

Spatial-Scale Effects on Relative Importance of Physical Habitat Predictors of Stream Health

EMMANUEL A. FRIMPONG

TRENT M. SUTTON*

Department of Forestry and Natural Resources
Purdue University
715 W. State Street
West Lafayette, Indiana 47907, USA

BERNARD A. ENGEL

Department of Agricultural and Biological Engineering
Purdue University
225 S. University Street
West Lafayette, Indiana 47907, USA

THOMAS P. SIMON

US Fish and Wildlife Service
Bloomington Field Office
620 S. Walker Street
Bloomington, Indiana 47403, USA

ABSTRACT / A common theme in recent landscape studies is the comparison of riparian and watershed land use as predictors of stream health. The objective of this study was to compare the performance of reach-scale habitat and remotely assessed watershed-scale habitat as predictors of stream health over varying spatial extents. Stream health

was measured with scores on a fish index of biotic integrity (IBI) using data from 95 stream reaches in the Eastern Corn Belt Plain (ECBP) ecoregion of Indiana. Watersheds hierarchically nested within the ecoregion were used to regroup sampling locations to represent varying spatial extents. Reach habitat was represented by metrics of a qualitative habitat evaluation index, whereas watershed variables were represented by riparian forest, geomorphology, and hydrologic indices. The importance of reach- versus watershed-scale variables was measured by multiple regression model adjusted- R^2 and best subset comparisons in the general linear statistical framework. Watershed models had adjusted- R^2 ranging from 0.25 to 0.93 and reach models had adjusted- R^2 ranging from 0.09 to 0.86. Better-fitting models were associated with smaller spatial extents. Watershed models explained about 15% more variation in IBI scores than reach models on average. Variety of surficial geology contributed to decline in model predictive power. Results should be interpreted bearing in mind that reach habitat was qualitatively measured and only fish assemblages were used to measure stream health. Riparian forest and length-slope (LS) factor were the most important watershed-scale variables and mostly positively correlated with IBI scores, whereas substrate and riffle-pool quality were the important reach-scale variables in the ECBP.

Physical habitat assessments are important as part of stream health evaluations for many reasons, including (i) evaluation of improvements made by fishery enhancement and stream habitat restoration; (ii) identification, estimation, and prediction of alterations due to anthropogenic or natural causes; (iii) identification and protection or avoidance of stream reaches or segments that are vulnerable or critical; and (iv) facilitation of stream classification for management purposes (Oswood and Barber 1982; Osborne and others 1991; Wang and others 1998; Maddock 1999). Efforts to

predict fish assemblage attributes with reach or watershed habitat attributes have been persistent (e.g., Oswood and Barber 1982; Berkman and Rabeni 1987; Roth and others 1996; Allan and others 1997; Wang and others 2003). Most habitat models use reach-scale indices relating to channel geomorphic features, water velocity, substrate, in-stream cover for fish, and condition of riparian zones (Bain and others 1999).

Indices of habitat quality are scale dependent (Rankin 1995; Maddock 1999) and management efforts tend to be concentrated at the scale where anthropogenic activity is perceived to affect the biological system (Poole and others 1997; Fausch and others 2002). The scale of habitat assessment determines the cost and reliability of results. On-site habitat evaluations may be subject to observer biases (Poole and others 1997; Maddock 1999). With a growing need for stream health evaluations and ever-present logisti-

KEY WORDS: Scale; Habitat; Predictive models; Stream health; Biotic integrity; Fish

Published online: October 18, 2005.

*Author to whom correspondence should be addressed; *email:* tsutton@purdue.edu

cal constraints, managers would benefit from tools that allow evaluation of streams without field measurements or observations. The increased availability of digital spatial data and geographic information system (GIS) software has facilitated watershed-scale evaluations of stream health. Numerous studies (e.g., Richards and others 1996; Davies and others 2000; Stauffer and others 2000; Fitzpatrick and others 2001; Sutherland and others 2002; McRae and others 2004) have shown that in certain regions, watershed characteristics like vegetative cover, geology, geomorphology, and hydrology could be used to predict fish or macroinvertebrate community attributes used as indicators of stream health.

Many watershed- or multiscale studies have taken advantage of the availability of spatial data and GIS (e.g., Hunsaker and Levine 1995; Richards and others 1996; Allan and others 1997; Lammert and Allan 1999; Fitzpatrick and others 2001; Sponseller and others 2001; Townsend and others 2003; Wang and others 2003; Weigel and others 2003). These studies often addressed multiple objectives with one question in common—the importance of riparian versus watershed land-cover influence on stream health or integrity as measured by in-stream habitat, fish, or macroinvertebrate indices. A single conclusive answer has not emerged from the numerous efforts (Allan and Johnson 1997; Allan 2004). There is evidence to suggest that fish and macroinvertebrates are sensitive to the habitat patterns at different scales, which could account for some of the inconsistency in patterns observed by studies relating different taxa to watershed and riparian land cover (Lammert and Allan 1999; Fitzpatrick and others 2001; Allan 2004). Effects of spatial extent on patterns of model predictive power have not received equal attention, but there is evidence that investigating the same question at different spatial extents can result in contradictory answers (Turner and others 1989; Wiens 1989; Lammert and Allan 1999).

Reframing the research question may help redirect research effort toward other important but unexplored areas. For the purpose of assessing stream health using physical habitat, a relevant question is “How well do in-stream (reach scale) indices independently predict the condition of biota compared to large-scale (watershed scale) variables obtainable from spatial data”? A clear answer to this question would also be a clue as to the scale at which habitat restoration efforts are likely to achieve greater biological recovery. Modeling at differing spatial extents will potentially result in differing strengths of observed biota–habitat relationships. Increasing spatial extent can increase, but not decrease, environmental variance or heterogeneity

(Palmer and others 1997). Therefore, we hypothesize that the ability of a fixed set of locally relevant environmental variables to account for variation in biological health of streams should decrease with increasing spatial extent of observations. Gordon and Majumder (2000) stated the same hypothesis as follows: “the ability of statistical models to explain variation in a fish index of biotic integrity (IBI) will decline as the size of the watersheds modeled increase.” They explained that “aggregation of smaller watersheds will cause a loss of information that will screen the causes of the changes in biological quality.” They tested this hypothesis with a design that held overall spatial extent constant and varied the level of aggregation of information within that space, and the result was no clear pattern of change in model predictive power. The objectives of this study were to (1) compare the performance of stream habitat indices derived using GIS databases with indices obtained by qualitative observation of the reach in the prediction of scores on a fish index of biotic integrity (IBI) and its metrics; and (2) investigate the effect of changing the spatial extent of observations on the relationships between IBI scores and its metrics and reach- and watershed-scale predictor variables.

Methods

Study Area

This study covered a large portion of the 44,000 km² geographic extent of the Eastern Corn Belt Plain (ECBP) ecoregion of Indiana (Omernik 1987), including the part of the upper Wabash (UW) River watershed within this ecoregion (Figure 1). Land use in the ECBP is greater than 75% row-crop agriculture in mainly corn–soybean rotation. The entire landscape is traversed by roads and isolated subdivisions and few urban areas. Data from 95 first to fifth Strahler-order streams were used in the study. Individual watershed sizes of the streams averaged 65.0 km² and ranged from 3.1 to 256.4 km², with the majority in the third and fourth orders. The dominant soil parent material of the region is glacial till (Franzmeier and others 2001) and soils fall primarily in hydrologic groups B and C (Natural Resources Conservation Service 1994). The major surface lithologic classes are loam and silty clay-loam to clay-loam (Gray 1989).

Fish Sampling and Reach-Scale Habitat Assessment

The 95 sampled stream reaches represented a combination of more recent and historical data. The

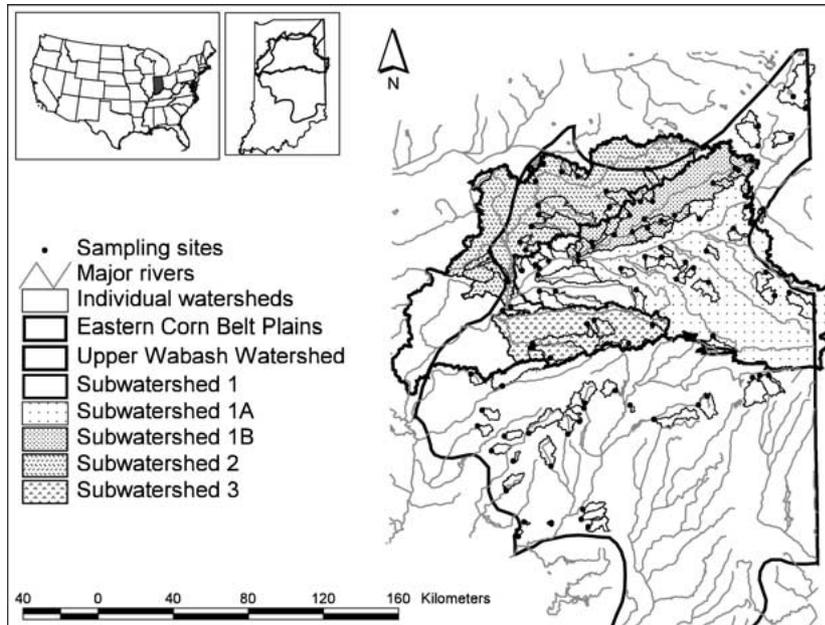


Figure 1. Map showing the Eastern Corn Belt Plain ecoregion in Indiana and hierarchically nested watersheds with stream sampling locations. Smaller polygons are individual watersheds of streams with the downstream end of sampled reaches as outlets.

historical data consisted of 56 fish assemblage samples collected by one-pass backpack electrofishing from 1990 through 1994 by the Indiana Department of Environmental Management. Additional 39 reaches were sampled in 2002 and 2003 using the same electrofishing protocol. Sampled reaches ranged in length from 15 to 20 mean stream widths in the entire data set. Fish sampling took place from June to September during which time reach habitat assessments were also undertaken. Fish collected were identified to species, counted, classified into trophic, reproductive, and sensitivity guilds, and site scores on the IBI were computed following Simon and Dufour (1998) and Simon (1999). To aid in diagnosing underlying causes of variation in IBI score and its relationship with habitat variables, the individual IBI metrics were also retained for a separate analysis. The Indiana ECBP IBI includes metrics for species composition, trophic composition, and fish condition. Metric scoring criteria are adjusted for watershed size and some metrics are used only for small (area ≤ 52) or large ($52 < \text{area} < 2560$) km² watersheds. Species composition metrics for small watersheds include total number of species, number of darter (*Etheostomatini*), madtom (*Noturus*), and sculpin (*Cottus*) species, percent headwater species, number of minnow species, number of sensitive species, and percent abundance of tolerant individuals. For large watersheds, three metrics—number of darter species, number of sunfish species, and number of sucker species—replace the first three metrics of small watersheds. Trophic composition metrics for small

watersheds include percent omnivore individuals, percent insectivore individuals, and percent pioneer species individuals. Percent carnivore individuals replace the pioneer metric for large watersheds. Fish condition metrics for both small and large watersheds are catch-per-unit-effort, percent simple lithophilic individuals, and percent individuals with deformities, fin erosions, lesions, and tumors (DELT). The DELT metric was not included in the computation of IBI scores for this study because preliminary analysis of the data suggested that different sampling crews might not have recorded this information consistently.

At each site, geographic coordinates were recorded at the downstream end of the reach, and metrics of the qualitative habitat evaluation index (QHEI) were scored in the field on a data sheet similar to that of the Ohio Environmental Protection Agency (Rankin 1995). The calculation of QHEI is based on field observations and scoring of reach-scale habitat metrics organized under substrate quality, riffle-pool quality, bank and riparian quality, channel morphology development, and in-stream cover. Local stream gradient is also scored using topographic maps. The QHEI was chosen for reach-scale habitat assessment because the index was developed in another portion of the ECBP in an area with similar landform and land use. The index is used extensively in the Midwestern United States, including Indiana. In this study, local stream gradient was not scored because of lack of range in the variable. Instead, bank and riparian quality, which is normally scored with a maximum of 10, was double-weighted to

a maximum of 20. With this modification, all five metrics used in this study ranged in scores from 0 to 20. Because QHEI sums to a scale of 0 to 100, the final IBI score was converted to a 0 to 100 scale to facilitate comparisons.

GIS-Derived Habitat Indices

All habitat metrics derived using spatial data in GIS are collectively called watershed-scale variables in this article. The total set of watershed-scale habitat variables was watershed area, stream order, stream network length, main channel length, basin length, main channel sinuosity, main channel slope, drainage shape, relief ratio, drainage density, riparian forest, runoff curve number (CN), and a length-slope factor (LS). The first four variables are proxies for stream size and were determined to be strongly correlated; therefore, only watershed area was used to represent stream size.

To delineate all watersheds, US Census Bureau (1990) line streams were embedded in a US Geological Survey (USGS) 30-m (1:24,000) NED Digital Elevation Model (DEM; US Geological Survey 1999) for Indiana. The purpose of this process was to force DEM-generated stream networks to align with known permanent streams and generate networks at a greater detail than was provided by the original line streams. Watershed delineations were performed with the Watershed Delineator extension in ArcView 3.3 (Environmental Systems Research Institute and Texas Natural Resources Conservation Commission 1997; Environmental Systems Research Institute 2002). A threshold area of approximately 0.5 km² was used to define a first-order stream to generate the new stream networks. Watershed areas were computed from delineated polygons using the XTools extension of ArcView.

In order to determine land cover in watersheds that approximates the time of sampling, the following two sources of 30-m-resolution digital land cover data were used: the 1992 National Land Cover Data (NLCD) (US Geological Survey, unpublished data) for streams sampled from 1990 to 1994 and the 2001 edition of the National Agricultural Statistical Service (NASS) crop-use data (US Department of Agriculture and National Agricultural Statistical Service 2001) for streams sampled in 2002 and 2003. Land-cover grids were reclassified as forest (predominantly wooded but also including all natural vegetation such as grasses, shrub, and herbaceous wetlands) or nonforest (mainly agricultural but also including developed areas, which constituted less than 3% of the land cover in most watersheds). The detection of roads and developed areas was enhanced in the NASS data by extracting

developed areas from the NLCD, adding it to a 30-m-resolution grid of Indiana roads, and embedding the resulting layer in the NASS data. A study in the agricultural landscape of the Willamette Valley, western Oregon, comparing aerial photos and Thematic Mapper (TM) land-cover imagery suggested that the pixel resolution of TM imagery such as those used in this study is sufficient for characterizing the association between riparian cover and fish IBI (Lattin and others 2004). Because percent forested and nonforested watershed areas are perfectly correlated variables, we focused only on forested area. Furthermore, forested area was more relevant for other studies that depended on the outcome of this modeling effort to further evaluate the potential effectiveness of riparian forest restoration for recovering IBI scores in the upper Wabash River watershed. Land cover was quantified as the forested riparian area within 30 m on either side of a stream and 600 m upstream of the watershed outlet. This buffer dimension has been previously shown to optimize the statistical association between fish IBI and forested buffer in the ECBP ecoregion (Frimpong and others 2005).

Runoff curve numbers are empirically derived family of curves ranging in value from 0 to 100 that quantify the potential of watershed land surface to generate runoff from precipitation based on soils and land use (Soil Conservation Service 1986). Computation of a CN grid for all watersheds was performed in ArcView using a series of avenue scripts via the spatial analyst extension (Engel 1999a). Length-slope factor derived from unit stream power theory accounts for sediment transport capacity of overland flow in the Universal Soil Loss Equation (Moore and Burch 1986a; Moore and Wilson 1992). It incorporates the length (L) and the steepness (S) of slopes into a single topographic index, LS. Steeper slopes produce high overland flow velocities and longer slopes accumulate runoff from larger areas and also result in higher overland flow velocities. Thus, both L and S result in increased erosion potential, but in a nonlinear manner. Moore and Birch (1986a, 1986b) proposed a modified formula for estimating LS using flow accumulation and slope steepness derived from a DEM. A step-by-step implementation of that formula for computing a grid of LS in ArcView has been developed (Engel 1999b). The values of CN and LS were computed for every 30-m × 30-m cell in all watersheds. To choose an area within which to average cell values for CN and LS, a preliminary comparison of the correlation coefficient of average cell values and IBI scores was made for three predefined areas using all 95 sites. Cell values were averaged for the area 30 m on either side of

a stream and 600 m upstream, 300 m on either side of a stream and 1000 m upstream, and the entire watershed. Correlation coefficients for both CN and LS were highest for the 300-m \times 1000-m area and lowest for the entire watershed. The 300-m \times 1000-m area was therefore chosen to summarize CN and LS. The remaining variables—basin length, main channel sinuosity, main channel slope, drainage shape, relief ratio, and drainage density—were computed using basic tools in ArcView. These variables are described in more detail by Gallagher (1999). Definition and methods for all the watershed-scale variables used in modeling are summarized in Table 1.

Model Development and Evaluation

Prior to modeling, distribution of reach- and watershed-scale predictors were checked for normality and transformations applied where necessary (Table 1). The appropriate transformations were determined based on all 95 observations. Unlike most watershed-scale habitat variables, the QHEI metrics were not strongly skewed in their distributions, and therefore not transformed. The basic statistical tool used was multiple linear regression with C_p and adjusted- R^2 model selection (Neter and others 1996). The C_p statistic is a measure of bias in a model, and the

Table 1. Watershed-scale habitat variables derived in Geographic Information Systems

Predictor variable	Method/definition	Transformation
Watershed area	Computed from watershed polygons delineated from a 30-m digital elevation model (DEM). Polygons created with Watershed Delineator software ^a	$\text{Log}_{10}(x)$
Basin length	Straight distance from basin outlet to farthest point on drainage divide ^b	Square root
Main channel sinuosity	A measure of the degree of meander in the main stream channel. A ratio of the channel meander length to down valley distance ^b	Square root
Main channel slope	Estimate of the typical rate of elevation change along the length of channel (main stem) that drains the basin ^b	Square root
Drainage shape	A unitless measure of watershed elongation. Basin area divided by the square of basin length. For a given area, longer basins have smaller peaks but longer floods ^b	Square root
Relief ratio	Dividing the difference in altitude between the outlet and the highest point on the watershed by the basin length. Standardizes change in elevation over distance ^b	Square root
Drainage density	Total (cumulative) stream length divided by watershed area ^b	Square root
Riparian forest	Percent of woods, grasses, and wetlands within an area 30 m on either side of a stream and extending for 600 m upstream from watershed outlet ^c	$\text{Log}_{10}(1+x)$
Runoff curve number (CN)	An index of runoff potential combining land use and hydrologic soil group. Average in an area 300 m on either side of stream and 1,000 m upstream from outlet ^d	None
Length-slope factor (LS)	An index of topography incorporating slope length and steepness and indicating sediment transport capacity by runoff. Derived from a DEM and averaged for an area 300 m on either side of stream and 1000 m upstream from watershed outlet ^e	None

^aEnvironmental Systems Research Institute and Texas Natural Resources Conservation Commission (1997).

^bGallagher (1999).

^cFrimpong and others (2005).

^dSoil Conservation Service (1986); Engel (1999a).

^eMoore and Burch (1986a,b); Moore and Wilson (1992); Engel (1999b).

criterion seeks to minimize bias. Adjusted- R^2 measures the predictive power of the selected model with a penalty for model complexity. Collinearity in models was controlled with the tolerance criterion (Neter and others 1996). The specific criteria that had to be met for a model to be selected were applied in the following order: (i) C_p was smaller than or approximately equal to the number of parameters in the model; (ii) the model had the highest adjusted- R^2 among candidate models; and (iii) tolerances of all parameters in the model were above 0.10 (generally much greater than 0.10). All analyses were implemented in SAS 8.02.

A systematic large-scale geographic trend in IBI or its metrics was not known to exist in the study area, but was assumed and tested with the intent to remove such a pattern from the response variable if necessary. Trend surface analysis of IBI and its metrics for the 95 sites in the ECBP was performed using the centered geographic coordinates, their quadratic and cubic terms, and interactions between the longitude and latitude terms following Legendre and Legendre (1998). The strength of the surface trends was weak and was not statistically significant when other reach- or watershed-scale habitat variables were added to the model. The geographic coordinates were therefore excluded in subsequent analyses.

To investigate how spatial extent affected model strength and the relative importance of predictor variables, data from six additional watershed areas hierarchically nested within the ECBP were further analyzed (Figure 1). The methodology of using the same set of variables over a range of spatial areas to investigate relative importance of predictors was recommended by Turner and others (1989). The union of individual watersheds of sampled streams was used to extract the composition of surficial geology (Indiana Geological Survey 2002) and hydrologic soil groups (Natural Resource Conservation Service 1994) from the respective grid maps for each nested watershed or spatial extent. The Soil Conservation Service (now Natural Resource Conservation Service) organizes soils into four Hydrologic Soil Groups (HSG) based on runoff potential. The four HSGs are A, B, C, and D. Soil textural sizes and permeability decrease from group A through D; therefore, the As have the smallest runoff potential and Ds the greatest (Soil Conservation Service 1986). Surficial geology was organized by lithology, which includes mineral content in addition to grain sizes, texture, and color of rocks in the classification. The proportional compositions of each study area by lithologic description and the HSG were the data used to determine variety or number of types (an index of heterogeneity), and dominance (an index of

homogeneity ranging from 0 to 1) for the ECBP and the nested watersheds. Turner and others (2001) provide the formula for calculating landscape dominance based on proportions of land surface categories, which is the same as the information theoretic formula for calculating species dominance in a community. Quantifying the spatial extent of study areas presented major challenges: First, although watersheds were used to subdivide the study area, the sampled streams and their individual watersheds covered only fractions of the designated study areas (Figure 1). Second, neither the sampled reaches nor their watersheds were regularly arranged in space and therefore any polygon drawn to encompass any set of streams or their watersheds would not be unique. The average distance between all pairs of sampling sites based on a distance matrix was used as an index of spatial extent for each designated study area.

Although the ECBP was made up of 59% historical data and 41% current data, the balance of composition was not as close for some of the nested study areas. Historical data were mostly outside the upper Wabash River watershed. Unknown sources of variability in the data due to samples collected 8 to 12 years apart could not be accounted for in a meaningful way (for instance with dummy variables) because sample sizes were small in the nested study areas. Therefore, historical data were not used below the ecoregion level. This was to ensure that patterns below the ecoregion would not be confounded by variability due to the changing weights in the mix of historical and current data. Where sample sizes would not permit multiple regression with all available variables, Pearson correlation analysis was used to select a fewer number of variables for analysis (Neter and others 1996). Sample sizes were not large enough to split data sets for independent model validation. After a model had passed the selection criteria, the jackknife resampling method (Manly 1997) was used to obtain an average value for each regression coefficient. Model R^2 tends to increase as the number of predictors (k) approaches the sample size (Ohtani 2000). The possibility of this phenomenon affecting adjusted- R^2 was assumed. The bootstrap procedure (Manly 1997), based on 1000 iterations of resampling of observations with replacement, was applied to all spatial extents to obtain average adjusted- R^2 for each selected model. Because models had differing numbers of predictors, a single bootstrap subsample size could not be used for all models. We used a subsample size (n_s) such that the ratio $k:n_s$ approximated 1:5. A single model for each defined spatial extent was developed independently for the reach-scale using the QHEI metrics as additive predictors and for the watershed-

scale using the GIS-derived variables. Because the QHEI is a sum of the scores from five scored categories, the QHEI itself was not entered into the multiple regression models with its metrics as a separate variable. A separate simple linear regression of IBI on QHEI was performed for the entire ecoregion to gain an insight on the underlying relationship between the two indices in the dataset. The general linear test (Neter and others 1996), available in SAS through the TEST statement in the REG procedure, was used to compare the IBI-QHEI relationship to that reported by Rankin (1995) with the null hypothesis that the two relationships have the same slope and intercept.

In order to test which of the reach- and watershed-scale predictors were more important within a particular spatial extent, the full and reduced model framework of the general linear test (Neter and others 1996) was used. Predictors of the best model from the reach-scale and watershed-scale were combined to create one full model. The predictors in the reach-scale and watershed-scale models were then considered as two subsets of predictors of the full model. Assuming that the reach-scale predictors were r_1, r_2, \dots, r_k and the watershed-scale predictors were w_1, w_2, \dots, w_k , then the following models were developed for each defined spatial extent:

(1) Full Model:
$$IBI = f(r_1, r_2, \dots, r_k, w_1, w_2, \dots, w_k);$$

(2) Reduced Model

(reach - scale):
$$IBI = f(r_1, r_2, \dots, r_k);$$

(3) Reduced Model (watershed - scale):

$$IBI = f(w_1, w_2, \dots, w_k).$$

Based on model 1, two separate null hypotheses, one for the reach- and the other for the watershed-scale, were tested using the TEST statement in the REG procedure of SAS. The null hypothesis 1 was that model 1 can be reduced to model 2 without a significant drop in how much variability in IBI among sites can be explained. In other words, the extra model sum of squares added to the full model by the additional watershed-scale predictors was not significant when we move from model 2 to model 1. The null hypothesis 2 was that model 1 can be reduced to model 3 without a significant drop in how much variability in IBI among sites can be explained. It follows a similar explanation, that is, the extra model sum of squares added to the full model by the additional reach-scale predictors is

not significant when we move from model 3 to model 1. The probability of a type-I error for the two null hypotheses were compared to conclude whether reach-scale variables on their own or watershed-scale variables on their own better explain the biological health of streams. The general linear test was not performed for Sub3 with a sample size of 5 because of limited degrees of freedom.

Within each spatial extent and scale, the relative importance of predictors retained in the model was determined by standardized regression coefficients. In addition, type-II partial regression coefficients of determination, indicating the remaining variability explained by a particular predictor when all other significant predictors have been taken into account, were computed. These two coefficients are useful only for comparing the importance of variables included in this study (Neter and others 1996). For each extent, the most important IBI metrics driving the response of IBI to reach- and watershed-scale habitat variables were determined. This was done by regressing the habitat variables retained at a particular scale and extent on all IBI metrics individually and selecting the three IBI metrics that had the strongest relationship with the habitat variables based on adjusted- R^2 of the regression. A model reported as significant had a P value ≤ 0.05 for the global F-test and < 0.1 for individual variable t-tests. The relations among watershed- and reach-scale habitat variables were examined using Pearson product-moment correlations (Neter and others 1996).

Results

IBI score ranged from 24 to 93, with a median of about 60 in most study areas (Table 2). Sub2 had the lowest median of 54.5 and Sub3 the highest of 71. All IBI metrics, except the proportion of carnivore individuals, maintained considerable ranges throughout the study areas. Qualitative habitat evaluation index scores ranged between 17 and 92, with the highest median of 66 occurring in the ECBP and the lowest of 42 in Sub3 (Table 3). The metrics of the QHEI also mostly spanned almost the entire score range of 0–20 in the ECBP. Median watershed sizes were close to 40 km² with all watershed-scale variables except drainage density and CN exhibiting wide ranges in most study areas. As expected from the nested hierarchy of study areas, all variables had their widest ranges in the ECBP extent and generally decreased in the smaller study areas. The composition of surficial geology varied from 22 types in the ECBP to 3 in Sub1A and Sub3, with the

Table 2. Median, minimum, and maximum values of IBI and its metrics in nested study areas

	ECBP <i>n</i> ^a = 95	UW <i>n</i> = 39	Sub1 <i>n</i> = 24	Sub1A <i>n</i> = 13	Sub1B <i>n</i> = 8	Sub2 <i>n</i> = 10	Sub3 <i>n</i> = 5
Index of biotic integrity (IBI) score	60 24–93	60 35–85	60 35–78	67 35–78	58 49–75	55 42–82	71 45–85
Number of species	15 1–31	15 6–28	15 6–26	15 6–26	12.5 8–22	13.5 7–28	17 15–23
Number of darter/madtom/sculpin species	3 0–9	3 0–9	2.5 0–9	2 0–9	2.5 1–5	2.5 1–5	4 4–6
Number of darter species	2 0–7	2 0–7	2 0–7	2 0–7	1.5 1–4	2 0–4	4 3–5
Number of sunfish species	2 0–7	2 0–4	1 0–4	2 0–4	1 0–2	1.5 0–4	2 2–4
Number of sucker species	1 0–5	1 0–4	1 0–3	1 0–3	1.5 0–3	1 0–4	1 1–3
Number of minnow species	7 0–14	7 1–14	7 4–14	7 4–10	7 5–14	6.5 1–11	7 5–12
Number of sensitive species	3 0–11	2 0–11	2 0–8	2 0–8	1.5 0–5	1.5 0–11	4 1–6
Proportion of headwater species	4.3 0–73.9	17.0 0–70.7	17.3 0–70.7	6.1 0–47.4	28.3 4.3–70.7	21.8 0–68.5	1.7 0–47.0
Proportion of tolerant individuals	47.9 0–96.6	59.4 14.9–96.6	62.3 26.4–96.6	60.7 36.5–96.6	75.1 26.4–92.2	54.2 14.9–74.1	42.4 19.4–67.1
Proportion of omnivore individuals	14.1 0–67.1	15.8 0.2–61.3	15.5 0.2–61.3	23.6 8.8–57.5	11.7 1.2–61.3	12.7 2.2–49.4	16.2 7.0–52.0
Proportion of carnivore individuals	0.8 0–100	0.0 0–18.9	0.0 0–7.5	0.0 0–7.5	0.0 0–1.1	1.0 0–18.9	1.6 0.1–5.1
Proportion of insectivore individuals	43.3 0–86.5	44.7 6.6–84.5	39.2 6.6–77.2	47.0 23.1–71.6	24.0 6.6–75.3	51.3 28.5–84.5	44.7 33.2–58.9
Proportion of pioneer species individuals	44.4 0–94.6	56.7 7.9–94.6	59.7 23.5–94.6	63.4 42.5–94.6	63.1 23.5–76.7	35.9 7.9–67.7	60.3 37.5–66.6
Proportion of simple lithophil individuals	22.9 0–87.0	24.8 0–67.9	24.6 2.9–47.8	24.3 2.9–47.8	23.5 5.1–40.0	20.8 0–67.9	29.6 1.6–34.6
Catch-per-unit-effort	181 3–1000	195 13–1000	210 78–1000	202 78–455	330 115–1000	53.5 13–215	239 137–801

^a*n*, number of sampled streams included in study area.

dominant proportion shifting between loam and silty clay-loam to clay loam in different study areas (Table 4). Dominant hydrologic soil group in study areas was either B or C, with group A constituting a minor part of some watersheds. Dominance of surficial geology ranged from 0.29 in Sub2 to 0.98 in Sub1A and dominance of hydrologic soil group from 0.02 in Sub3 to 0.79 in Sub1A. The results of statistical analyses are organized under (1) identity and importance of reach-scale predictors, (2) identity and importance of watershed-scale predictors, (3) reach- versus watershed-scale predictors and the general linear test, (4) effects of spatial extent, and (5) importance of IBI metrics.

Identity and Importance of Reach-Scale Predictors

Considering the larger extents of the ECBP and UW, substrate and riffle-pool quality were the only significant predictors of IBI score, with substrate being a slightly stronger predictor than riffle-pool quality (Table 5). Below the UW, reach-scale models had only one

significant predictor. The single most important reach-scale predictor differed among the three subwatersheds of the UW. Bank stability, substrate (driven by composition and embeddedness), and in-stream cover (driven by maximum pool depth and abundance of large woody debris) scores were the respective single most important predictors in the Sub1, Sub2, and Sub3 watersheds. The important predictors within the two subwatersheds of the Sub1 were also different. Channel morphology score, which incorporates sinuosity and channelization, was not selected as a predictor in any model. Regression coefficients were all positive, consistent with the functions of the habitat components, and indicate minimal collinearity in models. At the ecoregional extent, substrate and riffle-pool quality alone predicted IBI (Adjusted-R² = 0.10) as well as the QHEI (Figure 2; Adjusted-R² = 0.09). The hypothesis of equal slope and intercept of our observed relationship with that of Rankin (1995) was rejected (*p* = 0.0029; general linear test). Our observed IBI-QHEI relationship had a gen-

Table 3. Median, minimum, and maximum values of habitat variables of stream reaches and their watersheds in nested study areas

	ECBP <i>n</i> ^a = 95	UW <i>n</i> = 39	Sub1 <i>n</i> = 24	Sub1A <i>n</i> = 13	Sub1B <i>n</i> = 8	Sub2 <i>n</i> = 10	Sub3 <i>n</i> = 5
Reach-Scale							
Qualitative Habitat Evaluation Index	66	52	51	49	46	52	42
	17–92	17–86	21–86	21–79	25–86	25–64	17–72
Substrate score	14	12	12	12	13	6.5	13.5
	2–19	2–19	2–19	2–16	6–17	5–15	5–18
Riffle-pool score	10	7	7	6	7	8	6
	0–19	3–16	3–16	4–13	3–16	3–15	3–14
Bank/riparian score	16	11	11	12	8	12	6
	4–20	4–20	4–20	4–18	8–18	4–20	4–12
Channel morphology score	15	11	12	12	11	8	8
	4–20	4–17	5–17	6–17	5–17	4–15	5–14
Cover complexity score	12	10.5	11	7	11	11	8
	0–19	0–19	1–19	1–18	4–19	2–18	0–16
Watershed-Scale							
Watershed area (km ²)	44.7	40.4	40.7	40.9	39.1	41.1	37.7
	3.1–256.4	10.0–170.3	10.0–117.0	12.3–107.2	10.0–117.0	14.9–170.3	17–67.1
Riparian forest (%)	21	16.8	19.3	21.3	17.6	12.3	4.9
	0–100	0–100	0–100	0–62.9	0–100	0–65.3	0–83.7
Length-slope factor	0.46	0.40	0.41	0.31	0.42	0.39	0.34
	0.15–1.55	0.18–1.26	0.18–1.26	0.18–1.08	0.21–1.26	0.19–0.58	0.19–0.57
Runoff curve number	71.7	73.6	77.4	78.5	75.3	67.2	74.1
	59.4–82.9	59.4–81.5	59.4–81.3	60.1–81.3	59.4–80.1	60.9–74.4	65.9–81.5
Basin length (km)	10.2	8.5	8.7	8.4	9.0	8.1	8.8
	2.4–38.5	5.2–26.7	5.7–20.2	5.7–20.2	6.8–14.1	5.2–26.7	7.5–14.5
Sinuosity	1.3	1.4	1.5	1.4	1.6	1.3	1.4
	1.1–4.5	1.2–4.5	1.2–2.0	1.2–1.9	1.2–2.0	1.2–2.3	1.2–4.5
Channel slope (%)	0.18	0.16	0.18	0.16	0.18	0.12	0.23
	0.06–1.91	0.06–0.41	0.06–0.41	0.09–0.39	0.06–0.31	0.07–0.41	0.09–0.26
Drainage shape	0.4	0.4	0.4	0.4	0.6	0.3	0.3
	0.1–2.5	0.2–1.3	0.2–0.8	0.3–0.7	0.2–0.6	0.2–1.3	0.2–0.7
Drainage density (km km ⁻²)	1.0	1.0	1.0	1.0	0.9	0.9	1.1
	0.8–1.5	0.8–1.2	0.9–1.2	0.9–1.2	0.9–1.2	0.8–1.1	1.0–1.2

^a*n*, number of sampled streams included in study area.

tlar slope (0.18 versus 0.41), a larger intercept value (24.5 versus 13.3), and a smaller Pearson correlation coefficient ($r = 0.30$ versus 0.69). Slopes and intercepts are reported with IBI score on a scale of 0–60, and correlation coefficients (r) are reported here for direct comparison with Rankin (1995) to avoid confusion with the small values of the coefficient of determination (r^2) and the even smaller adjusted- R^2 s, which we report for our models. The larger watersheds nested in the ECBP had slightly stronger correlation between IBI and QHEI. Specifically UW ($r = 0.48$, $p = 0.0023$), Sub1 ($r = 0.59$, $p = 0.0025$), and Sub1A ($r = 0.61$, $p = 0.0262$) had statistically significant relationships, but Sub1B, Sub2, and Sub3 did not.

Identity and Importance of Watershed-Scale Predictors

Like reach-scale models, best watershed-scale models included different habitat variables at different

spatial extents, with some variables appearing more frequently than others. Considering the different spatial extents together, LS and the riparian forest were the leading predictors of IBI score (Table 6). At the ecoregional extent, where the largest range of LS was captured, the relationship of LS with IBI was nonlinear and the relationship was similar between LS and most IBI metrics (Figure 3). The IBI increased with average LS to approximately 0.85 and decreased thereafter. Drainage density, drainage shape, basin length, and main channel slope were also significant predictors. In terms of regression coefficients, these variables were always subordinate to riparian forest, except for Sub2 where basin length and channel slope were the only significant predictors. At the ecoregional extent, a multiplicative interaction term of riparian forest and watershed area had a negative relationship with IBI score, but watershed area on its own was not significant, suggesting a decreasing importance of 30-m × 60-

Table 4. Composition (%) of land surface of the area drained by groups of streams in the Eastern Corn Belt Plain ecoregion and nested areas

Characteristic	Category	Spatial extent ^a						
		ECBP 94.7	UW 61.2	Sub1 50.9	Sub1A 39.7	Sub1B 26.1	Sub2 39.7	Sub3 29.7
Surficial geology	Loam	53.62	32.82	18.95		26.46	47.71	73.30
	Silty clay-loam to clay-loam	28.32	44.67	68.29	99.76	48.24	3.40	19.52
	Mixed drift	6.80	9.40	6.22		18.46	16.99	7.17
	Lake sand	3.85	4.96	3.07			10.80	
	Blanket sand	2.02	3.19	0.64			9.80	
	Undifferentiated outwash	1.62	0.30	0.22	0.09	0.51	0.57	
	Muck	0.70	0.90	0.44		0.86	2.21	
	Outwash-fan deposits	0.62	1.10	1.46		4.34	0.74	
	Dune sand	0.54	1.14	0.48		0.68	2.95	
	Intensely pitted outwash	0.47	1.47	0.14		0.42	4.83	
	Clay-loam to silt-loam	0.40						
	Loess	0.33						
	Limestone	0.20						
	Lake silt and clay	0.13	0.05	0.08	0.15			
	Ice-contact stratified drift	0.12	0.01	0.01		0.03		
	Alluvium	0.08						
	Limestone and dolomite	0.07						
	Siltstone and shale	0.04						
	Loam to sandy loam	0.03						
	Lowland silt complex	0.02						
Karst	0.01							
Variety (s) ^b	21	12	12	3	9	10	3	
Dominance (D) ^c	0.56	0.42	0.59	0.98	0.42	0.29	0.33	
Hydrologic soil group	C	55.87	46.41	66.78	96.76	48.37	3.74	42.74
	B	42.62	51.16	32.82	3.24	50.47	88.55	57.26
	A	1.51	2.43	0.40		1.16	7.71	
	Variety	3	3	3	2	3	3	2
	Dominance	0.32	0.28	0.40	0.79	0.32	0.61	0.02

^aAverage distance between all pairs of sampling sites in kilometers.

^bs = Number of types.

^c $D = \frac{\ln(s) + \sum_{i=1}^s P_i \ln(P_i)}{\ln(s)}$, P_i = proportion of type i (Turner and others 2001).

Table 5. Identity and relative importance of reach-scale predictors^a of index of biotic integrity (IBI)^b score

Spatial extent ^c	Bootstrap sample size ^d	Standardized regression coefficients ^e (partial R ² in parentheses)					Average Adj-R ²
		Substrate	Riffle-pool	Bank/riparian	Channel	Cover	
ECBP ($n = 95$) ^f	10	0.21 (0.03)	0.17 (0.02)				0.09
UW ($n = 39$)	10	0.36 (0.13)	0.30 (0.09)				0.26
Sub1 ($n = 24$)	5			0.58 (0.34)			0.32
Sub1A ($n = 13$)	5					0.61 (0.37)	0.33
Sub1B ($n = 8$)	5			0.67 (0.45)			0.47
Sub2 ($n = 10$)	5	0.58 (0.34)					0.26
Sub3 ($n = 5$)	5					0.91 (0.82)	0.86

^aMetrics of a qualitative habitat evaluation index (QHEI; Rankin 1995).

^bBased on IBI scoring criteria for the Eastern Corn Belt Plain ecoregion (Simon and Dufour 1998).

^cECBP: Eastern Corn Belt Plains; UW: Upper Wabash River Watershed; Sub1: Subwatershed 1 of UW; Sub1A: Subwatershed A of Sub1; Sub1B: Subwatershed B of Sub1; Sub2: Subwatershed 2 of UW; Sub3: Subwatershed 3 of UW.

^d1,000 iterations of resampling with replacement from the n observations; used to obtain average adjusted-R².

^eJackknife resampling average based on n observations.

^f n , number of streams included in study area.

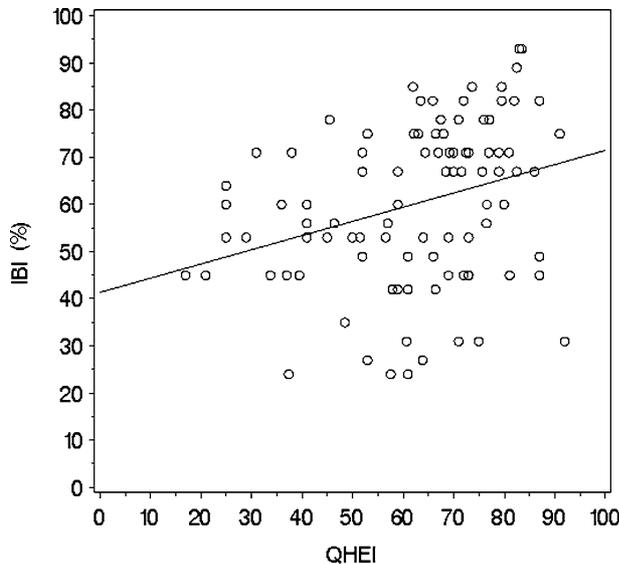


Figure 2. Relationship between the index of biotic integrity (IBI) and a qualitative habitat evaluation index (QHEI) for 95 streams of the Eastern Corn Belt Plain ecoregion of Indiana. The regression model is $IBI = 41.4 + 0.30 \times QHEI$ ($R^2 = 0.10$; adjusted- $R^2 = 0.09$; $p = 0.003$).

m riparian forest as a predictor of IBI in larger streams. Runoff curve number had a moderate negative relationship with IBI, but was not significant as a predictor whenever riparian forest was in a model.

Reach- versus Watershed-Scale Predictors and the General Linear Test

Watershed-scale habitat variables were stronger predictors of IBI score than reach-scale variables. For a given extent, the watershed-scale model adjusted- R^2 explained an average of about 15% more variation in IBI than did a reach-scale model (Figure 4). The probabilities of a type-I error associated with the general linear tests were generally smaller for the watershed-scale reduced models than for the corresponding reach-scale reduced models (Table 7). Note, however, that these probabilities were not corrected for the comparison of many nonindependent spatial extents. In most cases, there was sufficient collinearity in the full model involving both reach- and watershed-scale variables to result in a smaller adjusted- R^2 than the reduced model containing only watershed-scale predictors. Each of the variables LS and riparian forest predicted IBI with about the same model fit as the QHEI. For example, at the ecoregional extent, the IBI-LS relation had an adjusted- R^2 of 0.12 compared to the IBI-QHEI relation (adjusted- $R^2 = 0.09$).

All reach-scale habitat variables were positively correlated. Within the entire data set, strongest correlations were channel morphology with substrate ($r = 0.69$, $p <$

0.0001) and bank/riparian ($r = 0.77$, $p < 0.0001$) scores (Table 8). Watershed-scale habitat variables did not all have significant correlations and where correlations occurred, signs of the coefficient were mixed. Some noteworthy correlations were LS with CN ($r = -0.62$, $p < 0.0001$) and riparian forest (0.46, $p < 0.0001$). The highest correlation was between watershed area and basin length ($r = 0.81$, $p < 0.0001$). Riparian forest and LS had significant positive correlations with all and CN had significant negative correlations with all reach-scale variables except substrate.

Effects of Spatial Extent

For both the reach- and watershed-scale models, model adjusted- R^2 generally decreased with increasing spatial extent (Figure 4; Tables 5 and 6). Increasing spatial extent resulted in increasing variety of surficial geology, but no such clear trend was observed in the variety of hydrologic soil groups (Table 4). Consequently, there was a decreasing trend in model predictive power as the variety of surficial geology increased (Figure 5). There was no such trend in model adjusted- R^2 with variety of hydrologic soil groups or any of the geologic and hydrologic soil group dominance indices.

Importance of IBI Metrics

All but two of the 15 individual IBI metrics used in this study appeared among the three most important IBI metrics for some spatial extent (Table 7). The two metrics that did not appear in the three at any spatial extent were the number of darter species and percent simple lithophilic individuals. In Sub2 where both reach- and watershed-scale models had considerably weak relationships with IBI scores, catch-per-unit-effort metric (CPUE) and headwater species had fairly strong linear relations with substrate (adjusted- $R^2 = 0.55$ and 0.53, respectively) and species richness and sensitive species metrics also had even stronger relationships with basin length and channel slope (adjusted- $R^2 = 0.74$ and 0.76, respectively). In the smaller, non-nested watersheds (Sub1A, Sub1B, Sub2, and Sub3), individual metrics tended to relate more strongly to both reach- and watershed-scale habitat than did their composite IBI score. However, that trend faded and appeared to reverse as these watersheds were aggregated into larger ones (Sub1 and UW; Table 7). Similar IBI metrics were most sensitive to the selected habitat variables at both scales for a given spatial extent. For all but Sub2, at least two of the top three IBI metrics were the same, suggesting that habitat models of the two scales were measuring variation in similar biological indicators of stream health. The most fre-

Table 6. Identity and relative importance of watershed-scale predictors of index of biotic integrity (IBI)^a score

Spatial extent ^c	Bootstrap sample size ^d	Standardized regression coefficients ^b (partial R ² in parentheses)							Average adj-R ²
		Length-slope factor	Riparian forest	Riparian forest × watershed Area	Drainage density	Drainage shape	Basin length	Channel slope	
ECBP (n = 95) ^e	20	0.51 (0.08)	0.46 (0.12)	-0.37 (0.09)					0.25
UW (n = 39)	10		0.55 (0.33)		0.25 (0.09)				0.33
Sub1 (n = 24)	15		0.65 (0.54)		0.33 (0.23)	0.30 (0.19)			0.62
Sub1A (n = 13)	5		0.69 (0.48)						0.44
Sub1B (n = 8)	5	0.92 (0.84)							0.73
Sub2 (n = 10)	10						0.69 (0.34)		0.37
Sub3 (n = 5)	5	0.94 (0.88)							0.93

^aBased on IBI scoring criteria for the Eastern Corn Belt Plain ecoregion (Simon and Dufour 1998).

^bJackknife resampling average based on *n* observations.

^cECBP: Eastern Corn Belt Plains; UW: Upper Wabash River Watershed; Sub1: Subwatershed 1 of UW; Sub1A: Subwatershed A of Sub1; Sub1B: Subwatershed B of Sub1; Sub2: Subwatershed 2 of UW; Sub3: Subwatershed 3 of UW.

^d1000 iterations of resampling with replacement from the *n* observations; used to obtain average adjusted-R².

^e*n*, number of streams included in study area.

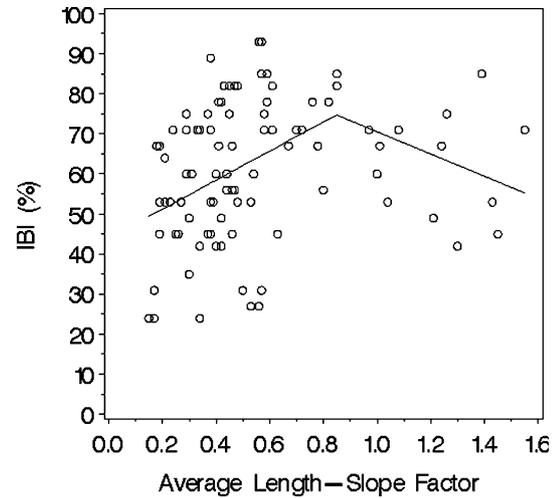


Figure 3. The relationship between the index of biotic integrity (IBI) and average of a length-slope factor within a 300-m × 1000-m buffer of 95 streams of the Eastern Corn Belt Plain ecoregion of Indiana. The piecewise regression relation $IBI = 43.9 + 36.3 \times LS - 64.0 \times sLS$ ($R^2 = 0.13$; adjusted- $R^2 = 0.12$; $p = 0.001$) has a parameter (sLS) accounting for the negative slope occurring from approximately $LS = 0.85$.

quently appearing IBI metrics among the top three were the number of sensitive species, percent tolerant individuals, the number of headwater species, the number of pioneer species, and percent omnivore individuals.

Discussion and Conclusions

The importance of the variables of a particular scale for predicting IBI scores depended on the study extent. The pattern of prediction of IBI and its metrics by the reach-scale QHEI and its metrics suggests that not all habitat metrics were needed. No additional predictive power was gained by using more than one or two of the QHEI metrics at any spatial extent. A single reach habitat assessment criterion for the entire ecoregion would probably be less reliable than setting different criteria for different watersheds based on a few most important habitat variables identified for that watershed. The channel morphology score was not found to be a useful habitat metric in any watershed in this study. This may be due to a real overlap or confusion over what is measured by this metric and the riffle-pool quality metric. Water depth and mean wetted channel width during low flow (the usual time for fish sampling and habitat evaluation) are required parameters for measuring aquatic habitat, but do not relate to the geomorphic

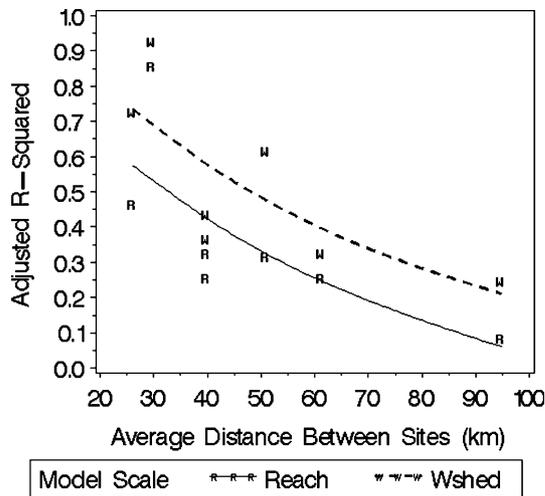


Figure 4. Trend in a measure of fit of reach- and watershed-scale habitat models predicting index of biotic integrity score (adjusted- R^2) of streams in the Eastern Corn Belt Plain ecoregion of Indiana as spatial extent of observations increase. Lines are spline interpolations of adjusted- R^2 (INTERPOL = sm80 using SAS version 8.02).

condition of the channel (Fitzpatrick 2001). Observer judgment of channel habitat unit development and changes resulting from land cover alteration can be biased in the absence of uniform training of observers (Roper and Scarnecchia 1995) and training in geomorphology (Fitzpatrick 2001). The small amount of variability in IBI score explained by QHEI at the ecoregional level and several nested watersheds may be accounted for by several of the following reasons: (1) lack of adequate observer training in geomorphology; (2) lack of uniform training for different sampling crews; (3) loss of statistical power of a habitat index if not adjusted to regional conditions (Rankin 1995); (4) the metrics in the index are not unique in describing geomorphic changes occurring with alteration of watersheds at different spatial and temporal scales (Fitzpatrick and others 2004); (5) the metrics are not sensitive enough to quantify geomorphic changes, especially in a sampling scheme that substitutes space for time (Fitzpatrick and others 2004); and (6) a potential effect of spatial extent on model predictive power (discussed further in later paragraphs). Local (reach)-scale factors are (supposedly) easier to measure, identify, and correlate with fish distributions than large-scale processes, but are also more temporally variable (Jackson and others 2001), and condition of fish that range widely will not necessarily reflect habitat at the exact spot they are captured (Schlosser 1991; Cooper and others 1998).

The importance of riparian forest as a watershed-scale predictor of stream health for many of the defined extents in this study is supported by accumulated evidence as reviewed by several authors (Waters 1995; Allan 2004). The mechanism of effect may be a mix of physical (control of erosion, sediment loading, and woody debris input) and trophic (temperature moderation, nutrient filtering, and allochthonous input of insect prey and vegetative forage) factors (Gregory and others 1991; Naiman and Decamps 1997). Furthermore, riparian forest was not the most important watershed-scale predictor in every study extent and, where significant, the strength of the relationship depended on spatial extent. The importance of landform and hydrologic context in evaluating the capacity of riparian buffers has been stressed previously (Wilkin and Hebel 1982; Hunsaker and Levine 1995; Baker and others 2001). The general consensus is that buffers may not perform their function with the same effectiveness in different locations of the landscape. Also, effects such as point discharges of pollutants, sewer outfalls, and subsurface drainage (which is very common in our study area), and even channelization will be missed by land cover maps and amplify error in prediction. In some study extents, LS was more important than forested buffer and the two variables together with individual watershed size constituted the best subset of predictors at the ecoregion extent. The variable LS has not been reported in any study we know of as a predictor of IBI or any biotic response. However, slopes are known to influence the function of riparian buffers and have been incorporated into regulations and guidelines for protecting streams (Waters 1995). Within the range captured in this study, LS had a largely positive relationship with IBI as shown by the sign of the standardized regression coefficient. However, at the ecoregion extent where the range in LS was largest, there was an apparent nonlinearity, suggesting that relatively high slopes in the watershed, in particular, within the 300 m on either side of the stream and 1 km upstream, adversely influenced fish communities. Because sediment has an adverse effect on stream fish communities (Waters 1995), a negative IBI-LS relationship is possible because the LS is a measure of sediment transport capacity of runoff from the landscape. However, the observed relationship is similar to a subsidy-stress response function (Odum and others 1979; Allan 2004). Thus, gentle slopes confer some (possibly trophic) benefits on fish communities to a certain threshold level before sedimentation potential outweighs possible benefits. The observed threshold of approximately 0.85 (Figure 3) was not unique. Different buffer dimensions gave different ranges of mean

Table 7. Top index of biotic integrity (IBI) metrics responding to selected habitat variables and results of general linear tests^a

Spatial extent (<i>n</i>)	Best predictors of IBI based on models selected at each scale		Dominant IBI metrics as response variables (model adjusted-R ² in parentheses) ^b		General linear test <i>p</i> value	
	Reach scale	Watershed scale	Reach scale	Watershed scale	Reach variables	Watershed variables
ECBP (95)	Substrate riffle-pool	Length-slope factor Riparian forest	Sensitive sp. (0.31) ^c Tolerant Ind. (0.24) ^c	Pioneer sp. (0.25) Tolerant Ind. (0.24) ^c	0.1340	0.0184
UW (39)	Substrate riffle-pool	Watershed area Riparian forest	Sucker sp. (0.21) Pioneer sp. (0.34)	Sensitive sp. (0.21) ^c Omnivores (0.18) ^c	0.0592	0.0416
Sub1 (24)	Bank/riparian	Drainage density Riparian forest	Headwater sp. (0.26) ^c Omnivores (0.21) ^c	Headwater sp. (0.17) ^c DMS sp. (0.16)	0.4112	0.0040
Sub1A (13)	Cover	Drainage shape Riparian forest	Tolerant Ind. (0.29) ^c Headwater sp. (0.18) ^c	Headwater sp. (0.36) ^c Tolerant Ind. (0.33) ^c	0.4623	0.1298
Sub1B (8)	Bank/Riparian	Length-slope factor	Omnivores (0.36) ^c Headwater sp. (0.27) ^c	CPUE (0.37) ^c Headwater sp. (0.52) ^c	0.7778	0.0172
Sub2 (10)	Substrate	Basin length Channel slope	Insectivores (0.65) ^c Carnivores (0.59) ^c	Carnivores (0.91) ^c Insectivores (0.46) ^c	0.3100	0.4282
Sub3 (5)	Cover	Length-slope factor	Tolerant Ind. (0.55) CPUE (0.55)	Pioneer sp. (0.44) No. of species (0.74)	—	—
			Headwater sp. (0.53) Sucker sp. (0.37)	Sensitive sp. (0.60) Minnow sp. (0.51)		
			Sunfish sp. (0.86) ^c Omnivores (0.86) ^c	Sensitive sp. (0.97) ^c Sunfish sp. (0.63) ^c		
			Sensitive sp. (0.82) ^c	Omnivores (0.60) ^c		

DMS sp.: Darter/Madtom/Sculpin species metric; CPUE: Catch-per-unit-effort metric.

^aThe full general linear test model combined habitat variables of both scales; *p* values are probability of type I error under H₀; Parameters of variables from the respective scale = 0 (i.e., variables are not useful as additional set of predictors).

^bMetrics ranked by adjusted-R² of regressions where corresponding habitat variables were used as predictors; only top three are shown.

^cCommon among the top three metrics selected by ranking reach- and watershed-scale models at that spatial extent.

LS and different locations of the potential threshold. For watershed mean LS, the threshold was approximately 0.20. Further studies should investigate the mechanisms underlying the IBI–LS relationship. Like LS, further data are needed to investigate why all other watershed geomorphology variables had positive though weaker relationships with IBI scores. The combination of riparian forest and LS hold some potential for developing a watershed-scale index of stream condition for the ECBP ecoregion for fish assemblages. The important relation of riparian forest and IBI has been documented elsewhere in the US Midwest (Lammert and Allan 1999), but the LS is new information and warrants further exploration and expansion to macroinvertebrates in future studies. It is not surprising that watershed area was not an important predictor of IBI score. If the metric scoring procedure adjusts properly for apparent relationships between metrics and watershed area, IBI score should correlate with watershed area only if there is an underlying monotonic relationship between habitat

quality and stream size. Our results suggest that habitat quality is not a function of stream size in the ECBP.

There was some redundancy when the best reach-scale and watershed-scale variables were combined in a single model. The linear interpolation of adjusted-R² show watershed-scale habitat as slightly but consistently better predictor of IBI scores. Correlations in Table 8 suggest that riparian forest, LS, CN, basin length, slope, and to a limited extent watershed area are linked to reach habitat, which mediate the effect of watershed habitat on fish assemblages. It is intuitive that reach habitat mediates watershed-habitat effect on fish, and some specific causalities have been documented (Richards and others 1996). However, it would be speculative to infer direct causality of reach variables by watershed variables in this study because the reach variables are composites and qualitative in measure. It requires a separate, more quantitative measurement of the components of reach variables to enable an investigation to be conducted as to which components of these variables are caused by specific watershed char-

Table 8. Pearson correlation among reach- and watershed-scale habitat variables^a of first- to fifth-order streams ($n = 95$) of the Eastern Corn Belt Plains of Indiana

	Qualitative habitat scores (reach scale)					Quantitative habitat (watershed scale)								
	SUBS	COV	CHAN	BANK	RI-PO	FORS	LS	AREA	CN	BSNL	SINU	SLOP	SHAP	DDEN
SUBS						0.48	0.33	—	—	0.24	—	0.23	—	—
COV	0.44					0.37	0.30	—	-0.29	—	—	—	—	—
CHAN	0.69	0.48				0.54	0.48	—	-0.29	0.26	—	0.28	—	—
BANK	0.51	0.52	0.77			0.52	0.41	—	-0.33	0.21	—	—	—	—
RI-PO	0.64	0.60	0.62	0.49		0.53	0.31	0.44	-0.25	0.44	—	—	—	—
FORS														
LS						0.46								
AREA						0.32	—							
CN						-0.43	-0.62	—						
BSNL						0.31	—	0.81	—					
SINU						—	—	—	—	-0.22				
SLOP						—	0.36	-0.56	—	-0.47	—			
SHAP						—	—	—	—	-0.48	0.42	—		
DDEN						—	—	—	—	—	—	—	—	—

^aSUBS: Substrate; COV: Cover; CHAN: Channel; BANK: Bank/riparian; RI-PO: Riffle-Pool; FORS: Riparian forest; LS: Length-slope factor; AREA: Watershed area; CN: Runoff curve number; BSNL: Basin length; SINU: Sinuosity; SLOP: Channel slope; SHAP: Watershed shape; DDEN: Drainage density.

Omitted correlation coefficients (—): ($p > |r|$ under $H_0: \rho = 0 > 0.05$) or $|r| < 0.20$.

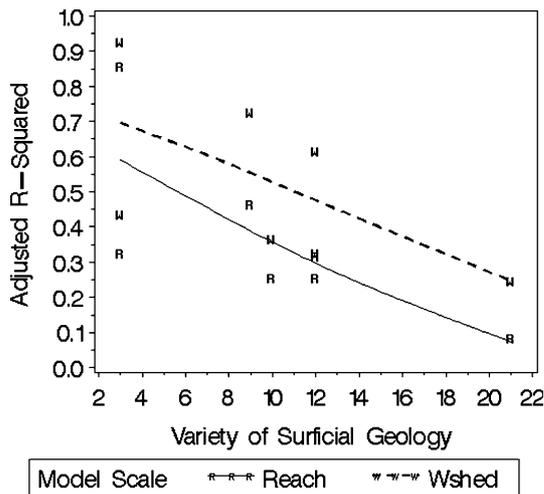


Figure 5. Trend in a measure of fit (adjusted-R²) of reach- and watershed-scale habitat models predicting index of biotic integrity score of streams in the Eastern Corn Belt Plain ecoregion of Indiana as the variety of surficial geology in the study area increase. Lines are spline interpolations of adjusted-R² (INTERPOL = sm80 using SAS version 8.02).

acteristics. Such studies have also been recommended by other researchers (Poff 1997; Papanicolaou and others 2003). The importance of bank stability and riparian quality index measured at the reach-scale did not reflect the relative importance of riparian forest found at the watershed-scale. This disparity can partially be attributed to the subjectivity of assessing riparian quality from qualitative observations at the

reach. In a study of the accuracy and precision of stream habitat estimates, bank vegetation or land use was one of the least precise (Wang and others 1996). A distinctly high variability in the assessment of bank vegetative protection and bank stability among untrained observers is also reported by Hannaford and others (1997). A more accurate assessment of the riparian quality is provided by a spatial view such as that afforded by aerial photos or remote sensing land cover data of the type used in this study. Managers can save time, reduce costs, be more precise, and greatly increase their geographic coverage by conducting spatial screening assessments and focusing reach assessments on segments identified to be vulnerable.

The trends in both reach- and watershed-scale model predictive power in relation to spatial extents should be expected because increased environmental heterogeneity caused by increasing variety of surficial geology means increased variation of responses of stream biota to similar geomorphology, land cover, and land use. There was much less variation in hydrologic soil groups compared to surficial geology and consequently no discernible relationship between model predictive power and hydrologic soil group variety. The changing types and variety of surficial geology are important in explaining the changing strength of models with extent. Although the study area is largely of loam and silty clay-loam to clay loam geology, the additional types of geology making up small percentages of the entire study area tended to be concentrated in individual watersheds, making them significant in

influencing the response of particular streams to land use and geomorphology. Eliminating these smaller components in land surface by lumping them with larger groups would obscure their potential significance. This result supports growing evidence that surficial geology is influential in the distribution of species and health of biotic communities. Richards and others (1996) reported that the status of benthic invertebrates from 58 watersheds in Michigan was highly influenced by surficial geology through channel morphology and patterns of hydrology. Davies and others (2000) used large-scale variables including volcanic rocks, metasediments, dominant geology, and soil type to classify stream reference site groups in the upper Murrumbidgee River catchment, Australia. Measures of surficial geology were the most effective watershed-scale variables determining the distribution of freshwater mussels in southeastern Michigan (McRae and others 2004). Not all sources of increasing heterogeneity with increasing spatial extent may have been accounted for, but it is evident that surficial geology is a significant component, although harder to separate from the effect of land use because the two are always correlated, especially in the US Midwest (Fitzpatrick 2001). The lack of trends in model predictive power in relation to surface dominance may be because the dominant geology and soil was not the same for each extent. Dominance is probably not a good descriptor of the land surface when the dominant group or groups differ among entities as in this study (Table 4). Furthermore, the range in hydrologic soil groups (and consequently, CN) was limited, and its importance in structuring fish communities and IBI (Stauffer and others 2000) may not have been captured in this study. We need to add that we may be seeing a trend of stronger models for smaller spatial extents because of the suite of predictors we used and the level at which stream health was quantified (reach). All predictors, even watershed-scale ones, were measured at fine resolutions and therefore would be expected to be more locally than regionally relevant. Thus, even for the smallest spatial extents there was considerable range in most variables for their significance for fish to be observed. Results may differ if broad categories of land use, soil type, etc., are used to predict watershed average of stream health at the continental scale, for instance.

The leading IBI metrics responding to the selected subset of habitat variables changed with spatial extent. Whereas substrate quality featured at the reach scale for several of the spatial extents, the strongly responding IBI metrics of these extents were those chosen for their sensitivity to more general environ-

mental stresses (Simon and Dufour 1998), including the number of sensitive species, number of tolerant individuals, number of pioneer species, and number of headwater species. The proportion of simple lithophilic spawners, the reproductive guild metric chosen for its sensitivity to siltation (Balon 1975; Simon and Dufour 1998), did not emerge as an important IBI metric in response to substrate or any other habitat variable used in this study. Although the general environmental stresses include siltation, it would be expected that the simple lithophilic metric would feature strongly, and especially when substrate quality appeared to be the most important habitat metric. The hypothesis that simple lithophilic spawners decline with siltation, which is the basis for its inclusion in the IBI, has been supported by some studies (e.g., Berkman and Rabeni 1987; Sutherland and others 2002), but needs further examination for the agricultural streams in the ECBP ecoregion.

The following are the major conclusions of this study: Modeling based on watershed-scale habitat variables of land use and geomorphology derived with spatial data provided better predictive power for stream health measured with fish than modeling with reach-scale qualitative habitat. Increasing the spatial extent of study resulted in decreased model predictive power irrespective of the scale of the predictor variables used. The source of decreased model predictive power may be an increasing heterogeneity in surficial geology. The relative importance of variables for predicting fish IBI and its metrics changed with spatial extent. Predictive modeling of fish IBI for the purpose of stream health evaluation would gain predictive power by reducing the ecoregion to smaller homogeneous areas such as smaller watersheds and developing separate models for those watersheds. In the ECBP, the combination of forested buffer and LS were the most important watershed-scale predictors, and substrate and riffle-pool quality were the most important reach-scale predictors of stream health based on stream fish. The LS-IBI relationship needs to be further investigated and expanded to invertebrates.

Acknowledgments

We wish to thank the Indiana Department of Environmental Management for providing the 1990–1994 biological dataset and the Purdue University Department of Agricultural and Biological Engineering for the use of their GIS database. We especially thank Dr. K. J. Lim for developing Avenue scripts to facilitate riparian land cover computations in ArcView. We also

thank Peter Hrodey and Cameron Guenther of Purdue University for their field support with sampling and fish identification. The ArcView extensions for calculating Strahler stream orders by Duncan Hornby (2003 version) and distance matrix by Hanna Maoh (2001 version) were obtained from ESRI support online. We are thankful to the authors of these programs. We also thank Dr. Faith A. Fitzpatrick of the USGS, and two anonymous reviewers for constructive reviews that improved this article. This research, funded by the Purdue University Department of Forestry and Natural Resources, was approved for publication as manuscript 2005-17617 by the Purdue University Agricultural Research Program.

Literature Cited

- Allan, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Reviews in Ecology, Evolution, and Systematics* 35:257–284.
- Allan, J. D., and L. B. Johnson. 1997. Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology* 37:107–111.
- Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use and stream integrity across multiple spatial scales. *Freshwater Biology* 37:149–161.
- Bain, M. B., T. C. Hughes, and K. K. Arend. 1999. Trends in methods for assessing freshwater habitats. *Fisheries* 24:16–21.
- Baker, M. E., M. J. Wiley, and P. W. Seelbach. 2001. GIS-based hydrologic modeling of riparian areas: implications for stream water quality. *Journal of the American Water Resources Association* 37:1615–1628.
- Balon, E. K. 1975. Reproductive guilds of fishes: A proposal and definition. *Journal of the Fisheries Research Board of Canada* 32:821–864.
- Berkman, H. E., and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285–294.
- Cooper, S. D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* 23:27–40.
- Davies, N. M., R. H. Norris, and M. C. Thoms. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. *Freshwater Biology* 45:343–369.
- Engel, B. 1999a. Estimating runoff depth using the SCS CN method. Purdue University Department of Agricultural and Biological Engineering, West Lafayette, Indiana, 21 pp.
- Engel, B. 1999b. Estimating soil erosion using RUSLE (Revised Universal Soil Loss Equation) using ArcView. Purdue University Department of Agricultural and Biological Engineering, West Lafayette, Indiana, 10 pp.
- Environmental Systems Research Institute. 2002. ArcView GIS 3.3. ESRI, Inc., Redlands, California.
- Environmental Systems Research Institute, and Texas Natural Resources Conservation Commission. 1997. The Watershed Delineator. ESRI, Inc., Redlands, California.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and W. H. Li. 2002. Riverscapes to landscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–498.
- Fitzpatrick, F. A. 2001. A comparison of multi-disciplinary methods for measuring physical condition of streams. *Water Science and Application* 4:7–18.
- Fitzpatrick, F. A., B. C. Scudder, B. N. Lenz, and D. J. Sullivan. 2001. Effects of multi-scale environmental characteristics on agricultural stream biota in eastern Wisconsin. *Journal of the American Water Resources Association* 37:1489–1507.
- Fitzpatrick, F. A., M. A. Harris, T. L. Arnold, and K. D. Richards. 2004. Urbanization influences on aquatic communities in Northeastern Illinois streams. *Journal of the American Water Resources Association* 40:461–475.
- Franzmeier D. P., G. C. Steinhardt, and B. D. Lee. 2001. Indiana soils: Evaluation and conservation. Purdue University Cooperative Extension Service Publication ID-727-01.
- Frimpong, E. A., T. M. Sutton, K. J. Lim, P. J. Hrodey, B. Engel, T. P. Simon, J. G. Lee, and D. C. Le Master. 2005. Determination of optimal riparian forest buffer dimensions for stream biota-landscape association models using multimeric and multivariate responses. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1–6.
- Gallagher, A. S. 1999. Drainage basins. Pages 25–34 in M. B. Bain, and N. J. Stevenson (eds.), *Aquatic habitat assessment: Common methods*. American Fisheries Society, Bethesda, Maryland.
- Gordon, S. I., and S. Majumder. 2000. Empirical stressor-response relationships for prospective risk analysis. *Environmental Toxicology and Chemistry* 19:1106–1112.
- Gray, H. H. 1989. Quaternary geologic map of Indiana. Indiana Geological Survey Miscellaneous Map 49. Indiana Geological Survey, Bloomington, Indiana.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective on riparian zones. *BioScience* 41:540–551.
- Hannaford, M. J., M. T. Barbour, and V. H. Resh. 1997. Training reduces observer variability in visual-based assessments of stream habitat. *Journal of the North American Benthological Society* 16:853–860.
- Hunsaker, C. T., and D. A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. *BioScience* 45:193–203.
- Indiana Geological Survey. 2002. Surficial_geol_mm49_IN: Quaternary geology map of Indiana (Indiana Geological Survey 1:500,000 polygon shapefile). Indiana Geological Survey, Bloomington, Indiana.
- Jackson, D. A., P. R. Peres-Neto, and J. O. Olden. 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Lammert, M., and J. D. Allan. 1999. Assessing biotic integrity of streams: Effects of scale in measuring the influence of

- land use/cover and habitat structure on fish and macroinvertebrates. *Environmental Management* 23:257–270.
- Lattin, P. D., P. J. Wigington Jr., T. J. Moser, B. E. Peniston, D. R. Lindeman, and D. R. Oetter. 2004. Influence of remote sensing imagery source on quantification of riparian land cover/land use. *Journal of the American Water Resources Association* 40:215–227.
- Legendre, P., and L. Legendre. 1998. Numerical ecology, second English edition. Developments in environmental modeling 20. Elsevier, New York, 853 pp.
- Maddock, I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* 41:373–391.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology, second edition. Chapman and Hall, New York, 399 pp.
- McRae, S. E., J. D. Allan, and J. B. Burch. 2004. Reach- and catchment-scale determinants of distribution of freshwater mussels (*Bivalvia*: Unionidae) in southeastern Michigan, U.S.A. *Freshwater Biology* 49:127–142.
- Moore, I. D., and G. J. Burch. 1986a. Physical basis of the length-slope factor in the universal soil loss equation. *Soil Science Society of America Journal* 50:1294–1298.
- Moore, I. D., and G. J. Burch. 1986b. Modeling erosion and deposition: Topographic effects. *Transactions of the American Society of Agricultural Engineers* 29:1624–1630, 1640.
- Moore, I. D., and J. P. Wilson. 1992. Length-slope factors for the universal soil loss equation: Simplified method of estimation. *Journal of Soil and Water Conservation* 47:423–428.
- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28:621–658.
- Natural Resources Conservation Service. 1994. State Soil Geographic (STATSGO) database for Indiana (1:250,000). US Department of Agriculture, NRCS, Fort Worth, Texas.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models, fourth edition. McGraw-Hill, New York, 1408 pp.
- Odum, E. P., J. T. Finn, and E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* 29:349–352.
- Ohtani, K. 2000. Bootstrapping R^2 and adjusted R^2 in regression analysis. *Economic Modelling* 17:473–483.
- Omerik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118–125.
- Osborne, L. L., B. Dickson, M. Ebberts, R. Ford, J. Lyons, D. Kline, E. Rankin, D. Ross, R. Sauer, P. Seelbach, C. Speas, T. Stephanavage, J. Waite, and S. Walker. 1991. Stream habitat assessment programs of the AFS North Central Division. *Fisheries* 16:28–35.
- Oswood, M. E., and W. E. Barber. 1982. Assessment of fish habitat in streams: Goals, constraints, and a new technique. *Fisheries* 7:8–11.
- Palmer, M. A., C. C. Hakenkamp, and K. Nelson-Baker. 1997. Ecological heterogeneity in streams: Why variance matters. *Journal of the North American Benthological Society* 16:189–202.
- Papanicolaou, A. N., A. Bdour, N. Evangelopoulos, and N. Tallebeydokhti. 2003. Watershed and instream impacts on the fish population in the south fork of the Clearwater River, Idaho. *Journal of the American Water Resources Association* 39:191–203.
- Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- Poole, G. C., C. A. Frissell, and S. C. Ralph. 1997. In-stream habitat unit classification: Inadequacies for monitoring and some consequences for management. *Journal of the American Water Resources Association* 33:879–895.
- Rankin, E. T. 1995. Habitat indices in water resource quality assessments. Pages 181–208 in W. S. Davis, and T. P. Simon (eds.), Biological assessment and criteria. Lewis Publishers, Boca Raton, Florida.
- Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences* 53(suppl 1):295–311.
- Roper, B. B., and D. L. Scarnecchia. 1995. Observer variability in classifying habitat types in stream surveys. *North American Journal of Fisheries Management* 15:49–53.
- Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11:141–156.
- Schlösser, I. J. 1991. Stream fish ecology: A landscape perspective. *BioScience* 41:704–712.
- Simon, T. P. 1999. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida, 671 pp.
- Simon, T. P., and R. Dufour. 1998. Development of index of biotic integrity expectations for the ecoregions of Indiana: V Eastern Corn Belt Plain. United States EPA, Region 5, Chicago, Illinois. EPA 905-R-96-004, 68 pp.
- Soil Conservation Service. 1986. Urban hydrology for small watersheds. TR-55, second edition. SCS, United States Department of Agriculture, Washington, DC, 164 pp.
- Sponseller, R. A., E. F. Benfield, and H. M. Vallet. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409–1424.
- 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.
- Sutherland, A. B., J. L. Meyer, and E. P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology* 47:1791–1805.
- Townsend, C. R., S. Doleddec, R. Norris, K. Peacock, and C. Arbuckle. 2003. The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48:768–785.
- Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: Theory development and testing. *Landscape Ecology* 3:245–252.

- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: Pattern and process. Springer-Verlag, New York, 401 pp.
- US Census Bureau. 1990. US Census Bureau (TIGER) 1:100,000 hydrography. USCB, Washington, DC.
- US Department of Agriculture, and National Agricultural Statistical Service. 2001. USDA–National Agriculture Statistics Service's 1:100,000-scale 2001 cropland data layer, a crop-specific digital data layer for Indiana. USDA-NASS Marketing Division, Washington, D.C.
- US Geological Survey. 1999. National elevation data set. USGS, Sioux Falls, South Dakota.
- Wang, L., T. D. Simonsen, and J. Lyons. 1996. Accuracy and precision of selected stream habitat estimates. *North American Journal of Fisheries Management* 16:340–347.
- 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, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela, and P. M. Stewart. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U. S. A. *Canadian Journal of Fisheries and Aquatic Sciences* 60:491–505.
- Waters, T. F. 1995. Sediment in streams: Sources, biological effects and control. American Fisheries Society Monograph 7. AFS, Bethesda, Maryland, 251 pp.
- Weigel, B. M., L. Wang, P. W. Rasmussen, J. T. Butcher, P. M. Stewart, T. P. Simon, and M. J. Wiley. 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes and Forests ecoregion, U. S. A. *Freshwater Biology* 48:1440–1461.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wilkin, D. C., and S. J. Hebel. 1982. Erosion, redeposition, and delivery of sediments to Midwestern streams. *Water Resources Research* 18:1278–1282.