

Impacts of Urbanization on Stream Habitat and Fish Across Multiple Spatial Scales

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ABSTRACT / We analyzed the relation of the amount and spatial pattern of land cover with stream fish communities, in-stream habitat, and baseflow in 47 small southeastern Wisconsin, USA, watersheds encompassing a gradient of predominantly agricultural to predominantly urban land uses. The amount of connected impervious surface in the watershed was the best measure of urbanization for predicting fish den-

sity, species richness, diversity, and index of biotic integrity (IBI) score; bank erosion; and base flow. However, connected imperviousness was not significantly correlated with overall habitat quality for fish. Nonlinear models were developed using quantile regression to predict the maximum possible number of fish species, IBI score, and base flow for a given level of imperviousness. At watershed connected imperviousness levels less than about 8%, all three variables could have high values, whereas at connected imperviousness levels greater than 12% their values were inevitably low. Connected imperviousness levels between 8 and 12% represented a threshold region where minor changes in urbanization could result in major changes in stream condition. In a spatial analysis, connected imperviousness within a 50-m buffer along the stream or within a 1.6-km radius upstream of the sampling site had more influence on stream fish and base flow than did comparable amounts of imperviousness further away. Our results suggest that urban development that minimizes amount of connected impervious surface and establishes undeveloped buffer areas along streams should have less impact than conventional types of development.

Recent studies indicate that stream hydrology, geomorphology, water chemistry, and biota are largely determined by a combination of regional factors, such as geology and climate, and local land cover and land use (Richards and others 1996, Seelbach and others 1997, Wehrly and others 1998, Zorn and others 1998). There is increasing interest in understanding the mechanisms by which watershed land uses influence stream ecosystems so that appropriate land management can be undertaken to improve or maintain stream quality (Booth and Jackson 1997, Lammert and Allan 1999).

Urban land use can severely degrade stream ecosystems (Wang and others 1997, 2000). A growing body of literature documents substantial alterations in flow patterns, channel morphology, water quality, and biotic communities associated with watershed urbanization (e.g., Ferguson and Suckling 1990, Lenat and Crawford 1994, Masterson and Bannerman 1994, Crunkilton and

others 1996, Booth and Jackson 1997, May and others 1997). As the amount of urban land grows, precipitation runoff volume and rate increase, causing the frequency and magnitude of floods to rise and base flows to fall. Greater flooding makes the channel less stable, leading to excessive bank erosion, loss of pool habitat and instream cover, and excessive streambed scour and deposition. Urban runoff typically also contains a variety of pollutants that degrade water quality. All of these physical and chemical alterations restructure biotic communities and cause declines in the diversity and productivity of invertebrates and fishes. Relatively small amounts of urban land use in a watershed can lead to major changes in biota, and there appear to be threshold values of urbanization beyond which degradation of biotic communities is rapid and dramatic (May and others 1997, Wang and others 2000).

Efforts to conserve stream biological communities in urbanizing watersheds require quantitative and predictive models that describe the relation between urbanization and the biological integrity of the community (Wang and others 1997, 2000). One challenge in constructing such models is the identification of appropriate indicators of the amount and extent of urbanization

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to use in statistical analysis and model building. Urban land use encompasses a wide range of interrelated human activities that can be difficult to summarize numerically. Moreover, not only the type, but also the intensity and the location of the land use within the watershed are likely to determine its impact on the biological community of the stream (Booth and Jackson 1997, May and others 1997).

In previous studies, several different measures have been used to characterize the degree of urbanization and its relation to stream biota and their habitat. Biological diversity and integrity have been shown to be negatively correlated with percentage urban land cover (Klein 1979, Steedman 1988, Limburg and Schmidt 1990, Lenat and Crawford 1994, Weaver and Garman 1994, Wang and others 1997, Klauda and others 1998), human population density (Jones and Clark 1987, Schueler 1997), and house density (Benke and others 1981). However, Wang and others (1997) did not find a strong correlation between stream habitat for fish and the percentage of urban land cover within either the entire watershed or the riparian corridor.

Recently, the amount of impervious surface within the watershed, which strongly influences the pattern and magnitude of precipitation infiltration and surface runoff, has been proposed as a key environmental indicator of urban land-use effects (Schueler 1994, Arnold and Gibbons 1996). The extent of imperviousness has an obvious direct effect on stream hydrology and water quality and an indirect but strong effect on stream habitat and biota (Booth and Jackson 1997). An impervious surface is also one of the few urban land-use attributes that can be explicitly quantified and managed at each stage of land development. However, only a few studies have examined relations between watershed imperviousness and stream fish communities (Klein 1979, Booth and Jackson 1997, May and others 1997, Wang and others 2000).

Proximity to the stream also appears to be an important consideration in estimating the impact of urban land uses on stream biological communities. A positive relation has been reported between the width of forested riparian corridors and fish and invertebrate biotic integrity in urbanizing watersheds of forested regions of southern Ontario and western Washington state (Steedman 1988, May and others 1997). In analyzing 45 agriculture- or forest-dominated catchments of a river basin in central Michigan, Richards and others (1996) found that stream riparian areas (buffers) were more important than whole-catchment data for predicting sediment-related habitat variables, but that channel morphology was more strongly related to attributes of entire catchments. For three first-order tributaries of

the River Raisin in southeastern Michigan with mixed agriculture and forest land cover, Lammert and Allan (1999) reported that land use immediately adjacent to the tributaries predicted biotic condition better than regional land use but was less important than local in-stream habitat variables.

In this study, we compared a variety of measures of urbanization to identify which one(s) had the strongest relation with fish habitat quality, fish community structure, and biotic integrity. Once we had identified the best measure, we developed quantitative models to predict the characteristics of the fish habitat and fish community that could be attained at a given level of watershed urbanization. Finally we analyzed the amount of urbanization at different spatial scales to examine how the pattern and proximity of urban development influenced stream ecosystems.

Methods

Study Area

We analyzed land use, fish habitat, and fish communities for 47 small watersheds in southeastern Wisconsin, USA, the same watersheds used in Wang and others (2000). All study watersheds were located within the Southeastern Wisconsin Till Plains Ecoregion (Omerik and Gallant 1988); 28 were in the Lake Michigan basin and 19 in the Mississippi River basin. Nearly all the soils in this region were formed, at least in part, from glacial materials. Nearly two thirds of the soils of the region are on glacial till, about a quarter on glacial outwash, and remainder on glaciolacustrine deposits (Hole 1976). Most of this area has low relief, and hill slopes are nearly level to rolling. Stream drainage systems are poorly developed and undrained depressions are common.

Owing to its rich soil and flat topography, southeastern Wisconsin has long been an important agricultural region. It has also been the most important urban area of the state, centered on the city of Milwaukee. In 1990 about 2 million people, 38% of Wisconsin's population, lived in this region. Over the last 70 years the urban population of southeastern Wisconsin has doubled, leading to a substantial increase in urban land and a major decrease in agricultural land.

A single stream site was sampled within each watershed in 1997, and the sites were chosen to minimize potential variation in natural biological attributes, such as watershed soil type, stream size and slope, and natural hydrological and temperature regimes, while maximizing variation in amount of urban and agricultural land use. At the sampling sites the streams were warm-

water (summer maximum daily mean temperature $>25^{\circ}\text{C}$), second to third order in size, and had low to moderate gradients (<6 m/km). In the absence of differing watershed land uses, these sites would be expected to have similar habitat and fish communities (Lyons 1996).

Watershed Land Use

An existing digital land-use database for 1990, prepared and maintained by the Southeastern Wisconsin Regional Planning Commission, was used to abstract watershed land-cover data for the study sites. This database contained 63 urban and rural land-use categories, including residential (six categories), commercial (three categories), industrial (four categories), transportation (20 categories), communication and utilities (two categories), government and institutional (nine categories), recreation (seven categories), agriculture (six categories), and open or forested lands (six categories). The database had been developed from 1:4800 air photos and had resolutions of about 0.40 ha for rural areas and as small as 0.06 ha for urban areas. Watershed boundaries above each sampling site were delineated by hand on 1:24,000 topographic maps using ARC/INFO software (ESRI 1994). We quantified watershed land cover by overlaying watershed boundaries on top of the land-use database with ARC/INFO software. We analyzed land-use data for a 50-m-wide region along each side of the stream upstream from the site, a region between 50m and 100m from the stream, and a region beyond 100m. We also extracted land-use data within the watershed for an area within a 1.6-km radius upstream of the site, between a 1.6- and 3.2-km radius, and beyond a 3.2-km radius. We chose these buffer and radius distances based on results from previous studies of agriculture- and forest-dominated watersheds (Large and Petts 1994, Richards and others 1996, Wang and others 1997, Harding and others 1998, Lammert and Allan 1999).

Fish and Habitat Sampling

Habitat, fish communities, and baseflow were sampled at each stream site during 1997. The length of site was about 35 times mean stream width, or a minimum of 100 m, a length sufficient to characterize the fish assemblage and to encompass about three meander sequences (Lyons 1992a, Simonson and others 1994). As a result, stations ranged in length from 100 to 315 m.

Fish sampling occurred between late May and late August in 1997, when low stream flows facilitated sampling effectiveness and large-scale seasonal fish movements were unlikely to occur (Lyons and Kanehl 1993). The entire length of each site was electrofished with

either two backpack units in tandem or a single tow-barge unit with three anodes (Lyons and Kanehl 1993, Simonson and Lyons 1995). Efforts were made to collect all fish observed and all captured fish were identified and counted. Previous studies have shown that this sampling procedure yields an accurate and precise picture of the fish community, with a measurement error of about $\pm 10\%$ – 20% (Simonson and Lyons 1995).

Habitat sampling occurred within a day of fish sampling. At each site, 28 habitat variables, encompassing channel morphology, bottom substrates, cover for fish, bank conditions, riparian vegetation, and land use, were measured or visually estimated along 13 transects using standardized procedures described in Simonson and others (1994). These procedures yield data with known levels of accuracy and precision, typically $\pm 5\%$ – 10% (Wang and others 1996).

Stream base-flow was measured at a single transect near the downstream end of each site using a Flow-Mate model 2000 portable flowmeter. All measurements were made during a three-day period in October when flows were likely to have been at or near their annual minimum, based on an analysis of gauged sites in the region. No rainfall had occurred for at least 10 days before this sampling.

Data Analysis

We summarized the 63 watershed land-use types into 15 major categories and expressed each as a percentage of total watershed land use. We also determined the percentage of the watershed as connected impervious land cover, defined as those surfaces impervious to infiltration by precipitation (e.g., roads, sidewalks, parking lots, roofs) that had a direct hydraulic connection (e.g., surface drainage way, storm sewer) to the downstream drainage system (Booth and Jackson 1997). The connected impervious area was calculated based on a previous study that had estimated typical levels of connected imperviousness for different types of urban land uses in southern Wisconsin (Bannerman, WDNR unpublished data). The different land-cover types and the connected impervious area within the three buffer and three radius categories were also expressed as a percentage of total watershed area.

From the habitat data, we calculated in-stream fish habitat scores using a habitat rating system for low gradient streams (Wang and others 1998). This habitat rating system was specifically developed for Wisconsin stream fishes, was not species specific, and was designed to assess the suitability of a stream segment for an entire fish assemblage. It consists of differentially weighted measures of channelization, instream cover, bank ero-

sion, sinuosity, variation in thalweg depth, and riparian vegetation.

From the fish data, we determined the number of fish species, total fish density (number/100 m²), and percentage of individuals that were tolerant of environmental degradation (Lyons 1992b). Fish data were also used to calculate the Shannon diversity index (Magurran 1988) and an index of biotic integrity (IBI) (Lyons 1992b). The IBI is a widely used measure of the quality of fish community, and an effective method to assess the overall condition or “health” of the stream ecosystem (Fausch and others 1990). The IBI used here was specifically developed for Wisconsin warmwater streams and could range from 0 to 100, with higher values indicating better fish communities.

For base flows, we calculated a value “adjusted” for differences among sites in the sizes of their watersheds. Our adjusted values were expressed as the quotient of the measured base flow divided by the area of the watershed in square kilometers, multiplied by 1000. Such an adjusted base flow is relatively consistent for streams with similar amounts of groundwater inputs and can be used to measure base flow changes resulting from watershed land modification (Seelbach and others 1997).

We analyzed the relation of each of the 16 land-use variables (i.e., 15 land cover types and connected imperviousness) with each of the fish, habitat, and base-flow (“stream”) variables to identify the best measure of urban land use for predicting stream fish and habitat attributes. We first examined bivariate plots to determine if data transformations were required to stabilize variance and approximate normality. After any necessary transformations, we correlated land-use variables with stream variables using simple linear regression (SAS Institute 1990). The land-use variable with the highest significant ($P < 0.05$) r^2 value was considered to be the best estimator of urbanization.

We next developed predictive models that related selected stream attributes to the amount of urban land use in the watershed. Our goal in this analysis was to identify the best possible conditions that could be expected at a given level of urbanization. Consequently, we applied 90% quantile regression to estimate the upper bounds of each of the correlations between variables (BLOSSOM software; Slauson and others 1994).

Finally, we used simple linear regression to analyze the relation of agricultural, woodland, wetland, and urban land uses with selected stream variables at the differing spatial scales represented by our buffer and radius categories. For each combination of variables, we compared P and r^2 values among the buffer and radius categories to estimate the relative importance of the

proximity of a given land use to the stream in influencing habitat, fish, and flow characteristics. When P and r^2 values were similar for different variables, we compared regression slopes, with higher slopes indicating stronger relations.

Results

Watershed and Land Cover

Our data set encompassed a wide range of watershed areas and land covers. Watershed areas upstream of the sampling sites ranged from less than 10 to 101 km² with a mean of 27.6 km². The watersheds were dominated by either urban (3%–97%) or agricultural (0–89%) land uses; woodland ranged from 0.2% to 18% with a mean of 6.1%; and water–wetland ranged from 0.2% to 25% with a mean of 8.7%. Details on the location, watershed size, and land use of each site are given in Wang and others (2000).

In general, the percentages of each land-use type were highly and significantly correlated among the three buffer and the three radius categories. Among the buffer categories, Pearson correlations for imperviousness and for urban, agriculture, and water–wetland land uses ranged from 0.70 to 0.99. Correlations for woodland land covers were more variable, ranging from 0.40 to 0.99. Among the radius categories, correlations were 0.80–0.99 for urban land uses and 0.35–0.92 for imperviousness and agriculture, woodland, and water–wetland land uses. However, correlations were not significant between the within-1.6-km and beyond-3.2-km categories for imperviousness, agriculture, woodland, and water–wetland land uses and between the 1.6-km-to-3.2-km and the beyond-3.2-km categories for imperviousness and agriculture land uses.

Best Land-Use Variables for Explaining Stream Attributes

Among the 16 land-use variables considered, connected imperviousness was the best at explaining variation in fish community attributes (Table 1). Percentage watershed connected imperviousness explained the most variance in the number of fish species (55%), Shannon diversity index (50%), fish density (39%), and the second-most variance for percent tolerant fish (19% vs 21% for the best variable) and third for IBI score (32% vs 34% and 33%). The next 10 best variables for explaining fish attributes were, from best to worst, highways–streets–parking lots, commercial land, total urban land, agricultural land, government land, residential land, environmental corridor (undisturbed land connected to the stream), woodland, vegetated

Table 1. Coefficients of determination (r^2) for regressions between land use variable (% of watershed) and fish and habitat variables^a

Land cover Variables (%)	Fish							
	Species number (Ln)	IBI score (Ln)	Shannon index (Ln)	Individuals of tolerant fish (%)	number/100 m ² (Ln)	Habitat score	Erosion	Base flow (Ln)
Connected imperviousness	0.55* (-)	0.32* (-)	0.50* (-)	0.19* (+)	0.39* (-)	—	0.27* (+)	0.09 (-)
Highway, street, parking	0.48* (-)	0.23* (-)	0.48* (-)	0.17* (+)	0.28* (-)	—	0.25* (+)	0.10 (-)
Commercial land	0.41* (-)	0.33* (-)	0.30* (-)	0.21* (+)	0.31* (-)	—	0.21* (+)	0.14 (-)
Urban land	0.35* (-)	0.22* (-)	0.33* (-)	0.13 (+)	0.28* (-)	—	0.21* (+)	0.10 (-)
Agricultural land	0.33* (+)	0.13 (+)	0.31* (+)	—	0.22* (+)	—	0.13 (-)	—
Residential land	0.23* (-)	0.16* (-)	0.20* (-)	—	0.22* (-)	—	0.20* (+)	0.10 (-)
Government land	0.30* (-)	0.31* (-)	0.20* (-)	0.11 (+)	0.29* (-)	—	—	0.10 (-)
Environmental corridor (Ln)	0.17* (+)	0.34* (+)	0.10 (+)	0.11 (-)	0.26* (+)	0.09 (+)	0.14 (-)	0.24* (+)
Woodland (Ln)	0.15* (+)	0.27* (+)	0.13 (+)	0.11 (-)	0.28* (+)	0.13 (+)	—	0.16* (-)
Vegetated land (Ln)	0.10 (+)	0.23* (+)	—	0.09 (-)	0.23* (+)	0.11 (+)	—	0.15* (+)
Industry	0.08 (-)	—	0.14 (-)	—	—	—	—	—
Water/wetland	0.12 (+)	0.22* (+)	—	0.09 (-)	—	—	—	0.35* (+)
Other transportation	0.18* (-)	0.15* (-)	—	—	0.15* (-)	—	—	—
Recreational land	0.14 (-)	—	0.22* (-)	0.10 (+)	0.10 (-)	—	—	—
Pasture	0.10 (+)	0.15* (+)	0.10 (+)	—	0.21* (+)	—	—	—
Unused land	0.18* (-)	0.27* (-)	0.11 (-)	—	—	0.10 (-)	—	0.14 (-)

^aLn indicates natural log transformed variables; base flow = m³/sec/1000 km² watershed area. Coefficients were listed only for regression slopes that were significant at $P < 0.05$; *indicates significant at $P < 0.01$. (+) indicates the relationship is positive and (-) is negative.

land, and water-wetland. Most of these variables explained the greatest variance for number of species and the least for percent tolerant fish.

Correlations were much weaker between land-use and habitat variables (Table 1). Environmental corridor, woodland, vegetative land, and unused land were the only variables that were significantly related to habitat score, but none explained more than 13% of the variation. Connected imperviousness and one of its major components—highways, streets, and parking lots—explained the most variation in streambank erosion (25%–27%). Water-wetland ($r^2 = 0.35$) and environmental corridor ($r^2 = 0.24$) had the best correlations with base flows. A plot suggested that connected imperviousness limited the maximum values for base flow, but the overall correlation was very weak ($r^2 = 0.09$).

Predictive Models Based on Connected Imperviousness

Percentage watershed connected imperviousness had similar relations with number of fish species, IBI scores, and adjusted base flows (Figure 1). For watersheds with connected imperviousness less than 8%, which corresponded to areas of relatively high agriculture (>40%), fish species number, IBI scores, and base flows were highly variable. Some sites had healthy fish communities (>15 species and IBI scores >50) and

high base flows (>4 m³/sec/1000 km²), whereas others had poor-quality fish communities (<8 species and IBI scores <30) and very low base flows (<1 m³/sec/1000 km²). Watersheds with connected imperviousness greater than 12% had poor-quality fish communities and low base flows. Connected imperviousness levels from 8% to 12% appeared to represent a threshold zone, where there was a dramatic drop in the maximum possible value for species number, IBI score, and base flow with a small increase in connected imperviousness.

The 90% quantile regressions between connected imperviousness and numbers of species ($r^2 = 0.40$), IBI scores ($r^2 = 0.42$), and base flows ($r^2 = 0.26$) had similar forms and were best fit with a negative exponential model (Figure 1). The regression lines quantified the pattern of relatively high maximum values at connected imperviousness levels less than 8%, a sharp decline in maximum values between 8% and 12%, and consistently low maximum values above 12% connected imperviousness.

Influence of Spatial Distribution of Land Use

Analysis of the radius data emphasized the importance of urbanization and the effect of land-use proximity on in-stream conditions. Within the 1.6-km radius and between the 1.6- and 3.2-km radius, connected imperviousness tended to have stronger correlations with fish, habitat, and flow variables than did agricul-

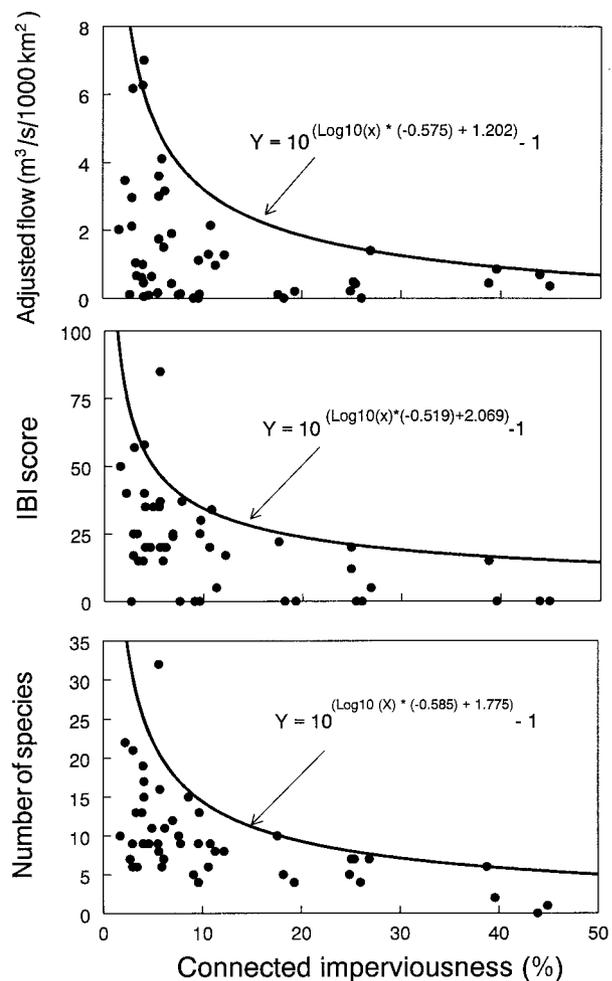


Figure 1. Plots between watershed percent connected imperviousness and number of fish species, IBI score, and base flow ($\text{m}^3/\text{sec}/1000 \text{ km}^2$ of watershed area). The models were developed by first \log_{10} -transforming the dependent variables, then performing 90% quantile regression on these semitransformed data to develop linear models, and finally back-transforming the linear models into nonlinear models using anti-logarithms. The coefficients of determination of the models, equivalent to r^2 in least square regression, are 0.40 for number of fish species, 0.42 for IBI score, and 0.26 for adjusted base flow.

tural, woodland, and water-wetland land-uses (Table 2). For connected imperviousness, the r^2 values were nearly identical for these two radius categories, but the slope was consistently steeper for the within-1.6-km class, suggesting that connected imperviousness immediately adjacent to the stream had the strongest influence on in-stream conditions. Beyond a 3.2-km radius, the correlation with imperviousness declined precipitously, and the other three land uses explained more of the

variation in stream attributes. Interestingly, for these other land uses, the beyond-3.2-km category usually explained substantially more variation than the within-1.6-km or the 1.6-km-to-3.2-km categories. This result indicates that within 3.2 km of the study sites the effects of connected imperviousness were overwhelming, or at least obscuring, any influence of these other land uses.

Buffer analysis yielded a different pattern. For number of fish species, IBI scores, and Shannon index, the connected imperviousness had the highest r^2 values for all buffer categories, but woodland land cover had the steepest slopes (Table 3). With the exception of woodland beyond 100 m ($r^2 = 0.14$), none of the four land uses explained a significant amount of variation in habitat scores. Water-wetland land cover and connected imperviousness both were significantly related to baseflow for all three buffer categories. Water-wetland explained more variation but imperviousness tended to have steeper slopes.

Discussion

Imperviousness as an Indicator of Urbanization

Our results show that watershed connected imperviousness was the best single indicator of urbanization effects on stream fish communities in southeastern Wisconsin. This finding supports similar conclusions from previous studies of stream fish communities from Maryland (Klein 1979, Schueler 1994) and Washington state (Booth and Jackson 1997, May and others 1997). Our next-best indicator, land cover by highways, streets, and parking lots, was a major component of imperviousness. Overall urban land use, which has been widely used in previous studies (e.g. Steedman 1988, Wang and others 1997), was an adequate indicator, but it explained substantially less of the variation in fish community attributes than did imperviousness.

Surprisingly, we found little relation between connected imperviousness (or any other measure of urbanization) and our habitat quality index. This is consistent with an earlier statewide study of urbanization impacts on Wisconsin streams (Wang and other 1997), but appears to contradict findings from other parts of the United States. In other studies, researchers have documented increased erosion, channel destabilization and widening, loss of pool habitat, excessive sedimentation and scour, and reduction in large woody debris and other types of cover as a consequence of urbanization (Lenat and Crawford 1994, Schueler 1994, Arnold and Gibbons 1996, Booth and Jackson 1997, May and other 1997). We did find a significant negative correlation between connected imperviousness and ero-

Table 2. Coefficients of determination (r^2) and regression slopes for relations between selected fish and habitat variables and selected land-use variables^a

Fish or habitat variable and distance from site	Land use (% of watershed area)							
	Agricultural		Woodland		Water-wetland		Connected imperviousness	
	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope
Number of species (Ln)								
Within 1.6 km radius	0.01	+0.01	0.00	-0.01*	0.02	+0.05	0.46	-0.12
Between 1.6 and 3.2 km	0.08	+0.01	0.02	+0.16*	0.02	+0.03	0.48	-0.07
Beyond 3.2 km	0.31	+0.02	0.18	+0.30*	0.16	+0.05	0.16	-0.04
Index of biotic integrity (Ln)								
Within 1.6 km radius	0.01	-0.02	0.00	+0.12*	0.06	+0.22	0.34	-0.25
Between 1.6 and 3.2 km	0.03	+0.02	0.09	+0.74*	0.04	+0.10	0.35	-0.14
Beyond 3.2 km	0.16	+0.03	0.38	+1.05*	0.24	+0.14	0.04	-0.05
Shannon index (Ln)								
Within 1.6 km radius	0.02	+0.01	0.00	+0.04*	0.00	+0.00	0.43	-0.06
Between 1.6 and 3.2 km	0.09	+0.01	0.02	+0.07*	0.02	+0.01	0.45	-0.03
Beyond 3.2 km	0.27	+0.01	0.11	+0.11*	0.27	+0.02	0.14	-0.02
Habitat score								
Within 1.6 km radius	0.00	-0.17	0.01	+3.11*	0.00	+0.40	0.14	-1.76
Between 1.6 and 3.2 km	0.03	-0.23	0.05	+6.42*	0.01	+0.40	0.15	-1.02
Beyond 3.2 km	0.10	+0.24	0.16	+7.39*	0.05	+0.70	0.02	-0.31
Adjusted base flow (m ³ /sec/1000 km ² watershed area) (Ln)								
Within 1.6 km radius	0.02	-0.01	0.01	-0.04	0.12	+0.02	0.15	-0.30*
Between 1.6 and 3.2 km	0.01	+0.00	0.11	+0.09	0.12	+0.08	0.09	-0.18*
Beyond 3.2 km	0.03	+0.00	0.10	+0.04	0.24	+0.05	0.01	-0.08*

^aCalculated as % watershed land use within a given radius upstream from the stream sampling site. Values significant at $P < 0.05$ are in bold type. Ln indicates natural log transformed; *indicates land-use variables were also natural log transformed.

sion, but the other habitat impacts (several of which are incorporated into the habitat quality index) were not correlated with urbanization. Many of our non-urban sites had degraded habitat from agricultural land uses in their watersheds, and this may have obscured the relation between increasing urbanization and decreasing habitat quality. Furthermore, our habitat scoring system seems to be most affected by local riparian conditions, as evidenced here by the significant correlations of habitat scores with stream corridor and vegetative land-cover variables (see Table 2). Some of our suburban and urban sites had well-vegetated riparian corridors, and these sites had at least fair-quality fish habitat.

The relation between connected imperviousness and baseflow was complex. Connected imperviousness appeared to limit the base flow in moderately to heavily urbanized watersheds but had little influence on base flow in rural watersheds. The low base flows we observed in urban watersheds agreed with findings from other studies, where impervious surfaces caused reduced infiltration of precipitation into the groundwater, a lowered water table, and a decrease in stream flow (Riggs 1965, Klein 1979, Simmons and Reynolds 1982,

Ferguson and Suckling 1990, Schueler 1994). However, in nonurban areas other factors besides imperviousness controlled base flow. For these areas, the amount of surface water (i.e., lakes and impoundments) and wetlands in the watershed was a better predictor of base flow, suggesting that the surface water storage capacity of the watershed strongly influenced the volume of flow in the stream channel in the absence of runoff.

We expect that only a small increase in connected imperviousness occurred between 1990, when the land use data were captured, and 1997, when the stream fish and habitat data were collected. Between 1970 and 1990, the average annual increase in connected imperviousness for all 47 study watersheds was 0.09% (Wang and others 2000). For watersheds with less than 10% connected imperviousness, the increase was 0.03%. In addition, there is evidence to support a time lag between watershed land-use changes and responses of the biological community. In agricultural watersheds the time lag is typically two to three years (Wang, WDNR unpublished data). Therefore, we believe that the difference in collection dates for the watershed land use data and the stream fish and habitat data in this study

Table 3. Coefficients of determination (r^2) and regression slopes for relations between selected fish and habitat variables and selected land-use variables^a

Fish or habitat variable and distance from stream	Land use (% of watershed area)							
	Agricultural		Woodland		Water-wetland		Connected Imperviousness	
	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope
Number of species (Ln)								
Within 50 m buffer	0.16	+0.09	0.04	+0.42*	0.10	+0.06	0.48	-0.33
Between 50 and 100 m	0.19	+0.09	0.09	+0.56*	0.10	+0.14	0.45	-0.41
Beyond 100 m	0.34	+0.02	0.14	+0.28*	0.11	+0.05	0.48	-0.04
Index of biotic integrity (Ln)								
Within 50 m buffer	0.01	+0.06	0.09	+1.59*	0.19	+0.22	0.29	-0.51
Between 50 and 100 m	0.04	+0.10	0.23	+2.35*	0.04	+0.45	0.26	-0.75
Beyond 100 m	0.16	+0.03	0.25	+0.92*	0.18	+0.16	0.31	-0.08
Shannon Index (Ln)								
Within 50 m buffer	0.18	+0.05	0.03	+0.02*	0.05	+0.17	0.37	-0.14
Between 50 and 100 m	0.19	+0.04	0.04	+0.20*	0.02	+0.03	0.35	-0.17
Beyond 100 m	0.32	+0.07	0.12	+0.12*	0.05	+0.02	0.48	-0.02
Habitat score								
Within 50 m buffer	0.00	+0.07	0.01	+6.81*	0.04	+1.13	0.03	-2.19
Between 50 and 100 m	0.00	+0.39	0.05	+12.28*	0.02	+1.81	0.07	-4.21
Beyond 100 m	0.03	+0.13	0.14	+7.46*	0.02	+0.62	0.06	-0.40
Adjusted base flow (m ³ /sec/1000 km ² watershed area) (Ln)								
Within 50 m buffer	0.01	-0.03	0.01	-0.11	0.20	+0.08	0.16	-0.47*
Between 50 and 100 m	0.00	-0.04	0.02	+0.12	0.31	+0.23	0.19	-0.57*
Beyond 100 m	0.03	+0.00	0.14	+0.04	0.35	+0.08	0.12	-0.02*

^aCalculated as % of watershed area at various distances from the stream upstream of the site. Values significant at $P < 0.05$ are in bold type. Ln indicates natural log transformed; * indicates land-use variables were also natural log transformed.

should not have a major effect on our results or conclusions.

Connected Imperviousness as a Limiting Factor and Values of Quantile Regression

Base flow and most of the fish community attributes that we measured had a wedge-shaped relation with connected imperviousness. High levels of imperviousness were always associated with low values of these attributes, but low levels had both high and low values. Traditional linear regression does not perform well with this sort of data structure. We analyzed relations with the recently developed technique of quantile regression, which is ideal for wedge-shaped relations (Terrell and others 1996, Thomson and others 1996, Scharf and others 1998, Cade and others 1999).

Quantile regression is superior to least-square linear regression in several regards. Least-square techniques are particularly sensitive to outlying values for dependent variables and irregularities in the distribution of observations, and they frequently produce inconsistent estimates of slope for upper and lower bounds (Scharf and others 1998). Estimates of means from least-square regressions are unbiased only for linear monotonic

transformation (Bassett 1992). In contrast, quantile regression techniques based on least absolute value models are more robust to outlying values of the dependent variable and to sparseness within data sets, while providing consistent estimates of upper and lower bound slopes (Scharf and others 1998). In addition, quantile regression is proficient in dealing with curvilinear edges of scatter diagrams as nonlinear (e.g., logarithmic) transformations of data do not bias coefficient estimates (Bassett 1992). In previous biological applications, quantile regressions have been used to model stream fish habitat for standing stock estimation (Terrell and others 1996); estimate changes in glacier lily seedling numbers as a function of lily flower numbers, rockiness, and pocket gopher activity (Thomson and others 1996); examine patterns between prey size and predator size in animal populations and the relation between animal abundance and body size (Scharf and others 1998); and study changes in annual acorn biomass due to forest canopy cover of oak and oak species diversity (Cade and others 1999). All of these studies have demonstrated that quantile regression is an appropriate statistical technique for modeling relations with a wedge-shaped form.

Quantile regression has enhanced our understanding of how and when connected imperviousness acts as a limiting factor for stream fish communities. The 90% quantile estimates are calculated such that they are greater than 90% of the observations and less than the remaining 10%. The products of our models could be interpreted as predictions, with 90% probability, of the highest possible number of fish species, IBI score, and adjusted base flow that can be achieved for a given imperviousness level. Our model predicts that high values of these variables are possible, but not inevitable, at low levels of imperviousness, but that at high levels of imperviousness only low values of base flow and fish community characteristics can be achieved.

Previous studies of fish communities in urban watersheds have reported both wedge-shaped and linear relations. Wedge-shaped relations have been found mainly in areas where rural land-uses are dominated by agriculture, whereas linear relations are more typical of areas where the rural landscape has been less modified and remains mainly forest. Watershed agriculture can strongly impact stream fishes, but degradation of fish communities is not inevitable in predominantly agricultural watersheds (Wang and others 1997, 2000). For example, in a survey of 270 stream sites from watersheds with a mix of forest, agriculture, and urban land uses in Maryland, Klauda and others (1998) reported a wedge-shaped relation between urbanization and IBI score. Sites with greater than 50% total urban land use had IBI scores in the poor to very poor range, but among sites with less than 25% urban land use, a wide range of IBI scores was observed from good to very poor. However, when the analysis was restricted to 61 sites in the Patapsco basin, where agricultural land-use impacts were limited (Klauda and others 1998, Klauda, Maryland Department of Natural Resources unpublished data), a strong linear negative relation between IBI scores and urban land was observed. Similarly, in an early study of 27 small Maryland watersheds with limited agriculture, Klein (1979) reported a near-linear negative relation between watershed total imperviousness and a fish diversity index. Steedman (1988) also reported a negative linear correlation between watershed urban land use and IBI scores in largely forested watersheds in southern Ontario.

Regardless of the type of land use in rural areas, all studies to date comparing the relation between imperviousness and stream fishes, including this one, have noted a sharp decline in fish community attributes at 8%–12% imperviousness (Scheuler 1994, Booth and Jackson 1998, May and others 1997, Wang and others 2000). Below about 8% imperviousness, fish species

richness, diversity, and IBI scores may be either high or low, but above 10%–12% they are consistently poor.

Impacts of Spatial Distribution of Urbanization on Stream Quality

The influence of the spatial distribution of land cover, especially in riparian areas, has long been recognized in watersheds with a mix of forest and agriculture or forest and urban lands. In otherwise predominantly agricultural or urban watersheds, riparian forests can stabilize streambanks and reduce erosion, provide woody debris that improves in-stream habitat, and filter sediment in nutrients from upland runoff (Castelle and others 1994). Establishment and maintenance of well-vegetated riparian buffer strips along streams has become one of the most visible and widely accepted applications of watershed management.

Buffer strips have a disproportionate influence on some aspects of stream biological communities and their habitats. In comparing the importance of buffer versus watershed land covers for mixed forest–agriculture watersheds, Richards and others (1996) reported that land cover from a 100-m-wide buffer explained more of the variance in the percent of fine substrate in the stream channel and in bank erosion than land cover in the entire catchment. However, catchment data explained more of the variance in channel morphological variables such as width, depth, and sinuosity. In a study attempting to distinguish the relative importance of local (riparian) versus regional (catchment) land uses on streams in a mixed forest–agriculture area, Allan and others (1997) concluded that the influence of land use on stream integrity was scale-dependent. Instream habitat structure and organic matter inputs were determined primarily by riparian conditions such as the vegetative cover adjacent to a stream site, whereas nutrient supply, sediment delivery, hydrology, and channel characteristics were influenced more by regional conditions, including landscape features and land cover upstream from and lateral to the site. In analyzing urbanization impacts on streams in primarily forested watersheds, Steedman (1988) and May and others (1997) have concluded that riparian buffers can offset some of the negative effects of urban land uses. They developed graphical models that predicted urbanization impacts on stream quality based on the amount of urban land use in the entire watershed and the amount of woodland in the riparian zone.

We can find no previous studies that have analyzed the spatial influence of different land uses in mixed agricultural–urban watersheds. Several factors make such an analysis difficult. Agricultural land uses appear to have more variable influences on stream attributes

than do forest land uses (Wang and others 1997, 2000). Land uses at different spatial scales are, at best, often highly intercorrelated and, at worst, not statistically independent, which has limited the application of multiple regression techniques. To avoid this problem, most previous investigators have compared regression coefficients of determination (i.e., r^2 values) from separate simple linear regressions for each land use and each spatial scale (Steedman 1988, Richards and others 1996, Roth and others 1996, Allan and others 1997, Harding and others 1998). However, such an approach can only indicate which spatial scale and land cover is a better predictor of stream quality, and it says little about how much of a change in stream quality will result from a change in the amount or spatial pattern of a land-use category.

Our study looked specifically at how the spatial pattern of different land-uses affected stream quality in an urbanizing agricultural region. We compared not only regression coefficients of determination but also regression slopes to assess the relative importance of location and type of land use. We found that urban land uses (i.e., connected imperviousness) in buffer areas along the stream (within 50 m and from 50 to 100 m) and in watershed areas immediately upstream (within a 1.6-km radius and between a 1.6- and 3.2-km radius) had much more influence on the fish community and on base flow than did urbanization further away from the site or stream. The closest buffer (within 50 m) and radius distances (within 1.6 km) had the steepest slopes, indicating that a given land use change in these areas would have a greater effect on the stream than a comparable change in a different part of the watershed. Weaver and Garman (1994) reported a significant correlation between fish community attributes and urbanization within a 1.4-km radius in a Virginia watershed.

We found relatively little influence of nonurban land uses near the stream or site on stream quality. We do not think that this finding means that the amount or location of these other land uses has no effect on the stream, but rather that the effects of connected imperviousness are so overwhelming that relations with other land uses are obscured (see also Wang and others 2000).

Summary and Management Implications

Our study has confirmed that the amount of connected impervious surface in the watershed is the best available indicator of urbanization impacts on stream fish communities and base flow. However, imperviousness may not be a good indicator of habitat quality, although it does accurately predict the amount of bank

erosion present. Using connected imperviousness as our measure of urbanization, we developed quantile regressions that can be used to predict the maximum possible values for fish species richness, fish community biotic integrity, and base flow for a given level of urban development. High values for these three variables are possible (but not inevitable) if connected imperviousness is less than 8% of the watershed area, but low values are inevitable above 12% connected imperviousness. Levels of connected imperviousness between 8% and 12% represent a threshold zone where minor increases in urbanization are associated with sharp declines in fish community quality and baseflow. Connected imperviousness within a 100-m buffer along the length of the stream or within a 3.2-km radius upstream of the sampling site has substantially more influence on stream quality than comparable levels of imperviousness further away. Above about 12% connected imperviousness, the influence of urbanization on stream quality is so dominant that nonurban land uses showed little influence on stream fish communities or base flow.

Our results have several implications for watershed management. First, urban development schemes that minimize the amount of connected impervious surface (e.g., see Schueler 1994, Arnold and Gibbons 1996) should reduce the impact of urbanization on stream ecosystems. Urban watershed best management practices, such as detention ponds, should ease the dramatic increase in flooding caused by urbanization (e.g., Booth and Jackson 1997), although they will not reverse declines in base flow. Establishment of "green spaces" or other types of undeveloped buffer areas at least 50 m wide along streams should also be beneficial. However, even with more environmentally friendly urban development practices, urbanization probably will eventually degrade stream ecosystems once it exceeds a certain threshold level. All the urban best management practices can do is to raise such a threshold level. For the conventional types of urban development that are currently in widespread use, this threshold is between 8% and 12% connected impervious surface. Note that this level of imperviousness corresponds to a suburban rather than a downtown urban landscape. Studies from forested watersheds suggest that better development practices and the establishment of riparian buffers may increase the amount of watershed urbanization that a stream ecosystem can withstand before it becomes degraded (e.g., Steedman 1988, Booth and Jackson 1997). Whether this is the case in agricultural watersheds is as yet unknown. In any event, even under the best-case urban development scenarios, our results and those of previous studies indicate that stream fish communities will decline substantially in quality even while the wa-

tershed remains largely rural in character. Unlike in agricultural landscapes, where implementation of best-management land-use practices can allow for relatively healthy stream fish communities in watersheds that are almost completely farmed (Wang and others 1997, 2000), relatively low levels of watershed urbanization inevitably lead to serious degradation of the fish community.

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Literature Cited

- Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology* 37:149–161.
- Arnold, C. L., Jr., and C. J. Gibbons. 1996. Impervious surface coverage: The emergence of a key environmental indicator. *Journal of the American Planning Association* 62(2):243–258.
- Benke, A. C., G. E. Willeke, F. K. Parrish, and D. L. Stite. 1981. Effect of urbanization on stream ecosystems. Completion Report OWRT Project No. A-055-GA. School of Biology in Cooperation with Environmental Resources Center, Georgia Institute of Technology, Atlanta, Georgia.
- Bassett, G. 1992. The Gauss Markov property for the median. Pages 23–31 in Y. Dodge (ed.), *L₁ Statistical analyses*. North-Holland, Amsterdam.
- Booth, D. B., and C. R. Jackson. 1997. Urbanization of aquatic systems: Degradation thresholds, stormwater detection, and the limits of mitigation. *Journal of the American Water Resources Association* 33(5):1077–1090.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80(1):311–323.
- Castelle, A. J., A. W. Johnson, and C. Conolly. 1994. Wetland and stream buffer size requirements—a review. *Journal of Environmental Quality* 23:878–882.
- Crunkilton, R., J. Kleist, J. Ramcheck, W. De Vita, and D. Villeneuve. 1996. Assessment of the response of aquatic organisms to long-term in situ exposures of urban runoff. Pages 95–111 in L. A. Roesner (ed.), *Effects of Watershed Development and management on aquatic ecosystems*, Proceedings of an engineering Foundation conference, Snowbird, Utah.
- ESRI, 1994. PC ARC/INFO Version 3.4.2. Environmental System Research Institute, Redlands, California.
- Fausch, K. D., J. Lyons, J. R. Karr, and P. L. Angermeier. 1990. Fish communities as indicator of environmental degradation. *American Fisheries Society Symposium* 8:123–144.
- Ferguson, B. K., and P. W. Suckling. 1990. Changing rainfall-runoff relationships in the urbanizing Peachtree Creek watershed, Atlanta, Georgia. *Water Resources Bulletin* 26(2):313–322.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of National Academy of Science USA* 95:14843–14847.
- Hole, F. D. 1976. Soils of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, 223 pp.
- Jones, R. C., and C. C. Clark. 1987. Impact of watershed urbanization on stream insect communities. *Water Resource Bulletin* 23(6):1047–1055.
- Klauda, R., P. Kazzyak, S. Stranko, M. Southerland, N. Roth, and J. Chaillou. 1998. Maryland biological stream survey: a state agency program to assess the impact of anthropogenic stress on stream habitat quality and biota. *Environmental Monitoring and Assessment* 51:299–316.
- Klein, R. D. 1979. Urbanization and stream quality impairment. *Water Resources Bulletin* 15(4):948–963.
- 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(2):257–270.
- Large, A. R. G., and G. E. Petts. 1994. Rehabilitation of river margins. Pages 401–418 in P. Calow and G. E. Petts (eds.), *The rivers handbook: Hydrological and ecological principles*, volume 2. Blackwell Scientific Publications, Oxford, England.
- Lenat, D. R., and J. K. Crawford. 1994. Effects of land use on water quality and aquatic biota of three North Carolina piedmont streams. *Hydrobiologia* 294:185–199.
- Limburg, K. E., and R. E. Schmidt. 1990. Patterns of fish spawning in Hudson River tributaries: Response to an urban gradient? *Ecology* 71(4):1238–1245.
- Lyons, J. 1992a. The length of stream to sample with a towed electrofishing unit when fish species richness is estimated. *North American Journal of Fisheries Management* 12:198–203.
- Lyons, J. 1992b. Using the index of biotic integrity (IBI) to measure environmental quality in warmwater streams of Wisconsin. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota. General Technical Report NC-149.
- Lyons, J. 1996. Patterns in the species composition of fish

- assemblages among Wisconsin streams. *Environmental Biology of Fishes* 45:329–341.
- Lyons, J., and P. Kanehl. 1993. A comparison of four electroshocking procedures for assessing the abundance of small-mouth bass in Wisconsin streams. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota. General Technical Report NC-149, NC-159.
- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, 179 pp.
- Masterson, J. P., and R. T. Bannerman. 1994. Impacts of stormwater runoff on urban streams in Milwaukee county, Wisconsin. Wisconsin Department of Natural Resources Project Report. Grant Number CP995252-01, 13 pp.
- May, C. W., R. R. Horner, J. R. Karr, B. W. Mar, and E. B. Welch. 1997. Effects of urbanization on small streams in the Puget Sound Lowland Ecoregion. *Watershed Protection Techniques* 2(4):485–494.
- Omernik, J. M., and A. L. Gallant. 1988. Ecoregions of the Upper Midwest states. US Environmental Protection Agency, Washington, DC. EPA/600/3-88/037.
- 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.
- Riggs, H. C. 1965. Effect of land use on the low flows of streams in Rappahannock County, Virginia. US Geological Survey, Washington, DC, Professional Paper 525-C, pp. 196–198.
- 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(3):141–156.
- SAS Institute. 1990. SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Cary, North Carolina, 1686 pp.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationship from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79(2):448–460.
- Schueler, T. 1994. The importance of imperviousness. *Watershed Protection Techniques* 1(3):100–111.
- Schueler, T. 1997. Fish dynamics in urban streams near Atlanta, Georgia. *Watershed Protection Techniques* 2(4): 100–111.
- Seelbach, P. W., M. J. Wiley, J. C. Kotanchik, and M. E. Baker. 1997. A landscape-based ecological classification system for river valley segments in Lower Michigan. State of Michigan, Department of Natural Resources, Fisheries Division. Research Report Number 2036.
- Simmons, D. L., and R. J. Reynolds. 1982. Effects of urbanization on base flow of selected South-shore streams, Long Island, New York. *Water Resources Bulletin* 18:797–805.
- Simonson, T. D., and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. *North American Journal of Fisheries Management* 15:419–427.
- Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Guidelines for evaluating fish habitat in Wisconsin streams. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota. General Technical Report NC-164, St. Paul, Minnesota.
- Slauson, W. L., B. S. Cade, and J. D. Richards. 1994. User manual for BLOSSOM statistical software. Midcontinental Ecological Science Center, National Biological Survey, Fort Collins, Colorado, 59 pp.
- Steedman, R. J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 45:492–501.
- Terrell, J. W., B. S. Cade, J. Carpenter, and J. M. Thomson. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. *Transactions of the American Fisheries Society* 125:104–117.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. *Ecology* 77(6):1698–1715.
- Wang, L., T. D. Simonson, 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, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries* 22(6):6–12.
- 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. Kanehl, R. Bannerman, and E. Emmons. 2000. Watershed urbanization and changes in fish communities in southeastern Wisconsin streams. *Journal of the American Water Resources Association* 36(5):1173–1189.
- Weaver, L. A., and G. C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. *Transactions of the American Fisheries Society* 123:162–172.
- Wehrly, K. E., M. J. Wiley, and P. W. Seelbach. 1998. A thermal habitat classification for Lower Michigan rivers. Michigan Department of Natural Resources. Research Report 2038, 50 pp.
- Zorn, T. G., P. W. Seelbach, and M. J. Wiley. 1998. Pattern in the distributions of stream fishes in Michigan's Lower Peninsula. Michigan Department of Natural Resources. Research Report 2035, 43 pp.