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Utility of Species-specific, Multiple Linear Regression Models for Prediction of Fish Assemblages in Rivers of Michigan's Lower Peninsula

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Abstract.–Models for predicting abundance of fishes in rivers are desired by fishery managers and the public to facilitate protection and management of stream resources, and are also used to gauge our scientific understanding of systems. Movement toward ecosystem management has stressed the need for models to predict fish assemblage structure in rivers, but such models are rare. Since fish assemblages are essentially collections of individual populations, we explored development of species-specific, predictive models for 68 commonly-occurring fishes in rivers of Michigan's Lower Peninsula using multiple linear regression techniques. We developed models for each species from All Sites (AS models) and from Sites Of its Occurrence (SOO models) in the database. We incorporated data describing site-, reach-, catchment-, and drainage network-scale aspects of habitat, species distribution ranges, and abundances of co-occurring fishes at sites to produce best predictive models. We developed two sets of significant regression models for the 68 species. Most commonly occurring variables were similar in both sets of models and included catchment area, July mean temperature, channel gradient, total phosphorus, substrate, and variables indicating connections to specific upstream and downstream aquatic habitats. Variables characterizing anthropogenic land use change and habitat connectivity were often significant for fishes in models. Landscape-scale habitat variables were slightly more common in AS models, while local-scale habitat variables occurred in higher proportions in SOO models. Strong effects of piscivores on fish abundance were not apparent in either set of models. The SOO models generally had fewer variables, explained more variance, and had lower estimation error than the AS models. Preliminary success in applying the SOO models to a river in which the list of occurring species is available and their generally good fit suggest that these models (in combination with some simple, species-specific tests to identify likely occurring fishes) show promise for predicting fish assemblage structure in Lower Michigan streams.

Introduction

The ability to predict species assemblages in aquatic systems has long been a goal of both research and management. Researchers use prediction to gauge our scientific understanding of systems, and as a tool for organizing, testing, and honing scientific theories (Pace 2001). Biologists and the public desire predictive models to aid in management and protection of our precious aquatic resources. Accurate predictions from models are particularly valuable when decisions need to be made and site-specific data are unavailable.

Predictive models are especially needed for assessing the effect of human activities on the biological integrity of river systems due to acute demands for drinking water, hydroelectric power, and irrigation, as well as industrial, recreational, and navigational uses by an ever-increasing human population (Karr and Chu 2000). Such management issues occur across the landscape at all spatial scales. Ecologists assessing the biological integrity of rivers at local sites and across broad geographic regions need the ability to predict fish assemblage structure under reference conditions or at differing levels of human disturbance (Karr and Chu 2000; Wiley et al. 2000; Oberdorff et al. 2001). Local fishery managers need to understand how local-scale habitat alterations or biotic changes might affect fish assemblage structure (Riley and Fausch 1995; Wiley et al. 1998) and how regional events (e.g., global climate change) may influence local assemblages.

Prediction of fish assemblage structure (species composition and relative abundance) in rivers is complicated due to issues of spatial scale and heirarchical relationships among habitat elements (Frissell 1986; Levin 1992), as well as dynamics of biological populations (Wiley et al. 1997). As a landscape system, a river represents a complex mosaic of interactions and relationships involving the regional climate and the many smaller landscape elements in its catchment (Wiley and Seelbach 1997). Studies of river fishes often occur at different spatial or temporal scales, with the scale of the study often relating to different pattern-process relationships (Jackson et al. 2001). For example, regional- or larger-scale studies of factors influencing salmonid biomass typically emphasize the importance of habitat factors (e.g., Binns and Eiserman 1979; Rahel and Hubert 1991; Zorn et al. 1998), while reach- or site-scale studies may be more likely to highlight biotic interactions (e.g., Waters 1983). Understanding relationships between pattern and scale (Levin 1992) is undoubtedly critical to successful prediction in river ecosystems.

The use of models to predict the structure of lotic assemblages has been steadily increasing over the last couple of decades. Longitudinal zonation studies (e.g., Huet 1959; Hawkes 1975), and later the River Continuum Concept (Vannote et al. 1980), provided early base models for describing predictable, upstream to downstream patterns in physical and biotic characteristics of many rivers. Exceptions to these general patterns (e.g., Wiley et al. 1990), however, limit the utility of these models as predictive tools. More recently, multivariate approaches to looking at fish assemblage patterns (e.g., Lyons 1996; Maret et al. 1997; Angermeier and Winston 1999; Waite and Carpenter 2000) have been useful for identifying important habitat gradients influencing fishes across large regions, but such coarse-grained analyses were not necessarily intended for predicting fish assemblages at local scales. Multivariate approaches can aid in identification of important habitat axes for coarse-scale characterization of rivers and fish assemblages, especially in regions having high spatial variation in habitat conditions. However, such analyses may also mask the effects of subtle, but important, local-scale factors such as substrate or woody debris (Jackson et al. 2001).

Others have taken a more species-specific approach to predicting fish assemblage structure in rivers. Habitat Suitability Index (HSI) models (Terrell et al. 1982) were developed to characterize how frequently fish used different types of key habitat parameters (e.g., depth, velocity, substrate, cover), and the Instream Flow Incremental Methodology (IFIM) combined these data with hydrology models to predict fish population and assemblage responses to alternate flow conditions (Bovee 1982). While HSI studies provided a good information base for many fishes, IFIM studies often had limited success in applying HSI data to predict fish biomass (Orth and Maughan

1982; Conder and Annear 1987; Zorn and Seelbach 1995). Lack of predictive ability was likely due to insufficient understanding of physical and biotic components of the river system and interactions among them (Mathur et al. 1985; Osborne et al. 1988). Researchers (e.g., Lamouroux et al. 1999) continue to modify the IFIM approach and have had limited success in generating species-specific predictions of fish assemblage structure.

Index of Biotic Integrity (IBI) studies (Karr 1981) require predictions of fish and invertebrate assemblages in rivers for use as benchmarks for comparison with actual survey data. Logistic regression approaches (e.g., Wright 1995; Oberdorff et al. 2001) are inherently appealing for some IBI applications because of their ability to predict probabilities of occurrence. However, logistic modeling algorithms that produce models with good overall fits may be biased predictors for many fishes (Olden et al. 2002). For example, Zorn (2000) found that logistic models developed for relatively rare fishes (e.g., occurring at fewer than 25% of study sites) were consistently poor predictors of species presence, while models built for very common species (e.g., present at more than 75% of sites) were consistently poor predictors of species absence. In addition, predicted probabilities of presence are too coarse for addressing biotic integrity and fisheries management issues where information on relative abundance of fishes is required.

Since fish assemblages in rivers are essentially collections of individual populations (Ricklefs 1987), a logical approach to predicting assemblage structure would be to develop models for each species and summarize findings across the collection of models to produce assemblage-level predictions. Multiple linear regression models have been used for many years to predict fish abundance from habitat correlates (Fausch et al. 1988), and their use in predicting fish assemblage structure is appealing in several regards. Models can be tailored to individual species, can incorporate various types of information, and each prediction has explicit error bounds associated with it. The species-specific modeling approach will allow determination of the extent to which each species' abundance can or cannot be reliably predicted. In addition, species-based predictions can be combined to produce expected values for a variety of functional- or life history group metrics used in studies of biotic integrity. Though models are useful for quantifying relationships among fish abundance and habitat variables, collinearities among input variables can complicate interpretation of causal relationships. Still, species-based, multiple linear regression modeling of fish assemblages would provide an opportunity to explore factors potentially related to fish assemblage structure from each species' perspective.

The primary objective of this study was to explore the use of multiple linear regression for predicting fish assemblage structure in Lower Peninsula (lower Michigan) rivers. We developed two complementary sets of multiple linear regression models for 68 fishes common to rivers of lower Michigan (Table 1). The first set of models (All Sites or AS models) was based on an array of sites on lower Michigan rivers with assemblage level data and should be applicable to unsampled rivers in lower Michigan. The second set of models was based on sites where each species occurred, and were referred to as the Sites Of Occurrence (SOO) models. By eliminating sites with standing crop values of zero from each modeling exercise, the SOO models were hypothesized to have better predictive ability and be more likely to identify local factors related to fish standing crops. Secondary objectives of this study were: 1) to compare AS and SOO sets of models in regards to their predictive ability and relative contributions of physical habitat, connectivity, distribution range, and biological parameters in explaining variation in fish standing crops; and 2) to test the hypothesis that landscape-scale variables would be relatively more common in AS models, and local-scale variables would be more common in SOO models.

Methods

Data sources

We obtained the fish survey data used in this study from the Michigan Rivers Inventory database for lower Michigan rivers (Seelbach and Wiley 1997). Standing crop estimates exist for all, or nearly all, fishes at 263 sites in the

database (Figure 1), and estimates just for salmonids occur at additional sites. This pseudo-random sample of sites provided good representation of most stream types found in lower Michigan. Fish populations were sampled once at each site between 1982 and 1995 using rotenone, electrofishing depletion, or mark-recapture techniques. Further discussion of techniques used to sample fishes and estimate fish standing crops at these sites occurs elsewhere (Seelbach et al. 1988; Seelbach and Wiley 1997; and Zorn et al. 1998). We used data from these 263 sites to develop the AS models, and a SOO model was developed for each species based only on sites where its standing crop was more than 0.000 kg/ha (Table 1). Standing crop (biomass density) was modeled rather than numerical density because it is less affected by yearly variation in year class strength.

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; Fausch et al. 1988; Lyons 1996). We obtained data for most variables from the Michigan Rivers Inventory database. Included were variables describing catchment-, reach-, and site-scale geology and land cover/use; measured or estimated exceedence streamflows and July temperatures; site-scale channel habitat data; and upstream-downstream connectivity (Table 2). Quadratic transformations of catchment area and July mean temperature variables were included in models to enable better fits for species preferring intermediate river size and temperature conditions. We also obtained additional data (or model predictions) for additional variables specifically for this study. We used multiple linear regression models based on Kleiman (1995) to make predictions of summer total phosphorus levels. Three variables described downstream connectivity of sites and one described upstream connectivity. Variable LNKDLINK indicated whether a barrier did (value = 1) or did not (value = 0) occur between the sample site and its confluence with a substantially larger channel located downstream. A substantially larger channel was defined as one whose link number, or its number of first order tributaries, was at least 10% higher than the link number of the site of interest. Variable BIGRIVER indicated whether a site was on or connected to a big river (catchment area greater than 1000 km^2), with values of 1 and 0 corresponding to yes and no answers. Variable G_LKS indicated whether a site was (1) or was not (0) connected to the Great Lakes. Variable PONDUPST indicated whether a site was (1) or was not (0) located less than 3.5 km downstream of a lake or pond in the drainage network. We thought that such proximity to upstream lentic habitats would likely alter stream habitat conditions (e.g., temperature) or export lentic fishes to sites.

Data analysis

Due to the large number of species and independent variables involved, we took a structured approach when developing regression modeling of fish standing crops. We placed abiotic variables into one of five categories generally based on the directness and proximity of their hypothesized effect on fishes (Table 2). Categories of variables and order of their entry into regressions were: 1) energetic; 2) site-scale hydraulic and hydrology; 3) site-scale channel characteristics; 4) reach-scale channel character and connectivity; and 5) catchment-scale. This allowed variables hypothesized to have a more direct or proximal influence on fishes to enter regressions prior to larger-scale variables having less direct effects. Variables were individually entered into the model using the former sequence until entry of all had been attempted. The entry method was used to manually enter or remove all regression variables (SPSS 2001). Fish standing crop values (in kg/ha) used in modeling were log-transformed ($\log_{10}(x + 0.001)$) to improve normality, as were values of many independent variables (Table 2). Since our objectives were to have models that made biological sense and explained as much variance in species abundance as possible, variables in latter categories were allowed to displace variables existing in a model if their inclusion increased the model's overall fit. We noted independent variables significant at P-values less than 0.10, 0.05 and 0.01, and included independent variables significant at $P<0.10$ due to the exploratory nature of the models. We

used these final models in making predictions. We compared the AS and SOO sets of models in regards to number of model parameters, model fit, estimation error, and the frequency of occurrence of individual variables and categories of variables.

Statistically significant multiple linear regression variables and their coefficients can provide insight regarding potential effects of anthropogenic changes to the landscape on fishes. However, regression coefficient values are influenced by other variables in the model (Neter et al. 1990). Therefore, we only noted the sign of regression coefficients for habitat connectivity and urban and agricultural land use when they were significant in both the AS and SOO models for a species.

Incorporation of piscivore variables and species distribution data

In regional-scale studies of distribution patterns of stream fishes, abiotic factors usually are more closely related to fish distributions than biotic factors (Jackson et al. 2001). We expected similar results in this study, but wanted to see if information on each species current distribution range (which may to some degree reflect historic constraints to movement) or potential predators could explain variance not accounted for by habitat parameters. So, we examined the final models further to assess the extent to which additional variance in fish density patterns could be explained by standing crops of piscivorous fishes at the sites and data on a species' geographic distribution range.

To assess the influence of piscivores, we correlated the residuals of each final model with standing crops of each piscivorous species and of piscivorous fishes grouped by general thermal preferences, of cold-, cool-, and warm-water (Table 3). We added piscivores (or groups of piscivores) with significant negative correlations to final models to assess their effect on regressions. Piscivore variables (though proximal in effect) entered regressions after abiotic variables because we assumed a species' abiotic habitat requirements needed to be met before it could potentially be affected by piscivores.

To assess the extent to which known range distributions could explain additional variance, we used maps of historical distribution housed at the University of Michigan Museum of Zoology, Fish Division, to develop a presence-absence data layer organized by major watershed for the 68 species of interest. We used this layer to develop a binary variable for each species that indicated whether or not a given site was within its potential distribution range. We added the appropriate distribution variable to each final model and noted when it explained additional variance in fish density.

Collinearities

We expected and found (Table 4) significant intercorrelations among many habitat variables important to fishes (Table 4) because rivers are large-scale systems that reflect interactions among climate, geology, landform, and land use/cover on multiple spatial scales (Wiley and Seelbach 1997). Rather than attempting to eliminate all correlated independent variables from this analysis, we included them to aid in identifying important predictor variables and to gain insight into potential mechanisms. To further aid in identifying potential mechanisms, we recorded each significant habitat variable displaced from the regression and the variable that replaced it. Further analysis of these complex relationships is reported elsewhere (Zorn and Wiley 2004).

Model application

We predicted standing crops for fishes at one site on a lower Michigan river, the Raisin River at Academy Road, to demonstrate how the set of multiple linear regression models could be used to predict fish assemblage structure for the most common fishes. We ran the SOO models for each species of fish observed at the site in a 1988 survey (these data were used in building SOO models), and compared model predictions and their 68% confidence limits to observed standing crop values from a survey conducted at the same site in 1984. Then, we noted whether observed standing crop values for each species

fell above, below, or between the predicted 68% confidence limits.

Results

General model overview

We developed two significant regression models (AS and SOO) for each of the 68 species (Appendices A and B; Table 5). Common patterns in significant variables were apparent when AS models were grouped according to membership of fishes in clusters identified in Zorn et al. (1998). Densities of fishes in cluster 1 (creek chub cluster), commonly thought of as a headwater group, were often negatively associated with catchment area variables and positively with agricultural land use (Appendix A). Coefficients for July temperature variables and catchment area variables in blacknose dace and mottled sculpin (cluster 3) regression models indicated their affinities for small, cool streams. Models for fishes in clusters 10 (walleye cluster) and 11 (freshwater drum cluster) often had positive coefficients for catchment area variables and negative coefficients for stream gradient indicating positive associations with large, low-gradient rivers. Fishes in cluster 13 (grass pickerel, hornyhead chub, and lake chubsucker) were positively associated with total phosphorus levels and the occurrence of lentic habitats in upstream reaches. Six of seven fishes in cluster 15 (smallmouth bass cluster) were positively associated with variables describing the prevalence of gravel or coarser-sized substrates.

Variables in SOO models were not shared as commonly among fishes within a cluster, possibly because sites with standing crop values of zero were excluded from species regression models (Appendix B). Still, a few general relationships existed, such as negative associations between catchment area and fishes in the creek chub cluster, and positive associations between coarse substrates and fishes in the smallmouth bass cluster.

Frequency of occurrence of variables

The most commonly occurring variables were quite similar in both sets of models (Table 6). For both sets, catchment area occurred most frequently followed by July mean temperature. Channel gradient, total phosphorus, and substrate variables were the next most frequently occurring variables, though the order differed between model sets. Variables indicating connections to specific upstream and downstream aquatic habitats were also significant in many models.

To assess the relative importance of different categories of variables, we grouped variables by types identified in Table 2, and calculated weighted frequency of occurrence for each category. This prevented categories with many, but infrequently-occurring, variables from appearing to be the most important. Once this was done, the two sets of models identified the same five variables (or types of variables) as most often associated with fish standing crops (Table 7). Catchment size and the energetic variables, mean July temperature and total phosphorus, occurred most frequently in both sets of models. These variables were not grouped with other variables due to their uniqueness relative to other variables of the same type. Reach-scale channel and connectivity variable types ranked fourth and fifth in both sets of models.

As hypothesized, landscape-scale variables were more common in the AS models, while local-scale variables occurred in higher proportions in the SOO models. Catchment- and reach-scale variables were proportionately more common in AS models, while site-scale and energetic variables occurred in higher proportions in SOO models (Figure 2). Looking more closely, two of three classes of catchment-scale variables and all three types of reach-scale variables occurred in higher proportions in the AS models (Figure 3). Both types of site-scale variables and one of two energetic variables (mean July temperature) occurred in higher proportions in the SOO models.

Model coefficients

Variables characterizing anthropogenic land use changes and habitat connectivity were often significant for fishes in both AS and SOO models (Table 8). Coefficients for variables characterizing urban land use in catchments and riparian corridors were negative for six fishes, including species such as rock bass, rainbow darter, and hornyhead chub, but positive for only one species (white sucker). Agricultural land use variables at these spatial scales had positive coefficients for five species, including tolerant fishes such as common carp, white sucker, and bluntnose minnow.

Connections to specific upstream and downstream habitats may be important for many fishes in lower Michigan rivers. Upstream water body variables were positively associated with eight species (mostly lake fishes such as bluegill, pumpkinseed, largemouth bass, black crappie, and rock bass), and had negative coefficients for three species (Table 8). Variables indicating connections to larger, downstream water bodies were positively associated with standing crops of four fishes and negatively associated with one (striped shiner).

Connectivity variables were especially common in AS models. Significant positive coefficients for variables indicating the presence of water bodies and wetlands upstream occurred for 28 species, mostly warmwater fishes, while negative coefficients occurred for 8 fishes, many of which were coldwater species (Appendix A). Densities of seventeen fishes were positively associated with variables indicating occurrence of connections to downstream habitats (Appendix A). Such connections are also required by chinook salmon and coho salmon, species that only occurred in (and whose regressions were built solely from) river sites connected to the Great Lakes. Ten species were positively associated with a lack of connections to larger downstream habitats (Appendix A).

Piscivore and species distribution variable effects

Strong effects of piscivores on fish standing crops were not apparent in either AS or SOO sets of models. When piscivores had significant negative effects in a model, it was often difficult to ascertain whether the effect was associated with biotic interactions or other factors. For example, piscivore variables were statistically significant in 20 of 68 SOO species models and increased R^2 values by 0.02 to 0.17 (Table 9). These variables were statistically significant in 21 of 68 AS models. However, in many cases, the modeled species and piscivores seldom co-occurred at sites. For example, the piscivore co-occurred with the modeled species at fewer than 20% of sites for 10 of the 25 occasions where piscivore variables were statistically significant in the SOO models (Table 9). To further complicate matters, addition of piscivore variables caused habitat variables to be displaced (i.e., no longer significant) in 8 of the 20 SOO models.

Biotic interactions seemed most likely in situations where species frequently co-occurred and when addition of a piscivore variable to the model did not displace a habitat variable. In only seven SOO models did piscivores have significant coefficients, co-occur with the modeled species at more than half of sites, and not displace habitat variables when added to the model (Table 9). Based on the above criteria, spatial patterns in standing crops of brook trout, creek chub, golden shiner, central mudminnow, river chub, sand shiner, and spotted sucker may be negatively affected by the co-occurring piscivores.

Information regarding recent, watershed-based distribution range of fishes had a limited contribution to AS models for the 68 species. After all habitat variables had been added to models, the distribution range variable was statistically significant in models for two species, black redhorse and flathead catfish.

Comparison of AS and SOO model sets

Despite similarities in coefficients used, the AS and SOO models differed considerably in their fit of the data. The SOO models had considerably higher fits than the AS models (average adjusted R^2 values of 0.43 and 0.26, respectively) though there was considerable variation in fits among species models (Figure 4; Table 5). The SOO models generally had fewer independent variables (average of 3.9 v. 5.7

variables per equation, respectively) than the AS models (Figure 5). Estimation error was lower for the SOO models than the AS models (Figure 6).

There were also substantial differences in how effectively each modeling approach could explain patterns in standing crops of individual species. In general, it appeared that poorly-fitting models of one type for a species were often accompanied by better-fitting models of the other type (Figure 7). This suggested that the AS and SOO modeling sets of data presented quite different patterns of variance in fish standing crops. Still, good AS and SOO model fits could be produced for some species (e.g., brook trout, slimy sculpin, mottled sculpin, and chinook salmon), while other species (e.g., hornyhead chub and rainbow darter) could not be modeled effectively using either approach.

The large number of standing crop values equal to zero appeared to influence the predictive ability of the AS models. In general, the SOO models were less biased predictors of fish standing crops than the AS models (Figure 8). The AS models tended to under-predict a species' standing crop at sites where the observed value was greater than zero, and often over-predicted standing crops when observed values were zero. This was even more clearly shown when predicted and observed standing crops for a representative species, such as brown trout, were plotted (Figure 9). Here, the 68% confidence interval from the AS brown trout model captured many of the observed standing crop values of zero, but only a fraction of observed values greater than zero. The 68% confidence interval from the SOO model, however, bounded most of the range in observed standing crop values for brown trout.

Collinearities

Correlation among variables included in both sets of regression models often resulted in numerous displacements of variables as each model was developed. Variables most commonly displaced from AS and SOO models were July mean temperature, total phosphorus, depth at 90% exceedence flow, and velocity at 90% exceedence flow (Table 10). Variables that most frequently displaced other variables were catchment area, channel gradient, 90% exceedence flow yield, and proportion of agricultural land use in catchment (Table 10). July mean temperature and catchment area were involved in many more displacements than other variables for several reasons. We sometimes used linear and quadratic forms of these variables in models because many species are intermediate in their preference of stream temperature and size conditions, so either of these forms could have been involved in displacements during modeling. They were involved in most models and were often involved in sequential displacements, which resulted in our recording multiple displacement events for these variables. For example, when depth displaced July temperature and depth was subsequently replaced by catchment area, we recorded depth as displacing temperature and catchment area as displacing both depth and temperature.

The most common displacements of variables during AS modeling occurred between parameters that were well correlated. Three of the four most common displacements involved July mean temperature being displaced by catchment area, channel gradient, and depth (Table 11). Simple correlations (r-values) of July mean temperature with these variables were all higher than 0.5 (Table 4). In fact, simple correlations higher than 0.5 occurred between variables in the six most frequent displacements among AS models (Tables 11 and 4).

Similar patterns of variable displacement also occurred in the SOO models, though to a lesser extent (Tables 10 and 11). Fewer displacements may have been due to the reduced number of sites (and range of physical conditions) in each model-building dataset.

Model application

Given a list of potentially-occurring species, the predicted values and 68% confidence intervals from SOO models provided a reasonable picture of expected fish assemblage structure for the Raisin River at Academy Road for use in comparison with actual survey data (Table 12). Observed standing crop values fell within confidence intervals for 16 of the 20 most common species. Higher than expected standing

crops occurred for bluntnose minnow and river chub, while lower than expected standing crops occurred for smallmouth bass and bluegill. Channel catfish were absent at the site, though moderate standing crops were predicted.

Discussion

Overview

The two modeling approaches used in this study represent filters that influence both the pattern observed and underlying processes (Levin 1992). The AS models collectively imply that spatial patterns in fish assemblage structure are more closely related (based on frequency of occurrence of variables) to catchment- and reach-scale variables than site-scale or energetic variables (Figure 2). The SOO models, on the other hand, suggest that site-scale variables are most closely related to fish assemblage structure. That these two approaches represent different patterns in the data is also supported by differences in the degree of similarity between the AS and SOO models when regressions are grouped into clusters based on species co-occurrence (Zorn et al. 1998). All Sites models for a cluster of species often shared variables that related to general habitat requirements of the fishes in the cluster (Appendix A). Such patterns were not as apparent in the SOO models when they were grouped this way (Appendix B). Differences between AS and SOO model fits for the same species further indicate that the two approaches reveal distinct patterns (Table 5; Figure 7).

To our knowledge, this study was the first to use the same base dataset to demonstrate that the selection of sample sites used in analyses influences the relative importance of different spatial scales of habitat variables to stream fishes (Figures 2 and 3). Our findings support the notion that the relative importance of large-scale variables (e.g., climate or zoogeography) increases as the spatial-scale of the study, and range of environmental conditions encountered, grows (Levin 1992; Jackson et al. 2001). Still, variables associated with patterns in both AS and SOO analyses are consistent with other studies relating fish standing crops to stream attributes. For example, large-scale studies of fish assemblages in other regions also identified the large-scale variables of river size and channel gradient as important correlates of fish assemblage structure (e.g., Zalewski and Naiman 1985; Degerman and Sers 1993; Lyons 1996). Site-scale variables, such as instream cover and depth at the sample site, occurred most commonly in a set of 98 regression models (Fausch et al. 1988) that were mostly based on fewer sites (79 models had fewer than 50 total degrees of freedom). Differences between the AS and SOO models support the view that pattern and process do indeed vary with scale, and that there is no single or "correct" scale for addressing all ecological questions (Levin 1992). What is needed is a fluid understanding of pattern-process relations at different scales and how they change as one moves between scales (Levin 1992).

Important variables

Despite the above differences, the two sets of models were quite similar in terms of which variables occurred most frequently. Variables significant in regression equations and the sign of their coefficients generally related to information in life history accounts (e.g., Scott and Crossman 1973; Trautman 1981; Becker 1983), and in some cases, provided new hypotheses for exploration. Frequent occurrences of catchment area, July mean temperature, and channel gradient (Table 6) supported numerous other studies which identify river size, temperature, and gradient as important correlates with fish assemblage structure (e.g., Hynes 1972; Hawkes 1975; Vannote et al. 1980; Zalewski and Naiman 1985; Rahel and Hubert 1991; Degerman and Sers 1993; Lyons 1996; Newall and Magnuson 1999; Wehrly et al. 1999). Total phosphorus, though correlated with these variables, was also among the most common factors associated with fish densities. Some studies suggest phosphorus levels may limit production of fishes in rivers (Johnston et al. 1990; Hoyer and Canfield 1991; Waite and Carpenter 2000). These variables, in addition to variables characterizing substrate, occurred most frequently in both sets of models. These findings also provide some support for the use of depth and velocity (both correlates of

size, gradient, and temperature), and substrate in instream flow (Bovee 1982) and HSI (Terrell et al. 1982) studies, but suggest a need for additional parameters, especially temperature and possibly nutrient levels.

Statistically significant associations between fish abundance and human changes to the landscape provide a number of interesting areas for further investigation. In this discussion, the term positive or negative association refers to a positive or negative coefficient for significant variables in multiple linear regression equations. Several questions quickly arise from looking at associations between fishes and urban land use in Table 8. Urban land use was positively associated with white sucker abundance, but negatively associated with standing crops of six species. Other studies support some of these associations. Lyons et al. (1996) identified white sucker as a tolerant species, and rock bass and rainbow darter as intolerant fishes. However, they also classified central mudminnow, and hornyhead chub and bluegill as neither tolerant nor intolerant. Other authors (e.g., Steedman 1988; Wang et al. 1997) have shown strong negative relationships between urban land use and IBI scores, which themselves are largely influenced by fish species richness and abundance. Are all these species really adversely affected by urbanization, and if so, to what extent? If these species are indeed negatively affected, what is the mechanism (e.g., increased fluctuations in current velocity or thermal conditions, sedimentation, etc.)? Does urbanization really benefit white sucker populations? If so, how (e.g., release from competition with fishes negatively affected by urbanization)?

Relatively few authors have studied effects of downstream barriers (Winston et al. 1991) or upstream wetlands, lakes, and impoundments on entire fish assemblages at a regional scale. However, numerous studies (e.g., Rieman and McIntyre 1995; Dunham et al. 1997) have examined relations between habitat fragmentation and current distributions of individual species of fish. Results of this exploratory modeling suggest that for many fishes the configuration of the site within the larger river system (i.e., its proximity and existence of connections to other aquatic habitats and their source populations) may be as important as other habitat characteristics (Osborne and Wiley 1992). Relatively low correlations between connectivity variables and other habitat variables in this analysis make these findings intriguing. Further investigation is needed to determine the influence of connectivity variables on biotic integrity of stream fish assemblages.

Variables describing connectivity of downstream habitats to sites were significant in AS regression models for many fishes. All Sites model results are more pertinent for discussing connectivity than SOO models because they include data on species absence as well as presence. Connection of a site to the Great Lakes was positively associated with densities of eight species (rainbow trout, walleye, gizzard shad, and shorthead redhorse), many of which reside in larger river reaches and whose populations may be bolstered by runs of fishes from the Great Lakes (Appendix A). Though not apparent from the AS model coefficients, Great Lakes connections are also key for chinook salmon and coho salmon. Such connections are also important for migratory fishes (e.g., lake sturgeon *Acipenser fulvescens*) not included in this analysis due to their rarity which, ironically, is often attributed to barriers on tributaries (Smith 1972). With the exception of northern pike, the three fishes negatively associated with connections to the Great Lakes were all headwater fishes (i.e., central stoneroller, northern redbelly dace, and slimy sculpin). A connection to the Great Lakes may provide a source of potential competitors or relate to other factors negatively correlated with densities of these three species. Construction of dams may benefit upstream populations of northern pike through formation of impoundments and creation of delta wetlands where rivers enter. Connections to larger downstream reaches were positively associated with densities of 10 species (including flathead catfish, spotted sucker, blacknose dace, and creek chub), but negatively associated with densities of 8 species, including northern hog sucker, northern pike, and blackside darter (Appendix A). Explaining all these associations is difficult because life history accounts (e.g., Scott and Crossman 1973; Trautman 1981; Becker 1983) document migrations for species having positive and negative associations. In

addition, some associations may have other explanations, such as spurious collinearities among model variables.

Variables describing upstream lentic habitats and their connectivity to sites were also significant in AS regression models for many fishes. Eight species were negatively associated with occurrence of wetlands and lentic habitats upstream (Appendix A). Included were coldwater and coolwater fishes (brown trout, rainbow trout, mottled sculpin, and blacknose dace) which may have reduced abundance in reaches below lentic habitats due to the thermal effects of ponds and lakes on coldwater rivers. Twenty-four species were positively associated with occurrence of wetlands and lentic habitats upstream (Appendix A). Included were fishes commonly associated with wetland habitats (e.g., northern redbelly dace), fishes that reproduce on vegetation (e.g., grass pickerel and golden shiner), and many fishes typical of lakes and large warm rivers (e.g., numerous sunfishes, channel catfish, and logperch). The positive association between upstream wetlands and slimy sculpin (a coldwater species) is largely due to one site on Stover Creek (a tributary to Lake Charlevoix), which has extensive cedar swamps (often associated with groundwater input) in its riparian corridor.

Biotic interactions

In their review of models that predict stream fish standing crops from habitat variables, Fausch et al. (1988) stated that few investigators addressed whether biotic interactions may be limiting fish standing crops below what the environment could support. In this study, we added potential predators to models (after all significant habitat variables had been included) to find out how much additional variance in fish biomass they might explain that could not be accounted for by habitat variables. Though predatory fishes were significant in several models, it is still unclear how often a significant negative regression coefficient for a piscivore variable indicated an actual biotic interaction. Nevertheless, that only 7 of 68 models suggested a likely influence of piscivory (Table 9) implies that piscivory may not be a dominant factor influencing fish assemblage structure at the fairly coarse AS and SOO scales of analysis.

Results of this study demonstrated the difficulty in using spatially extensive data to assess biotic interactions. Large contrasts in environmental conditions often capture so much variance in fish standing crops that effects of local, but important, biotic interactions are often not apparent (Jackson et al. 2001). This point is demonstrated by our experience with brook trout and brown trout, the two species in Table 9 for which predator-prey relations may be understood best. Displacement of brook trout by brown trout has been well-documented in individual streams (Waters 1983), and biomass values for the two species within individual streams (e.g., Au Sable River) where long-term data exists show a negative correlation (A. Nuhfer, Michigan Department of Natural Resources, unpublished data). However, a plot of brook trout biomass against brown trout biomass for Michigan Rivers Inventory sites where both species occurred shows a positive relationship (Zorn, unpublished data), and addition of brown trout to the brook trout SOO model explained little additional variability in standing stocks (Table 9). In this study, positive partial correlations likely represent shared habitat preferences rather than biotic interactions, and negative partial correlations often may indicate biotic interactions or just differences in preferred habitat between species not accounted for by habitat variables used in modeling (Oberdorff et al. 2001). Use of spatially-extensive data and correlation-based analyses to demonstrate biotic interactions is further complicated when habitat conditions, such as stream temperature, mediate outcomes of interspecific interactions (De Staso and Rahel 1994). These findings suggest the need for finer-scale studies (e.g., within a stream) over longer temporal scales to address questions regarding biotic interactions. Extrapolation from finer-scale studies of biotic interactions, however, cannot occur without knowledge of environmental constraints on populations. This suggests a general need for studies spanning a range of spatial and temporal scales (Levin 1992) and other analytic approaches (e.g., Zorn and Wiley 2004).

Limitations

Though often used to predict fish standing crops, multiple linear regression approaches suffer some common pitfalls. In their review of models that predict standing crop of stream fishes from habitat variables, Fausch et al. (1988) identified the following problem areas common in model development and testing: inadequate sample size; error in measuring independent variables; choice of the best model; inadequate testing of models; and making predictions from data outside the range of the model-building data. A brief discussion of each in relation to this study follows.

Inadequate sample size was generally not a major problem in this study. All of the AS models, except those for chinook salmon and coho salmon, were based on more than 200 sites. Sample sizes were large for most species in SOO models. For example, SOO models for 33 species had total degrees of freedom of at least 50. However, models for 16 relatively uncommon fishes had fewer than 20 total degrees of freedom. For comparison, 59 of the 98 models reviewed by Fausch et al. (1988) were based on 20 or fewer samples.

Some error occurred in measurement of independent variables, especially site-scale channel morphology variables, several of which were subjective. However, there is no reason to suspect that these measures were consistently biased in one direction or another. GIS-based land use/cover summary data were limited by the accuracy of base maps. The accuracy of predicted independent variables (Table 2) was limited by predictive ability of source models (e.g., Kleiman 1995; Wehrly et al. 1997). All of these errors would have contributed additional unexplained variance. In addition, data on some important variables (e.g., abundance of large woody debris) were not available for inclusion this study.

Choosing the multiple linear regression modeling approach seemed appropriate in this study since the primary objective was to develop predictive models. Using them to gain insight into important variables influencing densities of individual species was an additional benefit. The structured, well-documented approach to variable entry and removal was intended to result in a greater understanding of functional relations both among variables and between variables and fishes. However, it is possible that not all independent and dependent variables were related in a linear fashion, and other types or combinations of models would also have been appropriate.

The models developed here were not tested. Model testing would be a logical area for further research. For example, model predictions could be used as benchmarks for comparison with absolute or relative abundance data collected at the species- or assemblage-level.

Predictive models may perform poorly when applied to streams having physical or biological conditions substantially different from those under which the model was developed. To facilitate successful application of regression models, Fausch et al. (1988) recommended that readers be provided with the range of values for independent variables and the standard error of regression estimates. Such data are provided for models in this study (Tables 2 and 5). As suggested by Fausch et al. (1988), we caution against application of these models to regions outside of geographic area of their source data (lower Michigan).

Collinearities

Correlations were expected among many habitat variables in this study because rivers, by nature, are integrative, heirarchical systems (Frissell et al. 1986; Wiley and Seelbach 1997). Even locally-measured variables (e.g., depth, velocity, substrate) are heavily affected by large-scale factors (e.g., climate, topography, geology, land use, etc.) that control the flow of water from the landscape to stream channel to river mouth. Natural and anthropogenic changes, both in the landscape and along a river's course, often keep downstream river habitats from being entirely predictable (Seelbach et al. 1997). As a result, models for predicting even easily measured parameters, such as stream temperature, are often complex and require information on factors at site-, reach-, catchment-, and regional-scales (Wehrly et al. 1997). Given this complexity, it is not surprising that models for predicting fish assemblages, which themselves are built in part on predictions (and associated error) of other

models, cannot account for much variation in fish standing crops. Nevertheless, by documenting how variables interacted during the model-building process (Tables 10 and 11), this study provided some insight regarding relationships among habitat variables and the relative performance of different habitat variables in predicting standing crops at both the species and assemblage level. For example, correlations between catchment area and many key habitat variables in this study (Tables 4 and 11) provided insights as to why it is a key macro-habitat variable for lower Michigan rivers (Zorn et al. 1998).

Many variables and variable types were included in this study from the outset due to the array of requirements of fishes studied, the objective of developing a set of best predictive models, and the exploratory nature of modeling. Interpreting of the meaning of regression coefficients can be difficult when habitat variables are inter-correlated, as occurred in the AS and SOO models. In such cases, the variable's occurrence in the model may indicate a mechanistic relationship between it and the dependent variable, or simply an artifact resulting from its correlation with other variables in the model. Additional analyses or other types of experiments may help to further elucidate mechanisms. For example, covariance structure analysis (Mauryama 1998) provides an avenue for statistically exploring mechanistic relations among variables. It uses a dataset's variance-covariance matrix to assess direct and indirect effects of "independent" variables on each other and on the dependent variable. Use of this tool to examine relations among habitat variables and fishes in lower Michigan rivers occurs elsewhere (Zorn and Wiley 2004).

Management Implications

Accurate models would provide useful predictions of historic, current, or future fish assemblages for use as benchmarks in biotic integrity or other studies. The objective of this study was to explore the feasibility of using multiple linear regression models for predicting stream fish assemblages in Michigan. Biases inherent in the AS and SOO approaches influence the extent to which each set of models can be applied for this purpose. For example, frequent occurrence of zero standing crop values in the AS dataset resulted in models that generally under-predicted densities at sites where a species occurred (Figures 8 and 9). In this case, the desire for a general, state-wide model represented a trade-off against predictive ability. The SOO models, on the other hand, fit their range of data much better (Figures 8 and 9). However, the SOO models had limited success in predicting zero standing crop values for sites in the AS dataset, which were not part of the SOO model-building dataset (Zorn, unpublished data).

Models can help in setting realistic management objectives by providing predictions and confidence intervals for comparison with field survey data. For example, the SOO models were used to predict the fish assemblage at a site on the Raisin River, in southeast Michigan, for comparison with independent survey data from the site (Table 12). Comparison between the predicted standing crop ranges and actual data showed that most fishes were within the predicted confidence intervals. Actual abundances outside the confidence intervals may necessitate further inquiry by managers. For example, channel catfish were not collected in the survey, though the model predicts a modest standing crop for the species (Table 12). This difference likely relates to a change in fishery management practices (i.e., increased stocking of channel catfish in large, warm rivers) between this 1984 survey and the more recent surveys used in building models for this study. Hatchery practices would likely have relatively little influence on predictive models for other species stocked into Michigan streams, since highest standing crops of species stocked in rivers (e.g., brown trout, rainbow trout, chinook salmon) generally occur in rivers having naturally-reproducing populations of these species.

Success in applying the SOO models to a river in which the list of occurring species is available (Table 12) and their generally good fits suggest that these models show promise for use in predicting fish assemblage structure (at least for the 68 most common fish species in lower Michigan). Further testing of these models is still needed. If tests prove successful, the SOO models in combination with some simple, species-specific tests to identify likely-occurring

fishes (e.g., Wiley et al. 1998; Zorn et. al 1998), may allow researchers to predict fish assemblage structure at sites on rivers throughout lower Michigan. Further work is needed in this area.

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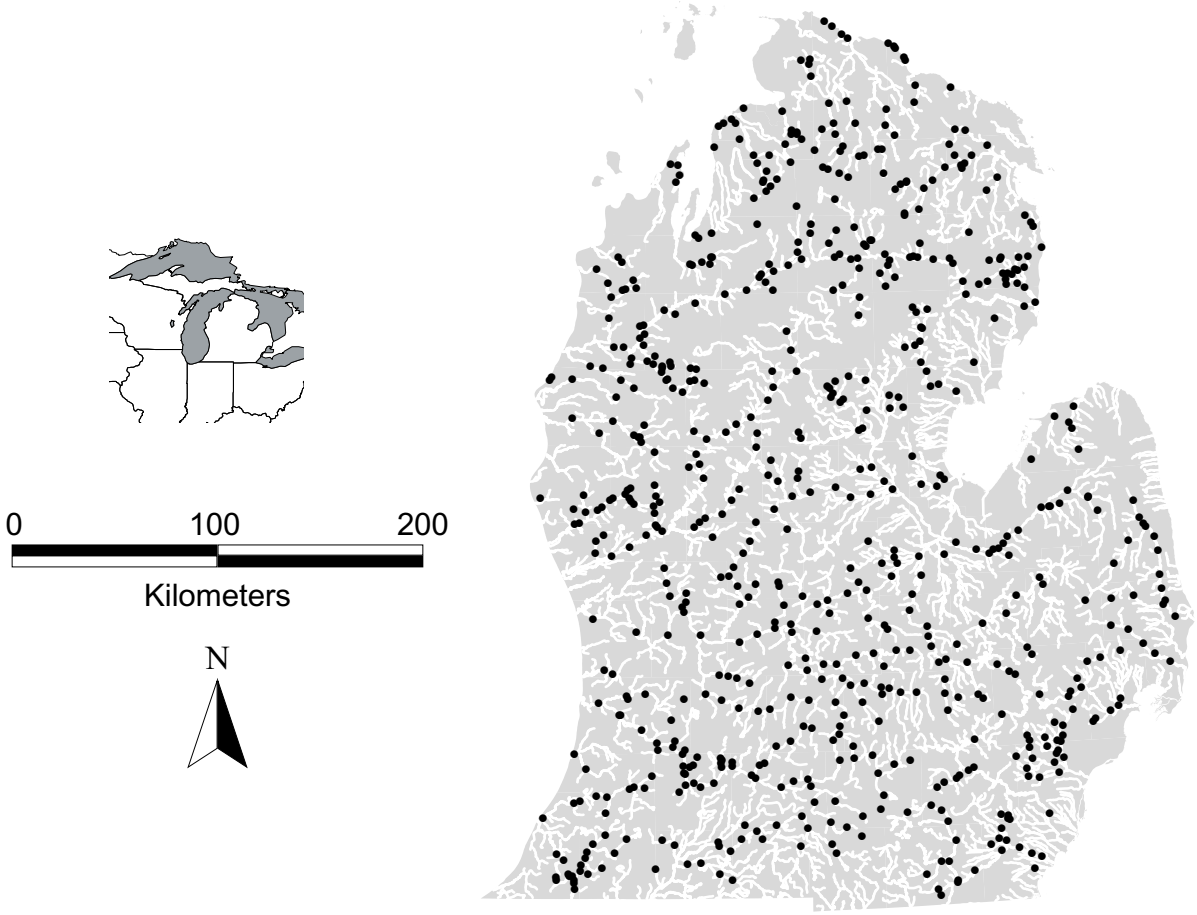

Figure 1.–Maps of the Great Lakes region and of Michigan showing major river drainages of Michigan's Lower Peninsula and locations of 263 fish sampling sites used to develop All Sites (AS) models.

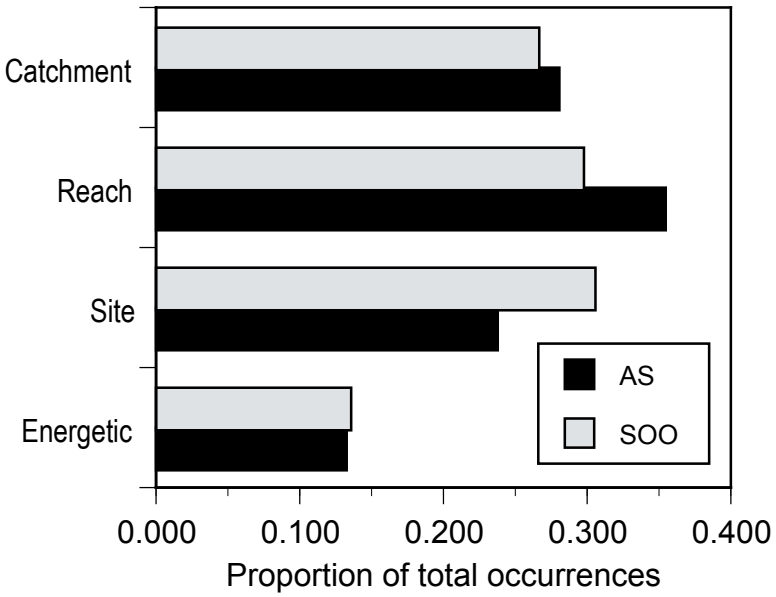

Figure 2.–Proportional occurrence of four general classes of variables in two sets of regression models for 68 common fishes in lower Michigan rivers. Model sets are All Sites (AS) and Sites of Occurrence (SOO) species models.

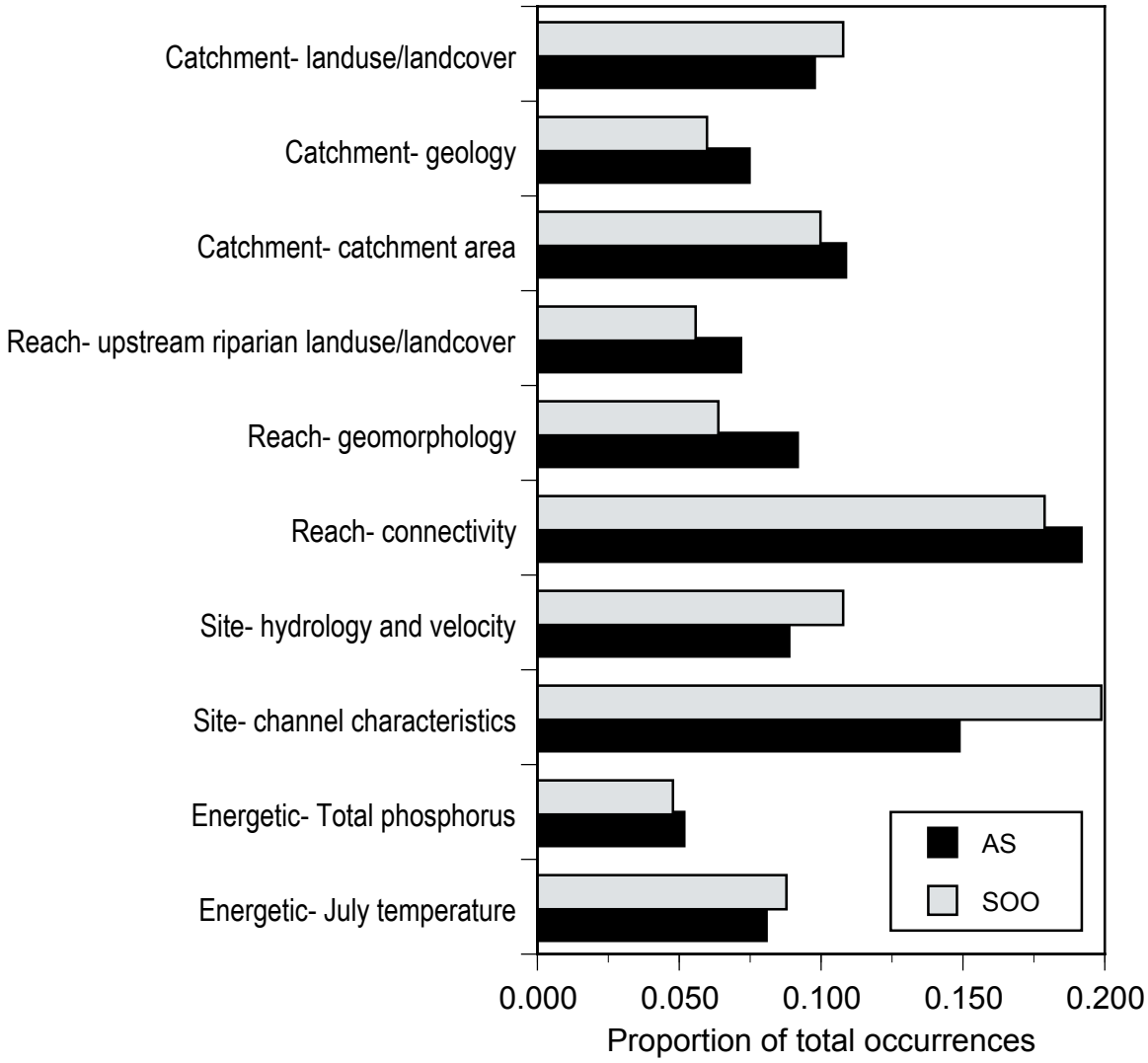

Figure 3.–Proportional occurrence of different types of variables in two sets of regression models for 68 common fishes in lower Michigan rivers. Model sets are All Sites (AS) and Sites Of Occurrence (SOO) species models.

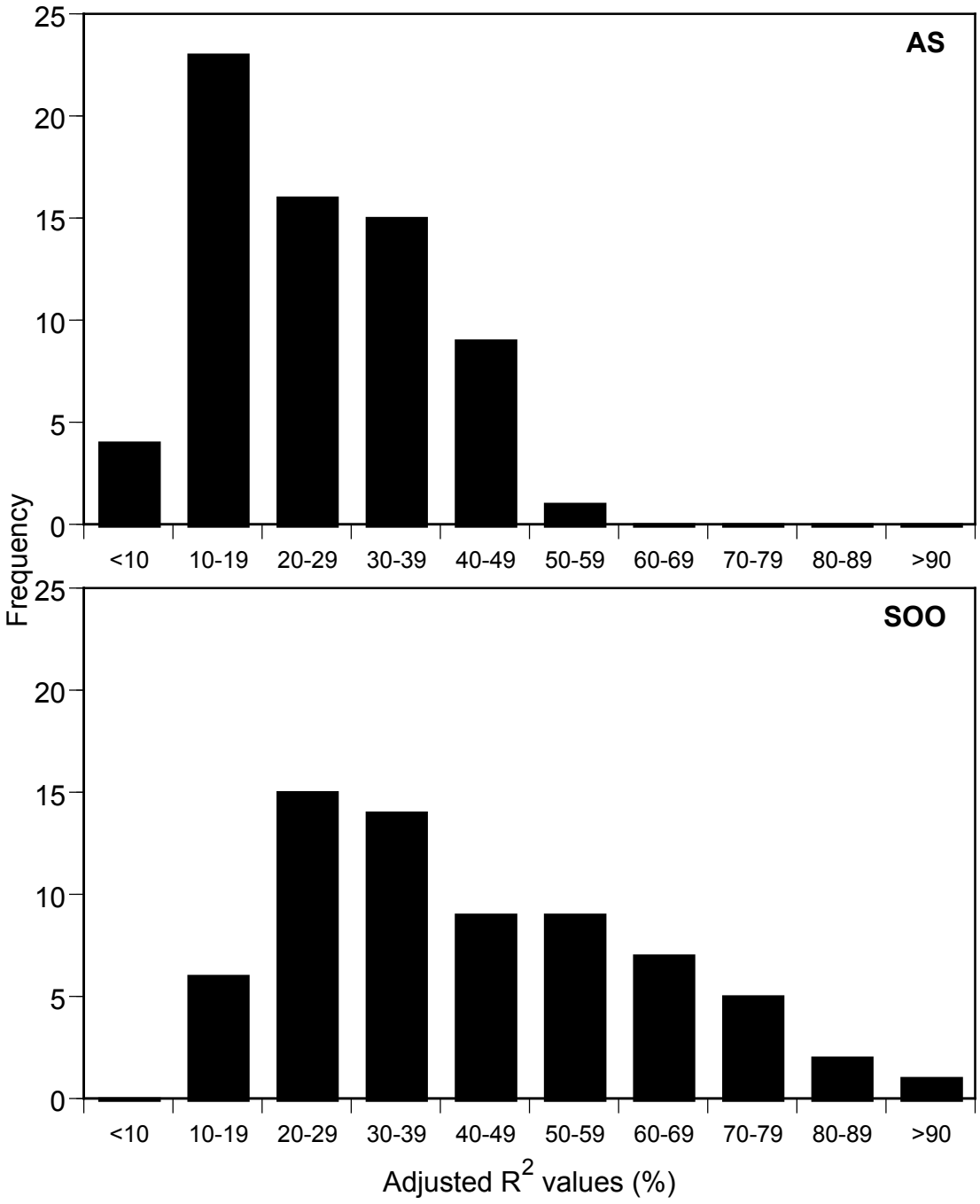

Figure 4.–Histogram of adjusted R^2 values for multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Histogram AS is for models based on all 263 sites having abundance data for the entire fish assemblage, and histogram SOO is for models based only on sites where each species occurred.

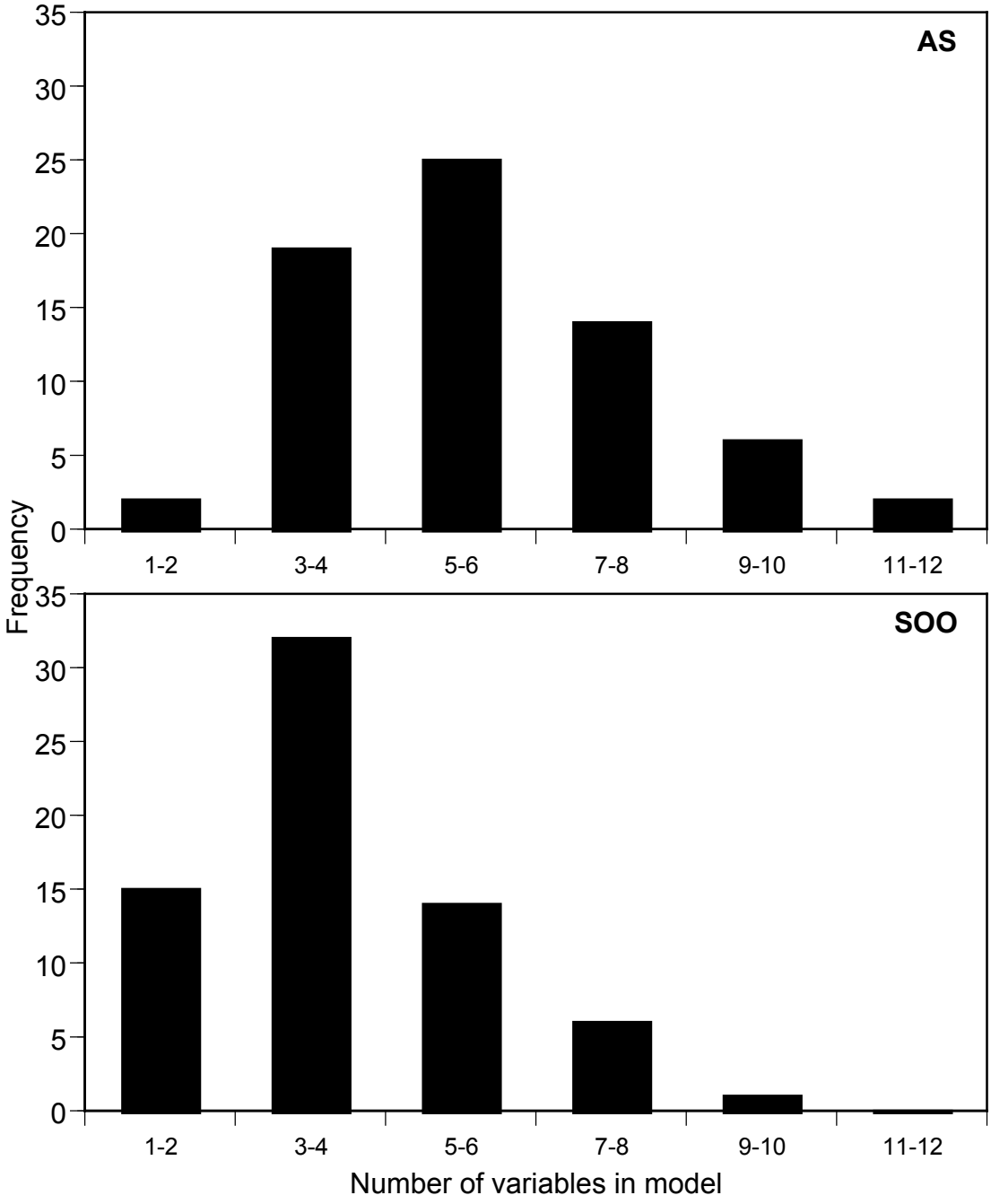

Figure 5.–Histogram of number of independent variables in multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Histogram AS is for models based on all 263 sites having abundance data for the entire fish assemblage, and histogram SOO is for models based only on sites where each species occurred.

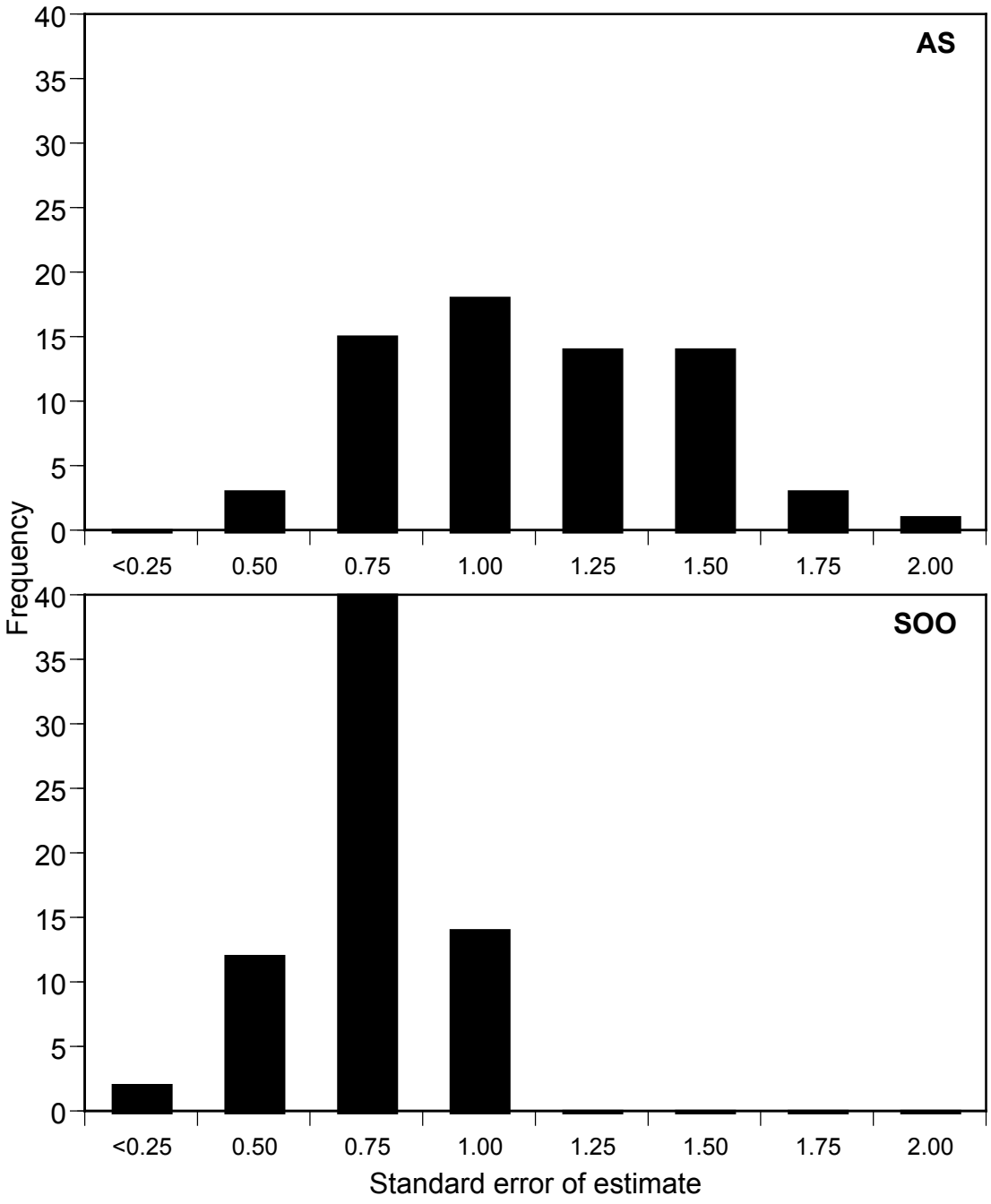

Figure 6.–Histogram of standard error of the estimate values in multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Histogram AS is for models based on all 263 sites having abundance data for the entire fish assemblage, and histogram SOO is for models based only on sites where each species occurred.

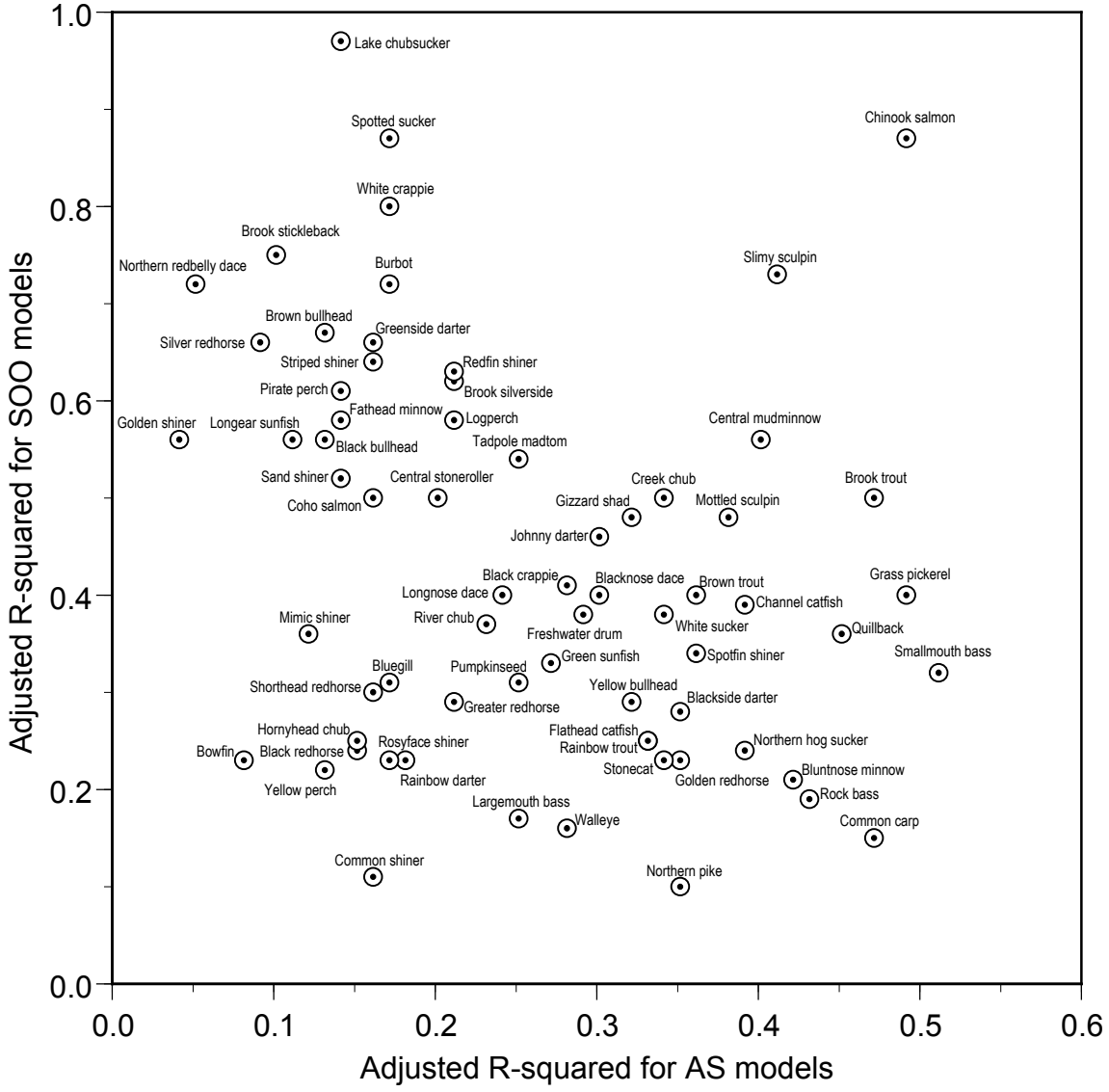

Figure 7.–Comparison of adjusted R^2 values from multiple linear regression models for 68 common common fishes in rivers of Michigan's Lower Peninsula. Models were developed for each species based on All Sites (AS) and Sites Of Occurrence (SOO) for each species.

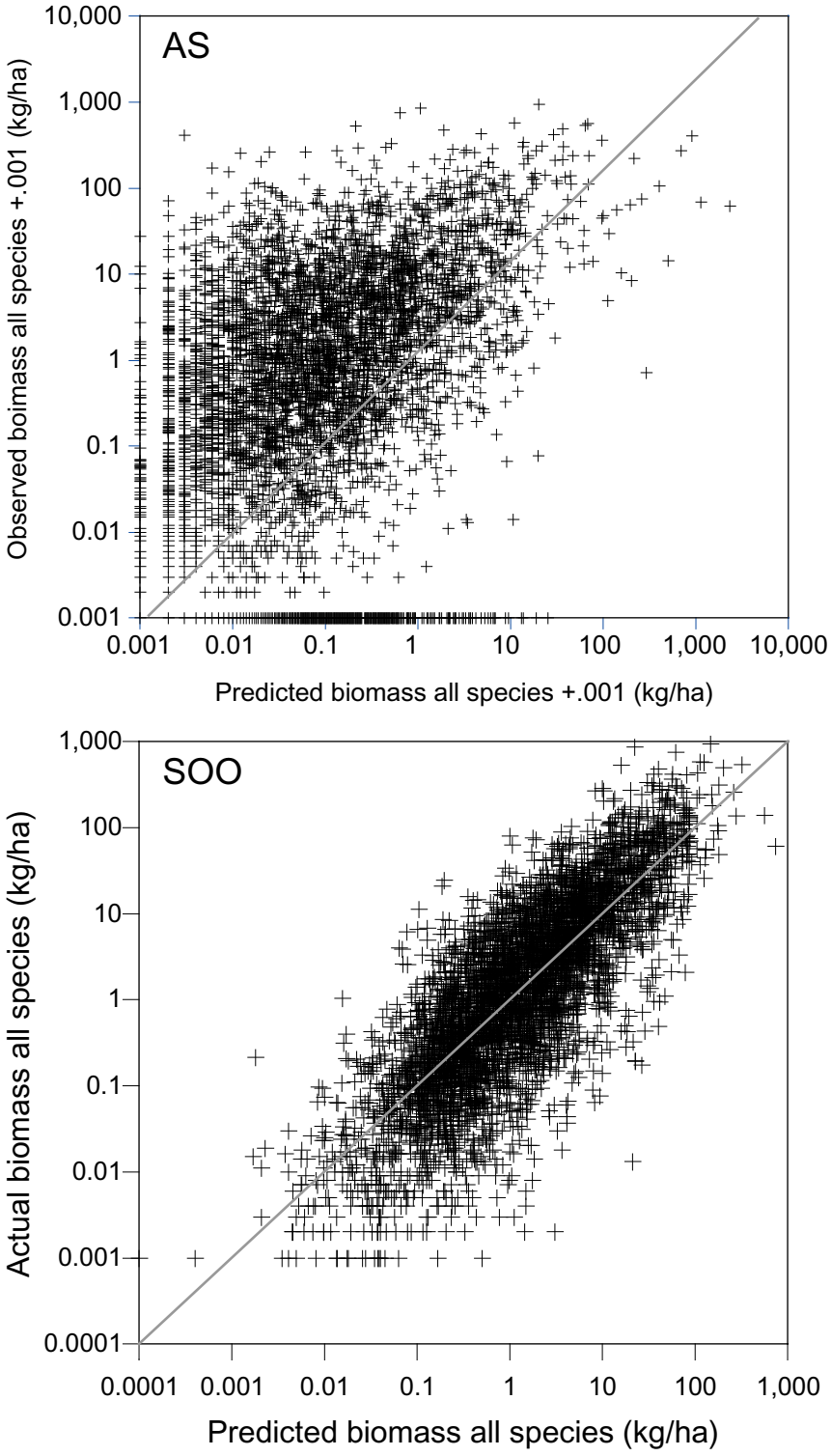

Figure 8.–Observed standing crops of 68 common fishes in lower Michigan rivers and predicted values from multiple linear regression models. Models were developed for each species based on All Sites (AS) and Sites Of Occurrence (SOO) for each species. A line indicating fit between observed and predicted values is shown.

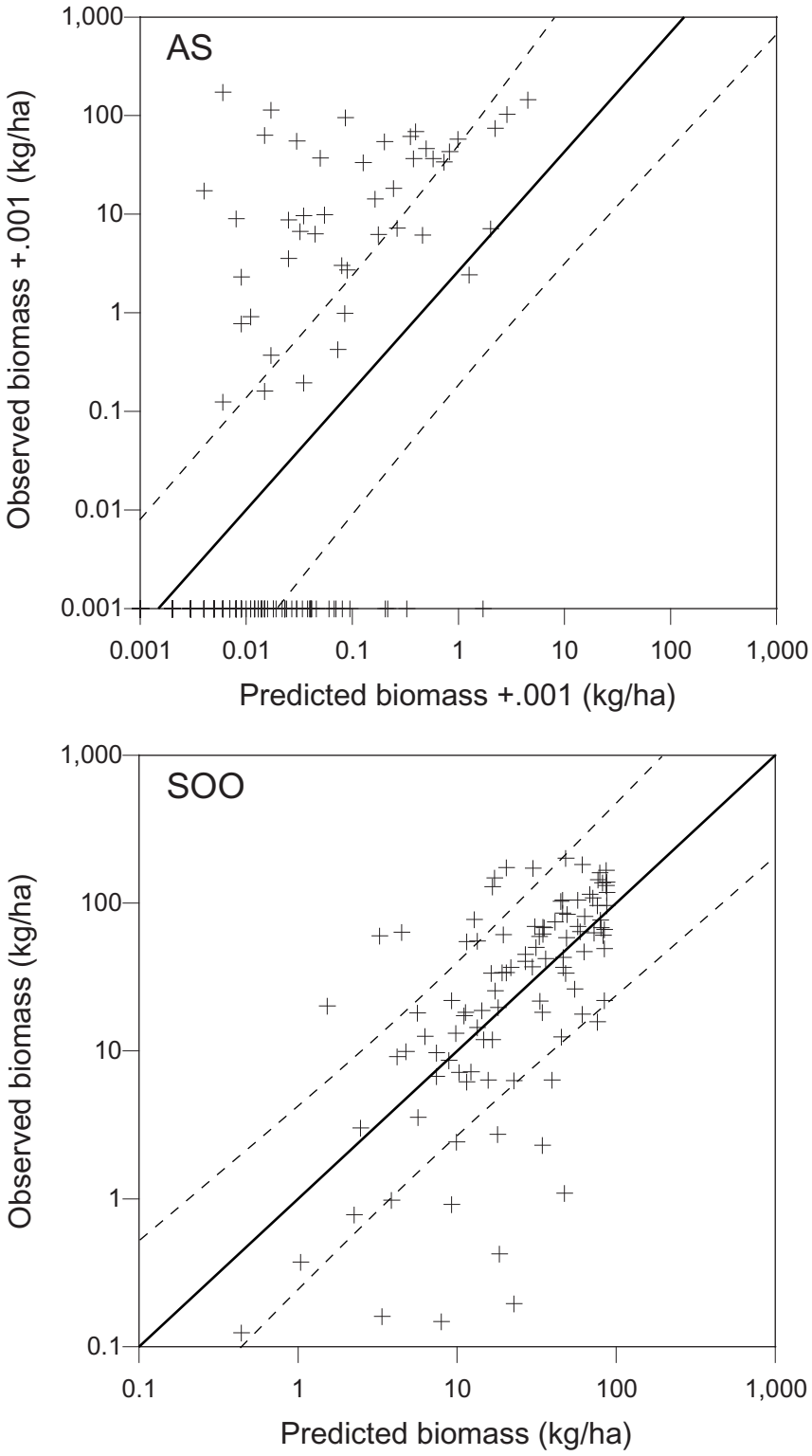

Figure 9.–Observed standing crops of brown trout in lower Michigan rivers and predicted values from multiple linear regression models. Models were developed from All Sites (AS) and brown trout Sites Of Occurrence (SOO). A line indicating fit between observed and predicted values, and 68% confidence intervals for individual predictions, are shown.

Table 1.–Standing crop values of 68 common fishes at 263 sites on rivers in Michigan's Lower Peninsula. Units are in kg/ha and the minimum value was 0.000 kg/ha for all species.

Common name	Scientific name	N	Maximum	Mean	Standard deviation
Black bullhead	*Ameiurus melas*	262	62.044	0.886	4.661
Black crappie	*Pomoxis nigromaculatus*	256	10.806	0.328	1.202
Black redhorse	*Moxostoma duquesnei*	262	257.015	3.275	19.343
Blacknose dace	*Rhinichthys atratulus*	262	64.081	2.631	8.625
Blackside darter	*Percina maculata*	246	7.218	0.423	0.847
Bluegill	*Lepomis macrochirus*	255	28.306	1.196	3.043
Bluntnose minnow	*Pimephales notatus*	239	53.653	1.685	4.824
Bowfin	*Amia calva*	263	14.628	0.235	1.283
Brook trout	*Salvelinus fontinalis*	263	205.950	4.824	20.612
Brook silverside	*Labidesthes sicculus*	259	3.897	0.050	0.352
Brook stickleback	*Culea inconstans*	262	6.481	0.061	0.447
Brown trout	*Salmo trutta*	263	173.350	5.733	21.004
Brown bullhead	*Ameiurus nebulosus*	263	31.722	0.357	2.516
Burbot	*Lota lota*	263	17.963	0.379	1.943
Central mudminnow	*Umbra limi*	257	214.778	2.676	15.823
Central stoneroller	*Campostoma anomalum*	262	116.559	1.058	7.701
Channel catfish	*Ictalurus punctatus*	261	79.703	2.805	9.804
Chinook salmon	*Oncorhynchus tshawytscha*	263	7.780	0.081	0.694
Coho salmon	*Oncorhynchus kisutch*	263	0.334	0.003	0.029
Common carp	*Cyprinus carpio*	263	943.123	65.025	137.078
Common shiner	*Luxilis cornutus*	244	89.107	4.687	9.462
Creek chub	*Semotilus atromaculatus*	256	284.483	11.566	32.464
Fathead minnow	*Pimephales promelas*	263	3.341	0.032	0.240
Flathead catfish	*Pylodictis olivaris*	263	52.597	0.664	4.288
Freshwater drum	*Aplodinotus grunniens*	263	88.081	0.449	5.518
Gizzard shad	*Dorsoma cepedianum*	263	266.037	1.675	17.128
Golden redhorse	*Moxostoma erythrurum*	251	479.090	18.196	49.982
Golden shiner	*Notemigonus crysoleucas*	260	6.553	0.076	0.591
Grass pickerel	*Esox americanus*	259	17.187	0.489	1.728
Greater redhorse	*Moxostoma valenciennesi*	258	92.563	1.892	8.352
Green sunfish	*Lepomis cyanellus*	252	29.244	1.613	3.825
Greenside darter	*Etheostoma blennioides*	262	1.859	0.065	0.252
Hornyhead chub	*Nocomis biguttatus*	259	62.581	2.142	6.843
Johnny darter	*Etheostoma nigrum*	245	21.687	0.543	1.702
Lake chubsucker	*Erimyzon sucetta*	263	16.595	0.098	1.072
Largemouth bass	*Micropterus salmoides*	257	18.340	0.782	2.220
Logperch	*Percina caprodes*	251	11.373	0.333	1.215
Longear sunfish	*Lepomis megalotis*	255	12.201	0.207	1.189
Longnose dace	*Rhinichthys cataractae*	263	6.860	0.112	0.606
Mimic shiner	*Notropis volucellus*	263	4.112	0.060	0.376
Mottled sculpin	*Cottus bairdi*	263	80.818	2.047	7.707
Northern hog sucker	*Hypentelium nigricans*	261	309.662	9.765	25.719
Northern pike	*Esox lucius*	260	87.166	2.826	7.360
Northern redbelly dace	*Phoxinus eos*	263	6.444	0.063	0.507
Pirate perch	*Aphredoderus sayanus*	263	23.035	0.217	1.695

Table 1.–continued.

Common name	Scientific name	N	Maximum	Mean	Standard deviation
Pumpkinseed	*Lepomis gibbosus*	253	22.063	1.079	3.074
Quillback	*Carpoides cyprinus*	263	65.848	1.098	6.605
Rainbow darter	*Etheostoma caeruleum*	259	8.429	0.234	0.793
Rainbow trout	*Oncorhynchus mykiss*	262	71.644	1.323	7.504
Redfin shiner	*Lythrurus umbratilis*	263	8.215	0.045	0.523
River chub	*Nocomis micropogon*	261	21.518	0.467	2.298
Rock bass	*Ambloplites rupestris*	258	79.631	6.108	11.169
Rosyface shiner	*Notropis rubellus*	260	3.489	0.156	0.497
Sand shiner	*Notropis stramineus*	247	2.352	0.064	0.296
Shorthead redhorse	*Moxostoma macrolepidotum*	258	264.955	4.583	22.455
Silver redhorse	*Moxostoma anisurum*	262	47.913	0.949	4.718
Slimy sculpin	*Cottus cognatus*	263	23.200	0.429	2.491
Smallmouth bass	*Micropterus dolomieu*	261	76.178	3.977	8.412
Spotfin shiner	*Cyprinella spiloptera*	241	12.148	0.319	1.267
Spotted sucker	*Minytrema melanops*	263	10.536	0.236	1.130
Stonecat	*Noturus flavus*	263	66.930	3.089	8.747
Striped shiner	*Luxilis chrysocephalus*	254	24.758	0.453	2.554
Tadpole madtom	*Noturus gyrinus*	262	10.052	0.190	0.935
Walleye	*Stizostedion vitreum*	263	23.828	0.601	2.500
White crappie	*Pomoxis annularis*	263	8.391	0.087	0.695
White sucker	*Catostomus commersoni*	263	420.831	24.348	48.844
Yellow bullhead	*Ameiurus natalis*	256	62.776	2.592	6.606
Yellow perch	*Perca flavescens*	256	4.187	0.143	0.474

Table 2.–Descriptions of variables occurring in multiple linear regression models for 68 fishes at 263 sites on Lower Michigan rivers. 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 different transformations of the independent variables (x's) used in models. Transformed forms were: 1) x and x^2; 2) x and $\log_{10}x$; 3) $\log_{10}x$; 4) x and $\log_{10}(x + 0.01)$; 5) $\log_{10}(x + 0.001)$; 6) x and $\log_{10}(x + 1)$; and 7) $\log_{10}x$ and $(\log_{10}x)^2$. Species combined for predator variables occur in Table 3.

Variable name	Variable description (units)	N	Min.	Max.	Mean	Standard deviation	Type
	Energetic						
BESTMEAN	July mean temperature (^oC)	263	9.2	26.40	21.1	3.0	C-1
TOTPPPM	Total phosphorus (mg/L)	263	0.004	0.31	0.08	0.040	C-2
	Site-scale hydraulic and hydrology						
LGVEL90	Velocity at 90% exceedence flow (m/s)	263	0.00	29.66	0.31	1.83	P-3
DEPMBEST	Depth at 90% exceedence flow (m)	263	0.02	1.47	0.48	0.28	C-2
LG90CMSK	90% exceedence flow yield ($m^3 \cdot s^{-1} \cdot km^{-2}$)	263	<0.0000	0.032	0.0031	0.0036	C-3
LG10CMSK	10% exceedence flow yield ($m^3 \cdot s^{-1} \cdot km^{-2}$)	263	0.0038	0.059	0.018	0.0046	C-3
	Site-scale channel characteristics						
SUBSI	Percent of substrate as silt (%)	247	0	100	16.7	19.3	M
SUBSA	Percent of substrate as sand (%)	247	0	100	37.9	25.6	M
SUBGR	Percent of substrate as gravel (%)	247	0	90	22.9	18.9	M
SUBCO	Percent of substrate as cobble (%)	247	0	75	12.5	14.3	M
SUBBE	Percent of substrate as bedrock (%)	247	0	75	1.4	8.4	M
SUBOR	Percent of substrate as organic (%)	247	0	30	0.4	2.4	M
SUBBO	Percent of substrate as boulder (%)	247	0	25	3.1	5.2	M
SUBCL	Percent of substrate as clay (%)	247	0	93	5.2	15.8	M
SANDSM	Proportion sand and finer substrates	247	0	1	0.5	0.3	M-4
GRAVELLG	Proportion gravel and coarser substrates	247	0	1	0.4	0.3	M-4
RIFFLE	Percent site as riffle (%)	235	0	100	20.3	26.6	M-6
BNKST	Percent of streambank as stable (%)	241	0	100	75.8	37.8	M-6
BNKMOSE	Percent of streambank as moderately or severely eroding (%)	241	0	100	16.0	32.5	M-6
BRDCO1_1	Percent of streambank within 0-3m of channel as brush, decidious, or coniferous (%)	244	0	100	76.7	29.8	M-6
BRDCO10_	Percent of streambank within 3-33m of channel as brush, decidious, or coniferous (%)	244	0	100	68.6	33.2	M-6

Table 2–.Continued.

Variable name	Variable description (units)	N	Min.	Max.	Mean	Standard deviation	Type
	Reach-scale channel character and connectivity						
GRADPERC	Percent channel gradient (%)	263	0.004	5.12	0.19	0.539	M-1,5
SINUOSIT	Sinuousity (channel length/valley length)	263	1.00	2.64	1.4	0.30	M-2
L4WATWET	Proportion of water and wetlands within 4 km upstream of site	263	0	0.23	0.02	0.02	M-4
BWATER	Proportion of water in the upstream river network	259	0	0.10	0.02	0.02	M-4
BURBAN	Proportion of urban land use in 2 km total width upstream riparian buffer	259	0	0.75	0.07	0.08	M-4
BAGRIC	Proportion of agricultural land use in 2 km total width upstream riparian buffer	259	0	0.91	0.46	0.24	M-4
BNFORWET	Proportion of non-forested wetlands in 2 km total width upstream riparian buffer	259	0	0.17	0.05	0.04	M-4
G_LKS	Is site accessible to Great Lakes fishes (yes=1)?	253	0(214)	1(39)	0.1542	0.362	M
PONDUPST	Is a lake or pond <3.5 km upstream of site (yes=1)?	253	0(209)	1(44)	0.1739	0.380	M
BIGRIVER	Is site on or connected to a river having a catchment > 1000 km2 (yes=1)?	251	0(192)	1(59)	0.2351	0.425	M
LNKDLNK	Is a barrier between the site and the next considerably larger (link# at least 10% greater) reach downstream (yes=1)?	253	0(195)	1(58)	0.2292	0.421	M
	Catchment-scale						
LOGDAKM	Catchment area (km^2)	263	1.0	14287.6	1051.0	2073.6	M-7
OUTWGEO	Proportion of outwash geology in catchment	263	0.00	1.00	0.30	0.25	M-4
COARSGEO	Proportion of coarse geology in catchment	263	0.00	1.00	0.25	0.24	M-4
FINEGEO	Proportion of fine geology in catchment	263	0.00	1.00	0.14	0.25	M-4
URBAN	Proportion of urban land use in catchment	263	0.00	0.79	0.06	0.08	M-4
AGRIC	Proportion of agricultural land use in catchment	263	0.00	0.92	0.48	0.25	M-4
FOREST	Proportion of forest in catchment	263	0.03	1.00	0.34	0.25	M-4
WATWETLA	Proportion of water and wetlands in catchment	263	0.00	0.13	0.02	0.02	M-4
CRSNOUTW	Proportion of coarse and outwash geology in catchment	263	0.00	1.00	0.55	0.35	M-4
	Predation						
COLDPRED	Biomass of coldwater predators (kg/ha)	263	0	173.35	5.733	21.004	M-5
COOLPRED	Biomass of coolwater predators (kg/ha)	260	0	87.16	3.210	7.677	M-5
WARMPRED	Biomass of warmwater predators (kg/ha)	245	0	137.21	19.442	25.438	M-5

Table 3.–Piscivorous fishes whose standing crop values were correlated against residuals of habitat-based multiple linear regression models of 68 species common in lower Michigan streams. Fishes were also categorized by general thermal preference as shown below and their standing crop values combined into the predator biomass variables shown in Table 2.

General thermal preference	Species
Coldwater	Brown trout
Coolwater	Burbot
	Northern pike
Warmwater	Black crappie
	Black bullhead
	Bowfin
	Brown bullhead
	Channel catfish
	Flathead catfish
	Grass pickerel
	Largemouth bass
	Rock bass
	Smallmouth bass
	Walleye
	White crappie
	Yellow bullhead
	Yellow perch

Table 4.–Pearson-product moment correlation matrix of variables* commonly used in regression models of fish density in lower Michigan rivers. Correlations significant at P< 0.05 level (2-tailed) are shown in italics and correlation coefficients higher than 0.5 are in bold type. Correlations were calculated from raw or transformed variables described in Table 2. Log-transformed variables begin with "LG" or "LOG".

	BESTMEAN	LGTOTP	LGVEL90	DEPMBEST	LG90CMSK	LG10CMSK	SANDSM	GRAVELLG	RIFFLE	BNKST	LGGRADPE	SINUOSIT	L4WATWET	BWATER	BURBAN	BAGRIC	BNFORWET	G_LKS	PONDUPST	BIGRIVER	LNKDLNK	LOGDAKM	OUTWGEO	COARSGEO	FINEGEO	URBAN	AGRIC	FOREST	WATWETLA
BESTMEAN	1.00																												
LGTOTP	***0.51***	1.00																											
LGVEL90	0.02	*-0.35*	1.00																										
DEPMBEST	***0.51***	0.10	*0.40*	1.00																									
LG90CMSK	*-0.19*	*-0.31*	***0.67***	*0.23*	1.00																								
LG10CMSK	*-0.29*	-0.06	0.07	*-0.16*	*0.43*	1.00																							
SANDSM	*-0.19*	*-0.15*	0.02	-0.08	-0.02	0.00	1.00																						
GRAVELLG	*0.20*	0.09	*0.14*	*0.15*	*0.21*	0.03	***-0.85***	1.00																					
RIFFLE	*-0.18*	*-0.14*	0.09	*-0.22*	*0.27*	*0.21*	*-0.41*	***0.52***	1.00																				
BNKST	*-0.14*	*-0.25*	*0.25*	0.06	*0.34*	0.09	-0.11	*0.21*	0.11	1.00																			
LGGRADPE	***-0.72***	*-0.39*	*-0.12*	***-0.61***	0.11	*0.25*	-0.10	0.09	*0.42*	0.11	1.00																		
SINUOSIT	*0.24*	-0.04	*0.25*	*0.20*	*0.15*	-0.07	0.02	-0.04	0.05	*-0.13*	*-0.26*	1.00																	
L4WATWET	-0.01	*0.15*	*0.19*	*0.15*	*0.22*	0.10	0.03	0.05	0.12	*0.15*	-0.09	0.05	1.00																
BWATER	0.07	0.08	*0.31*	0.05	*0.36*	0.00	0.06	0.03	*0.17*	*0.15*	-0.11	*0.21*	*0.23*	1.00															
BURBAN	0.06	*0.31*	0.00	0.01	0.05	0.05	-0.07	0.07	*0.15*	-0.07	0.04	-0.03	*0.16*	*0.32*	1.00														
BAGRIC	*0.45*	***0.72***	*-0.45*	0.09	*-0.49*	-0.11	-0.10	-0.01	*-0.28*	*-0.26*	*-0.38*	*-0.14*	-0.10	*-0.33*	*-0.19*	1.00													
BNFORWET	0.12	*0.12*	*0.34*	0.11	*0.34*	-0.02	0.03	0.09	0.05	*0.25*	*-0.14*	*0.19*	*0.27*	***0.54***	*0.17*	*-0.30*	1.00												
G_LKS	*-0.18*	*-0.19*	-0.03	-0.02	-0.08	0.11	-0.04	-0.04	*0.15*	0.05	0.10	-0.01	0.06	*-0.20*	*-0.13*	-0.04	*-0.28*	1.00											
PONDUPST	*0.15*	*0.16*	*0.13*	0.10	*0.15*	0.04	-0.08	*0.15*	0.08	0.01	-0.07	0.06	*0.14*	*0.23*	*0.13*	0.03	*0.20*	-0.08	1.00										
BIGRIVER	*-0.26*	0.08	0.03	*-0.28*	*0.14*	*0.17*	*0.23*	*-0.22*	-0.02	0.10	0.11	-0.10	*0.16*	*0.32*	0.04	-0.11	*0.31*	*-0.23*	0.07	1.00									
LNKDLNK	*0.21*	0.12	*0.17*	*0.19*	*0.14*	0.01	*-0.20*	*0.24*	0.13	0.06	-0.10	0.05	*0.14*	*0.15*	0.10	0.01	*0.22*	*-0.23*	*0.22*	*0.14*	1.00								
LOGDAKM	***0.77***	*0.25*	*0.32*	***0.75***	0.10	*-0.27*	*-0.25*	*0.35*	-0.11	0.01	***-0.71***	*0.30*	0.06	0.08	-0.05	*0.26*	0.12	-0.09	*0.15*	*-0.34*	*0.30*	1.00							
OUTWGEO	*-0.14*	*-0.31*	***0.78***	*0.20*	***0.54***	0.00	0.02	0.09	0.12	*0.24*	-0.02	*0.18*	0.10	*0.35*	0.02	*-0.39*	*0.31*	-0.05	*0.15*	0.08	*0.13*	*0.14*	1.00						
COARSGEO	*-0.15*	-0.08	*0.13*	-0.01	*0.49*	*0.27*	0.05	0.05	0.10	*0.28*	0.12	0.02	*0.33*	*0.30*	0.00	*-0.28*	*0.45*	-0.07	0.09	*0.20*	0.12	-0.09	0.03	1.00					
FINEGEO	0.06	*0.16*	*-0.38*	*-0.21*	*-0.47*	-0.08	0.02	*-0.20*	-0.11	*-0.23*	0.01	0.00	*-0.20*	*-0.30*	0.00	*0.31*	*-0.33*	*0.15*	-0.06	0.00	-0.09	-0.10	*-0.41*	*-0.40*	1.00				
URBAN	0.09	*0.33*	-0.01	0.05	0.03	0.02	-0.09	0.09	*0.13*	-0.08	0.00	-0.02	*0.14*	*0.30*	***0.98***	*-0.17*	*0.16*	-0.12	0.11	0.02	0.10	0.01	0.01	-0.03	-0.02	1.00			
AGRIC	*0.45*	***0.77***	*-0.41*	0.11	*-0.43*	-0.08	-0.11	0.02	*-0.29*	*-0.25*	*-0.38*	*-0.13*	-0.07	*-0.29*	*-0.17*	***0.98***	*-0.24*	-0.05	0.06	-0.08	0.04	*0.26*	*-0.34*	*-0.21*	*0.28*	*-0.14*	1.00		
FOREST	*-0.46*	***-0.94***	*0.38*	-0.12	*0.33*	0.03	*0.16*	-0.10	*0.17*	*0.27*	*0.36*	0.10	-0.06	0.04	*-0.27*	***-0.83***	0.08	*0.13*	*-0.13*	0.01	-0.09	*-0.24*	*0.32*	*0.14*	*-0.19*	*-0.30*	***-0.87***	1.00	
WATWETLA	0.07	*0.18*	*0.32*	0.07	*0.37*	-0.01	-0.03	0.11	*0.20*	*0.15*	-0.09	*0.24*	*0.31*	***0.80***	*0.23*	*-0.34*	***0.70***	*-0.20*	*0.20*	*0.31*	*0.16*	0.10	*0.33*	*0.36*	*-0.28*	*0.23*	*-0.28*	0.03	1.00

* Variable names (and descriptions): BESTMEAN (July mean temperature); LGTOTP (total phosphorus); LGVEL90 (current velocity at 90% exceedence flow); DEPMBEST (depth at 90% exceedence flow); LG90CMSK (90% exceedence flow yield); LG10CMSK (10% exceedence flow yield); SANDSM (% sand and finer substrate); GRAVELLG (% gravel and larger substrate); RIFFLE (% riffle); BNKST (% of banks that are stable); LGGRADPE (reach gradient); SINUOSIT (reach sinuosity); L4WATWET (% water and wetlands within 4 km upstream); BWATER (% water in upstream buffer); BURBAN (% urban land use in upstream buffer); BAGRIC (% agricultural land use in upstream buffer); BNFORWET (% nonforested wetlands in upstream buffer); G_LKS (1=Great Lakes connection); PONDUPST (1=pond <3.5km upstream); BIGRIVER (1=on or connected to a large river downstream); LNKDLNK (1=a barrier occurs before junction with next large downstream tributary); LOGDAKM (catchment area); OUTWGEO (% outwash geology in wetlands in catchment); COARSGEO (% coarse geology in catchment); FINEGEO (% fine geology in catchment); URBAN (% urban land use in catchment); AGRIC (% agricultural land use in catchment; FOREST (% forest cover in catchment); WATWETLA (% water and wetlands in catchment).

Table 5.–Adjusted R^2 (R^2), standard error of the estimate (SEE), ANOVA significance level (P), and total degrees of freedom (n) for multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Species densities were transformed as $\log_{10}(x + 0.001)$ where x equals fish density in kg/ha. Models for species with an asterisk were developed only from sites accessible to the Great Lakes.

	All Sites models				Sites Of Occurrence models			
Common name	R^2	SEE	P	n	R^2	SEE	P	n
Black bullhead	0.13	1.18	<0.001	237	0.56	0.67	<0.001	54
Black crappie	0.28	1.05	<0.001	255	0.41	0.57	<0.001	85
Black redhorse	0.15	1.24	<0.001	231	0.24	0.83	0.010	29
Blacknose dace	0.30	1.30	<0.001	259	0.40	0.94	<0.001	79
Blackside darter	0.35	1.04	<0.001	215	0.28	0.52	<0.001	133
Bluegill	0.17	1.34	<0.001	229	0.31	0.67	<0.001	140
Bluntnose minnow	0.42	1.13	<0.001	212	0.21	0.75	<0.001	141
Bowfin	0.08	0.81	<0.001	262	0.23	0.55	0.023	18
Brook silverside	0.10	0.54	<0.001	244	0.62	0.72	0.013	11
Brook stickleback	0.21	0.66	<0.001	245	0.75	0.44	<0.001	38
Brook trout	0.47	0.98	<0.001	262	0.50	0.64	<0.001	62
Brown bullhead	0.13	0.84	<0.001	230	0.67	0.44	<0.001	24
Brown trout	0.36	1.29	<0.001	240	0.40	0.59	<0.001	102
Burbot	0.17	0.85	<0.001	262	0.72	0.43	<0.001	23
Central mudminnow	0.40	1.11	<0.001	238	0.56	0.79	<0.001	137
Central stoneroller	0.20	1.07	<0.001	228	0.50	0.75	<0.001	64
Channel catfish	0.39	1.14	<0.001	250	0.39	0.79	<0.001	43
Chinook salmon*	0.49	0.78	<0.001	45	0.87	0.26	<0.001	15
Coho salmon*	0.16	0.37	0.006	38	0.50	0.64	0.014	9
Common carp	0.47	1.75	<0.001	262	0.15	0.77	<0.001	119
Common shiner	0.16	1.55	<0.001	243	0.11	0.80	<0.001	167
Creek chub	0.34	1.41	<0.001	232	0.50	0.83	<0.001	161
Fathead minnow	0.14	0.53	<0.001	240	0.58	0.49	0.001	19
Flathead catfish	0.33	0.70	<0.001	252	0.25	0.76	0.049	12
Freshwater drum	0.29	0.56	<0.001	252	0.38	0.53	0.045	8
Gizzard shad	0.32	0.72	<0.001	252	0.48	0.86	0.011	13
Golden redhorse	0.35	1.71	<0.001	231	0.23	0.78	<0.001	92
Golden shiner	0.04	0.67	0.007	243	0.56	0.67	<0.001	29
Grass pickerel	0.49	0.95	<0.001	234	0.40	0.53	<0.001	74
Greater redhorse	0.21	1.13	<0.001	241	0.29	0.37	0.007	25
Green sunfish	0.27	1.29	<0.001	230	0.33	0.65	<0.001	151
Greenside darter	0.16	0.75	<0.001	241	0.66	0.38	<0.001	30
Hornyhead chub	0.15	1.49	<0.001	224	0.25	0.80	<0.001	101
Johnny darter	0.30	0.99	<0.001	222	0.46	0.58	<0.001	160

Table 5.–Continued.

	All Sites models				Sites Of Occurrence models			
Common name	R^2	SEE	P	n	R^2	SEE	P	n
Lake chubsucker	0.14	0.47	<0.001	257	0.97	0.18	0.001	8
Largemouth bass	0.25	1.24	<0.001	231	0.17	0.82	<0.001	125
Logperch	0.21	1.02	<0.001	246	0.58	0.53	<0.001	48
Longear sunfish	0.11	0.82	<0.001	250	0.56	0.57	<0.001	26
Longnose dace	0.24	0.69	<0.001	234	0.40	0.46	0.006	21
Mimic shiner	0.12	0.62	<0.001	230	0.36	0.72	0.022	18
Mottled sculpin	0.38	1.14	<0.001	230	0.48	0.74	<0.001	69
Northern hog sucker	0.39	1.57	<0.001	238	0.24	0.57	<0.001	127
Northern pike	0.35	1.42	<0.001	247	0.10	0.59	0.001	125
Northern redbelly dace	0.05	0.56	0.002	252	0.72	0.58	<0.001	17
Pirate perch	0.14	0.76	<0.001	236	0.61	0.65	<0.001	30
Pumpkinseed	0.25	1.25	<0.001	238	0.31	0.58	<0.001	145
Quillback	0.45	0.73	<0.001	244	0.36	0.67	0.017	16
Rainbow darter	0.18	1.07	<0.001	242	0.23	0.70	<0.001	103
Rainbow trout	0.33	0.90	<0.001	231	0.25	0.78	<0.001	53
Redfin shiner	0.21	0.50	<0.001	242	0.63	0.47	<0.001	23
River chub	0.23	0.88	<0.001	238	0.37	0.65	0.003	27
Rock bass	0.43	1.31	<0.001	241	0.19	0.57	<0.001	180
Rosyface shiner	0.17	0.99	<0.001	243	0.23	0.61	0.002	53
Sand shiner	0.14	0.73	<0.001	224	0.52	0.53	<0.001	28
Shorthead redhorse	0.16	1.39	<0.001	235	0.30	0.63	0.001	42
Silver redhorse	0.09	1.00	<0.001	251	0.66	0.25	<0.001	18
Slimy sculpin	0.41	0.61	<0.001	240	0.73	0.35	<0.001	15
Smallmouth bass	0.51	1.31	<0.001	228	0.32	0.60	<0.001	113
Spotfin shiner	0.36	0.93	<0.001	217	0.34	0.64	<0.001	53
Spotted sucker	0.17	0.77	<0.001	244	0.87	0.16	<0.001	15
Stonecat	0.34	1.43	<0.001	242	0.23	0.71	<0.001	98
Striped shiner	0.16	0.87	<0.001	234	0.64	0.68	<0.001	21
Tadpole madtom	0.25	0.80	<0.001	257	0.54	0.57	<0.001	31
Walleye	0.28	1.00	<0.001	248	0.16	0.83	0.024	39
White crappie	0.17	0.57	<0.001	240	0.80	0.39	<0.001	11
White sucker	0.34	1.39	<0.001	258	0.38	0.63	<0.001	198
Yellow bullhead	0.32	1.42	<0.001	245	0.29	0.65	<0.001	103
Yellow perch	0.13	1.00	<0.001	255	0.22	0.55	0.001	58
Averages	0.26	1.00	<0.001	235	0.43	0.61	0.004	65

Table 6.–Total occurrences of variables significant at $P < 0.10$ in All Sites (AS) and Sites of Occurrence (SOO) regression models for 68 common fishes in Lower Michigan Rivers.

Variable description	Total occurrences	
	SOO models	AS models
Catchment area	25	38
July mean temperature	22	28
Gravel or coarser substrates	17	17
Channel gradient	13	24
Sand or finer substrates	12	8
Total phosphorus	12	18
Percent water and wetlands within 4 km upstream	11	11
Depth at 90% exceedence flow	10	9
Site is accessible to Great Lakes	10	13
Percent urban land use in catchment	10	8
Percent riffle	9	10
Percent agricultural land use in catchment	9	14
Barrier occurs between site and the next considerably larger reach downstream	8	9
Velocity at 90% exceedence flow	7	4
Bank stability	7	15
Percent water in the upstream river network	7	14
A lake or pond is <3.5 km upstream of site	7	11
Percent outwash geology in catchment	6	6
Percent water and wetlands in catchment	6	10
90% exceedence flow yield	5	12
10% exceedence flow yield	5	6
Percent urban land use in 2 km total width upstream riparian buffer	5	6
Percent agricultural land use in 2 km total width upstream riparian buffer	5	8
Percent fine geology in catchment	5	7
Percent of riparian corridor as brush, decidious, or coniferous	4	2
Percent non-forested wetlands in 2 km total width upstream riparian buffer	4	11
Sinuousity	3	8
Percent coarse geology in catchment	3	11
Site is on or connected to a river having a CA > 1000 km2	2	9
Percent forest in catchment	2	2
Percent coarse and outwash geology in catchment	1	2
Recent distribution range	n/a	2
Total	252	353

Table 7.–Frequency of occurrence of different categories of variables in All Sites (AS) and Sites of Occurrence (SOO) regression models for 68 fishes common in lower Michigan rivers. Data are sorted by the weighted frequency of occurrence of each category in SOO models. Variable names (in capital letters) or types (lower case letters) for each category are listed within parentheses.

Category (and variables included)	Variables in category	Total occurrences		Weighted frequency of occurrence	
		SOO	AS	SOO	AS
Catchment- catchment area (LOGDAKM)	1	25	38	25.0	38.0
Energetic- July temperature (BESTMEAN)	1	22	28	22.0	28.0
Energetic- Total phosphorus (TOTPPPM)	1	12	18	12.0	18.0
Reach- geomorphology (GRADPERC, SINUOSIT)	2	16	32	8.0	16.0
Reach- connectivity (BWATER, L4WATWET, G_LKS, PONDUPST, BIGRIVER, LNKDLNK)	6	45	67	7.5	11.2
Site- hydrology and velocity (LG90CMSK, LG10CMSK,LGVEL90, DEPMBEST)	4	27	31	6.8	7.8
Catchment- landuse/landcover (URBAN, AGRIC, FOREST, WATWETLA)	4	27	34	6.8	8.5
Reach- upstream riparian landuse/landcover (BURBAN, BAGRIC, BNFORWET)	3	14	25	4.7	8.3
Catchment- geology (OUTWGEO, COARSGEO, CRSNOUTW, FINEGEO)	4	15	26	3.8	6.5
Site- channel characteristics (substrate, RIFFLE, bank stability, riparian cover)	14	50	52	3.6	3.7

Table 8a.–Sign of coefficients of urban land use variables that were significant at $P < 0.10$ for fishes in both the All Sites and Sites of Occurrence regression models. Variables described the proportion of urban land use in upstream riparian buffer or catchment of site. An asterisk indicates use of the $\log_{10}$-transformed form of the variable.

	Variable description (and variable name)	
Species common name	Buffer (BURBAN)	Catchment (URBAN)
Bluegill	-	
Lake chubsucker	-	
Rock bass		-
Central mudminnow		-*
Hornyhead chub		-*
Rainbow darter		-*
White sucker		+*

Table 8b.–Sign of coefficients of agricultural land use variables that were significant at $P < 0.10$ for fishes in both the All Sites and Sites of Occurrence regression models. Variables described the proportion of agricultural land use in upstream riparian buffer or catchment of site.

	Variable description (and variable name)	
Species common name	Buffer (LGBAGRIC)	Catchment (AGRIC)
Common carp	+	
White sucker	+	
Longnose dace		+
Redfin shiner		+
Bluntnose minnow		+

Table 8c.–Sign of coefficients of upstream connectivity variables that were significant at $P < 0.10$ for fishes in both the All Sites and Sites of Occurrence regression models. Variables described the following: proportion of water and wetlands in local (4 km) riparian buffer upstream of site; proportion of water in riparian buffer of upstream river network; and occurrence of a lake or pond < 3.5 km upstream of site. An asterisk indicates use of the $\log_{10}$-transformed form of the variable.

	Variable description (and variable name)		
Species common name	Local buffer (L4WATWET)	Network buffer (BWATER)	Pond upstream (PONDUPST)
Northern hog sucker	-		
White sucker	-		
Mottled sculpin			-
Bluegill	+		+
Pumpkinseed	+	+	
Largemouth bass	+*		+
Black crappie		+	+
River chub		+	
Golden shiner		+	
Rock bass		+	

Table 8d.–Sign of coefficients of downstream connectivity variables that were significant at $P < 0.10$ for fishes in both the All Sites and Sites of Occurrence regression models. Variables described whether the site was: connected to the Great Lakes; on or connected to a big river (draining > 1000 km^2); separated from the next larger reach downstream by a dam.

	Variable description (and variable name)		
Species common name	Great Lakes (G_LKS)	Big river (BIGRIVER)	Larger reach (LNKDLNK)
Striped shiner			+
Walleye	+		
Spotted sucker	+		
Blacknose dace		+	
Bluegill			-

Table 9.–Changes to regression models when predators were added to the model and had significant, negative regression coefficients. Shown are changes in adjusted R^2 values and variables displaced (i.e. no longer significant at P = 0.10) when potential predators were added to Sites Of Occurrence (SOO) models for 68 fishes in lower Michigan rivers. Predator variables in bold were significant in the regression model (P < 0.10), occurred at more than 50% of sites with the modeled species, and did not displace habitat variables when added to the regression model. The three right-most columns indicate the proportion of times potential predators and prey co-occurred in the data. Letters A, B, and C in these columns follows the ordered list of potential predators in a model (e.g., predator B for the blacknose dace model is smallmouth bass).

Common name	Original R^2	R^2 with predators	Change in R^2	Potential predators in model	Variables displaced*	n	Predator A	Predator B	Predator C
Brook trout	0.50	0.51	0.02	**Brown trout**		56	0.66		
Blacknose dace	0.40	0.53	0.13	rock bass smallmouth bass yellow perch	BESTMEAN LGVEL90 BIGRIVER	86	0.52	0.21	0.16
Creek chub	0.50	0.53	0.04	**COOLPRED** **WARMPRED**		184	0.51	0.88	
Common shiner	0.11	0.14	0.03	Flathead catfish		168	0.01		
Golden redhorse	0.23	0.33	0.10	Flathead catfish	DEPMBEST	93	0.08		
Golden shiner	0.56	0.63	0.07	**Black crappie**		33	0.52		
Johnny darter	0.46	0.49	0.03	Smallmouth bass	BESTMEAN GRAVELLG	182	0.52		
Longnose dace	0.40	0.61	0.21	Black crappie	LOGDAKM	22	0.41		
Mimic shiner	0.36	0.49	0.14	Bowfin		20	0.15		
Mottled sculpin	0.48	0.56	0.09	Rock bass, burbot	DEPMBEST	72	0.42	0.17	
Central mudminnow	0.56	0.58	0.02	**Rock bass**		150	0.70		
Rainbow darter	0.23	0.30	0.07	black bullhead white crappie		109	0.22	0.03	
River chub	0.37	0.54	0.17	**COOLPRED**		29	0.86		
Rock bass	0.19	0.22	0.03	Flathead catfish	AGRIC	176	0.08		
Sand shiner	0.52	0.57	0.05	**COOLPRED**		31	0.87		
Silver redhorse	0.66	0.79	0.14	Yellow bullhead	AGRIC	19	0.68		
Spotfin shiner	0.34	0.39	0.05	White crappie		57	0.12		
Spotted sucker	0.87	0.94	0.07	**Largemouth bass**		17	0.82		
Slimy sculpin	0.73	0.80	0.08	Northern pike		16	0.13		
Stonecat	0.23	0.27	0.04	White crappie	SUBSI	103	0.05		

* Names (and descriptions) of displaced variables: BESTMEAN (July mean temperature); LGVEL90 (current velocity at 90% exceedence flow); BIGRIVER (1=on or connected to a large river downstream); DEPMBEST (depth at 90% exceedence flow); GRAVELLG (% gravel and larger substrate); LOGDAKM (catchment area); AGRIC (%agricultural land use in catchment); SUBSI (% silt).

Table 10.–Variables that displaced other variables or were displaced during development of All Sites (AS) and Sites Of Occurrence (SOO) multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. General variable descriptions are used because different forms of many variables were combined. Values are shown only for variables involved in more than five displacements.

Frequency		
SOO	AS	Variable description
		Variable entering
29	57	Catchment area
7	21	Channel gradient
7	11	Proportion agricultural land use in catchment
6	11	90% exceedence flow yield
6	-	Gravel or coarser substrates
6	-	Proportion fine geology in catchment
-	8	Depth at 90% exceedence flow
-	8	Proportion water in the upstream river network
-	7	Proportion non-forested wetlands in 2 km total width upstream riparian buffer
-	6	Proportion water and wetlands within 4 km upstream
-	6	Proportion water and wetlands in catchment
		Variable displaced
21	50	July mean temperature
16	14	Total phosphorus
15	21	Depth at 90% exceedence flow
15	16	Velocity at 90% exceedence flow
7	-	Gravel or coarser substrates
7	-	Channel gradient
6	8	90% exceedence flow yield
6	8	Sand or finer substrates

Table 11.–Most common displacements of variables that occurred during development of All Sites (AS) and Sites Of Occurrence (SOO) multiple linear regressions for 68 common fishes in rivers of Michigan's Lower Peninsula. Values are shown only for displacements occurring three or more times. General variable descriptions are used because different forms of many variables were combined.

SOO	AS	Variable entering	Displaced variable
7	22	Catchment area	July mean temperature
5	15	Catchment area	Depth at 90% exceedence flow
4	6	90% exceedence flow yield	Velocity at 90% exceedence flow
4	-	Catchment area	Channel gradient
3	6	Depth at 90% exceedence flow	July mean temperature
3	-	Catchment area	Total phosphorus
3	-	Catchment area	Velocity at 90% exceedence flow
-	7	Channel gradient	July mean temperature
-	5	Channel gradient	Sand or finer substrates
-	4	Proportion agricultural land use in catchment	Proportion agricultural land use in 2 km total width upstream riparian buffer
-	3	90% exceedence flow yield	July mean temperature
-	3	Channel gradient	Depth at 90% exceedence flow
-	3	Channel gradient	Velocity at 90% exceedence flow
-	3	Proportion agricultural land use in 2 km total width upstream riparian buffer	Total phosphorus
-	3	Catchment area	Sinuousity
-	3	Catchment area	Site is on or connected to a river having a CA > 1000 km2

Table 12.–Example showing use of predicted standing crop values from Sites Of Occurrence (SOO) models, and their upper and lower 68% confidence intervals, as benchmarks for comparison with observed standing crops of fishes from an independent, 1984 survey of the Raisin River at Academy Road in southeast Michigan (T6S R4E Section 32). Standing crop predictions were made only for species that occurred in a 1988 fisheries survey of the site. Status column indicates whether observed values were above (High), below (Low), or between (Ok) predicted confidence interval values.

	Standing crop (kg/ha)		68% Confidence Interval		
Common name	Observed	Predicted	Lower	Upper	Status
Common carp	51.518	160.763	27.211	949.788	Ok
Golden redhorse	34.160	6.332	1.055	38.006	Ok
White sucker	14.910	16.123	3.780	68.773	Ok
Northern hog sucker	8.679	7.289	1.957	27.142	Ok
Northern pike	7.678	2.590	0.670	10.006	Ok
Bluntnose minnow	4.451	0.598	0.107	3.340	High
Yellow bullhead	3.672	2.022	0.450	9.079	Ok
River chub	3.561	0.531	0.116	2.430	High
Rock bass	3.227	4.382	1.172	16.382	Ok
Spotfin shiner	3.227	3.639	0.830	15.946	Ok
Stonecat	2.893	4.238	0.818	21.947	Ok
Green sunfish	1.113	0.753	0.170	3.339	Ok
Smallmouth bass	0.890	5.244	1.327	20.719	Low
Blackside darter	0.445	0.198	0.060	0.661	Ok
Largemouth bass	0.445	0.078	0.012	0.514	Ok
Grass pickerel	0.334	0.168	0.049	0.572	Ok
Creek chub	0.111	0.106	0.016	0.708	Ok
Johnny darter	0.111	0.096	0.025	0.367	Ok
Bluegill	0.056	0.321	0.069	1.489	Low
Black crappie	0.056	0.194	0.052	0.728	Ok
Greenside darter	0.056	0.156	0.064	0.378	Low
Central stoneroller	0.056	0.047	0.008	0.266	Ok
Redfin shiner	0.056	0.016	0.005	0.048	High
Channel catfish	0.000	34.373	5.569	212.150	Low
Black redhorse	0.000	2.974	0.427	20.707	Low
Sand shiner	0.000	0.215	0.062	0.746	Low
Mottled sculpin	0.000	0.204	0.037	1.123	Low
Rosyface shiner	0.000	0.179	0.044	0.734	Low
Central mudminnow	0.000	0.017	0.003	0.107	Low
Mimic shiner	0.000	0.010	0.002	0.053	Low

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Appendix A.–Coefficients of variables in multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Models are based on All Sites (AS) with standing crop estimates for the entire fish assemblage (n= 263). Species densities were transformed as log10(x + 0.001) where x equals fish density in kg/ha. An asterisk following the coefficient indicates that variable is $\log_{10}$ transformed. Fishes with a model based only on sites with Great Lakes access are indicated by "**". Font indicates significance of coefficients as follows: <0.01 (regular); 0.01<p<0.05 (**bold**); 0.05<p<0.10 (*italic*), >0.1 (***bold and italic***).

Cluster#	Common name	constant	distrib	BESTMEAN	BESTMEA2	TOTPPPM	LGVEL90	LG90CMSK	LG90CMK2	LG10CMSK	DEPMBEST	SUBCL	SUBSI	SUBSA	SANDSM	SUBGR	SUBCO	SUBBE	GRAVELLG	RIFFLE	BNKST	BNKMOSE
1	Bluntnose minnow	-4.44		*0.08*																-0.01		
1	Central stoneroller	***0.63***				**0.67***									-1.30	-0.02				0.31*	-0.01	
1	Common shiner	-4.45																				
1	Creek chub	-16.26		1.78	-0.04																-0.01	
1	Johnny darter	-2.35																	-1.03			
1	Redfin shiner	-3.06										0.01										
2	Bluegill	3.28				0.95*					1.16										-0.01	
2	Brook stickleback	-5.73		**0.25**	*-0.01*		-0.28												**-0.19***			
2	Northern redbelly dace	-1.89				-2.80																
3	Blacknose dace	-13.23		1.31	-0.03																	
3	Mottled sculpin	**-5.31**		0.80	-0.02			1.13						**0.01**						0.01		
4	Fathead minnow	-1.65		-0.04																		**0.1***
4	White sucker	***-0.97***		**-0.13**							**0.76***											
5	Burbot	-11.02		0.57	-0.01	-1.46*																
5	Longnose dace	-10.43		0.55	-0.01	-1.58*														0.01		
6	Brown trout	-9.66		0.85	-0.03			0.69											1.21			
6	Chinook salmon**	***-3.58***		0.80	-0.02					3.81												
6	Rainbow trout	-3.32				**-4.69**		0.59												0.01		
7	Brook trout	1.24		-0.18																		
7	Coho salmon**	-3.71																				
7	Slimy sculpin	-4.99				**-0.5***										**0.01**						
8	Black bullhead	-5.43													0.81							
8	Green sunfish	1.12				1.94*																0.01
8	Yellow bullhead	8.15		-0.79	0.02	1.8*																
9	Blackside darter	-5.14																		-0.01	**0.00**	
9	Bowfin	-2.09		-0.07																		
9	Central mudminnow	-11.20		0.92	-0.02			-0.56				0.02			1.18							
9	Golden shiner	-3.47						-0.23														
9	Northern pike	-3.52																				
9	Pirate perch	-2.54						**-0.23**				0.01									**0.00**	
9	Pumpkinseed	-1.90				0.88*																

Appendix A.–Continued.

Cluster#	Common name	LGBRDC1	GRADPERC	SINUOSIT	BURBAN	BAGRIC	BNFORWET	L4WATWET	BWATER	G_LKS	PONDUPST	BIGRIVER	LNKDLNK	LOGDAKM	LOGDAKM2	OUTWGEO	COARSGEO	CRSNOUTW	FINEGEO	URBAN	AGRIC	FOREST	WATWETLA
1	Bluntnose minnow													*0.31*							2.42		
1	Central stoneroller									**-0.48**				**-0.24**									**-6.94**
1	Common shiner													3.57	-0.72						**0.5***		
1	Creek chub											0.75		-0.79									
1	Johnny darter					0.91*						**0.34**		1.69	-0.36								
1	Redfin shiner						**-2.18**														0.56		
2	Bluegill							**0.87***	1.09*				**-0.46**							**-3.22**			
2	Brook stickleback													**-0.25**						**-0.32***			
2	Northern redbelly dace							**0.29***		*-0.17*				**-0.10**									
3	Blacknose dace		0.75*						**-12.48**			0.84		*-0.32*									
3	Mottled sculpin										*-0.35*			-0.52			-1.55						
4	Fathead minnow																		0.52	**0.27***			
4	White sucker					1.44*		-13.17						4.23	-0.83					3.22			
5	Burbot																						**4.99**
5	Longnose dace													**0.20**							**0.41***		
6	Brown trout		**-0.53**						-1.34*		-0.64					1.84							
6	Chinook salmon**															1.90							
6	Rainbow trout									0.83	**-0.33**	**0.37**		1.56	-0.27	-0.41*	**-0.27***				*-0.65*		
7	Brook trout		0.92																	-1.99			
7	Coho salmon**			0.56																			
7	Slimy sculpin		0.62					1.01*		**-0.24**				1.11	-0.20		**-0.2***						-0.8*
8	Black bullhead								-1.9*			-0.78		1.50	-0.33								**1.2***
8	Green sunfish		*-0.33*																				
8	Yellow bullhead		-0.94*	**2.72***							0.83												0.67*
9	Blackside darter							*-0.5**				-0.57	**0.50**	2.80	-0.52								
9	Bowfin		-0.7*																				
9	Central mudminnow			*-0.47*	-2.52		8.05							-0.67									
9	Golden shiner				*-0.90*				*5.89*			*0.18*											
9	Northern pike		-0.91*							*-0.50*		-0.79		**0.43**					**-0.91**		1.18		
9	Pirate perch							**0.43***					*0.22*										
9	Pumpkinseed		-1.1*						15.76	**0.48**													

Appendix A.–Continued.

Cluster#	Common name	constant	distrib	BESTMEAN	BESTMEA2	TOTPPPM	LGVEL90	LG90CMSK	LG90CMK2	LG10CMSK	DEPMBEST	SUBCL	SUBSI	SUBSA	SANDSM	SUBGR	SUBCO	SUBBE	GRAVELLG	RIFFLE	BNKST	BNKMOSE
10	Black crappie	-1.77																				
10	Common carp	**7.44**		-1.41	0.04	10.88		*-0.39*														
10	Flathead catfish	-1.85	**0.21**								0.95											
10	Spotted sucker	-1.88											0.01									
10	Tadpole madtom	-3.85		-0.13		7.01					0.81											
10	Walleye	-3.66									1.50											
10	White crappie	-2.55									**0.36**										0.00	
11	Freshwater drum	-3.63																				
11	Gizzard shad	-3.88																				
11	Quillback	-3.96		*0.30*	**-0.01**										0.49*							
12	Brook silverside	-2.84		**0.03**																		
12	Channel catfish	***0.75***						**-0.33**		**2.05**												
12	Logperch	**-1.20**																				
12	Mimic shiner	-4.93		0.08							**-0.41**									*0.00*		
12	Sand shiner	-3.90																				0.00
12	Shorthead redhorse	-2.73					0.84														**-0.01**	
12	Spotfin shiner	***1.92***		-0.68	0.02													**0.02**				0.01
13	Grass pickerel	*-1.39*		-0.20		6.63							*0.01*									
13	Hornyhead chub	-14.22		0.78	-0.02	**7.26**				**-2.47**								**0.03**		**0.33***	**-0.01**	
13	Lake chubsucker	-3.63				5.16																
14	Brown bullhead	-3.49				4.62														**4.62***		
14	Largemouth bass	***-0.52***				**4.77**																0.33*
14	Longear sunfish	***-1.02***						-0.44		**1.41**												
14	Rainbow darter	-13.85		1.11	-0.03		**0.31**												0.54*			
14	Rock bass	-4.61																				
15	Black redhorse	-2.36	**0.39**														0.03				**-0.01**	
15	Greenside darter	-3.92		**0.06**							-0.69								0.51			
15	Northern hog sucker	-5.34						0.69											1.70			
15	River chub	-5.26		*0.04*		-0.78*		**0.31**		*-1.47*											-0.01	
15	Smallmouth bass	-5.22		**0.10**									**-0.01**				0.03			-0.01		
15	Stonecat	-5.04					**0.60**				**-1.20**						0.03					
15	Striped shiner	-3.58																	**0.44**			
16	Rosyface shiner	-7.46						**0.33**		-2.37							0.01					
16	Yellow perch	-1.98		-0.10																		
17	Golden redhorse	-5.39															0.03					
17	Greater redhorse	-2.65															0.03					
17	Silver redhorse	-3.66																				

Appendix A.–Continued.

Cluster#	Common name	LGBRDC1	GRADPERC	SINUOSIT	BURBAN	BAGRIC	BNFORWET	L4WATWET	BWATER	G_LKS	PONDUPST	BIGRIVER	LNKDLNK	LOGDAKM	LOGDAKM2	OUTWGEO	COARSGEO	CRSNOUTW	FINEGEO	URBAN	AGRIC	FOREST	WATWETLA
10	Black crappie							1.15*						0.70			**-0.60**						
10	Common carp													1.43							**0.8***		
10	Flathead catfish		**-0.35***	*-0.31*									-0.31	-1.14	0.24			**-0.30**					
10	Spotted sucker							0.85*					-0.43	0.26									**-5.65**
10	Tadpole madtom		-0.77*		**-0.38***		-0.4*							0.96	-0.21		**-0.2***						
10	Walleye		-0.46*				-7.99			0.56													**7.22**
10	White crappie		-0.32*	-0.40									-0.23										
11	Freshwater drum		**-0.21***							0.87				**0.16**									
11	Gizzard shad		-0.52*							1.11				*0.13*									
11	Quillback		**-0.39***							0.52				-2.12	0.56	**-0.53**							
12	Brook silverside							0.39*	12.01				*-0.12*										*-4.49*
12	Channel catfish		-0.65*								**0.46**			-2.16	0.61								
12	Logperch						-8.84		0.93*					0.55						-2.24	-1.00		
12	Mimic shiner				**-0.34***		-4.38		**7.91**									**0.40**					
12	Sand shiner													0.36					**-0.17***				
12	Shorthead redhorse									**0.60**				0.41							1.20		
12	Spotfin shiner										**0.41**			0.42									
13	Grass pickerel	**0.30**	-0.88*			**-3.91**	**0.65***				**0.40**			1.89	-0.44				-1.63		5.13		
13	Hornyhead chub								19.27										**-0.4***	-4.79			
13	Lake chubsucker				-0.30				8.69													*0.34**	
14	Brown bullhead						5.76																
14	Largemouth bass		-0.58*					1.52*	**12.97**														
14	Longear sunfish						6.65	**0.46***															
14	Rainbow darter																			-1.0*			
14	Rock bass		-0.75*		*-0.54**	0.7*			30.05		*0.45*	-0.72		2.52	-0.44		0.45*						*-11.76*
15	Black redhorse			**0.69**					**0.78***														
15	Greenside darter					0.78										0.26*							
15	Northern hog sucker			1.00		2.34		**-8.38**					0.85	2.18	**-0.34**								
15	River chub										**0.32**						0.31*		0.41*				9.56
15	Smallmouth bass										**0.52**			0.88			**0.35***						
15	Stonecat					-0.55*	-8.39							2.84	-0.47		**0.38***				2.27		
15	Striped shiner						4.24				**0.38**		0.39								0.71		
16	Rosyface shiner			**0.56**													0.3*				1.54	**1.06**	
16	Yellow perch		-0.74*											0.34									
17	Golden redhorse					2.23								1.11									
17	Greater redhorse		-0.46*													-1.34	**-0.83**		-1.12				
17	Silver redhorse		*-0.29**							0.53				**0.22**									

Appendix B.–Coefficients of variables in multiple linear regression models for 68 common fishes in rivers of Michigan's Lower Peninsula. Models are based only on sites of occurrence (SOO) for each species. Species densities were transformed as log10(x + 0.001) where x equals fish density in kg/ha. An asterisk following the coefficient indicates that variable is $\log_{10}$ transformed. Font indicates significance of coefficients as follows: <0.01 (regular); 0.01<p<0.05 (**bold**); 0.05<p<0.10 (*italic*), >0.1 (***bold and italic***).

Cluster#	Common name	constant	BESTMEAN	BESTMEA2	TOTPPPM	VEL90MPR	LG90CMSK	LG90CMK2	LG10CMSK	DEPMBEST	SUBCL	SUBSI	SUBSA	SANDSM	SUBGR	SUBCO	SUBBO	SUBBE	GRAVELLG	RIFFLE	BNKST	BNKMOSE	BRDCO1_1	BRDCO10_
1	Bluntnose minnow	**-0.54**												**-0.4***						**-0.01**				
1	Central stoneroller	***-1.50***	*0.11*																					
1	Common shiner	***-8.26***	**1.00**	**-0.02**			**0.24**																	
1	Creek chub	4.21	-0.15																	0.28*				
1	Johnny darter	1.64	**-0.06**																**-0.63**	**0.17***	**0.00**			
1	Redfin shiner	***0.49***																						
2	Bluegill	***0.21***			5.80																			
2	Brook silverside	-6.76																		1.31*				
2	Northern redbelly dace	3.69			-18.21																			
3	Blacknose dace	*2.93*	-0.21			-0.57*																		
3	Mottled sculpin	3.64	-0.17							**-0.95**														
4	Fathead minnow	***0.93***	*-0.12*		*10.02*							-0.03												
4	White sucker	-12.07	1.41	-0.04										0.76				0.02						
5	Burbot	**-3.82**			-5.19*					**-0.87**		-0.02												
5	Longnose dace	***-0.73***																						
6	Brown trout	***-3.18***	**0.72**	-0.03																				
6	Chinook salmon	***0.20***			79.58																			
6	Rainbow trout	**0.65**																						
7	Brook trout	-9.06	0.81	-0.03					-3.45															
7	Coho salmon	**6.24**	**-0.35**																					
7	Slimy sculpin	1.31								-2.06														
8	Black bullhead	***-0.43***			**6.13**	*-0.90*				-1.66														
8	Green sunfish	1.50																				0.27*		**0.00**
8	Yellow bullhead	***0.37***			6.25					*-0.44**					0.01					-0.01				-0.01
9	Blackside darter	2.17	-0.10		-5.28						**0.01**									**0.00**				
9	Bowfin	**-14.12**							**-8.14**															
9	Central mudminnow	**1.05**					-0.56				0.01													
9	Golden shiner	-3.15																	-1.3*					
9	Northern pike	***0.14***	*-0.04*				-0.38							*0.34*										
9	Pirate perch	***4.11***					-0.88		*4.26*															
9	Pumpkinseed	*0.43*																						

Appendix B.–Continued.

Cluster#	Common name	GRADPERC	GRADPER2	LGGRADPE	SINUOSIT	BURBAN	BAGRIC	BNFORWET	L4WATWET	BWATER	G_LKS	PONDUPST	BIGRIVER	LNKDLNK	LOGDAKM	LOGDAKM2	OUTWGEO	COARSGEO	CRSNOUTW	FINEGEO	URBAN	AGRIC	FOREST	WATWETLA
1	Bluntnose minnow																**-0.87**					0.91		
1	Central stoneroller														-1.23									**-1.03***
1	Common shiner														-0.42									
1	Creek chub														-0.64		-0.45*							
1	Johnny darter														-0.36			-0.27*			-2.64			
1	Redfin shiner														-1.03							*1.51*		
2	Bluegill					**-2.83**			**6.48**			0.38		-0.52	-0.37			*0.56*						
2	Brook silverside			-3.65								*1.06*												
2	Northern redbelly dace														-1.70									
3	Blacknose dace	4.10	-2.53										**0.46**											
3	Mottled sculpin											-0.87	**0.45**								**1.68**			
4	Fathead minnow																			*0.60*				
4	White sucker			**0.33**			0.42*		-7.91		-0.54										**0.32***			
5	Burbot																						**-4.78**	
5	Longnose dace														-0.28		1.73					**2.39**		
6	Brown trout																							
6	Chinook salmon						-6.60								-0.43									-21.64
6	Rainbow trout					**-0.87***									-0.51									
7	Brook trout									**16.50**					-0.61									
7	Coho salmon																							
7	Slimy sculpin																							
8	Black bullhead																							
8	Green sunfish	-2.31							**6.45**						-0.56									
8	Yellow bullhead						**-0.83**							**-0.33**										
9	Blackside darter																							
9	Bowfin																							
9	Central mudminnow							1.14*							-1.15						**-0.54***			
9	Golden shiner									23.42								-0.94*						
9	Northern pike																							
9	Pirate perch			1.17	**1.08**																			
9	Pumpkinseed			-0.54					*4.18*	13.31					-0.45		-1.33				-1.52			

Appendix B.–Continued.

Cluster#	Common name	constant	BESTMEAN	BESTMEA2	TOTPPPM	VEL90MPR	LG90CMSK	LG90CMK2	LG10CMSK	DEPMBEST	SUBCL	SUBSI	SUBSA	SANDSM	SUBGR	SUBCO	SUBBO	SUBBE	GRAVELLG	RIFFLE	BNKST	BNKMOSE	BRDCO1_1	BRDCO10_
10	Black crappie	-3.36			*0.7**		-0.57					0.02												
10	Common carp	1.30								**0.5***										**-0.22***				
10	Flathead catfish	***-0.55***																	**3.32**					
10	Spotted sucker	-0.98															-0.05							0.01
10	Tadpole madtom	*1.52*			2.22*	**-0.55***										**0.02**					**-0.01**			
10	Walleye	*-41.60*	*3.54*	*-0.08*																				
10	White crappie	**-1.81**																						
11	Freshwater drum	*-12.10*							**-7.02**															
11	Gizzard shad	*-1.09*																		**0.02**	0.02			
11	Quillback	1.42																		**-0.02**				
12	Brook stickleback	2.82	-0.12			-2.05				**-1.34**									-1.69					
12	Channel catfish	***-0.21***																					0.01	
12	Logperch	*22.44*	*-2.20*	*0.05*		0.78*																		
12	Mimic shiner	-2.24																	1.80		**0.01**			
12	Sand shiner	-2.64											0.05						3.02*					
12	Shorthead redhorse	2.88																						
12	Spotfin shiner	**-16.75**	**0.15**																			0.01		
13	Grass pickerel	2.75	*-0.06*																					
13	Hornyhead chub	1.97																						
13	Lake chubsucker	**0.92**																						
14	Brown bullhead	2.16																						
14	Largemouth bass	2.24																						
14	Longear sunfish	**7.30**							*3.38*															
14	Rainbow darter	***1.40***	-0.12													**0.01**								
14	Rock bass	***0.11***			8.94																			
15	Black redhorse	2.17								-1.99														
15	Greenside darter	**-11.62**	**-0.13**																**0.70**					
15	Northern hog sucker	1.13										*-0.01*						**0.01**						
15	River chub	**5.11**	-0.27												*0.01*									
15	Smallmouth bass	4.10			3.76*						**-0.01**	**-0.01**												
15	Stonecat	***0.47***								-1.19		**-0.01**												
15	Striped shiner	2.18																				-0.02		
16	Rosyface shiner	**37.74**	**-3.36**	**0.07**														-0.04						
16	Yellow perch	***0.03***																-0.07						
17	Golden redhorse	***0.94***				-2.10				-1.18														
17	Greater redhorse	0.91				**-2.44**													**0.72**					
17	Silver redhorse	1.18																						

Appendix B.–Continued.

Cluster#	Common name	GRADPERC	GRADPER2	LGGRADPE	SINUOSIT	BURBAN	BAGRIC	BNFORWET	L4WATWET	BWATER	G_LKS	PONDUPST	BIGRIVER	LNKDLNK	LOGDAKM	LOGDAKM2	OUTWGEO	COARSGEO	CRSNOUTW	FINEGEO	URBAN	AGRIC	FOREST	WATWETLA
10	Black crappie									33.42	0.50	0.45			0.48						-8.10			
10	Common carp				0.64		1.21*					*0.32*												
10	Flathead catfish																							
10	Spotted sucker							9.48	**6.31**		**0.28**													
10	Tadpole madtom																							
10	Walleye										*0.56*													
10	White crappie			-1.71		-31.87																		
11	Freshwater drum																							
11	Gizzard shad																							
11	Quillback										**-0.86**													
12	Brook stickleback			**0.53**																				
12	Channel catfish								**-9.72**	*26.51*				-0.89										
12	Logperch	12.07	-29.62					*-10.77*												-0.58*				*-1.19**
12	Mimic shiner													**-1.17**										
12	Sand shiner			**-0.90**							**-0.65**													
12	Shorthead redhorse								1.18*			**0.51**									**-9.80**			*11.85*
12	Spotfin shiner					1.4*									**9.56**	**-1.57**								
13	Grass pickerel														-0.66									
13	Hornyhead chub														-0.73						**-0.72***			*0.64**
13	Lake chubsucker					-10.90	-3.06	12.02						**-0.61**										
14	Brown bullhead				-1.83				9.60													**-0.56***		
14	Largemouth bass								1.24*			0.55			*-0.20*				**-0.63**					
14	Longear sunfish										*0.74*			*-0.53*	-0.65									
14	Rainbow darter														*-0.28*						-0.74*			
14	Rock bass									12.31							**-0.24***				-5.05	*-0.48*		
15	Black redhorse																			*-1.37*				
15	Greenside darter										-1.25				11.40	-2.02						**-2.84**		-14.06*
15	Northern hog sucker			0.62					**-6.51**						**0.26**									
15	River chub									**30.95**														
15	Smallmouth bass										**-0.38**											1.4*	5.10	
15	Stonecat														**0.48**		**0.51***					1.16*		
15	Striped shiner			1.81										0.88										
16	Rosyface shiner													*0.36*										
16	Yellow perch			**0.50**					**6.62**															
17	Golden redhorse														**0.53**					-1.75				
17	Greater redhorse																							
17	Silver redhorse										-0.65									-0.87		*-0.36**		