functional groups normally identified with prairie stream systems, specifically cyprinids that release semibuoyant eggs during high water (i.e., minnows *Hybognathus* spp., chubs *Macrhybopsis* spp., and some shiners *Notropis* spp.; Dodds et al. 2004), may be more appropriate for use in the Missouri River drainage. Differences observed in physical habitat and fish assemblages between the major river drainages are probably the result of natural physiographic variation (Griffith et al. 1994) and biogeographic differences (Abell et al. 2008) as well as anthropogenic influences. Identification of additional least impacted reference sites in the Missouri River drainage is needed to establish more appropriate regional criteria for fish and physical habitat in that portion of Iowa.

The collective evidence to date demonstrates strong, direct mechanistic linkages between fish assemblages and physical habitat in wadeable streams. The precise nature of these relationships varies with region and study methodology. The degree of human alteration also clearly influences the nature and strength of these relationships, as illustrated by our study and a previous study of Iowa streams (Heitke et al. 2006). Another strong line of evidence from previous studies suggests that physical habitat integrates effects of larger-scale phenomena (Hughes et al. 2006). In this view, physical habitat is seen as one of the important links between fish assemblages and landscape-level factors, such as geology, land cover, and anthropogenic disturbance. Because of the pervasiveness of land cover alteration in Iowa (Natural Resources Conservation Service 2000) and the associated degradation of aquatic habitats (Menzel 1983; Heitke et al. 2006), it is especially important to fully document these linkages in Iowa streams. In a companion article (Rowe et al. 2009, this issue), we explore relationships of landscape characteristics that influence fish assemblages through effects on physical habitat in wadeable Iowa streams.

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References

Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N. Mandrak, S. C. Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. P. Allen, P. Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E. Wikramanake, D. Olson, H. L. Lopez, R. E. Reis, R. J. Lundberg, M. H. S. Perez, and P. Petry. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater conservation. BioScience 58:403–414.

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

Allan, J. D., D. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149–161.

Angermeier, P. L., and J. R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 124:573–582.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, 2nd edition. EPA/841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Assessment and Watershed Protection Division, Washington, D.C.

Berkman, H. E., and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18:285–294.

Bogue, A. G. 1963. From prairie to corn belt: farming on the Illinois and Iowa prairies in the nineteenth century. Iowa State University Press, Ames.

Bulkley, R. V. 1975. Inventory of major stream alterations in Iowa. Completion report: a study of the effects of stream channelization and bank stabilization of warm water sport fish in Iowa. U.S. Fish and Wildlife Service, Contract Number 14-16-0008-745, Subproject Number 1, Ames, Iowa.

Campell, K. L., S. Kumar, and H. P. Johnson. 1972. Stream straightening effects on flood-runoff characteristics. Transactions of the ASAE (American Society of Agricultural Engineers) 15:94–98.

Cao, Y., D. D. Williams, and N. E. Williams. 1998. How important are rare species in aquatic community ecology and bioassessment? Limnology and Oceanography 43:1403–1409.

Davis, W. S. 1995. Biological assessment and criteria: building on the past. Pages 15–29 *in* W. S. Davis and T. P. Simon, editors. Biological assessment and criteria: tools for water resource planning and decision making. CRC Press, Boca Raton, Florida.

Diana, M., J. D. Allan, and D. Infante. 2006. The influence of physical habitat and land use on stream fish assemblages in southeastern Michigan. Pages 359–374 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54:205–216.

Fausch, K. D., J. R. Karr, and P. R. Yant. 1984. Regional application of an index of biotic integrity based on stream fish communities. Transactions of the American Fisheries Society 113:39–55.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507–515.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. BioScience 41:540–551.

Griffith, G. E., J. M. Omernik, T. F. Wilton, and S. M. Pierson. 1994. Ecoregions and subregions of Iowa: a framework for water quality assessment and management. Journal of the Iowa Academy of Science 101:5–13.

Gurnell, A. M., H. Piégay, F. J. Swanson, and S. V. Gregory. 2002. Large wood and fluvial processes. Freshwater Biology 47:601–619.

Heitke, J. D., C. L. Pierce, G. T. Gelwicks, G. A. Simmons, and G. L. Siegwarth. 2006. Habitat, land use, and fish assemblage relationships in Iowa streams: preliminary assessment in an agricultural landscape. Pages 287–304 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Hughes, R. M., L. Wang, and P. W. Seelbach, editors. 2006. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Infante, D. M., M. J. Wiley, and P. W. Seelbach. 2006. Relationships among channel shape, catchment characteristics, and fish in Lower Michigan streams. Pages 339–358 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6(6):21–27.

Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant, and I. J. Schlosser. 1986. Assessing biological integrity in running waters: a method and its rationale. Illinois Natural History Survey, Special Publication 5.

Karr, J. R., L. A. Toth, and D. R. Dudley. 1985. Fish communities of midwestern rivers: a history of degradation. BioScience 35:90–95.

Kaufmann, P. R., J. M. Faustini, D. P. Larsen, and M. A. Shirazi. 2008. A roughness-corrected index of relative bed stability for regional stream surveys. Geomorphology 99:150–170.

Kaufmann, P. R., and R. M. Hughes. 2006. Geomorphic and anthropogenic influences on fish and amphibians in Pacific Northwest coastal streams. Pages 429–455 *in* R. M. Hughes, L. Wang, and P. W. Seelbach, editors. Influences of landscapes on stream habitats and biological assemblages. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Kaufmann, P. R., P. Levine, E. G. Robinson, C. Seeliger, and D. Peck. 1999. Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. U.S. Environmental Protection Agency, Office of Research and Development, Environmental Monitoring and Assessment Program, Corvallis, Oregon.

Kwak, T. J. 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee River, Illinois. American Midland Naturalist 120:241–249.

Lammert, M., and J. D. Allan. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land cover/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23:257–270.

Lau, J. K., T. E. Lauer, and M. L. Weinman. 2006. Impacts of channelization on stream habitats and associated fish assemblages in east central Indiana. American Midland Naturalist 156:319–330.

Lee, K. H., T. M. Isenhart, and R. C. Schultz. 2003. Sediment and nutrient removal in an established multi-species riparian buffer. Journal of Soil and Water Conservation 58:1–8.

Lee, K. H., T. M. Isenhart, R. C. Schultz, and S. K. Mickelson. 2000. Multispecies riparian buffer system in central Iowa for controlling sediment and nutrient losses during simulated rain. Journal of Environmental Quality 29:1200–1205.

Legendre, P., and L. Legendre. 1983. Numerical ecology. Elsevier, Amsterdam.

Litvan, M. E., C. L. Pierce, T. W. Stewart, and C. J. Larson. 2008a. Fish passage in a western Iowa stream modified by grade control structures. North American Journal of Fisheries Management 28:1384–1397.

Litvan, M. E., C. L. Pierce, T. W. Stewart, and C. J. Larson. 2008b. Fish assemblages in a western Iowa stream modified by grade control structures. North American Journal of Fisheries Management 28:1398–1413.

Lyons, J. 1992. Using the index of biotic integrity (IBI) to measure environmental quality in warmwater streams of Wisconsin. U.S. Forest Service General Technical Report NC-149.

Lyons, J., L. Wang, and T. D. Simonson. 1996. Development and validation of an index of biotic integrity for coldwater streams in Wisconsin. North American Journal of Fisheries Management 16:340–347.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Kluwer, Dordrecht, Netherlands.

McMahon, G., S. M. Gregonis, S. W. Waltman, J. M. Omernik, T. D. Thorson, J. A. Freeouf, A. H. Rorick, and J. E. Keys. 2001. Developing a spatial framework of common ecological regions for the conterminous United States. Environmental Management 28:293–316.

Menzel, B. W. 1983. Agricultural management practices and the integrity of in-stream biological habitat. Pages 305–329 *in* F. W. Schaller and G. W. Bailey, editors. Agricultural Management and Water Quality. Iowa State University Press, Ames.

Menzel, B. W. 1987. Fish distribution. Pages 201–213 *in* J. R. Harlan, E. B. Speaker, and J. Mayhew, editors. Iowa fish and fishing. Iowa Department of Natural Resources, Des Moines.

Mundahl, N. D., and T. P. Simon. 1999. Development and application of an index of biotic integrity for coldwater streams of the upper midwestern United States. Pages 383–415 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Natural Resources Conservation Service. 2000. Natural resources inventory, 1997 summary report. U.S. Department of Agriculture, Ames, Iowa. Available: www.nrcs.usda.gov (January 2007).

Nerbonne, B. A., and B. Vondracek. 2001. Effects of local land use on physical habitat, benthic macroinvertebrates, and fish in the Whitewater River, Minnesota, USA. Environmental Management 28:87–99.

Oksanen, J., R. Kindt, P. Legendre, and B. O'Hara. 2007. The VEGAN Package: community ecology package. Available: cc.oulu.fi/~jarioksa/ (January 2007).

Paragamian, V. L. 1987. Standing stocks of fish in some Iowa streams, with a comparison of channelized and natural stream reaches in the southern Iowa Drift Plain. Proceedings of the Iowa Academy of Science 94:128–134.

Peck, D. V., A. T. Herlihy, B. H. Hill, R. M. Hughes, P. R. Kaufmann, D. J. Klemm, J. M. Lazorchak, F. M. McCormick, S. A. Peterson, P. L. Ringold, T. Magee, and M. R. Cappaert. 2006. Environmental monitoring and assessment program—surface waters western pilot study: field operations manual for wadeable streams. EPA 600/R-06/003, U.S. Environmental Protection Agency, Office of Research and Development, Washington, D.C.

Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606–627.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available: www.R-project.org (June 2006).

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647–659.

Roth, N., J. D. Allan, and D. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141–156.

Rowe, D. C. 2007. Relationships of fish assemblages, in-stream physical habitat, and landscape characteristics of wadeable Iowa streams. Master's thesis. Iowa State University, Ames.

Rowe, D. C., C. L. Pierce, and T. F. Wilton. 2009 (this issue).

Physical habitat and fish assemblage relationships with landscape variables at multiple spatial scales in wadeable Iowa streams. North American Journal of Fisheries Management 29:1333–1351.

SAS Institute. 1996. SAS/STAT user's guide for personal computers, Version 6. SAS Institute, Cary, North Carolina.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52:395–414.

Schumm, S. A. 1977. The fluvial system. Wiley, New York.

Shields, F. D., S. S. Knight, and C. M. Cooper. 1994. Effects of channel incision on base flow stream habitats and fishes. Environmental Management 18:43–57.

Simon, T. P., editor. 1999. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Simonson, T. D., and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. North American Journal of Fisheries Management 15:419–427.

Smale, M. A., and C. F. Rabeni. 1995. Influences of hypoxia and hyperthermia on fish species composition in headwater streams. Transactions of the American Fisheries Society 124:711–725.

Stauffer, J. C., R. M. Goldstein, and R. M. Newman. 2000. Relationship of wooded riparian zones and runoff potential to fish community composition in agricultural streams. Canadian Journal of Fisheries and Aquatic Sciences 57:307–316.

Stevens, D. L., and A. R. Olsen. 1999. Spatially restricted surveys over time for aquatic resources. Journal of Agricultural, Biological, and Environmental Statistics 4:415–428.

Talmage, P. J., J. A. Perry, and R. M. Goldstein. 2002. Relation of in-stream habitat and physical conditions to fish communities of agricultural streams in the northern Midwest. North American Journal of Fisheries Management 22:825–833.

Turner, T. M., J. C. Trexler, G. L. Miller, and K. E. Toyer. 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. Copeia 1994:174–183.

USEPA (U.S. Environmental Protection Agency). 2006. Wadeable stream assessment: a collaborative survey of the Nation's streams. EPA/641/B-06/002. USEPA, Office of Water, Washington, D.C.

USGS (U.S. Geological Survey). 1999. The National Hydrography Dataset. USGS fact sheet 106-99. Available: http://edc2.usgs.gov. (January 2007).

Wallerstein, N. P., and C. R. Thorne. 2004. Influence of large woody debris on morphological evolution of incised, sand bed channels. Geomorphology 57:53–73.

Wang, L., J. Lyons, and P. Kanehl. 1998. Development and evaluation of a habitat rating system for low gradient Wisconsin streams. North American Journal of Fisheries Management 18:775–785.

Wang, L., J. Lyons, and P. Kanehl. 2003. Impacts of urban land cover on trout streams in Wisconsin and Minnesota. Transactions of the American Fisheries Society 132:825–839.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22(6):6–12.

Waters, T. F. 1995. Sediment in streams: sources, biological effects and control. American Fisheries Society, Bethesda, Maryland.

Whittier, T. R., and S. G. Paulsen. 1992. The surface waters component of the Environmental Monitoring and Assessment Program (EMAP): an overview. Journal of Aquatic Ecosystem Health 1:119–126.

Wilton, T. F. 2004. Biological assessment of Iowa's wadeable streams. Project completion report. Iowa Department of Natural Resources, Des Moines. Available: http://wqm.igsb.uiowa.edu. (January 2007).

Yoder, C. O., and E. T. Rankin. 1995. Biological criteria program development and implementation in Ohio. Pages 109–144 *in* W. S. Davis and T. P. Simon, editors. Biological assessment and criteria: tools for water resource planning and decision making. CRC Press, Boca Raton, Florida.

Yoder, C. O., and M. A. Smith. 1999. Using fish assemblages in a state biological assessment and criteria program: essential concepts and considerations. Pages 17–56 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Zaimes, G. N., R. C. Schultz, and T. M. Isenhart. 2004. Stream bank erosion adjacent to riparian forest buffers, row-crop fields, and continuously grazed pastures along Bear Creek in central Iowa. Journal of Soil and Water Conservation 59:19–28.

Zimmer, D. W. 1976. The effects of long-reach channelization on habitat and invertebrate drift in some Iowa streams. Doctoral dissertation. Iowa State University, Ames.