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[Article]

Physical Habitat and Fish Assemblage Relationships with Landscape Variables at Multiple Spatial Scales in Wadeable Iowa Streams

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Abstract.—Landscapes in Iowa and other midwestern states have been profoundly altered by conversion of native prairies to agriculture. We analyzed landscape data collected at multiple spatial scales to explore relationships with reach-scale physical habitat and fish assemblage data from 93 randomly selected sites on second- through fifth-order wadeable Iowa streams. Ordination of sites by physical habitat showed significant gradients of channel shape, habitat complexity, substrate composition, and stream size. Several landscape variables were significantly associated with the physical habitat ordination. Row crop land use was associated with fine substrates and steep bank angles, whereas wetland land cover and greater sinuosity and catchment land area were associated with complex channel and bank morphology and greater residual pool volume, woody debris, and canopy cover. Thirteen landscape variables were significant predictors of physical habitat variables in multiple linear regressions, with adjusted R^2 values ranging from 0.07 to 0.74. Inclusion of landscape variables with physical habitat variables in multiple regression models predicting fish assemblage metrics and a fish index of biotic integrity resulted in negligible improvements over models based on only physical habitat variables. Physical habitat in wadeable Iowa streams is strongly associated with landscape characteristics. Results of this study and previous studies suggest that (1) landscape factors directly influence physical habitat, (2) physical habitat directly influences fish assemblages, and (3) the influence of landscape factors on fish assemblages is primarily indirect. Understanding how landscape factors, such as human land use, influence physical habitat and fish assemblages will help managers make more informed decisions for improving Iowa's wadeable streams.

Physical habitat is a key component of stream ecosystems and plays a major role in determining biotic assemblages and integrity (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, and appropriate substrates for spawning (Berkman and Rabeni 1987), have been shown to influence biotic assemblages. Diverse habitats have been shown to support more abundant and diverse assemblages of organisms (Gorman and Karr 1978; Beisel et al. 1998). Physical habitat has been shown to influence the composition of fish (Gorman and Karr 1978; Schlosser 1982; Rowe et al. 2009, this issue), macroinvertebrate (MacFarlane 1983; Richards et al. 1996; Maul et al. 2004; Litvan et al. 2008), and aquatic macrophyte (Gurnell et al. 2006) assemblages. Alteration of physical habitat can lead to brief or long-lasting changes in the composition of stream communities depending on the severity of the disturbance (Reice et al. 1990).

There is increasing recognition of the role played by landscape-level factors in determining biotic assemblages and integrity of streams (Hughes et al. 2006). Agricultural land use has been associated with reduced biotic integrity at the catchment scale (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997) and at local riparian scales (Lammert and Allan 1999; Stauffer et al. 2000; Heitke et al. 2006), while forest cover and wetland land cover have been associated with streams with higher biotic integrity (Roth et al. 1996; Wang et

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al. 1997; Stauffer et al. 2000; Diana et al. 2006). Urban land cover and impervious surfaces have been shown to reduce abundance and diversity of fish and benthic macroinvertebrates and reduce biotic integrity (Wang et al. 2001; Wang and Kanehl 2003). There is uncertainty regarding the relative influence of factors on stream biota at different spatial scales. Stream systems are spatially nested hierarchies of catchments, segments, reaches, macrohabitats, and microhabitats (Frissell et al. 1986). The features of larger scales constrain conditions at smaller scales, regulating local conditions through processes at multiple spatial scales and ultimately influencing stream biota. This view of control in stream systems implies that effects of landscape-level factors on biotic assemblages are primarily indirect, operating via direct effects on instream factors, such as water quality and physical habitat, which in turn affect biota directly (Poff 1997).

Landscapes in Iowa and other midwestern states have been profoundly altered by conversion of native prairies to agriculture (Whitney 1994). Beginning in the 1800s, as settlement by European-American immigrants pushed west, the vast prairies and wetlands of the eastern plains were converted to the Corn Belt by plowing the prairie, draining water from wetlands, and cutting down riparian forests. Between 1830 and 1900, Iowa lost over 99% or roughly 30 million acres of native tallgrass prairie to agriculture (Smith 1981). Wetlands declined similarly once drainage districts were created for the purpose of swamp reclamation in the late 19th century (Bogue 1963). Extensive networks of subsurface drainage tile and ditches were dug and connected to streams that were channelized to increase the rate at which water drained from the land. Once estimated to cover over 6 million acres of Iowa's landscape, wetland and wet prairie now cover less than 27,000 acres, less than 0.5% of the original area (Bishop 1981). Forests covered 19% of Iowa at the time of European-American settlement, and now less than 4% of the state is forested (Thomson and Hertel 1981). Over 80% of Iowa's land area was used for agriculture in 2000 (Natural Resources Conservation Service 2000), and the emerging bioeconomy (Jordan et al. 2007) threatens to intensify agricultural alteration of the Iowa landscape in the future (Widenoja 2007).

Stressor indicators quantify processes that cause changes in stream habitat or chemistry and thus have the potential to affect stream biota. These can be natural processes or more often changes from human disturbances. Stressor indicators are typically used to reflect human disturbances and are surrogates for phenomena that are hard to measure or quantify. Connected impervious surfaces (Wang et al. 2001), agricultural and urban land cover (Allan et al. 1997; Lammert and Allan 1999), and channelization age (Wang et al. 1998) are all examples of stressor indicators that have been used in previous stream assessments. Because stressors represent human disturbances, spatial scale is important when considering the effects of stressors on stream ecosystems. Stressors acting at large spatial scales impact all smaller scales. There is uncertainty about the scale at which land cover stressors have a greater influence on stream biota. Some studies have demonstrated that land cover has stronger effects on fish assemblages at a catchment scale (Roth et al. 1996; Wang et al. 1997), while other studies have demonstrated a greater influence at the local riparian or reach scale (Lammert and Allan 1999; Wang et al. 2003). Richards et al. (1996) found that different elements of physical habitat were more strongly influenced at different scales. It is important to understand the spatial scale at which land cover and catchment characteristics influence stream biota and habitat in Iowa's streams and rivers so that conservation or restoration activities can target the appropriate scales at which stressors are acting.

The overall goal of this study was to explore physical habitat and fish assemblage relationships with landscape-level characteristics at multiple spatial scales in wadeable Iowa streams. This study builds on a companion study (Rowe et al. 2009, this issue) that describes the fish assemblages and relationships with physical habitat in detail. Our specific objectives were to (1) quantify and characterize landscape variables at multiple spatial scales for the same stream reaches sampled for fish assemblages and reach-scale physical habitat in Rowe et al. (2009, this issue), (2) identify landscape variables that are significantly associated with physical habitat characteristics, (3) identify landscape variables that are significantly associated with fish assemblage characteristics, (4) evaluate the effects of spatial scale on landscape relationships, and (5) weigh the evidence for direct versus indirect effects of landscape variables on physical habitat and fish assemblages. 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).

Methods

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). Locations on all streams greater than first order, excluding the Mississippi and Missouri rivers, were eligible for selection. If greater than 60% of a selected location was judged to be nonwadeable at the time of sampling, the location was excluded. Coldwater streams and those suspected to be severely polluted were sampled but excluded from this analysis. The 93 sites sampled and retained for analysis ranged from second through fifth order and represented all four ecoregions of Iowa and the seven subregions within the Western Corn Belt Plains ecoregion. See Rowe et al. (2009, this issue) for more site selection and ecoregion details.

Fish assemblages and physical habitat.—Fish assemblages were sampled by following the Iowa Department of Natural Resources wadeable streams bioassessment protocol (Wilton 2004) using single-pass upstream electrofishing (Simonson and Lyons 1995; Yoder and Smith 1999). Reaches were isolated with block nets to prevent fish escape. An effort was made to sample all accessible habitats in the reach and collect all stunned fish. All fish collected were identified to species, counted, examined for external physical abnormalities, and returned to the stream. Fish assemblage metrics and a fish index of biotic integrity (FIBI) score were calculated according to Wilton (2004). A more detailed description of fish sampling is given in Rowe et al. (2009, this issue).

Physical habitat was sampled following the wadeable streams physical habitat protocol of USEPA EMAP (Peck et al. 2006), with data reduction and metric calculation as described by Kaufmann et al. (1999). Reaches that were 40 times the mean stream width were sampled, with 11 cross-sectional transects evenly spaced along each reach. Variables were quantified by measurement or observation 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 (Rowe 2007). A more thorough description of habitat sampling and physical habitat variables is given in Rowe et al. (2009, this issue) and Rowe (2007).

Landscape variables.—Variables describing catchment and riparian characteristics were quantified at four spatial scales using the Analytical Tools Interface for Landscape Assessments (ATtILA), an ArcView (ESRI 2008) extension developed by USEPA (2004). Catchments were delineated such that the center of the reach sampled for fish and physical habitat was the bottom of the catchment. Data layers used by ATtILA included 2002 land cover, elevation, slope, stream networks, roads, and human population density (2000 and 1990 census data; ISU 2007). The land cover data layer had 16 classes of land cover: (1) water, (2) wetland, (3) wet forest, (4) coniferous forest, (5) deciduous forest, (6) ungrazed grasslands, (7) grazed grasslands, (8) Conservation Reserve Program (CRP) lands (U.S. Department of Agriculture), (9) alfalfa *Medicago sativa* and lush grass, (10) corn *Zea mays*, (11) soybeans *Glycine max*, (12) other agriculture, (13) roads, (14) commercial and industrial, (15) residential, and (16) barren. Percentage of impervious surface was estimated using the approach described by Caraco et al. (1998). Assuming that 90% of commercial and industrial land cover, 60% of residential land cover, 2% of natural vegetated land cover, and none of the remaining land cover classes are impervious, we calculated the percentage of impervious surface as the sum of land cover classes multiplied by their impervious surface proportions.

Land cover classes were then simplified to the following six categories: wetland, forest, natural grassland, pasture, row crop, and urban. Three composite variables were created by summing land cover types. Total agriculture was defined as the sum of row crop and pasture; human land use was defined as the sum of total agriculture and urban; and total natural land cover was defined as the sum of wetland, forest, and natural grassland. Artificially drained agricultural land was estimated using the Iowa Soil Properties and Interpretation Database (Miller 2006) and 2002 land cover. Land with a slope less than 2%, drainage classified as poor to very poor, soils with slow infiltration rates, and usage in row crop cultivation was considered to be artificially drained (Jaynes et al. 2006). Stream and road densities were calculated as length : area ratios. Human population density was apportioned by area-weighting from census units. For example, if 30% of a census unit was in a catchment, then 30% of the population of that census unit was assigned to the catchment.

Variables were quantified at four different spatial scales extending upstream from the center of the reach sampled for fish and physical habitat variables. The four scales included catchment, riparian buffer, local catchment, and local riparian buffer. The catchment scale included the entire upstream catchment. The riparian buffer scale consisted of the area extending out 30 m on each side of the entire upstream channel network. The local catchment scale consisted of the portion of the upstream catchment that was within 1 km of the center of the sampled reach. The local riparian buffer scale was the portion of the riparian buffer upstream that was within 1 km of the center of the sampled reach.

Sinuosity was quantified at three scales: catchment, local, and segment. Sinuosity is the ratio of the curvilinear distance of the stream channel to the straight-line distance. Sinuosity was calculated for each stream segment, which was defined as a length of stream extending from a downstream confluence to the next upstream confluence. Catchment sinuosity was calculated as the average of all segments in the catchment, weighted by segment length. Local sinuosity was calculated as the average of all upstream segments within 1 km of the center of the reach, weighted by segment length. Segments that had sinuosity values of less than 1.5 were considered to be nonmeandering (Rosgen 1994). The proportion of nonmeandering segments was also quantified at the catchment and local scales for each site.

Data analysis.—A nonmetric multidimensional scaling (NMDS) ordination was created from the 30 physical habitat variables identified in Rowe et al. (2009, this issue) as significantly correlated with an ordination of fish species abundance and significantly different between sites with poor FIBI scores and sites with good or excellent FIBI scores. Canberra similarity coefficients were generated between all sites from the physical habitat variables. Canberra similarity coefficients weight all variables equally regardless of the magnitude of numeric values. The ordination was generated from the matrix of pairwise Canberra similarity coefficients between sites.

All landscape variables were fit to the physical habitat ordination as vectors. Vectors indicate the direction of the 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 landscape variable; vector length 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 generated using the metaMDS function and permutation tests were performed using the envfit function in the VEGAN package (Oksanen et al. 2007) for R software (R Development Core Team 2006).

Landscape variables that were significantly correlated with the ordination were then assessed for redundancy within each spatial scale. Pearson's product-moment correlation matrices were created for landscape variables at each spatial scale, and only the variable exhibiting the highest correlation with the ordination was retained from groups of highly correlated ($r > 0.75$) variables. 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 physical habitat variables from the retained set of landscape variables. The physical habitat variables used as dependent variables in these analyses were the 18 variables identified by Rowe et al. (2009, this issue) as being significant predictors of fish assemblage metrics and FIBI. Forward stepwise variable selection was used; the first variable chosen was the one that produced the single-variable model with the highest r^2, and subsequent variables were chosen to maximize the improvement in adjusted 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. Log_{10} transformations were performed on heteroscedastic dependent variables. Multiple linear regression analysis was performed in SAS (SAS Institute 1996) using PROC REG and the STEPWISE variable selection procedure.

All landscape variables were fit as vectors to the NMDS ordination of fish species abundance that was generated in Figure 2 of Rowe et al. (2009, this issue). This was performed to identify landscape variables that were related to fish assemblages independent of any relationship with physical habitat. Monte Carlo permutation tests identified landscape variables significantly related to the patterns of fish species abundance similarity. A Pearson's product-moment correlation matrix of these significant landscape variables was then examined, and only the variable with the highest correlation with the ordination was retained from groups of highly correlated ($r > 0.75$) variables. Permutation tests were performed using the envfit function in the VEGAN package (Oksanen et al. 2007) for R (R Development Core Team 2006), and correlation analyses were performed in SAS (SAS Institute 1996).

We attempted to improve the multiple linear regression models generated in Rowe et al. (2009, this issue) for fish assemblage metrics and FIBI based on physical habitat variables by adding landscape variables that explained additional variation. Assuming that landscape factors affect fish assemblages mainly indirectly through direct effects on physical habitat, the addition of landscape variables should not greatly improve the models. However, if the addition of landscape variables accounts for significant variation that was previously unexplained by physical habitat alone, then landscape effects may be at least partially independent of physical habitat effects. We used forward stepwise multiple regression, in this case

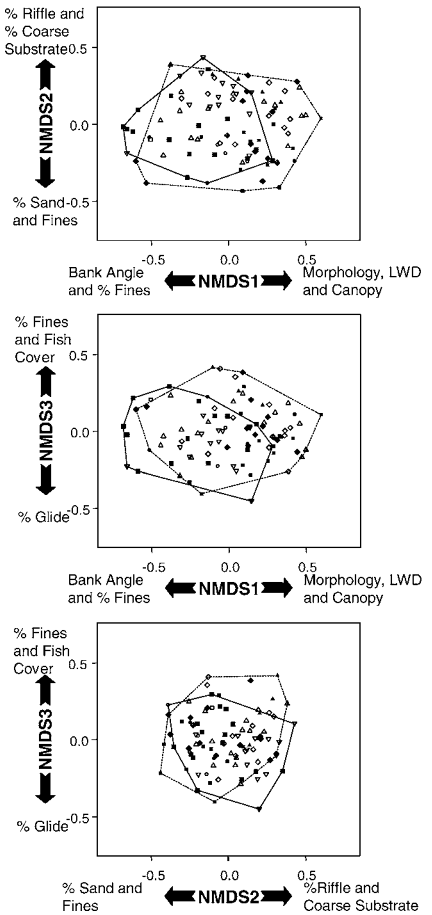

FIGURE 1.—Nonmetric multidimensional scaling (NMDS) ordination of 93 sites on wadeable Iowa streams based on the 30 physical habitat variables described in Table 2 of Rowe et al. (2009, this issue; LWD = large woody debris). Sites are represented by ecoregion or subregion symbols as follows: Central Irregular Plains ecoregion (solid squares), Northwest Iowa Loess Prairies subregion (inverted open triangles), Des Moines Lobe subregion (open triangles), Iowan Surface subregion (open diamonds), Missouri Alluvial Plain subregion (open squares), Loess Hills and Steeply Rolling Prairies subregion (× symbols surrounded by squares), Southern Iowa Rolling Loess Prairies subregion (crossed diamonds), Western Loess Hills subregion (open circles), Paleozoic Plateau ecoregion (solid triangles), and Interior River Lowland ecoregion (solid circles). Polygon hulls outline sites within the Mississippi River (dashed polygon) or Missouri River (solid polygon) drainages. The NMDS axis 1 is positively correlated with SDDEPTH, XWD_RAT, SDBKF_W, BFWD_RAT, C1TM100, V1TM100, RPGT50, RPMXDEP, RPXWID, RPV100R, and XC and negatively correlated with XBKA and PCT_FN. The NMDS axis 2 is positively correlated with PCT_RI, PCT_GF, and PCT_BIGR and negatively correlated with PCT_SAFN. The NMDS axis 3 is positively correlated with PCT_FN and XFC_NAT and negatively correlated with PCT_GL.

including the 18 physical habitat variables from Table 3 of Rowe et al. (2009, this issue) and the landscape variables identified above as potential predictors of fish assemblage metrics and FIBI. From this pool of variables, the first variable chosen was the one that produced the single-variable model with the highest r^2, and subsequent variables were chosen to maximize the improvement in adjusted R^2 while maintaining significance of all previously included variables. The significance level for inclusion of landscape variables was 0.05. Improvement of models over those based solely on physical habitat was expressed as the increase in adjusted R^2 (ΔR^2) and the decrease in root mean square error (ΔRMSE). Multiple linear regression analysis was performed in SAS (SAS Institute 1996) using PROC REG and the STEPWISE variable selection procedure.

Results

Fish Assemblages and Reach-Scale Physical Habitat

Fish assemblages were composed primarily of cyprinids, catostomids, percids, centrarchids, and ictalurids. Cyprinids represented 75% of the captured fish. The majority of species (94%) were tolerant or moderately tolerant of environmental disturbance. The creek chub *Semotilus atromaculatus*, bigmouth shiner *Notropis dorsalis*, sand shiner *Notropis stramineus*, bluntnose minnow *Pimephales notatus*, green sunfish *Lepomis cyanellus*, johnny darter *Etheostoma nigrum*, white sucker *Catostomus commersonii*, and fathead minnow *Pimephales promelas* were present at over half of the sites and constituted over 50% of the catch. Sites were often dominated by a few of these species, and the mean percentage of the top-three most abundant species was 70.6% (range = 35–100%). The mean FIBI score was 34 (range = 1–90). Most sites were characterized as poor (32%) or fair (53%) based on FIBI score, with a few classified as good (9%) and fewer as excellent (6%). A detailed description of fish assemblage characteristics is given in Rowe et al. (2009, this issue).

Most streams were low gradient, nonmeandering, and dominated by glide habitat. Substrates were often dominated by sand and silt, and banks were usually eroding. Often, the channels were actively incising and isolated from the floodplain. Some streams were beginning to deposit new bank material within an incised and widened channel. Visual evidence of past channel alteration and straightening was common. A variety of riparian conditions was observed, from well-vegetated banks with intact forest or grass riparian zones to sites with active erosion; steep, unvegetated banks; and little or no native vegetation between the

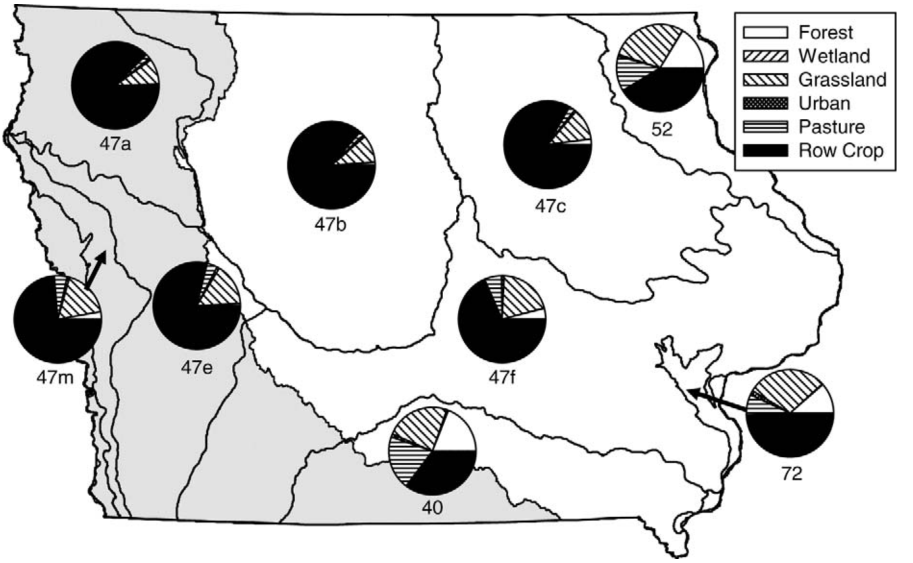

FIGURE 2.—Mean percent composition of catchment-scale land cover at 93 sites on wadeable Iowa streams, presented for each ecoregion or subregion (codes defined in Figure 1 of Rowe et al. 2009, this issue). Subregion 47d was omitted because it contained only one site. Shaded area indicates land in the Missouri River drainage; unshaded area represents land that drains to the Mississippi River.

stream channel and corn or soybean fields. Thirty reach-scale physical habitat variables from nine categories were significantly related to fish assemblage composition and were significantly different between sites with impaired versus healthy fish assemblages (Rowe et al. 2009, this issue). Eighteen of these variables were significant predictors of fish assemblage metrics and FIBI in multiple linear regressions (Rowe et al. 2009, this issue). A detailed description of reach-scale physical habitat variables and an analysis of relationships with fish assemblages are given in Rowe et al. (2009, this issue).

The NMDS ordination of sites based on physical habitat variables was evaluated at two and three dimensions. There was a sizeable improvement in stress values between ordinations with two dimensions (stress value = 20.2) and ordinations with three dimensions (14.7), so we used the three-dimensional ordination. The ordination did not separate sites by ecoregion or major river drainage (Figure 1). Axis 1 represented a gradient from (1) sites with steep banks, fine substrate, and close proximity of row crop agriculture to (2) sites with complex channel and bank morphology, increased residual pool volumes, large woody debris, and greater riparian vegetation canopy. Axis 1 was correlated with the standard deviation of depth (SDDEPTH, Pearson's product-moment correlation coefficient = 0.72); mean width : depth ratio (XWD_RAT, 0.73); mean bank angle (XBKA, −0.65); standard deviation of bank-full width (SDBKF_W, 0.67); bank-full width : depth ratio (BFWD_RAT, 0.72); proximity of row crop (W1H_CROP, −0.60); pieces of small, medium, large, or extra large woody debris per 100 m above the bank-full channel (C2DM100, 0.52); pieces of all sizes of woody debris per 100 m (C1TM100, 0.53); volume of woody debris per 100 m (V1TM100, 0.59); number of residual pools greater than 50 cm deep (RPGT50, 0.60); residual pool maximum depth (RPMXDEP, 0.66); mean width at residual pool volume (RPXWID, 0.86); residual pool volume per 100 m (RPV100R, 0.76); riparian vegetation canopy cover (XC, 0.75); and percent fines (PCT_FN, −0.48). Axis 2 represented a gradient from sand and fine substrates to coarse substrates and riffles. Axis 2 was correlated with percent riffle habitat (PCT_RI, 0.60), areal proportion of large fish cover types (XFC_BIG, 0.47), percent fine gravel (PCT_GF, 0.61), percent sand and fine substrates (PCT_SAFN, −0.75), and percent coarse substrate greater than 16 mm in diameter (PCT_BIGR, 0.63). Axis 3 represented a gradient from sites with higher proportions of natural types of fish cover and fine substrates to sites with large amounts of glide habitat. Axis 3 was correlated with percent glide habitat (PCT_GL, −0.47), proportion of natural types of fish cover (XFC_NAT, 0.55), and percent fines (PCT_FN, 0.52).

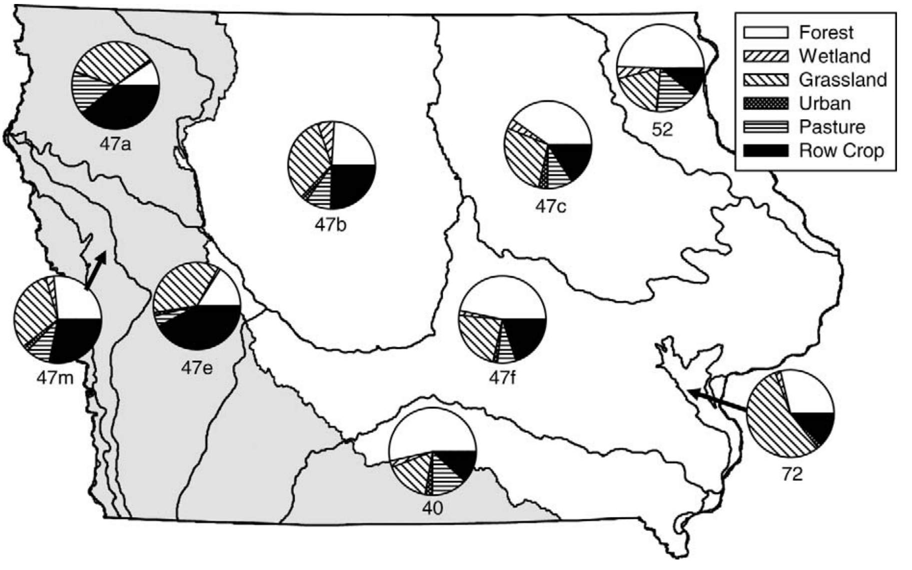

FIGURE 3.—Mean percent composition of local riparian buffer-scale land cover at 93 sites on wadeable Iowa streams, presented for each ecoregion or subregion (codes defined in Figure 1 of Rowe et al. 2009, this issue). Subregion 47d was omitted because it contained only one site. Shaded area indicates land in the Missouri River drainage; unshaded area represents land that drains to the Mississippi River.

Landscape Variables

We quantified 69 landscape variables at five spatial scales: 23 at the catchment scale, 12 at the riparian buffer scale, 20 at the local catchment scale, 12 at the local riparian buffer scale, and 2 at the segment scale (Table 1). Catchment land area varied in size from 5.2 to 2,123.1 km^2. Catchment land cover was dominated by agriculture (Table 1; Figure 2). Percent total agriculture averaged 77% and ranged from 42% to 93% (Table 1). Row crop agriculture averaged 71% at the catchment scale, ranging from 16% to 91%. Catchments in the Western Corn Belt Plains ecoregion had significantly greater amounts (mean = 80%) of row crop agriculture than the other ecoregions (mean = 37%; Figure 2). Catchments in the Mississippi River drainage averaged 68% row crop, 16% grasslands, 7% forest, and 6% pasture. In comparison, catchments in the Missouri River drainage averaged 76% row crop, 15% grasslands, 2% forest, and 5% pasture. Urban land cover was infrequent, averaging less than 1% and with a maximum of 6%. Estimated percentage of impervious surface was also low, with a mean of 1% and a maximum of 5% (Table 1). However, the mean percentage of catchment area estimated as artificially drained was 14%, with a maximum of 62% (Table 1). Natural land cover was much less prevalent than human land cover at the catchment scale. Natural grassland was the most common class of natural land cover (15%); forests (5%) were less common, and wetlands were the least common (0.2%).

At the riparian buffer scale, agricultural land cover was again more common than natural land cover, but the difference was much less than that at the catchment scale (Table 1). Mean total agriculture was 55% and mean row crop was 46% at the riparian buffer scale. Row crop agriculture was reduced at this scale, thereby increasing the amount of pasture and all natural land cover types. Natural land cover increased to 43% at the riparian buffer scale: grassland increased to 30%, forest increased to 13%, and wetland increased to 0.6%.

At the local catchment scale, the average amounts of total agricultural land use (61.4%) and row crop agriculture (53.4%) were less than—but more variable than—those at the catchment scale (Table 1). As the amount of row crop agriculture was reduced, all other land cover classes increased and also became more variable. Mean total natural land cover was 35%: grassland was 20%, forest was 14%, and wetland was 0.7% (Table 1).

At the local riparian buffer scale, natural land cover was dominant, with a mean of 62%. Total agriculture was reduced to a mean of 35% and row crop agriculture was 25%, but row crop percentages varied from 0% to 86% (Table 1). Local riparian buffers in the Mississippi River drainage had greater amounts of forest and wetland and lower amounts of row crop agriculture than sites in the Missouri River drainage.

TABLE 1.—Descriptions and summary statistics of landscape variables quantified at 93 sites on wadeable Iowa streams (variable names correspond to those in USEPA 2004). Landscape variables marked as retained were significantly correlated with the nonmetric multidimensional scaling ordination of 30 physical habitat variables and were retained for multiple linear regression analysis.

Variable	Description	Mean	SD	Min	Max	Retained
Catchment Scale						
LANDAREA	Catchment land area (km^2)	331.1	469.9	5.2	2,123.1	X
N_INDEX	% natural land cover	20.6	13.7	6.2	56.1	
PFOR	% forest	4.7	8.3	0.1	40.3	
PWETL	% wetland	0.2	0.2	0	1.1	X
PNG	% natural grassland	15.7	7.9	6	44	
U_INDEX	% human land cover	79.4	13.7	43.9	93.8	
PURB	% urban	0.9	0.9	0.1	6.3	
PAGT	% agriculture total	77.2	14.5	42.2	93.2	
PAGP	% pasture	5.9	6.9	0.3	26.5	
PAGC	% row crop	71.4	20.9	15.6	91.3	X
AGTSL9	% agriculture total on slope > 9%	54.6	22	0	100	
AGPSL9	% pasture on slope > 9%	12.5	9.8	0	50	X
AGCSL9	% row crop on slope > 9%	42.1	27.3	0	100	X
STRMLEN	Length of stream network (km)	254.1	369	4.3	1,911.8	
STRMDENS	Stream density (km/km^2)	0.8	0.2	0.3	1.2	
RDLEN	Length of roads (km)	451.1	649.1	6.7	3,045.7	
RDDENS	Road density (km/km^2)	1.3	0.2	1	2.4	
POPCHG	Population change from 1990 to 2000 (%)	0.8	15.1	−48.3	58.6	
POPDENS	Population density from 2000 census (number/km^2)	71.2	124.7	3.6	843.5	X
PCTIA_LC	% impervious surface estimated from land cover	1.1	0.8	0.2	5	
PTILE	% land with estimated artificial drainage	14.1	15.5	0	62.1	
SINU	Average sinuosity of all segments	1.2	0.1	1.1	1.5	X
PNMNDR	Proportion of nonmeandering segments	0.9	0.1	0.5	1	
Riparian Buffer Scale						
RNAT30	% natural land cover	43.1	14.4	7.6	78.7	
RFOR30	% forest	12.8	16.6	0	72	
RWETL30	% wetland	0.6	0.8	0	4.1	X
RNG30	% natural grassland	29.6	9.2	5.5	51.9	
RHUM30	% human land cover	56.9	14.4	21.3	92.4	
RURB30	% urban	0.9	0.8	0	5.4	
RAGT30	% agriculture total	55.2	14.7	18.8	92.4	
RAGP30	% pasture	9.4	7.5	0	39.1	
RAGC30	% row crop	45.8	19.3	3.8	92.4	X
RNS30	Length of road within buffer (km)	0	0	0	0.3	
STXRD	Stream road crossing density (number/km)	0.6	0.1	0.2	1.1	X
STXRD_CNT	Number of stream road crossings	162.4	242.6	1	1,271	
Local Catchment Scale						
1K_N_INDEX	% natural land cover	35.4	22	5.6	92.7	
1K_PFOR	% forest	14.2	17.9	0	71	
1K_PWETL	% wetland	0.7	1.3	0	9.8	X
1K_PNG	% natural grassland	20.2	10.1	2.5	58.5	
1K_U_INDEX	% human land cover	64.6	22	7.3	94.4	
1K_PURB	% urban	1.7	3.5	0	21.7	
1K_PAGT	% agriculture total	61.4	23.3	4.8	94	
1K_PAGP	% pasture	8	7.8	0	36.1	X
1K_PAGC	% row crop	53.4	27.3	1.4	93.8	X
1K_AGTSL9	% agriculture total on slope > 9%	42.6	34.1	0	100	
1K_AGPSL9	% pasture on slope > 9%	10.9	13.2	0	51.1	
1K_AGCSL9	% row crop on slope > 9%	31.7	34.8	0	100	X
1K_STRMLEN	Length of stream network (km)	1.7	0.7	0.9	4.6	
1K_STRMDENS	Stream density (km/km^2)	1.3	0.5	0.6	2.7	
1K_RDLEN	Length of roads (km)	1.9	1.6	0	9.3	
1K_RDDENS	Road density (km/km^2)	1.4	1.1	0	6.7	
1K_PCTIA_LC	% impervious surface estimated from land cover	1.8	2.4	0.2	15.2	X
1K_PTILE	% land with estimated artificial drainage	9.5	12.4	0	60.3	X
1K_SINU	Average sinuosity of all segments	1.3	0.5	1	4.8	
1K_PNMNDR	Proportion of nonmeandering segments	0.8	0.3	0	1	
Local Riparian Buffer Scale						
1K_RNAT30	% natural land cover	62	21.2	13.7	100	
1K_RFOR30	% forest	30.4	29.2	0	99.8	
1K_RWETL30	% wetland	2.7	5.6	0	27.1	X
1K_RNG30	% natural grassland	28.9	17.3	0.2	79	X
1K_RHUM30	% human land cover	37.9	21.2	0	86.3	

TABLE 1.—Continued.

Variable	Description	Mean	SD	Min	Max	Retained
1K_RURB30	% urban	1.9	3.2	0	19.2	
1K_RAGT30	% agriculture total	35.3	21.4	0	86.3	
1K_RAGP30	% pasture	9.9	10.9	0	52.4	
1K_RAGC30	% row crop	25.4	22	0	86.3	X
1K_RNS30	Length of road within buffer (km)	0	0	0	0.2	
1K_STXRD	Stream road crossing density (number/km)	0.5	0.5	0	2	
1K_STXRD_CNT	Number of stream road crossings	0.9	0.9	0	4	
	Segment Scale					
SEG_SIN	Segment sinuosity	1.3	0.3	1	2.5	X
GRADSEG	Segment gradient (m/km)	1.6	1.2	0	7.2	X

Local riparian buffers in the Mississippi River drainage averaged 40% forest, 25% grassland, 18% row crop, 9% pasture, and 4% wetland, while catchments in the Missouri River drainage averaged 36% row crop, 34% grassland, 16% forest, 11% pasture, and 1% wetland. There was a longitudinal gradient in the amount of row crop agriculture within the local riparian buffer, increasing from east to west (Figure 3). Western subregions of the Western Corn Belt Plains had the highest percentages of row crop in the local riparian buffer (subregion 47a, Northwest Iowa Loess Prairies: 39%; 47m, Western Loess Hills: 28%; 47e, Loess Hills and Steeply Rolling Prairies: 42%), and the eastern ecoregions (52, Paleozoic Plateau: 11%; 72, Interior River Lowland: 11%; 40, Central Irregular Plains: 12%) and the Iowan Surface subregion (47c: 16%) had the lowest (Figure 3). Forest was the most common natural land cover type, with a mean of 30% and a maximum of 100%. Percentages of grassland and wetlands were also greater than at the larger spatial scales. Variation in land cover percentages increased compared with that observed at the local catchment scale (Table 1).

Sinuosity values were low at all scales, indicating that most streams were nonmeandering (Table 1). At the catchment scale, average sinuosity was 1.20. At the local scale, the mean was slightly higher (1.35) and had greater variation, with a maximum of 4.8. The average segment-scale sinuosity was 1.29.

The majority of segment-scale gradients were low, with a mean of 1.6 m/km (0.16% slope), but exhibited a wide range between 0.0 and 7.2 m/km. Only 13 out of 93 (14%) stream segments had a gradient greater than 3 m/km.

Relationships between Landscape Variables and Physical Habitat

We identified 44 landscape variables as being significantly correlated with the physical habitat ordination of sites (Rowe 2007). At all spatial scales, percentages of total natural land cover, forest, total human land cover, total agriculture, and row crop were strongly correlated ($r > 0.75$) and considered redundant. The percentage of row crop agriculture was retained for further analysis at all spatial scales. At the catchment scale, pasture was removed because it was also correlated with percentages of row crop, total natural land cover, total human land cover, forest, and total agriculture. Catchment land area was correlated with stream length and road length; catchment land area was retained. Total agriculture on slopes greater than 9% was correlated with row crop on slopes greater than 9%; row crop on slopes greater than 9% was retained. Weighted mean sinuosity was correlated with the proportion of nonmeandering segments; weighted mean sinuosity was retained. At the local catchment scale, total agriculture on slopes greater than 9% was correlated with row crop on slopes greater than 9%; row crop on slopes greater than 9% was retained. In all, 21 landscape variables describing land cover, sinuosity, human disturbance, and gradient were retained for further analysis (Table 1).

Fifteen multiple linear regression models were constructed to predict individual physical habitat variables (Table 2). The predictors included 13 landscape variables representing all five spatial scales (Table 2). Two example relationships of physical habitat variables with their most strongly related landscape predictors are shown in Figure 4. Seventy-two percent of the model coefficients shown in Table 2 reflected catchment-scale (36%) or local riparian buffer-scale (36%) variables. Segment-scale (17%), local catchment-scale (9%), and riparian buffer-scale (2%) variables accounted for smaller percentages of the significant model terms. Forty percent of the coefficients shown in Table 2 accompanied variables that were expressions of percent row crop at various scales. Adjusted R^2 values of the 15 models ranged from 0.07 to 0.74, averaging 0.39.

The 13 landscape variables identified as predictors of physical habitat (Table 2) were plotted as vectors on the ordination of physical habitat variables (Figure 5).

TABLE 2.—Multiple linear regression models of physical habitat variables based on landscape variables in wadeable Iowa streams (adj. = adjusted; RMSE = residual mean square error). Models were created with stepwise multiple regression. Landscape variables (defined in Table 1) are listed in order of inclusion in models. Physical habitat variables are defined in Table 2 of Rowe et al. (2009, this issue).

	Model				
Habitat variable	Adj. R^2	RSME	Landscape variable	Coefficient	P
Log_{10}(SDDEPTH)	0.31	0.20	Intercept	1.096	<0.0001
			1K_RAGC30	−0.004	0.0006
			1K_RNG30	−0.003	0.0126
			SEG_SIN	0.196	0.0168
Log_{10}(XWD_RAT)	0.55	0.22	Intercept	1.684	<0.0001
			LANDAREA	0.001	<0.0001
			1K_RAGC30	0.006	<0.0001
			PAGC	−0.004	0.0026
			POPDENS	−0.001	0.0076
SDBKF_W	0.45	1.51	Intercept	2.222	<0.0001
			LANDAREA	0.002	<0.0001
			1K_RAGC30	−0.025	0.0013
Log_{10}(XINC_H)	0.43	0.17	Intercept	1.663	<0.0001
			SINU	−0.867	0.0005
			POPDENS	−0.001	<0.0001
			RAGC30	−0.007	<0.0001
			AGCSL9	0.004	0.0002
			LANDAREA	0.001	0.0085
BFWD_RAT	0.54	3.15	Intercept	0.979	<0.0001
			LANDAREA	0.006	<0.0001
			1K_RAGC30	−0.085	<0.0001
LRBS_BW6	0.07	0.59	Intercept	−1.836	<0.0001
			PWETL	0.670	0.0078
W1H_CROP	0.61	0.20	Intercept	0.442	0.0003
			1K_PAGC	0.004	0.0003
			1K_RAGC30	0.006	<0.0001
			SEG_SIN	−0.275	0.0011
RPXWID	0.74	1.10	Intercept	0.349	<0.0001
			LANDAREA	0.002	<0.0001
			POPDENS	−0.003	0.0040
			1K_RWETL30	0.093	0.0004
			1K_RNG30	−0.025	0.0017
			1K_RAGC30	−0.036	<0.0001
Log_{10}(RPV100R)	0.39	0.41	Intercept	1.563	<0.0001
			LANDAREA	0.001	0.0054
			1K_PAGC	−0.008	<0.0001
			1K_RWETL30	0.022	0.0137
Log_{10}(RPMXDEP)	0.20	0.23	Intercept	1.615	<0.0001
			1K_RAGC30	−0.004	0.0002
			SEG_SIN	0.205	0.0286
XC	0.55	0.18	Intercept	0.692	<0.0001
			1K_RAGC30	−0.003	0.0269
			GRADSEG	−0.037	0.0261
			1K_PAGC	−0.003	0.0113
			1K_RNG30	−0.005	0.0002
PCT_FN	0.35	18.70	Intercept	49.928	<0.0001
			PWETL	−28.521	0.0013
			1K_RAGC30	0.487	0.0002
			1K_PAGC	−0.232	0.0289
			LANDAREA	−0.015	0.0011
PCT_GF	0.21	7.19	Intercept	−24.028	0.0264
			SINU	20.358	0.0286
			1K_RNG30	0.133	0.0056
			1K_RAGC30	−0.118	0.0025
			PAGC	0.100	0.0159
PCT_SAFN	0.17	13.36	Intercept	107.341	<0.0001
			GRADSEG	−4.543	0.0002
			SEG_SIN	−16.694	0.0024
PCT_BIGR	0.27	9.20	Intercept	−11.960	0.0356
			GRADSEG	4.358	<0.0001
			SEG_SIN	12.832	0.0009
			1K_RAGC30	−0.099	0.0342

TABLE 3.—Multiple linear regression models of fish assemblage metrics in wadeable Iowa streams; the models were improved by addition of landscape variables. Potential predictors included both the 18 physical habitat variables from Table 3 of Rowe et al. (2009, this issue) and the 21 landscape variables retained for analysis (Table 1). Predictor variables are listed in order of inclusion in models. Model improvement is expressed as change in adjusted R^2 (ΔR^2) and change in residual mean square error (ΔRMSE). Physical habitat variables are defined in Table 2 of Rowe et al. (2009, this issue). Landscape variables (indicated by asterisks) are described in Table 1.

	Model						
Metric	R^2	ΔR^2	RMSE	ΔRMSE	Predictor variable	Coefficient	P
Number of sucker species	0.60	0.06	1.28	−0.10	Intercept	−2.479	<0.0001
					RPXWID	0.527	<0.0001
					PCT_GF	0.040	0.0269
					PAGC*	0.027	0.0002
					PCT_BIGR	0.047	0.0005
					RCHDMDLL	1.614	0.0028
Number of sensitive species	0.43	0.04	1.86	−0.08	Intercept	3.200	0.0180
					RWETL30*	0.966	0.0009
					PCT_SAFN	−0.069	<0.0001
					PAGC*	0.034	0.0010
					XC	3.185	0.0004
Number of benthic invertivore species	0.66	0.08	1.55	0.17	Intercept	2.884	0.1012
					RPXWID	0.466	<0.0001
					PCT_SAFN	−0.050	0.0049
					GRADSEG*	−0.497	0.0058
					1K_RURB30*	0.188	0.0006
					XC	2.653	0.0020
					PAGC*	0.026	0.0035
					PCT_BIGR	0.059	0.0226
Percent abundance of top-3 abundant species	0.33	0.05	12.78	−0.48	Intercept	59.080	<0.0001
					PCT_FN	0.184	0.0048
					1K_RNG30*	0.333	0.0002
					PCT_GF	−0.619	0.0009
Percent abundance of benthic invertivores	0.25	0.07	10.50	−0.46	Intercept	7.567	0.0005
					PCT_BIGR	0.480	<0.0001
					1K_RWETL30*	0.454	0.0238
					PCTIA_LC*	−2.916	0.0458
Percent abundance of top carnivores	0.41	0.05	5.56	−0.23	Intercept	−8.174	0.0001
					LANDAREA*	0.008	<0.0001
					LRBS_BW6	−3.057	0.0019
					XINC_H	1.101	0.0029
Percent abundance of simple lithophilous spawners	0.46	0.02	4.73	0.11	Intercept	6.671	0.0308
					1K_RWETL30*	0.301	0.0068
					XFC_RCK	32.864	0.0034
					LANDAREA*	0.004	0.0049
					RCHDMDLL	4.705	0.0162
					PCT_SAFN	−0.088	0.0210
Tolerance index	0.37	0.06	1.11	−0.05	Intercept	9.632	<0.0001
					PCT_BIGR	−0.055	<0.0001
					PAGC*	−0.016	0.0095
					1K_PWETL*	−0.225	0.0247
					PCT_GF	−0.033	0.0327
					RPXWID	−0.129	0.0298

In Figure 5, the upper and middle panels (NMDS axis 1) show that greater percentages of row crop at all scales, natural grassland at the local riparian buffer scale, and steeper gradient at the segment scale were associated with steep banks and fine substrates, whereas greater percentages of wetland at several scales, greater catchment area, and greater sinuosity were associated with complex channel and bank morphology and greater residual pool volume, large woody debris, and canopy cover. The upper and lower panels in Figure 5 (NMDS axis 2) show that greater sinuosity was associated with higher percentages of coarse substrate and riffle habitat. The middle and lower panels (NMDS axis 3) show that steeper gradients and higher population density were associated with greater percentages of fine substrate and more fish cover, whereas greater catchment area and percentage of wetland at several scales were associated with higher percentage of glide habitat.

Relationships between Landscape Variables and Fish Assemblages

The 13 landscape variables identified as predictors of physical habitat variables were plotted as vectors on

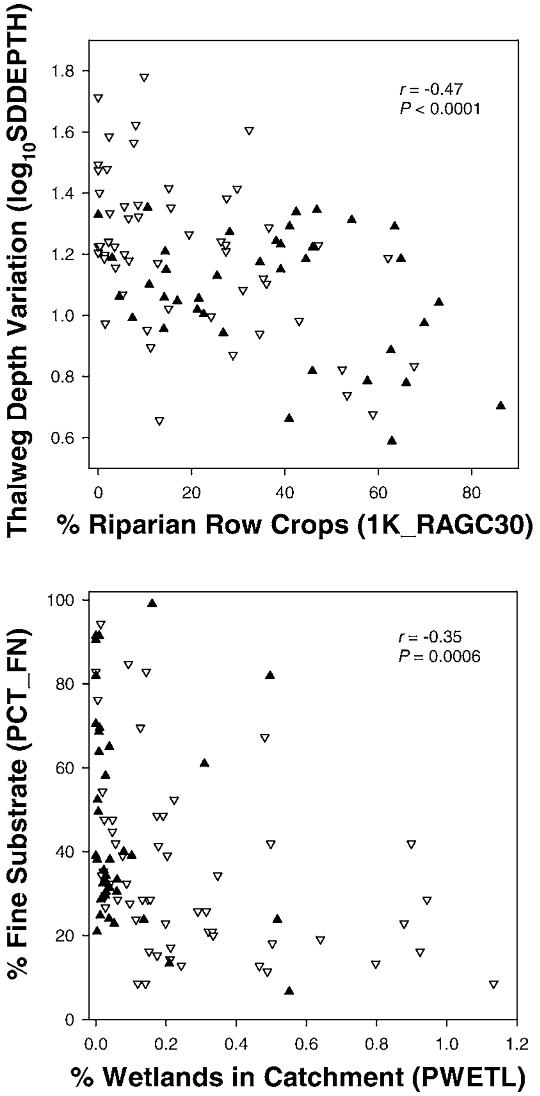

FIGURE 4.—Example relationships of physical habitat variables with their most strongly related landscape predictors in wadeable Iowa streams. Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites located in the Mississippi River drainage. Physical habitat variable codes in parentheses correspond to those in Table 2 of Rowe et al. (2009, this issue). Landscape variable codes in parentheses are defined in Table 1.

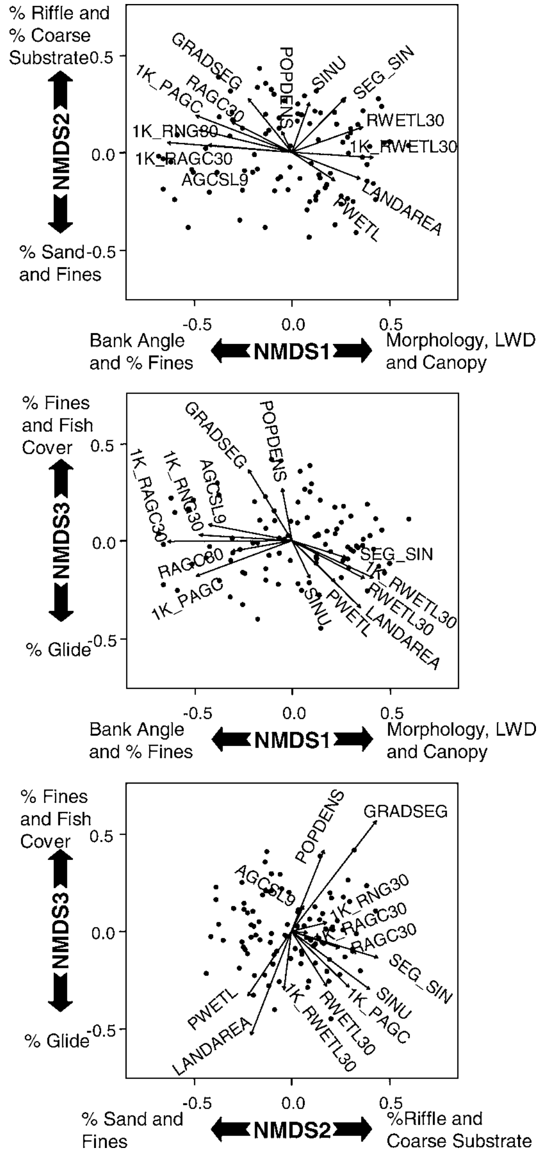

FIGURE 5.—Nonmetric multidimensional scaling (NMDS) ordination of 93 sites on wadeable Iowa streams based on the 30 physical habitat variables defined in Table 2 of Rowe et al. (2009, this issue; LWD = large woody debris). Physical habitat variables significantly related to NMDS axes are listed in Figure 1. Landscape variables (codes defined in Table 1) that were identified as significant predictors of physical habitat are plotted as vectors. Vectors indicate the direction of the most significant change, and arrow length is proportional to the strength of correlation with the ordination.

the ordination of fish assemblages from Rowe et al. (2009, this issue; Figure 6). Mean catchment and segment sinuosity were not significantly related to the ordination and were removed. Several land cover variables were strongly associated with NMDS axis 2. Percentages of wetland at the catchment, riparian buffer, and local riparian buffer scales were positively associated with axis 2. This pattern reflects, in part, the association of several species (including blackstripe topminnow *Fundulus notatus*, central mudminnow *Umbra limi*, grass (redfin) pickerel *Esox americanus*,

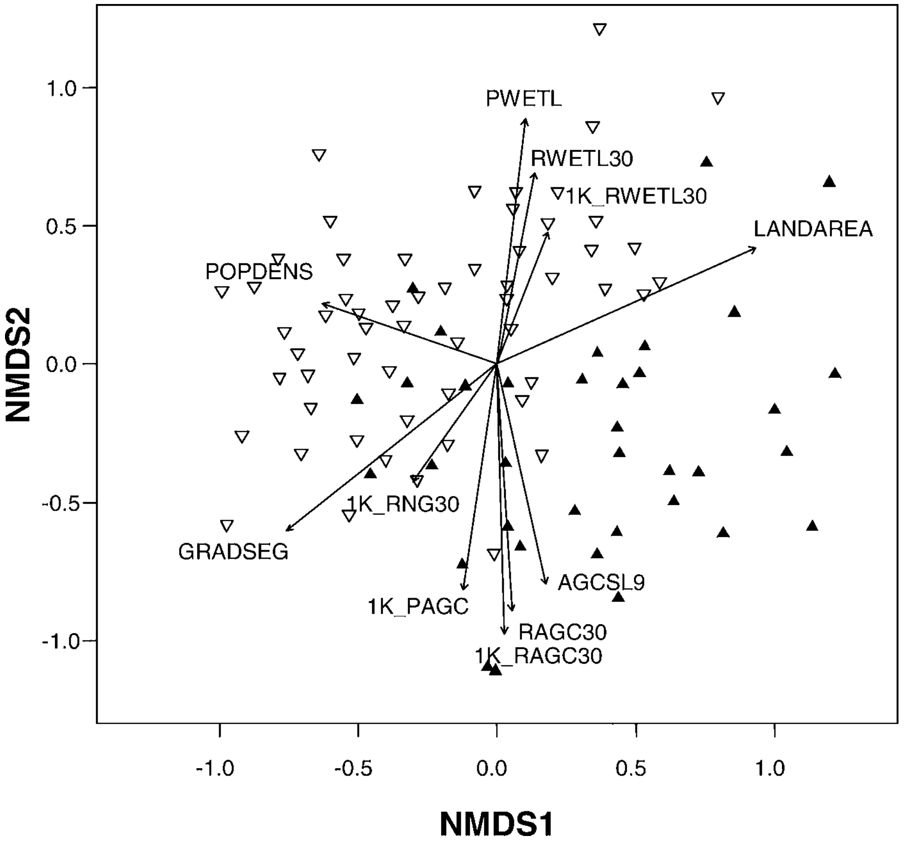

FIGURE 6.—Nonmetric multidimensional scaling (NMDS) ordination of fish species abundance at 93 sites on wadeable Iowa streams and relationships with landscape variables (defined in Table 1). Solid triangles represent sites located in the Missouri River drainage, and inverted open triangles represent sites located in the Mississippi River drainage. Landscape variables that were selected as significant predictors of physical habitat variables and significantly related to the ordination are plotted as vectors. Vectors indicate the direction of the most significant change, and arrow length is proportional to the strength of correlation with the ordination.

mud darter *Etheostoma asprigene*, pumpkinseed *L. gibbosus*, and warmouth *L. gulosus*) with the greater prevalence of wetlands in the Interior River Lowland subregion and other areas near the Mississippi River (Rowe et al. 2009, this issue; Figure 4). Percentage of row crop at several scales was negatively associated with axis 2. This pattern reflects, in part, (1) the association of brook sticklebacks *Culaea inconstans* and fathead minnow with heavily row-cropped north-central Iowa, (2) the association of flathead chub *Platygobio gracilis* and goldeyes *Hiodon alosoides* with heavily row-cropped western Iowa (Rowe et al. 2009, this issue; Figure 4), and (3) lower FIBI scores at sites with high percentages of row crop land use (Rowe et al. 2009, this issue; Figure 3). The catchment area vector illustrates a pattern previously shown in Figures 3 and 4 of Rowe et al. (2009, this issue); walleyes *Sander vitreus*, white bass *Morone chrysops*, gizzard shad *Dorosoma cepedianum*, and freshwater drum *Aplodinotus grunniens* were associated with larger streams that had larger catchment areas. Although the range of gradients was narrow, steeper gradients were associated with smaller streams (Rowe et al. 2009, this issue; Figure 3), which in turn were associated with a number of species, including ubiquitous species such as the creek chub, fathead minnow, and johnny darter, and rarer species such as the brook stickleback, brown trout *Salmo trutta*, and southern redbelly dace *Phoxinus erythrogaster* (Rowe et al. 2009, this issue; Figure 4). Population density was associated with the axis of separation between the major drainages and the gradient of stream health identified in Rowe et al. (2009, this issue; Figure 3); greater population density was associated with Mississippi River drainage sites and higher FIBI scores.

Addition of landscape variables resulted in only minor improvement for 8 of the 12 original physical habitat-based multiple linear regression models used for predicting fish assemblage metrics (Table 3). The average increase in percentage of variance explained (ΔR^2) for the eight improved models in Table 3 was 6.7%. No significant improvement was possible for the remaining four physical habitat-based models, which included models for number of native species and FIBI.

Discussion

Our results demonstrated strong relationships of physical habitat with landscape variables at several spatial scales. Sites with natural land cover at all spatial scales had more complex habitat, with wider and more variable channel form, greater residual pool volumes, more large woody debris, and more riparian vegetation canopy, whereas sites dominated by row crop land cover tended to have less-complex habitat, highly sloped banks, and more fine substrates. The majority of our multiple regression models with the greatest predictive power described conditions of the channel, such as residual pool measures (RPXWID, RPV100R), width : depth ratios (BFWD_RAT, XWD_RAT), bankfull width variation (SDBKF_W), and incision height (XINC_H). As Iowa's land was converted from prairie, wetland, and forest to cultivated row crops, the residence time of water in the soil decreased. Water drained from uplands faster because no natural vegetation was present to impede overland flow. Residence time in the soil was reduced through artificial drainage to convert poorly draining soils to arable land. Some areas of Iowa are estimated to have more than 60% of land area that is artificially drained (Jaynes et al. 2006). Subsurface drainage reduces peak flows by lowering the water table and creating greater space for water storage in clay soils with slow infiltration rates, but in loess and loamy soils there is evidence that peak flows are increased by subsurface drainage (Robinson and Rycroft 1999). To increase drainage, stream channels were straightened, thereby reducing sinuosity and increasing channel gradient, peak flow, and stream power (Campell et al. 1972; Robinson and Rycroft 1999). Segment-scale sinuosity was also positively related to channel and bank morphology, residual pool volumes, and bed stability. An unmodified, sinuous reach of an otherwise straightened river has a strong damping effect on peak stream power because of the increase in hydraulic roughness (Campell et al. 1972). Riparian forest and wetland vegetation can also increase hydraulic roughness and reduce stream power and current velocity when peak flows exceed the active channel and spill into the floodplain. Conversion of natural land cover to row crops, artificial drainage, and channelization in the late 1800s and early 1900s probably increased flow variability in Iowa streams. In Michigan's Lower Peninsula, stable flows are associated with natural land cover, whereas variable flows are associated with agricultural land use (Diana et al. 2006). Increased flow variability increases stream power at peak flows, increasing sediment transport and bank and bed erosion, whereas at base flow the ability to transport sediment is decreased and habitat volumes are reduced. Many of the channel morphology variables were correlated with catchment size because they increase with stream size, which is correlated with catchment size. Larger streams are associated with natural riparian zones, whereas small streams are associated with row crops. We attribute this to the tendency to farm up to the edge of a small stream that likely has been channelized. Larger streams are less likely to have been channelized and more likely to have forested riparian buffers. Large streams are also more likely to have glide habitat and fewer riffles and pools. Small streams with less stream power have more fine sediments and higher areal proportions of natural fish cover because similarly sized cover elements in a small stream have proportionally greater area than in a larger stream.

The majority of our models with the least predictive power described substrate characteristics, such as relative bed stability (LRBS_BW6), percent sand and fine substrate (PCT_SAFN), percent fine gravel (PCT_GF), and percent coarse substrate (PCT_BIGR). This may partially be attributable to the fact that substrates strongly reflect underlying geology, despite the land use influences emphasized in our suite of landscape variables. In contrast to some other regions of the USA, the lithology and soils in many parts of Iowa do not provide a wide and continuous range of sediment sizes. Consequently, the response to changes in sediment supply or bed shear stress may be more evident in altered channel morphology (aggradations, pool filling, bank cutting, incision) than in changes to mean particle size of the streambed that generally cause persistent changes in relative bed stability (Kaufmann et al. 2009). Fine substrates were associated with row crop agriculture at all scales and negatively associated with natural land cover at all scales, with the exception of natural grassland at the local riparian buffer scale. Upland and bank erosion acts to increase the proportion of small sediments, burying coarse substrates (Waters 1995). Riparian vegetation stabilizes streambanks with root networks, preventing bank erosion (Zaimes et al. 2004). Forested riparian buffers effectively reduce the velocity of overland flow and sequester sediment that otherwise would be washed into the stream (Lee at al. 2003). However, sand and fines are naturally the dominant substrates in most of Iowa except the Paleozoic Plateau ecoregion, where there are thinner soils and where coarse geological parent material is more available. Substrate diversity in Iowa streams is probably determined by interaction of the availability of coarse sediments, the extent of riparian land cover, and the stream's ability to transport sediment. Relative to southern Iowa streams, northern Iowa streams have more coarse sediments available from glacial deposits and flow through catchments with thin or no loess deposits (Menzel 1987). Streams in southern Iowa are more susceptible to bank and bed erosion because the finer substrates in their catchments are more easily mobilized than larger substrates. The east–west gradient of increasing row crop agriculture in the local riparian buffer also contributes by increasing sediment delivery from upland and bank erosion in western Iowa. Our results support the observation of a northeast to southwest gradient of increasing fine sediment and decreasing forested riparian land cover that has been mentioned previously (Heitke et al. 2006) based on several studies (Menzel 1987; Paragamian 1990; Griffith et al. 1994; Wilton 2004). Overall, our results are strong evidence that stream habitats, which are initially shaped by climate and physiography, can be significantly altered by human modification of the landscape at multiple spatial scales.

Our results also demonstrated relationships of fish assemblages with landscape variables at several spatial scales. We observed a catchment area gradient in fish assemblages, as has been documented previously (Schlosser 1982; Lyons 1996). Fish assemblages in small headwater streams tend to be small-bodied, generalist invertivores. As streams become larger and deeper, habitat diversity increases, species richness increases, and larger-bodied benthic invertivores and piscivores increase in relative abundance (Schlosser 1982). Fish assemblages were also associated with a gradient of land cover. Impaired assemblages were associated with row crop agriculture, whereas assemblages with higher FIBI scores were associated with greater percentages of wetland land cover. Conversion of natural land cover to agriculture has been the primary source of stream degradation in the upper Midwest (Karr et al. 1985; Waters 1995). Agricultural land uses have been shown to impair fish assemblages at the catchment scale (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997; Walser and Bart 1999) and at a local riparian buffer scale (Lammert and Allan 1999; Stauffer et al. 2000; Wang et al. 2003). The collective evidence to date suggests that stream fish assemblages, like physical habitat, are shaped by natural elements of the landscape, such as catchment size and physiography, but also by human modification of the landscape.

Previous studies are contradictory regarding the relative importance of different spatial scales on the effects of landscape and physical habitat variables on fish assemblages. Studies in Michigan and Wisconsin have shown that catchment-scale variables explain greater amounts of variation in stream biota than do local factors (Roth et al. 1996; Allan et al. 1997; Wang et al. 1997, 2003), but other studies have shown that local and riparian conditions were better at explaining variation in stream biota (Lammert and Allan 1999; Stauffer et al. 2000; Diana et al. 2006; Bouchard and Boisclair 2008). Wang et al. (2006) found that instream habitat explained more variation in fish assemblage measures than land use variables at all disturbance levels. Catchment variables increased in relative importance as disturbance increased, but their importance never exceeded that of instream and reach variables. In a recent comparison of the relative strengths of local, riparian, and longitudinal variables in fish habitat quality models, Bouchard and Boisclair (2008) reported that 98% of the explanatory power was attributed to local instream variables. Our results showed (1) strong relationships between fish assemblages and physical habitat variables measured at a relatively small scale and (2) little or no improvement from addition of landscape variables at larger spatial scales. However, comparing among our models of physical habitat based on landscape variables, the majority of significant predictor variables were split evenly between catchment-level effects and local riparian buffer-level effects. Presently, we are unable to conclude that one spatial scale has greater relative influence on fish assemblages than another, although we recognize that catchment-scale processes may ultimately dominate local processes because of the hierarchical nature of lotic systems. The collective evidence to date suggests that documented, spatial-scale-specific relationships may be the most useful in management and restoration applications. Unfortunately, sweeping generalizations about the overall relative importance of factors at different spatial scales remain elusive.

In a companion article (Rowe et al. 2009, this issue), we speculated that landscape characteristics influence fish assemblages primarily through effects on physical habitat. This implies that physical habitat influences on fish assemblages are direct, whereas landscape effects on fish assemblages are primarily indirect, operating via intermediate, direct effects on physical habitat (Poff 1997). A corollary of this hypothesis is that statistical relationships between landscape characteristics and fish assemblages should be fewer and weaker than those between physical habitat characteristics and fish assemblages. In comparison with the multiple linear regression models based solely on physical habitat variables in Rowe et al. (2009, this issue), addition of landscape variables resulted in little or no improvement in predicting fish assemblage metrics and FIBI, suggesting that physical habitat factors account for the majority of the stream fish assemblage variation that can be explained within the scope of our study and with current methods. Furthermore, landscape variable coefficients in the improved models often suggested relationships that were contrary to expectations, possibly a result of the lack of independence between the landscape and physical habitat variables. Our results support the view that landscape-level factors strongly influence many physical habitat characteristics in streams and that in turn these physical habitat characteristics strongly influence fish assemblages. This view does not imply that landscape factors are less important than physical habitat in determining fish assemblage characteristics. On the contrary, because landscape characteristics are the ultimate drivers of this simple two-step conceptual model, landscape-level factors clearly have profound effects on fish assemblages. Rather than comparing the relative importance of landscape versus physical habitat effects, we view the utility of this conceptual model in furthering understanding of the precise nature of effects and, perhaps more importantly, in predicting outcomes of remediation efforts.

Successful restoration of Iowa's wadeable streams and conservation of their fish assemblages will require management actions that account for the hierarchical nature of stream ecosystems and that focus on processes at the appropriate spatial scale (Rabeni and Sowa 1996). Efforts at the catchment scale should focus on restoring natural hydrographs and reducing upland soil erosion. Retaining water in the catchment to reduce peak flows and stream power would decrease the streams' erosive potential, reduce hydrological variation, and increase and stabilize base flows. The Iowa Conservation Reserve Enhancement Program (CREP) is a state and federal initiative (Smith 2000) to create wetlands that are strategically located within catchments and designed to remove sediments and dissolved nutrients from water drained from cropland. These wetlands will also help to retain water and reduce flow variability downstream. Since complete restoration of original wetlands is unlikely, these targeted CREP wetlands could play an important role in restoring more natural hydrology at the catchment scale. Best management practices, such as conservation tillage, contour farming, and establishment of grass waterways, can reduce sources of upland sediments (Wang et al. 2002). Efforts at the riparian and reach scales should focus on channel and bank stabilization, preventing upland sediments from entering the stream, and reconnecting the active channel with the floodplain. The most cost-effective bank stabilization methods may be (1) riparian buffer creation by establishing native woody and grassland vegetation along the bank and in the adjacent riparian zone and (2) streambank fencing to prevent livestock access (Lyons and Courtney 1990). Substrate composition should be taken into account. For example, in areas with little coarse substrate, woody vegetation (e.g. willows *Salix* spp.) should be used for bank stabilization because of its high root density and deep root structure (Shields et al. 1995). Riparian buffer strips are also effective at filtering and removing upland sediment and shallow groundwater nutrients from runoff before they can enter the stream (Lee et al. 2003), ultimately benefiting stream habitat and biota (e.g., Duehr et al. 2007).

Despite progress in recent decades toward improving management of midwestern U.S. agricultural landscapes for better stream health through programs such as the CRP and CREP (Ribaudo 1989; Smith 2000), significant challenges remain for Iowa (Zohrer 2006). In particular, the emerging bioeconomy (Jordan et al. 2007), with its current emphasis on agricultural production of corn for ethanol, threatens to intensify agricultural alteration of the Iowa landscape in the future and to reverse recent progress (Widenoja 2007). Our results clearly demonstrate that increasing the percentages of row crop agriculture in catchments and riparian areas, as will be necessary for increased corn production, will lead to further habitat degradation in Iowa streams, which in turn will be deleterious to fish assemblages. We urge decision makers to (1) consider the many recommendations of the American Fisheries Society Farm Bill Advisory Committee (Garvey et al. 2007) regarding decisions affecting landscapes in agricultural regions like Iowa and (2) hasten the transition from reliance on first-generation biofuels (e.g., corn ethanol) to second-generation, more environmentally friendly cellulosic sources (e.g., switchgrass *Panicum virgatum* and short-rotation poplars *Populus* spp. and willows; Graham et al. 1995).

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