Untangling Relationships between
River Habitat and Fishes in Michigan's Lower Peninsula
with Covariance Structure Analysis

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Abstract.–Biologists need to understand causal relationships among key habitat elements and fishes to effectively protect and manage river systems. Though much groundwork has been laid, development of an analytic framework that incorporates spatial hierarchy of river habitat to predict characteristics of habitat and fish assemblages has been challenging. A key issue is the complex web of direct and indirect effects that arises when one attempts to include all pertinent habitat parameters in analyses. Covariance structure analysis (CSA) was specifically developed for untangling such webs and was used throughout this study. We developed a Habitat Model to quantitatively describe relationships between landscape- and local-scale habitat variables commonly associated with fish distribution and abundance in rivers of Michigan's Lower Peninsula. Catchment-scale variables characterizing river size, land use, and surficial geology had significant direct and indirect effects on (and explained 48-84% of spatial variation in) mean depth, velocity, July mean temperature, 90% exceedence flow yield, and total phosphorus values at sites. These variables also had significant direct effects on substrate composition at sites, but could not account for more than 26% of the spatial variation in any individual substrate class. Covariance structure analysis also provided an excellent tool for examining the relative importance of abiotic and biotic causal factors on fish abundance because it allowed us to distinguish among direct effects of habitat and biota, and indirect effects of habitat as mediated through the biota. In addition, CSA enabled us to determine the extent to which the set of sample sites chosen for analysis influenced the relative importance of local-scale habitat and biotic factors to fish abundance. The direct effect of habitat variables on brook trout biomass was 32 times greater than that of brown biomass when all streams were studied, but declined to 0.3 times that of brown trout when the analysis was restricted to trout streams.   In a similar analysis for smallmouth bass, habitat factors had the strongest effects on fish standing crops when the analysis was based on all streams. However, when the sample was limited to smallmouth bass streams, direct effects of forage fish abundance and indirect effects of habitat via forage fish abundance were more prominent. In both the trout and smallmouth bass analyses, regional data sets (which included sites where the species of interest was absent) emphasized the importance of habitat factors on fish abundance, whereas restricting the sample to only sites where the species of interest was present, elevated the importance of biotic factors. Thus, both habitat and biotic factors are important to these species, with the set of streams being studied having an overriding influence on the relative importance of one versus the other. These findings help to resolve apparently conflicting results of other studies on the relative importance of biotic and abiotic factors to fish standing crops.

Introduction

Faced with rapid changes to watersheds and competing demands placed on rivers, biologists need to understand relationships among key habitat elements and fishes to effectively protect and manage river systems. Describing these relations seems deceptively simple at first glance because many physical and biotic characteristics often change predictably in a downstream direction. Such changes formed the basis for longitudinal zonation studies (e.g., Huet 1959; Hawkes 1975; Vannote et al. 1980) that represented early general models for river ecosystems. However, rivers may change abruptly at confluences of comparably sized tributaries and boundaries of landscape features such as glacial landforms, bedrock outcrops, impoundments, and lakes (Seelbach et al. 1997). In addition, variability between river systems is often great enough that no single model seems capable of describing all systems (Balon and Stewart 1983; Wiley et al. 1990; Zorn et al. 1998). Nevertheless, development of a general framework is desirable, and seems feasible, since the specific responses of fishes to a common suite of local factors (e.g., current velocity, temperature, predators) are often fairly consistent across each species' geographic range. These consistent relationships between local factors and fish distribution and abundance are the basis for widely used Habitat Suitability Index (HSI) models (Terrell et al. 1982).

Work by many authors has led to development of models for describing physical habitat in river systems and explaining contemporary patterns in fish assemblages. Early studies (e.g., Lotspeich and Platts 1982; Frissell et al. 1986) provided impetus for thinking about stream habitats in a hierarchical context. These concepts have been applied by others (e.g., Wiley et al. 1990) to quantitatively model stream habitat conditions. Biotic assemblages are commonly thought to result from a combination of local and regional processes acting on individual populations over time (Ricklefs 1987). For fishes, large-scale immigration and extinction processes (e.g., post-glacial dispersal and climate change) provide the available species pool for a region (e.g., Bailey and Smith 1981; Mahon 1983). Contemporary stream fish assemblages result from the effects of more localized immigration and extinction processes (e.g., present habitat conditions, fish introductions, and migration barriers) on individual populations from the species pool (Mahon 1983; Tonn 1990). Extinction processes have been viewed as a series of filters, in part to emphasize the different spatial and temporal scales of factors that may limit or eliminate local populations of fishes (Tonn 1990; Poff 1997). Filters represent local conditions that may be influenced by site-, reach-, catchment-, and regional-scale habitat characteristics, drainage network characteristics (e.g., barrier waterfalls, lakes, and wetlands), or biotic factors (Poff 1997). Models incorporating these filters could conceptually be linked to information on species habitat needs to make predictions of fish assemblage structure or identify habitat attributes limiting fish populations (Imhoff et al. 1996).

Analyses of habitat and fish assemblages in Michigan rivers have also demonstrated the utility of information from various spatial scales. Landscape-based models have been developed for rivers in Michigan's Lower Peninsula (lower Michigan) to predict habitat variables measured at the site, such as water temperature (Wehrly et al. 1997) and nutrient levels (Kleiman 1995; Baker et al. 2001). Large-scale variables characterizing river size and hydrology can provide a macro-habitat template for characterizing individual survey sites and making coarse-scale predictions of fish assemblage structure (Zorn et al. 1998). Use of multi-scale data in species-specific modeling of river fishes in Michigan has helped identify key predictive variables for individual fishes, and collectively for fish assemblages (Zorn et al. 2004). What is lacking, however, is a descriptive yet quantitative model representing interplay among different hierarchical levels of key habitat variables, and between these levels and fishes. With such a tool we could demonstrate the relative influence of stream habitat characteristics, measured at different spatial scales, on habitat parameters important to stream fishes. It would also allow a more complete assessment of the effects (both direct and indirect) of landscape and habitat alteration on stream fish assemblages. This would help in answering a variety of complex questions regarding fishes and habitat. For example, how

does increased urban land use affect streamflow attributes, stream temperatures, substrate conditions, and brown trout standing crops? To what extent is stream substrate composition in glaciated regions influenced by river hydraulics, local sediment supply, and land use activities?

Obviously, there is a need for synthesis of relations among key aspects of aquatic habitat and fishes. Despite the existing need, theory, and models, development of an analytic framework that incorporates spatial hierarchy to predict characteristics of habitat and fish assemblages has been challenging for several reasons. A key issue is the complex web of direct and indirect effects that arises when one attempts to include all pertinent habitat parameters in analyses (Zorn et al. 2004). This multi-collinearity often obscures discernment of mechanisms and violates the assumption of independence required by widely used analyses, such as multiple linear regression. Multivariate analysis techniques (e.g., Lyons 1996; Maret et al. 1997; Waite and Carpenter 2000) can accommodate these data in a more statistically appropriate manner, but may provide relatively little information regarding causal relationships among habitat variables. In addition, regional differences in mechanisms behind site-scale habitat characteristics will also cause empirical relations to vary regionally, and may limit broad application of correlation-based models. For example, altitude is closely associated with stream temperature variation in the mountain states (Keleher and Rahel 1996) but not in glaciated states, such as Michigan where groundwater is key (Wehrly et al. 1997). Such issues have hindered development of a comprehensive framework for lotic systems.

Covariance structure analysis (CSA) was specifically developed for untangling webs of direct and indirect effects, and can provide a useful analytic framework for studying interrelationships between physical and biotic features of river systems across multiple scales. In CSA, the researcher uses existing knowledge to generate hypotheses of how the system functions. These hypotheses are explicitly stated in the form of a causal model that depicts pathways, both direct and indirect, by which variables influence each other. The researcher's theoretical model can be evaluated by assessing the extent to which covariances among variables

in the model (whose structure was constrained by the researcher's theory) are consistent with those occurring in the actual data. Thus, a CSA model could be developed for rivers to depict and quantify the many linkages among inter-correlated habitat parameters. A CSA showing relationships for key habitat variables such as HSI parameters (Terrell et al. 1982) could serve as a common analytic framework for models tailored to individual fishes. Use of CSA in studies of fish habitat has been fairly rare to date, but its popularity is increasing (e.g., Sheldon and Meffe 1995; Hinz and Wiley 1998; Isaak and Hubert 2001; Infante 2001).

In this study, we used CSA to: 1) quantitatively describe the many relationships between key large-scale habitat variables and local-scale, HSI variables commonly associated with fish distribution and abundance in lower Michigan rivers (Zorn et al. 2004); and 2) determine the extent to which the set of sample sites chosen for analysis influences the relative importance of local-scale habitat and biotic variables to fishes.

Methods

Data sources

We obtained data for this study from sites included in the Michigan Rivers Inventory database for lower Michigan rivers (Seelbach and Wiley 1997). The basic unit of the database is the site, with information occurring for 675 sites on streams in lower Michigan. This includes GIS-based data for all sites, local-scale habitat observational data at over 350 sites, and fish population estimates at over 220 sites. This pseudo-random sample of sites provided good representation of most stream types found in lower Michigan. A detailed description of field sampling methods occurs elsewhere (Seelbach and Wiley 1997; Zorn et al. 1998).

Stream habitat variables included in this study were hypothesized to directly or indirectly influence fish assemblage structure, and have been identified in other studies as important correlates with fish assemblages (e.g., Hynes 1972; Lyons 1996; Richards et al. 1996; Zorn et al. 1998). Included were variables describing catchment-, reach-, and site-scale geology and

land cover/use; measured or estimated exceedence streamflow values and mean July temperature (hereafter referred to as temperature); site-scale channel habitat data; and estimates of fish standing crops (Tables 1 and 2).

Data analysis

We analyzed causal relationships among variables using CSA techniques. Covariance structure analysis techniques have been discussed in detail by other authors (e.g., Mitchell 1992; Wooton 1994a; Wooton 1994b; Klem 1995) so only a brief overview is given here. Covariance structure analysis allows partial correlation coefficients among variables in models to be decomposed and into direct, indirect, and spurious effects (Bollen 1989). The set of causal relationships being studied in a CSA are explicitly defined by a path diagram (Figure 1). Here, each effect is denoted by an arrow whose tail is at the cause and whose head points to its direct effect. A direct effect is represented by a single arrow, whereas indirect effects involve paths of two or more linked direct effects. Spurious effects (non-causal correlations) between variables are indicated by double-headed arrows. As an explicit hypothesis on how a system functions, a covariance structure (causal) model and its path diagram identify constraints on expected patterns of covariance in the study system (Wooton 1994a; Wooton 1994b). The causal model is evaluated by comparing the covariance matrix of observed data to the covariance matrix implied by the constraints of the causal model. Thus, the utility of CSA is its ability to allow researchers to assess the extent to which theoretical models for complex systems are consistent with the covariance structure of the observed data (Bollen 1989).

We constructed three CSA models for this study: Habitat, Trout, and Smallmouth bass. The Habitat Model (Figure 1) assessed relationships among catchment- and reach-scale variables (e.g., surficial geology and reach gradient) and traditional HSI-variables (i.e., depth, substrate, velocity, and temperature). Total phosphorus, a correlate of fish production (Johnston et al. 1990; Hoyer and Canfield 1991; Waite and Carpenter 2000), was also included.

The vertical position of the variables in Figure 1 generally represents the spatial scale at which each is measured, with site-scale variables at the top and catchment-scale variables at the bottom. Direct and indirect effects of catchment- and reach-scale variables on river habitat characteristics were specified based on findings from previous studies. For example, substrate conditions were hypothesized to be influenced by both the availability of different-sized particles (Farrand and Bell 1982), and the river's power (competency) to transport them (Leopold et al. 1964; Gordon et al. 1992). Catchments with coarse-textured geology and high-slopes provide increased groundwater contribution to streams, producing higher 90% exceedence flow (low-flow) yield values (Hendrickson and Doonan 1972; Wiley et al. 1997). July water temperatures of Michigan rivers are influenced by groundwater inputs, channel width, travel time, and incision of the water table in high-gradient reaches (Hendrickson and Doonan 1972; Wiley et al. 1997; Wehrly et al. 1997; Zorn et al. 1998). Flow-related variables influence each other as per hydraulic geometry relationships (Leopold et al. 1964). In addition, we included variables quantifying urban and agricultural land use in each catchment due to their demonstrated effects on physical, hydrologic, and chemical characteristics of rivers (Osborne and Wiley 1988; Wiley et al. 1990; Allan 1995; Kleiman 1995; Richards et al. 1996; Baker et al. 2001). Error terms for endogenous (often predicted) variables in the model were allowed to freely correlate with exogenous (independent) variables, in part to account for non-causal correlations due to characteristics of the sample (e.g., a lack of data from large catchments dominated by urban land use).

We used the other two models to examine the relative importance of different abiotic and biotic paths to standing crops of coldwater fishes (brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*) and a warmwater fish (smallmouth bass *Micropterus dolomieu*), and to assess the influence of sample set selection. We included physical variables that represented habitat features that fishes directly interact with, were common in HSI models (Terrell et al. 1982), and were important in previous modeling efforts on lower Michigan rivers (Zorn et al. 2004). We developed a Trout Model to quantify

the effects of temperature, mean depth, percent sand and gravel substrates, and biotic interaction (i.e., brown trout on brook trout) on brook trout and brown trout standing crops (Figure 2). We then made separate model runs (i.e., parameterizations of the Trout Model) with the following subsets of sites from the Michigan Rivers Inventory database: 1) all sites with standing crop data (including zero values) for brook trout and brown trout; 2) sites where brook trout and/or brown trout occurred; and 3) sites where brook trout occurred (with or without brown trout). We built a Smallmouth Bass Model for assessing the effects of depth, substrate, temperature, total phosphorus, and forage fish on smallmouth bass standing crops (Figure 3). Separate model runs occurred for 1) all sites with standing crop data (including zero values) for smallmouth bass and forage fishes, and 2) sites where smallmouth bass occurred and smallmouth bass and forage fish standing crop data existed.

We analyzed all model runs with Amos 4.0 software (Arbuckle and Wothke 1999). All runs were based on data from sites with no missing values for all variables involved. We used Asymptotic Distribution-Free (ADF) estimation procedures because significant departures from normality occurred for some variables, particularly those characterizing substrate composition (Arbuckle and Wothke 1999). We also used maximum likelihood estimation because ADF estimation is most effective on sample sizes of at least 1000 (Muthén 1993). Both methods produced similar results for all runs, suggesting that model results were robust. We used a Monte-Carlo parametric bootstrap procedure to estimate direct, indirect, and total effects (Grace and Pugesek 1997). Bootstrap-estimated, un-standardized regression coefficients, implied and observed (sample) correlation matrices, and total and direct effects matrices for each model run are shown in appendices A through G.

For the Trout and Smallmouth Bass models we estimated the total direct habitat effects and the biological effects on brook trout and smallmouth bass, as well as indirect effects of habitat mediated through the biota. Total direct habitat effects equaled the sum of the standardized direct effects of all habitat variables on these species. Direct biological effects were the standardized direct effect values for brown trout on brook trout and forage fishes on smallmouth bass. The ratio of the total direct habitat effect to the direct biological effect in each analysis indicated the relative extent that these local habitat or biological variables were explaining observed patterns of spatial variation in brook trout and smallmouth bass standing crops. Indirect effects of habitat variables (as mediated through the biota) equaled the sum of the differences between the standardized total effect and standardized direct effect of each habitat variable on brook trout or smallmouth bass.

We evaluated the CSA models in several regards. We used squared multiple correlations to assess the amount of variance explained for each endogenous variable. The theoretical soundness and statistical significance of total and direct effects were assessed using the 90% biased corrected confidence interval and t distribution based on the degrees of freedom for each model (Arbuckle and Wothke 1999). We assessed fit of the overall model for each run with a variety of fit statistics that measure the discrepancy between the implied covariance structure (as constrained by the model) and the covariance structure of the sample data. Statistics included chi-square (χ^2), Goodness of Fit Index (GFI), Tucker-Lewis Index, and root mean square error of approximation (RMSEA),

Results

Habitat relationships

Covariance structure analysis of habitat variables (the Habitat Model) demonstrated the importance of landscape-scale variables to local habitat characteristics of lower Michigan rivers. The sum of the total effects on endogenous variables was highest for catchment area, followed by gradient, then coarse-textured till and outwash geologic deposits, implying that these were the most pervasive organizers of fish habitat (Table 3). Catchment area, gradient, agricultural land use, and low-flow yield (in decreasing order) had the highest sums for direct effects (Table 3). Gradient had significant direct effects on seven variables while catchment area had significant direct effects on six variables.

Landscape scale variables had significant direct and indirect effects on all local habitat variables (Table 3). Variables significant at a P-value less than 0.05 and their direct effect values are discussed here. Coarse-textured till and outwash geologic deposits (0.697) and agricultural land use (-0.235) had significant direct effects on low-flow yield. Depth was directly affected by catchment area (0.634), low-flow yield (0.204), and gradient (-0.177), and indirectly affected by coarse-textured till and outwash geologic deposits and agricultural land use. Velocity was directly affected by low-flow yield (0.785), gradient (-0.170), and depth (0.131), and indirectly affected by agricultural land use, catchment area, and coarse-textured till and outwash geologic deposits. Some effect values on velocity should be interpreted with caution (e.g., negative direct effect of gradient), because velocity was initially predicted from flow values and hydraulic geometry equations. Temperature was directly influenced by catchment area (0.528), low-flow yield (-.276), gradient (-0.249), agricultural land use (0.133), and urban land use (0.096), and indirectly affected by coarse-textured till and outwash geologic deposits. Catchment area and gradient, the two components of stream power, had significant direct effects on all four substrate variables. Additional significant direct effects occurred for agricultural land use on percent silt (0.198) and coarse-textured till and outwash geologic deposits on percent gravel (0.201). Agricultural land use (0.671) and low flow yield (-0.183) had direct effects on total phosphorus, while gradient and coarse-textured till and outwash geologic deposits had indirect effects.

Landscape-scale variables explained a significant portion of variance in, and had significant effects on, many variables measured at the site. In this analysis, the amount of variation explained in low-flow yield, depth, velocity, and temperature variables ranged from 48-77% (Table 3). Eighty-four percent of the variation in total phosphorus was explained, mostly by urban and agricultural land use variables (Table 3). The percent of each substrate type was more difficult to explain, with only 16-26% of the variation being explained for each substrate category (Table 3).

Overall fit measures for the Habitat Model (Table 3) indicated good correspondence between the predicted and observed covariance structure. The χ^2 value of 38.7 (df = 34, p = 0.267) suggested no significant difference between the covariance matrix of the sample data and the covariance matrix implied by the model. The RMSEA, a measure of the average of the fitted residuals interpreted in relation to observed variances and covariances (Joreskog and Sorbom 1996), was 0.020. Both the chi-square and RMSEA statistics suggest a close fit of the Habitat Model to the observed data. Tucker-Lewis Index and GFI values were 0.993 and 0.990, both indicating a close fit of the Habitat Model to the observed data. Multivariate kurtosis values suggested the occurrence of non-normality (mostly due to substrate variable distributions) that could not be resolved without modifying hypotheses. However, other discrepancy estimation methods (i.e., maximum-likelihood), and bootstrapping efforts produced similar results, suggesting that the model was generally robust.

Influence of sample set selection on relationships among fishes and habitat in streams

Three sets of data fit to the Trout Model demonstrated the influence of sample selection on the relative strength of effects of habitat parameters and biotic interactions on brook trout and brown trout standing crops. Trout Model runs 1, 2, and 3 represented samples of trout and non-trout streams, trout streams with brook trout and/or brown trout, and brook trout streams (with or without brown trout), respectively (Table 4). Each run fit the sample data well (p > 0.3 for χ^2 statistic and RMSEA < 0.05), explained reasonable amounts of variation (21-54%) in fish standing crops, and exhibited only moderate (run 1) or no significant departures from multivariate normality.

The strength of direct effects on brook trout and brown trout changed as Trout Model runs were parameterized with increasingly restricted samples of streams. Average stream conditions became colder, shallower, and more sandy and gravelly as samples progressed from run 1 to run 3 (Table 2). The magnitude of direct effects of temperature and percent gravel substrate on brown trout declined going run 1 to run 3, while those of depth and percent sand substrate

increased (Table 4). The direct effect of depth on brown trout was statistically significant for run 3 (and almost for run 2), and that for percent sand substrate was significant in run 3. Similarly, direct effects of percent gravel substrate and temperature on brook trout all declined going from run 1 to run 3, though temperature effects remained significant in all three runs. Direct effects of percent sand substrate and depth on brook trout changed little from runs 1 to 3. The negative effect of brown trout on brook trout was most pronounced in run 2 (Table 4). In run 3, this effect was substantial, but not statistically significant, and its path coefficient was nearly significant ($p = 0.091$).

Two sets of data fitted to the Smallmouth Bass Model also demonstrated the influence of the sample on relative strength of effects of habitat parameters and potential forage fishes on smallmouth bass standing crops (Table 5). Run 1 was based on a sample of streams with and without smallmouth bass, while run 2 was based on a sample of streams where smallmouth bass occurred. Each run fit the sample data well ($p > 0.1$ for χ^2 statistic and RMSEA < 0.06), explained reasonable amounts of variation (23-46%) in fish standing crops, and exhibited significant departures from multivariate non-normality, largely due to substrate variables, particularly bedrock (Table 5). Bedrock was kept in the analysis because we thought it was correlated with abundance of crayfish, an important forage item for smallmouth bass (McClendon and Rabeni 1987; Rabeni 1992). Depth, percent cobble substrate, and temperature all had statistically significant, positive direct effects on smallmouth bass in run 1 (Table 5). Silt had a negative direct effect that was nearly significant ($p = 0.051$). Significant direct effects for run 1 indicated that forage fishes were positively affected by total phosphorus and warm temperatures, and negatively affected by percent cobble substrate. More variation in smallmouth bass and forage fish standing crops could be explained with the run 1 data than with the run 2 data (45% compared to 25% for smallmouth bass and 30% compared to 27% for forage fishes). Interestingly, in run 2, total phosphorus and forage fish biomass had the highest positive direct effects on smallmouth bass standing crops (Table 5), but only that of total phosphorus was statistically significant.

For both brook trout and smallmouth bass, the relative influence of biotic and habitat direct effects, and indirect effects, differed considerably depending upon which sites were included in analyses. When all sites were used, the direct effects of habitat variables on brook trout were about 32 times that of brown trout (Figure 4 and Table 4). However, the relative importance of brown trout to brook trout was much greater when analyses were conducted with a more restricted set of sites. For example, when the analysis was conducted only on trout streams the direct effect of brown trout on brook trout was 3 times greater than direct effects of habitat (Table 4). Here, indirect effects of habitat via brown trout were of similar magnitude to direct effects of habitat (Figure 4). Direct effects of brown trout and habitat were of similar magnitude when the analysis was based only on brook trout streams (Figure 4). Similar patterns were also observed for smallmouth bass. When the analysis was based on all sites, direct effects of habitat variables were 58 times greater than those of forage fishes (Figure 5 and Table 5). However, when the sample was restricted to streams with smallmouth bass, the direct effects of habitat were only 3.7 times greater than those of forage fishes (Table 5). Here, indirect effects of habitat via forage fishes were comparable to the direct effect of forage fishes (Figure 5).

Discussion

Habitat relationships

We used CSA to plainly demonstrate the importance of landscape-scale features as hierarchical constraints on local features of stream habitat. While other studies have shown the prevalence of large-scale variables (e.g., river size and gradient) as important correlates with fish assemblage structure (Zalewski and Naiman 1985; Degerman and Sers 1993; Lyons 1996), this study quantified the extent to which these variables affect local habitat variables important to fishes. Of the exogenous variables in this study, catchment area had the strongest total effect on depth, temperature, sand, and cobble (Table 3). Catchment area is undoubtedly a key force shaping these local

habitat conditions (Zorn et al. 1998) because it indexes stream discharge volume, which itself is a component of stream power (Leopold et al. 1964). Gradient, the other key variable in the stream power equation, had the strongest total effect on silt and gravel. As an index of permeability of glacial deposits in the basin, coarse-textured till and outwash geologic deposits had the strongest direct effect on 90% exceedence flow yield. Ninety percent exceedence flow yield, in turn, had the strongest effect on velocity, and strong direct effects on temperature and depth. Temperature, depth, velocity, and substrate have been identified as key correlates with standing crops of river fishes in Michigan (Zorn et al. 2004) and other regions (e.g., Fausch et al. 1988; Lyons 1996; Maret et al. 1997; Angermeier and Winston 1999; Waite and Carpenter 2000). In Lower Michigan, river size, catchment geology, and gradient are clearly major forces influencing site-level aspects of habitat important to river fishes.

The Habitat Model provided a first-cut look at the complex web of relations between spatial scale and local habitat (Figure 1). Though data from several spatial scales could be added to provide more realistic predictive models for each habitat variable, this analysis plainly showed that the landscape shapes and constrains local habitat conditions. For example, geology and land use variables influenced many site-scale aspects of river habitat (Table 3). Coarse-textured till and outwash geologic deposits are highly permeable, and in combination with sloping landscapes, produce groundwater-dominated streams (Hendrickson and Doonan 1972; Wiley et al. 1997) that have relatively high low-flow yields. That these streams, in the summer, tend to be colder, more gravelly, and have higher mean depths and velocities is supported by the direct effects of low-flow yield (Table 3). In addition, landscapes dominated by coarse-textured till and outwash geologic deposits are often ill-suited to agriculture, so streams draining these sandy landscapes also tend to be relatively poor in phosphorus and less silty than streams in agricultural areas (Table 3). This is just one example of the complex linkages between the landscape and microhabitat conditions and the utility of CSA in quantifying them. Exploring these and other paths between the landscape and local river habitat in further

detail to identify mechanisms would be an interesting area for further research.

Variation in some habitat variables was difficult to explain from river size, catchment geology, and gradient variables alone. For example, little variation in total phosphorus could be explained without the catchment-scale variable, percent agricultural land use, in the model. This was not unexpected since human activities are major contributors of nutrients to river systems (Osborne and Wiley 1988; Wiley et al. 1990; Kleiman 1995; Allan 1995; Baker et al. 2001). Catchment area (a correlate of bankfull discharge) and gradient, the two components of stream power (Leopold et al. 1964), had significant direct effects on each substrate category. As hypothesized, higher stream power (associated with higher gradient or larger catchments) favored coarser substrates (Table 3). Surprisingly, these variables, along with geology and land use variables, explained less than 27% of variation in abundance of any substrate type. Instream sediment transport processes and local geologic features (e.g., where the river cuts through a moraine) may add variation in substrate characteristics that is difficult to predict from catchment- and reach-scale variables alone. However, preliminary analyses suggest that use of local-scale geology variables may add little predictive power, since in lower Michigan, these variables are often correlated with reach gradient (Zorn, unpublished data). Approximately twice as much variation in composite substrate percentages (i.e., percent gravel and coarser substrates) could be explained for the sites in this study (Zorn, unpublished data), but we used individual categories of substrate because fishes often show preferences for distinct substrate types.

Influence of sample set selection on relationships among fishes and habitat in streams

Covariance structure analysis provided a useful means for evaluating the relative influence of both direct and indirect causal mechanisms on stream fishes because it allowed decomposition of the variance structure in the data. For example, because brown trout prey upon, and tolerate warmer water temperatures

than brook trout, increases in brown trout biomass and concurrent declines in brook trout biomass may relate to either warmer temperatures, biotic interactions, or some combination of the two. The model we developed for trout (Figure 2 and Table 4) allowed quantification of the direct effect of brown trout on brook trout, the direct effect of temperature on brook trout, and the indirect effect of temperature on brook trout via its influence on brown trout (i.e., the difference between the total and direct effects of temperature on brook trout). By summing habitat effects on brook trout and smallmouth bass, this study showed that the relative importance of direct and indirect effects of habitat varies substantially depending which sites are selected for study (Figures 4 and 5). Samples that included all sites emphasized the importance of direct effects of habitat to patterns in fish abundance. Restricting the sample to sites where pairs of interacting species occurred (e.g., trout streams) or just the species of interest occurred (e.g., smallmouth bass streams) elevated the importance of biotic and indirect factors in explaining patterns of fish abundance. These analyses showed that biotic, habitat, and indirect effects may all be important to a species, though the significance of each may only be revealed when specific sets of streams are studied (Levin 1992).

Restricting the sample set demonstrated the strong influence of sample selection on our ability to detect patterns and identify underlying processes (Levin 1992). For the Trout Model, colder, shallower, and more gravelly sites made up a progressively larger proportion of the sample as the analysis progressed from run 1 to run 3 (Table 4). Following this progression, gravel substrate and temperature appeared less limiting to brown trout standing crops (i.e., their direct effects declined), while sand substrate and depth appeared more limiting. Following the progression for brook trout, temperature remained significant (but became less important), gravel became less limiting, and brown trout became more limiting. These results support observations of trout distributions in Great Lakes rivers and reconcile apparently conflicting findings of positive correlations between brook trout and brown trout standing crops in some studies (e.g., Lyons

1996; Maret et al. 1997), and negative correlations in other studies (e.g., Waters 1983). For example, at the statewide scale, brown trout and brook trout biomass is generally highest in cold, high-gradient, gravelly streams and the fish are positively correlated in their distributions. Using a sample of streams where trout occur (run 2), restricts the sample to streams that are generally colder and more gravelly. Variation in temperature and gravel substrates is more limited among this set of streams, so fewer physical variables had significant direct effects on fish standing crops. The negative effect of brown trout on brook trout is greatest here, possibly because highest brown trout standing crops occur in streams on the warmer end of the range and highest brook trout standing crops occur on the cooler end of the range, particularly at sites without brown trout (Zorn, unpublished data). Indirect effects of habitat on brook trout via brown trout are most important here (Figure 4), possibly because physical conditions in this set of streams span the tolerance limits of these interacting species. When the sample consisted solely of brook trout streams, which are generally cold and small, depth becomes limiting for brown trout (a larger-bodied species). A significant negative effect occurred for sand on brown trout, possibly reflecting the species preference for coarser spawning gravels (Witzel and MacCrimmon 1983). This finding supported local-scale, field studies from Michigan and other areas that showed negative effects of sand sediments on trout populations (e.g., Alexander and Hansen 1986; Waters 1995). The two largest effects for brook trout in run 3 (temperature and brown trout abundance) reflect both the species sensitivity to thermal conditions (even in some of the coldest rivers in Michigan) and its vulnerability to predation by or competition with brown trout.

Results of the Smallmouth Bass Model analysis also illustrated the influence of sample selection on models of fish abundance patterns. We explained considerable variation (46%) in smallmouth bass standing crops at the statewide scale. The positive effects of depth, cobble substrate, and temperature, and negative effects of silt, on fish standing crops were clear in run 1 (Table 5) and are supported by other studies (e.g., Becker 1983; McClendon and Rabeni 1987; Zorn et al. 2004). We anticipated that for

streams where smallmouth bass occurred (run 2), variation in fish standing crops would be more difficult to explain and may likely relate to variables indexing food availability (e.g., forage fish standing crops, nutrient levels, or abundance of bedrock and coarse substrates favored by crayfishes) (McClendon and Rabeni 1987; Rabeni 1992; Waters et al. 1993). Only 23% of the variation in smallmouth bass standing crops could be explained in run 2 (Table 5). Variables related to food availability (i.e., total phosphorus and forage fish standing crop) had the highest direct effects, though the effect of forage fish standing crops was not statistically significant (Table 5). We expected percent bedrock substrate to have a positive effect on smallmouth bass, since highest smallmouth bass standing crops in lower Michigan occurred in streams flowing over bedrock outcrops. However, its effects were not significant in either run, possibly due to the variable's non-normal distribution and high variance resulting from its scarcity in lower Michigan's drift-dominated landscapes.

Limitations

Covariance structure analysis provided a powerful tool for evaluating hypotheses about complex interactions in multivariate systems where covariance was common and collinearity high (Wootton 1994b). Despite its utility, there are limitations that affect both the use and interpretation of CSA results. Covariance structure analysis techniques can only evaluate whether or not the theory and constraints of the specified model correspond to the structure of the sample data. CSA requires the user to supply a theoretically sound causal model (Wootton 1994b). Where theory on system function is sufficient, application of CSA to observed data may provide new insights into system processes by elucidating direct and indirect effects, or by falsifying theoretical assumptions. When theory is inadequate, as often occurs in ecological studies, CSA can contribute to evaluation of competing models. Since it is only a confirmatory statistical technique, CSA should not be used to propose direct causal linkages without clear mechanistic justification. Despite the causal implications of

structured models, CSA only provides a measurement of the fit of a causal theory to the data and does not prove causality.

Conclusions from CSA (and possibly any type of analysis) regarding mechanism are limited by the variables included or not included in the analysis. Thus, inadequate theory, or omission of key variables, may lead to misguided conclusions regarding mechanisms. Less than half of the variation in brook trout, brown trout, and smallmouth bass standing crops was typically accounted for in our analyses. This was not unexpected, since a large component of variability in fish abundance is likely due to temporal factors that were not accounted for here (Bovee et al. 1994; Wiley et al. 1997). Modest variation in brown trout standing crops might be explained by stocking activities, but the great majority of brown trout streams in this study were not stocked. Streams that are stocked typically support few fish relative to streams in which natural reproduction occurs, so stocking was probably not responsible for much spatial variation in brown trout standing crops in our data. Brook trout have not been stocked in lower Michigan streams for many years.

Variables included in this study, though informative, often do not point to a particular mechanism. For example, this study suggested the importance of July temperatures to fish but did not emphasize any particular mechanism. July temperatures may be lethal to trout, but they also index thermal conditions that fish, eggs, and fry experience in other seasons, and probably other factors such as forage production (Hinz and Wiley 1997). Numerous abiotic or biotic variables could potentially be added to models to explore mechanisms and account for additional unexplained variance. Since biotic and abiotic variables are often correlated with each other (e.g., fish biomass and temperature) care needs to be taken when bringing them into a model to ensure (as much as possible) that partial correlations between two species represent biotic interactions, rather than differences in habitat preferences. CSA is particularly useful in this regard because path diagrams allow habitat and biotic effects on a species to be explicitly partitioned amongst different paths. Nevertheless, researchers still

need to be as cognizant of variables not in models as they are of those that are included.

Characteristics of the data used in the stream habitat CSA (Figure 1) suggest the need for some caution when interpreting results. It was not possible to obtain all the data needed for these comprehensive analyses of river systems due to the number of sites studied and types of data needed (e.g., 90% exceedence flow yield measurements would require continuous data from streamflow gages at each site). As a result, several of the variables used in this study (Table 1) represented a combination of values that were measured or predicted from statistical models developed in other studies (e.g., Kleiman 1995; Wehrly et al. 1997; Seelbach and Wiley 1997). Models predicting these variables used some of the parameters in this study as inputs (e.g., catchment area and agricultural land use), along with numerous additional variables. Consequently, multiple correlation coefficient and path coefficient values for these variables may differ from what might be obtained from an analysis based strictly on measured values.

Assumptions of normality could not be met for some variables in this analysis. Some variables important to fishes, such as percent cobble or bedrock substrate, have a patchy distribution throughout Michigan and tend to occur in moderate to high abundance or not at all. Thus, transformation of the data may not be able to produce an entirely normal distribution for these variables. We used computational procedures (e.g., bootstrapping, distribution-free estimation, and bias-corrected confidence intervals) to help prevent non-normally distributed variables from erroneously influencing study results (Arbuckle and Wothke 1999). Maximum likelihood estimation was also used because ADF estimation is most effective on large sample sizes (Muthén 1993). Both methods produced similar results in all cases, suggesting that the models were robust. Further statistical exploration and modified sampling designs may help alleviate normality issues in future studies.

Research and management implications

Several authors have discussed conceptual frameworks whereby aquatic assemblages are seen as products of a series of filters, operating at different temporal and spatial scales, through which each species in the assemblage must pass (Tonn 1990; Poff 1997). The need to explicitly incorporate hierarchical relations among spatial scale and habitat conditions into such a model has been stressed by many (e.g., Poff 1997; Rabeni and Sowa 1996; Imhoff et al. 1996). Path diagrams can provide an analytic framework for studying influences of hierarchically-nested habitat variables on aquatic assemblages in rivers. Variables can be portrayed at the appropriate spatial scale, and hypothetical relationships among them explicitly represented via causal paths. Direct and indirect relationships among variables can be evaluated in terms of significance and magnitude of effect. Allowing multiple paths to and from individual variables alleviates, to some extent, statistical issues of collinearity and the conceptual problem of assigning a filter (e.g., temperature) to a single spatial scale (Poff 1997).

Our analyses demonstrated the ecological complexity and multi-scale nature of fish habitat in river ecosystems (Figure 1). One could easily envision other habitat attributes (and associated paths) that could be included to add realism. Path diagrams and associated outputs plainly showed, and quantitatively demonstrated, the importance of large-scale variables in terms of their direct and indirect effects on more proximal habitat attributes. For example, catchment area and 90% exceedence flow yield had significant total effects on depth, temperature, total phosphorus, velocity, and substrate. These variables, in turn, are important predictors of abundance for many common river fishes in lower Michigan (Zorn et al. 2004). These findings also support the use of catchment area and 90% exceedence flow yield as primary habitat axes for Michigan streams (Zorn et al. 1998). By quantifying linkages among habitat elements, managers can more readily show how changes to the landscape would likely influence particular local habitats and fishes. Based on total effects observed in this study (Table 3), increasing agricultural land use in Michigan watersheds could be expected to result in decreased 90% exceedence flow yields, reduced depth, slower current velocity, increased total phosphorus concentration, higher summer temperatures, and increased silt substrate. Such

effects could be quantitatively described using the equations developed in this study (Table 3; Appendices A and B). The quantitative effects described here, however, reflect patterns of variation observed in the collection of rivers included in this study and may not apply to other regions.

The CSA approach to modeling river systems may provide a general habitat framework that is useful for a variety of purposes. In this study, for example, the Habitat Model served as the basis for subsequent models developed for individual fishes (Trout and Smallmouth Bass models). Here, models for each species (e.g., Figures 2 and 3) consisted of statistically significant paths from the base habitat model plus additional variables that were significant just for the species of interest. Another interesting application would be to use a common path model to compare regional differences in the relative influence of different factors on habitat parameters. For example, a hypothetical model for stream temperature in North American rivers may likely include many measures (e.g., groundwater input, latitude, altitude, shading, river size, etc.), but the relative strength of each path would likely vary from region to region.

By allowing inter-correlations to be accounted for, CSA provided a more appropriate forum for exploring mechanistic relationships than linear regression. Still, a single CSA should not be considered the definitive test of how the system works, nor a substitute for development of a sound understanding of a particular study system. CSA analyses with brook trout, brown trout, and smallmouth bass in this study demonstrated that the sample of rivers (or sites) studied can have an overriding influence on the detection of pattern-process relationships and the relative strength of

different processes observable in a study system (Levin 1992). Thus, issues of scale should always provide the context for interpreting CSA (or any data analysis) results. If our goal is to build a functional assembly model that accurately predicts standing crops of stream fishes at individual sites, then a series of models built from progressively finer-scale data may be needed. These models should be tailored to individual species and based on datasets having increasingly narrower ranges in physical conditions.
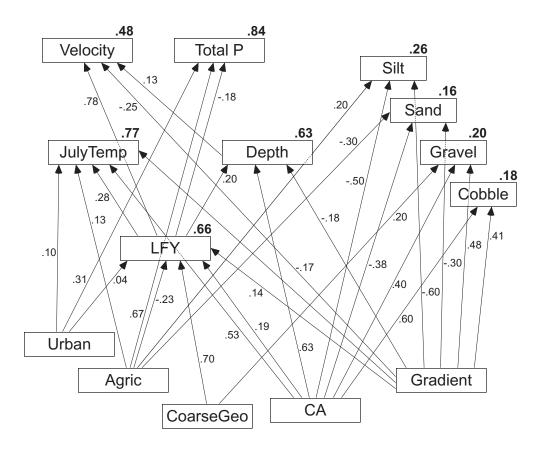
Acknowledgments

Figure 1.–Simplified path diagram for select catchment-, reach-, and site-scale habitat attributes of lower Michigan rivers (Model 1). Standardized direct effects (in regular type) from the covariance structure analysis are shown for each path along with squared multiple correlations for endogenous variables (bold type). Covariances and error terms associated with endogenous variables have been omitted from diagram for clarity.
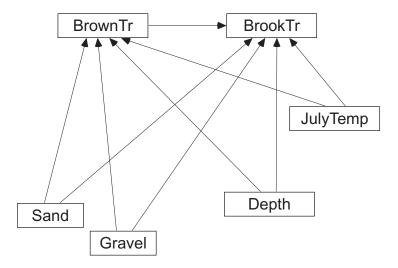
Figure 2.–Simplified path diagram for brook trout and brown trout in lower Michigan rivers (Model 2). Covariances and error terms associated with endogenous variables have been omitted from diagram for clarity. Standardized direct effects for each Model Run occur in Table 4.
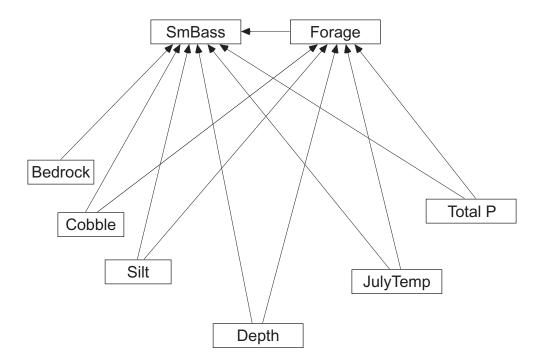

Figure 3.–Simplified path diagram for the smallmouth bass in lower Michigan rivers (Model 3). Covariances and error terms associated with endogenous variables have been omitted from diagram for clarity. Standardized direct effects for each Model Run occur in Table 5.
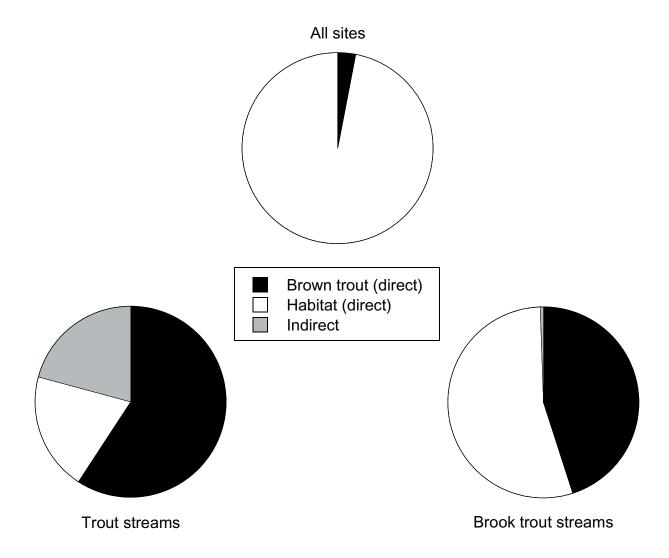
14

Figure 4.–Relative magnitude of direct effects of brown trout, direct effects of all habitat variables, and indirect effects of habitat mediated through brown trout on brook trout standing crops for three runs of the Trout Model. Runs were based on the following sets of sites on Lower Michigan rivers: 1) All Sites (sites with standing crop measurements (including zero values) for brook trout and brown trout, n = 271); 2) Trout Streams (sites where either brook trout and/or brown trout occurred, n = 74); and 3) Brook Trout Streams (sites where brook trout occurred, n = 39). Numeric values occur in Table 4.
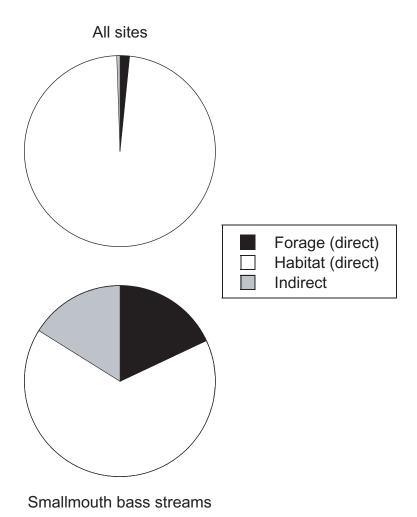
15

All sites

Smallmouth bass streams

Figure 5.–Relative magnitude of direct effects of forage fishes, direct effects of all habitat variables, and indirect effects of habitat mediated through forage fishes on smallmouth bass standing crops for two runs of the Smallmouth Bass Model. Runs were based on the following sets of sites on Lower Michigan Rivers: 1) All Sites (sites with standing crop measurements for forage fishes and smallmouth bass, n = 229); and 2) Smallmouth Bass Streams (sites where smallmouth bass occurred, n = 100). Numeric values occur in Table 5.

Table 1.–Name and description of variables included in this study. Variable name is the name used in models. Type indicates both source of the data (M- measured, P- predicted, C- combination of measured and predicted) and transformation used. Transformations were: 1) $\log_{10}(x + 0.001)$; 2) $\log_{10}x$; 3) $\log_{10}(x + 1)$; and 4) $\log_{10}(x + 0.01)$. The variable LSMBFOOD was the sum of standing crops of 25 forage species at the site, and included minnows other than common carp and darters in all clusters defined in Zorn et al. (1998), except clusters 3 and 5, plus biomasses of northern redbelly dace, brook silversides, brook stickleback, and pirate perch.

Simplified variable name	Variable name in analysis	Variable description (units)	Type
		Habitat variables	
JulyTemp	BESTMEAN	July mean temperature (^{o}C)	C
Total P	LGTOTP	Total phosphorus (mg/L)	C-1
Velocity	LGVEL90	Velocity at 90% exceedence flow (m/s)	P-2
Depth	DEPMBEST	Depth at 90% exceedence flow (m)	C
LFY	LG90CMSK	90% exceedence flow yield ($m^3 \cdot s^{-1} \cdot km^{-2}$)	C-2
Silt	SUBSI	Percent of substrate as silt (%)	M
Sand	SUBSA	Percent of substrate as sand (%)	M
Gravel	SUBGR	Percent of substrate as gravel (%)	M
Cobble	SUBCO	Percent of substrate as cobble (%)	M
Bedrock	LSUBBE	Percent of substrate as bedrock (%)	M-3
Gradient	LGRADPE	Percent channel gradient (%)	M-2
CA	LOGDAKM	Catchment area (km^2)	M-2
Urban	LGURBAN	Proportion of urban land use in catchment	M-4
Agric	LGAGRIC	Proportion of agricultural land use in catchment	M-4
CoarseGeo	CRSNOUTW	Proportion of coarse-textured till and outwash geologic deposits in catchment	M-4
		Biotic variables	
Brook trout	Brook trout	Biomass of brook trout (kg/ha)	M-1
Brown trout	Brown trout	Biomass of brown trout (kg/ha)	M-1
SmBass	LSMB	Biomass of smallmouth bass (kg/ha)	M-1
Forage	LSMBFOOD	Biomass of forage fishes (kg/ha)	M-1

Table 2a.–Sample mean and standard deviation values (prior to transformations) for variables in the Habitat Model for Lower Michigan rivers.

Variable (units)	Mean	SD
Habitat		
JulyTemp (°C)	20.4	3.2
Total P (mg/L)	0.068	0.042
Velocity (m/s)	0.36	1.63
Depth (m)	0.46	0.27
LFY ($m^3*s^{-1}*km^{-2}$)	0.0041	0.0044
Silt (%)	15.1	18.4
Sand (%)	39.6	26.3
Gravel (%)	24.7	20.5
Cobble (%)	12.0	15.1
Gradient (%)	0.21	0.45
CA (km^2)	872.7	1856.0
Urban	0.055	0.080
Agric	0.430	0.261
CoarseGeo	0.627	0.358
Sample size	356	

Table 2b.–Sample mean and standard deviation values (prior to transformations) for variables in each run of the Trout and Smallmouth Bass models.

Variable (units	Run 1		Run 2		Run 3	
	Mean	SD	Mean	SD	Mean	SD
Trout						
Brook trout (kg/ha)	4.50	19.81	16.49	35.38	31.30	43.92
Brown trout (kg/ha)	6.99	23.33	25.59	39.11	22.68	42.09
July temp (°C)	21.0	3.0	18.2	2.8	16.9	3.0
Depth (m)	0.48	0.28	0.36	0.22	0.29	0.21
Sand (%)	37.6	25.8	45.6	29.3	47.3	31.7
Gravel (%)	23.7	19.6	31.6	23.5	33.7	26.8
Sample size	271		74		39	
Smallmouth bass						
Smallmouth bass (kg/ha)	3.91	8.58	8.95	11.14		
Forage (kg/ha)	28.76	52.16	16.91	21.25		
JulyTemp (°C)	20.8	3.0	22.6	1.7		
Total P (mg/L)	0.074	0.042	0.077	0.029		
Depth (m)	0.45	0.25	0.59	0.26		
Silt (%)	16.4	19.7	13.7	14.4		
Cobble (%)	12.6	14.5	19.5	16.0		
Bedrock (%)	1.6	8.7	3.6	12.9		
Sample size	229		100			

Table 3a.–Squared multiple correlations for endogenous variables in the Habitat Model for Lower Michigan Rivers.

Variable name	Squared multiple correlation
LFY	0.66
Depth	0.63
Total P	0.84
Velocity	0.48
JulyTemp	0.77
Silt	0.26
Sand	0.16
Gravel	0.20
Cobble	0.18

Table 3b.–Fit statistics for the Habitat Model for Lower Michigan Rivers.

Model fit statistic	Value
χ^2	38.7
χ^2 Degrees of freedom	34
χ^2 p value	0.267
GFI	0.990
Tucker-Lewis index	0.993
RMSEA	0.020
P for test of close fit	0.981
Multivariate kurtosis	41.5

Table 3c.–Matrices of total and direct effects from the Habitat Model for lower Michigan rivers (Figure 1). Values in bold and italics are significant at P-values of 0.05 and 0.10, respectively. Sums are for absolute values for all total or direct effects.

Variable	Urban	Agric	CA	Gradient	CoarseGeo	LFY	Depth
Standardized Total Effects - Estimates							
LFY	0.035	**-0.235**	0.19	0.136	**0.697**	0	0
Depth	0.007	**-0.048**	**0.673**	**-0.15**	**0.142**	**0.204**	0
Total P	0.303	**0.713**	*-0.035*	**-0.025**	**-0.127**	**-0.183**	0
Sand	0	*-0.298*	**-0.378**	**-0.302**	0	0	0
Gravel	0	0	**0.4**	**0.478**	**0.201**	0	0
Velocity	0.029	**-0.191**	**0.237**	**-0.083**	**0.566**	**0.811**	**0.131**
JulyTemp	**0.086**	**0.197**	**0.475**	*-0.286*	**-0.192**	**-0.276**	0
Silt	0	**0.198**	**-0.502**	**-0.604**	0	0	0
<u>Cobble</u>	<u>0</u>	<u>0</u>	**<u>0.596</u>**	**<u>0.413</u>**	<u>0</u>	<u>0</u>	<u>0</u>
Sum	0.46	1.88	3.486	2.477	1.925	1.474	0.131
Standardized Direct Effects - Estimates							
LFY	0.035	**-0.235**	0.19	0.136	**0.697**	0	0
Depth	0	0	**0.634**	**-0.177**	0	**0.204**	0
Total P	0.31	**0.671**	0	0	0	**-0.183**	0
Sand	0	*-0.298*	**-0.378**	**-0.302**	0	0	0
Gravel	0	0	**0.4**	**0.478**	**0.201**	0	0
Velocity	0	0	0	**-0.17**	0	**0.785**	**0.131**
JulyTemp	**0.096**	**0.133**	**0.528**	**-0.249**	0	**-0.276**	0
Silt	0	**0.198**	**-0.502**	**-0.604**	0	0	0
<u>Cobble</u>	<u>0</u>	<u>0</u>	**<u>0.596</u>**	**<u>0.413</u>**	<u>0</u>	<u>0</u>	<u>0</u>
Sum	0.441	1.535	3.228	2.529	0.898	1.448	0.131

Table 4.–Squared multiple correlations, standardized direct effects, and fit measures for the Trout Model (Figure 2). Results were computed for model runs based on the following sets of sites on lower Michigan rivers: 1) sites with standing crop measurements for brook trout and brown trout (n = 271); 2) sites where brook trout and/or brown trout occurred (n = 74); and 3) sites where brook trout occurred (n = 39). Direct effect values in bold and italics are significant at P-values of 0.05 and 0.10, respectively.

		Model run		
		1	2	3
Types of streams		All	Trout	Brook Trout
Number of cases		271	74	39
Squared Multiple Correlations				
Brown Trout		0.21	0.233	0.416
Brook Trout		0.409	0.544	0.375
Standardized Direct Effects				
Effect of:	On:			
Gravel	brown trout	**0.298**	0.094	-0.021
Depth	brown trout	0.050	*0.226*	**0.412**
Sand	brown trout	0.096	-0.180	**-0.442**
July Temp	brown trout	**-0.364**	0.212	0.064
Gravel	brook trout	**0.223**	0.190	0.035
Depth	brook trout	-0.005	-0.006	-0.062
Sand	brook trout	*0.105*	0.115	0.085
July Temp	brook trout	**-0.576**	**-0.444**	**-0.397**
Brown Trout	brook trout	-0.008	**-0.430**	*-0.280*
Sum of effects on brook trout				
Brown Trout (direct)		-0.008	-0.430	-0.280
Habitat variables (direct)		-0.253	-0.145	-0.339
Habitat variables (indirect)		0.000	-0.151	-0.004
Habitat: Brown Trout direct effect ratio		31.63	0.34	1.21
Fit Measures				
χ^2		0.121	0.881	1.607
χ^2 Degrees of freedom		2	2	2
χ^2 p value		0.941	0.644	0.448
GFI		1	0.999	0.999
Tucker-Lewis index		1.09	1.059	1.013
RMSEA		0	0	0
P for test of close fit		0.969	0.692	0.481
Multivariate kurtosis		9.756	-1.028	-1.487

Table 5.–Squared multiple correlations, standardized direct effects, and fit measures for the Smallmouth Bass model (Figure 3). Results were computed for model runs based on the following sets of sites on lower Michigan rivers: 1) sites with standing crop measurements for smallmouth bass and forage fishes (Forage variable) (n = 229); 2) sites where smallmouth bass occurred and smallmouth bass and forage fish standing crop data existed (n = 110). Direct effect values in bold and italics are significant at P-values of 0.05 and 0.10, respectively.

		Model run	
		1	2
Types of streams		All	Smallmouth bass
Number of cases		229	100
Squared Multiple Correlations			
Forage		0.302	0.266
Smallmouth Bass		0.45	0.248
Standardized Direct Effects			
Effect of:	On:		
Total P	forage	**0.279**	-0.049
Depth	forage	-0.070	**-0.345**
Silt	forage	-0.018	-0.163
Cobble	forage	**-0.165**	-0.088
July Temp	forage	**0.368**	**-0.263**
Total P	smallmouth bass	0.004	**0.445**
Bedrock	smallmouth bass	0.078	0.044
Depth	smallmouth bass	**0.240**	0.083
Silt	smallmouth bass	-0.115	-0.138
Cobble	smallmouth bass	**0.265**	0.132
July Temp	smallmouth bass	**0.394**	0.046
Forage	smallmouth bass	-0.015	0.167
Sum of effects on smallmouth bass			
Forage (direct)		-0.015	0.167
Habitat (direct)		0.866	0.612
Habitat (indirect)		-0.006	-0.151
Ratio of Habitat: Forage direct effects		-57.73	3.66
Fit Measures			
χ^2		9.223	4.745
χ^2 Degrees of freedom		6	6
χ^2 p value		0.161	0.577
GFI		0.996	0.99
Tucker-Lewis index		0.954	1.054
RMSEA		0.049	0
P for test of close fit		0.448	0.709
Multivariate kurtosis		22.448	14.696

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Appendix A.–Observed (sample) and implied correlation matrices coefficients for the Habitat Model.

Sample Correlations - Estimates

	Urban	Agric	CA	Gradient	CoarseGeo	LFY	Depth	Total P	Sand	Gravel	Velocity	JulyTemp	Silt	Cobble
Urban	1	0.367	0.347	-0.312	-0.055	-0.042	0.336	0.6	-0.268	0.162	-0.019	0.428	0.092	0.086
Agric	0.367	1	0.326	-0.402	-0.218	-0.334	0.156	0.838	-0.363	-0.022	-0.358	0.535	0.248	0.141
CA	0.347	0.326	1	-0.726	-0.062	0.003	0.753	0.286	-0.25	0.061	0.175	0.765	-0.001	0.303
Gradient	-0.312	-0.402	-0.726	1	0.218	0.23	-0.589	-0.402	0.13	0.198	-0.015	-0.763	-0.316	-0.028
CoarseGeo	-0.055	-0.218	-0.062	0.218	1	0.756	0.064	-0.3	0.056	0.229	0.574	-0.326	-0.06	-0.006
LFY	-0.042	-0.334	0.003	0.23	0.756	1	0.155	-0.41	0.06	0.246	0.633	-0.323	-0.152	0.073
Depth	0.336	0.156	0.753	-0.589	0.064	0.155	1	0.136	-0.155	-0.013	0.301	0.494	0.115	0.131
Total P	0.6	0.838	0.286	-0.402	-0.3	-0.41	0.136	1	-0.334	0	-0.413	0.58	0.231	0.115
Sand	-0.268	-0.363	-0.25	0.13	0.056	0.06	-0.155	-0.334	1	-0.478	0.12	-0.28	-0.166	-0.457
Gravel	0.162	-0.022	0.061	0.198	0.229	0.246	-0.013	0	-0.478	1	0.089	-0.038	-0.37	0.139
Velocity	-0.019	-0.358	0.175	-0.015	0.574	0.633	0.301	-0.413	0.12	0.089	1	-0.138	-0.089	0.041
JulyTemp	0.428	0.535	0.765	-0.763	-0.326	-0.323	0.494	0.58	-0.28	-0.038	-0.138	1	0.138	0.219
Silt	0.092	0.248	-0.001	-0.316	-0.06	-0.152	0.115	0.231	-0.166	-0.37	-0.089	0.138	1	-0.332
Cobble	0.086	0.141	0.303	-0.028	-0.006	0.073	0.131	0.115	-0.457	0.139	0.041	0.219	-0.332	1

Implied Correlations - Estimates

	Urban	Agric	CA	Gradient	CoarseGeo	LFY	Depth	Total P	Sand	Gravel	Velocity	JulyTemp	Silt	Cobble
Urban	1	0.392	0.374	-0.31	0	-0.028	0.393	0.578	-0.246	0.147	0.082	0.429	0.077	0.095
Agric	0.392	1	0.267	-0.349	-0.212	-0.366	0.157	0.859	-0.294	-0.103	-0.323	0.499	0.275	0.114
CA	0.374	0.267	1	-0.699	0	0.046	0.768	0.243	-0.247	0.066	0.255	0.76	-0.027	0.308
Gradient	-0.31	-0.349	-0.699	1	0.179	0.198	-0.58	-0.366	0.066	0.234	-0.09	-0.748	-0.322	-0.004
CoarseGeo	0	-0.212	0	0.179	1	0.771	0.125	-0.283	0.009	0.286	0.591	-0.285	-0.15	0.074
LFY	-0.028	-0.366	0.046	0.198	0.771	1	0.201	-0.445	0.029	0.273	0.659	-0.313	-0.215	0.086
Depth	0.393	0.157	0.768	-0.58	0.125	0.201	1	0.151	-0.162	0.056	0.363	0.521	0.055	0.159
Total P	0.578	0.859	0.243	-0.366	-0.283	-0.445	0.151	1	-0.262	-0.091	-0.358	0.543	0.269	0.064
Sand	-0.246	-0.294	-0.247	0.066	0.009	0.029	-0.162	-0.262	1	-0.486	0.025	-0.217	-0.137	-0.466
Gravel	0.147	-0.103	0.066	0.234	0.286	0.273	0.056	-0.091	-0.486	1	0.182	-0.098	-0.381	0.136
Velocity	0.082	-0.323	0.255	-0.09	0.591	0.659	0.363	-0.358	0.025	0.182	1	-0.033	-0.13	0.089
JulyTemp	0.429	0.499	0.76	-0.748	-0.285	-0.313	0.521	0.543	-0.217	-0.098	-0.033	1	0.169	0.164
Silt	0.077	0.275	-0.027	-0.322	-0.15	-0.215	0.055	0.269	-0.137	-0.381	-0.13	0.169	1	-0.342
Cobble	0.095	0.114	0.308	-0.004	0.074	0.086	0.159	0.064	-0.466	0.136	0.089	0.164	-0.342	1

Appendix B.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) for the Habitat Model.

Dependent	Predictor	Coefficient	BC P-value
LFY	Coarse Geo	1.171	0.098
LFY	Gradient	0.194	0.119
LFY	CA	0.173	0.191
LFY	Agric	-0.248	0.000
LFY	Urban	0.049	0.309
Depth	CA	0.212	0.002
Depth	LFY	0.086	0.000
Depth	Gradient	-0.096	0.020
Cobble	Gradient	11.963	0.003
July Temp	LFY	-1.268	0.000
Silt	CA	-11.380	0.003
Cobble	CA	11.389	0.017
Velocity	LFY	0.667	0.003
Velocity	Gradient	-0.129	0.002
July Temp	Gradient	-1.616	0.025
Velocity	Depth	0.211	0.017
July Temp	CA	1.996	0.000
Gravel	Coarse Geo	11.397	0.002
Gravel	Gradient	17.512	0.000
Gravel	CA	10.101	0.000
Silt	Gradient	-21.441	0.003
Sand	Gradient	-11.372	0.000
Sand	CA	-10.071	0.000
July Temp	Urban	0.893	0.010
July Temp	Agric	0.873	0.009
Total P	Urban	0.339	...
Total P	Agric	0.448	0.000
Silt	Agric	7.417	0.008
Sand	Agric	-17.224	0.071
Total P	LFY	-0.102	0.002

Appendix C1.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) for run 1 (n = 271) of the Trout Model.

Dependent	Predictor	Coefficient	BC P-value
Brown Trout	Sand	0.006	0.162
	Depth	0.320	0.320
	Gravel	0.026	0.010
	JulyTemp	-0.217	0.010
Brook Trout	JulyTemp	-0.268	0.003
	BrownTr	-0.002	0.861
	Sand	0.006	0.054
	Gravel	0.016	0.008
	Depth	-0.030	0.942

Appendix C2.–Observed (sample) and implied correlation matrices, and total and direct effects matrices for run 1 (n = 271) of the Trout Model.

	Gravel	Depth	Sand	July temp	Brown trout	Brook trout
Sample Correlations - Estimates						
Gravel	1	-0.017	-0.42	-0.028	0.263	0.197
Depth	-0.017	1	-0.128	0.485	-0.142	-0.301
Sand	-0.42	-0.128	1	-0.278	0.067	0.167
JulyTemp	-0.028	0.485	-0.278	1	-0.368	-0.611
Brown trout	0.263	-0.142	0.067	-0.368	1	0.272
Brook trout	0.197	-0.301	0.167	-0.611	0.272	1
Implied Correlations - Estimates						
Gravel	1	0	-0.421	0	0.258	0.177
Depth	0	1	-0.134	0.483	-0.139	-0.296
Sand	-0.421	-0.134	1	-0.293	0.07	0.181
JulyTemp	0	0.483	-0.293	1	-0.368	-0.607
Brown trout	0.258	-0.139	0.07	-0.368	1	0.27
Brook trout	0.177	-0.296	0.181	-0.607	0.27	1
Standardized Total Effects - Estimates						
Brown trout	0.298	0.05	0.096	-0.364	0	
Brook trout	0.221	-0.005	0.105	-0.574	-0.008	
Standardized Direct Effects - Estimates						
Brown trout	0.298	0.05	0.096	-0.364	0	
Brook trout	0.223	-0.005	0.105	-0.576	-0.008	

Appendix D1.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) for run 2 (n = 74) of the Trout Model.

Dependent	Predictor	Coefficient	BC P-value
Brown Trout	Sand	-0.012	0.421
	Depth	2.115	0.032
	Gravel	0.008	0.605
	JulyTemp	0.117	0.131
Brook Trout	JulyTemp	-0.359	0.015
	Brown trout	-0.485	0.022
	Sand	0.008	0.382
	Gravel	0.018	0.211
	Depth	0.078	0.788

Appendix D2.–Observed (sample) and implied correlation matrices, total and direct effects matrices for run 2 (n = 74) of the Trout Model.

	Gravel	Depth	Sand	July temp	Brown trout	Brook trout
Sample Correlations - Estimates						
Gravel	1	-0.107	-0.769	-0.099	0.168	0.077
Depth	-0.107	1	-0.025	0.533	0.347	-0.407
Sand	-0.769	-0.025	1	-0.073	-0.252	0.101
JulyTemp	-0.099	0.533	-0.073	1	0.356	-0.623
Brown trout	0.168	0.347	-0.252	0.356	1	-0.57
Brook trout	0.077	-0.407	0.101	-0.623	-0.57	
Implied Correlations - Estimates						
Gravel	1	0	-0.775	0	0.233	0.001
Depth	0	1	-0.112	0.513	0.355	-0.399
Sand	-0.775	-0.112	1	-0.149	-0.309	0.167
JulyTemp	0	0.513	-0.149	1	0.355	-0.617
Brown trout	0.233	0.355	-0.309	0.355	1	-0.58
Brook trout	0.001	-0.399	0.167	-0.617	-0.58	1
Standardized Total Effects - Estimates						
Brown trout	0.094	0.226	-0.18	0.212	0	
Brook trout	0.15	-0.103	0.192	-0.535	-0.43	
Standardized Direct Effects - Estimates						
Brown trout	0.094	0.226	-0.18	0.212	0	
Brook trout	0.19	-0.006	0.115	-0.444	-0.43	

Appendix E1.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) for run 3 (n = 39) of the Trout Model.

Dependent	Predictor	Coefficient	BC P-value
Brown Trout	Sand	-0.032	0.093
	Depth	5.106	0.009
	Gravel	-0.002	0.845
	JulyTemp	0.003	0.423
Brook Trout	JulyTemp	-0.160	0.061
	Brown trout	-0.146	0.165
	Sand	0.002	0.876
	Gravel	0.002	0.995
	Depth	-0.046	0.625

Appendix E2.–Observed (sample) and implied correlation matrices, total and direct effects matrices for run 3 (n = 39) of the Trout Model.

	Gravel	Depth	Sand	July temp	Brown trout	Brook trout
Sample Correlations - Estimates						
Gravel	1	-0.143	-0.823	-0.011	0.278	-0.038
Depth	-0.143	1	0.025	0.527	0.444	-0.452
Sand	-0.823	0.025	1	-0.08	-0.394	0.147
JulyTemp	-0.011	0.527	-0.08	1	0.3	-0.542
Brown trout	0.278	0.444	-0.394	0.3	1	-0.441
Brook trout	-0.038	-0.452	0.147	-0.542	-0.441	1
Implied Correlations - Estimates						
Gravel	1	0	-0.838	0	0.349	-0.134
Depth	0	1	-0.085	0.52	0.482	-0.411
Sand	-0.838	-0.085	1	-0.069	-0.464	0.218
JulyTemp	0	0.52	-0.069	1	0.309	-0.521
Brown trout	0.349	0.482	-0.464	0.309	1	-0.46
Brook trout	-0.134	-0.411	0.218	-0.521	-0.46	1
Standardized Total Effects - Estimates						
Brown trout	-0.021	0.412	-0.442	0.064	0	
Brook trout	0.041	-0.178	0.209	-0.415	-0.28	
Standardized Direct Effects - Estimates						
Brown trout	-0.021	0.412	-0.442	0.064	0	
Brook trout	0.035	-0.062	0.085	-0.397	-0.28	

Appendix F1.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) of the Smallmouth Bass Model.

Dependent	Predictor	Coefficient	BC P-value
Forage	Cobble	-0.16	0.02
	Depth	-0.438	0.411
	JulyTemp	0.163	0.007
	Total P	1.076	0.002
	Silt	-0.002	0.864
SmBass	JulyTemp	0.241	0.003
	Cobble	0.033	0.003
	Silt	-0.01	0.032
	Depth	1.782	0.006
	Bedrock	0.637	0.004
	Forage	-0.011	0.675
	Total P	-0.069	0.752

Appendix F2.–Observed (sample) and implied correlation matrices, total and direct effects matrices for run 1 (n = 229) of the Smallmouth Bass Model.

	Total P	Bedrock	Depth	Silt	Cobble	JulyTemp	Forage	SmBass
			Sample Correlations - Estimates					
Total P	1	0.067	0.073	0.251	0.05	0.539	0.45	0.206
Bedrock	0.067	1	0.211	-0.065	0.093	0.219	0	0.273
Depth	0.073	0.211	1	0.097	0.157	0.436	0.04	0.459
Silt	0.251	-0.065	0.097	1	-0.344	0.128	0.152	-0.14
Cobble	0.05	0.093	0.157	-0.344	1	0.251	-0.09	0.443
JulyTemp	0.539	0.219	0.436	0.128	0.251	1	0.425	0.555
Forage	0.45	0	0.04	0.152	-0.09	0.425	1	0.119
SmBass	0.206	0.273	0.459	-0.14	0.443	0.555	0.119	1
			Implied Correlations - Estimates					
Total P	1	0	0.054	0.274	0	0.536	0.467	0.189
Bedrock	0	1	0	0	0	0.112	0.041	0.121
Depth	0.054	0	1	0.112	0.147	0.421	0.073	0.432
Silt	0.274	0	0.112	1	-0.34	0.16	0.165	-0.117
Cobble	0	0	0.147	-0.34	1	0.212	-0.091	0.425
JulyTemp	0.536	0.112	0.421	0.16	0.212	1	0.449	0.537
Forage	0.467	0.041	0.073	0.165	-0.091	0.449	1	0.141
SmBass	0.189	0.121	0.432	-0.117	0.425	0.537	0.141	1
			Standardized Total Effects - Estimates					
Forage	0.279	0	-0.07	-0.018	-0.165	0.368	0	
SmBass	-0.001	0.078	0.241	-0.115	0.268	0.389	-0.015	
			Standardized Direct Effects - Estimates					
Forage	0.279	0	-0.07	-0.018	-0.165	0.368	0	
SmBass	0.004	0.078	0.24	-0.115	0.265	0.394	-0.015	

Appendix G1.–Bootstrap-estimated, un-standardized regression coefficients (significance based on bias-corrected 90% confidence intervals) for run 2 (n = 100) of the Smallmouth Bass Model.

Dependent	Predictor	Coefficient	BC P-value
Forage	Cobble	-0.005	0.7
	Depth	-0.809	0.015
	JulyTemp	-0.075	0.005
	Total P	-0.107	0.602
	Silt	-0.007	0.2
SmBass	JulyTemp	0.017	0.656
	Cobble	0.006	0.271
	Silt	-0.006	0.166
	Depth	0.264	0.561
	Bedrock	0.172	0.908
	Forage	0.245	0.253
	Total P	1.282	0.002

Appendix G2.–Observed (sample) and implied correlation matrices, total and direct effects matrices for run 2 (n = 100) of the Smallmouth Bass Model.

	Total P	Bedrock	Depth	Silt	Cobble	JulyTemp	Forage	SmBass
Sample Correlations - Estimates								
Total P	1	0.058	-0.183	0.078	0.078	0.419	-0.093	0.423
Bedrock	0.058	1	0.139	-0.074	-0.014	0.222	-0.094	0.145
Depth	-0.183	0.139	1	0.223	-0.017	0.076	-0.4	-0.083
Silt	0.078	-0.074	0.223	1	-0.413	0.033	-0.216	-0.173
Cobble	0.078	-0.014	-0.017	-0.413	1	0.197	-0.092	0.198
JulyTemp	0.419	0.222	0.076	0.033	0.197	1	-0.299	0.212
Forage	-0.093	-0.094	-0.4	-0.216	-0.092	-0.299	1	0.122
SmBass	0.423	0.145	-0.083	-0.173	0.198	0.212	0.122	1
Implied Correlations - Estimates								
Total P	1	0	-0.225	0.114	0	0.393	-0.093	0.413
Bedrock	0	1	0	0	0	0.182	-0.048	0.044
Depth	-0.225	0	1	0.228	0.003	0.04	-0.382	-0.11
Silt	0.114	0	0.228	1	-0.413	0.093	-0.235	-0.157
Cobble	0	0	0.003	-0.413	1	0.166	-0.066	0.185
JulyTemp	0.393	0.182	0.04	0.093	0.166	1	-0.325	0.187
Forage	-0.093	-0.048	-0.382	-0.235	-0.066	-0.325	1	0.1
SmBass	0.413	0.044	-0.11	-0.157	0.185	0.187	0.1	1
Standardized Total Effects - Estimates								
Forage	-0.049	0	-0.345	-0.163	-0.088	-0.263	0	-0.049
SmBass	0.437	0.044	0.026	-0.165	0.117	0.002	0.167	0.437
Standardized Direct Effects - Estimates								
Forage	-0.049	0	-0.345	-0.163	-0.088	-0.263	0	
SmBass	0.445	0.044	0.083	-0.138	0.132	0.046	0.167	