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Patterns in the Distributions of Stream Fishes in Michigan's Lower Peninsula

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Abstract.–We examined distribution and abundance patterns of 69 commonly occurring fishes at several hundred sites in Lower Michigan streams. We used cluster analysis to group fishes that commonly occurred together at stream sites. These seventeen clusters explained about 39% of the variation in species abundances among the stream sites, providing a reasonable, albeit simplified picture of general associations of fishes in Lower Michigan streams. Known ecological differences among species and further analyses suggested that a single measure of cluster abundance should not be used to predict abundances of its constituent species.

We used measures of stream size and hydrology as landscape-scale, habitat axes (a "macro-template") for comparing streams. We identified catchment area (CA) and low-flow yield (90% exceedence flow divided by catchment area) as key driving variables that linked features of the landscape to multiple, site-scale characteristics of stream habitat (e.g. temperature, velocity, and depth) important to fishes. As a measure of groundwater loading to streams, low-flow yield (LFY) integrates geology, landform, and soil characteristics of catchments, reaching its highest values in basins with highly permeable soils and relatively steep topography. In Lower Michigan streams, high LFY values were generally associated with: greater portions of coarse-textured glacial deposits in catchments; higher stream gradients; coarser stream substrates; and cooler and less variable predicted July weekly temperatures. High CA values were generally associated with lower stream gradients, and warmer and less variable predicted July weekly temperatures.

Ordinations of fish clusters and species' abundances on LFY-CA axes provided insight into the structure of fish assemblages in Lower Michigan streams. The seventeen fish clusters spread out in a meaningful pattern when plotted on LFY-CA axes, reflecting stream size and temperature preferences of constituent species. Plots of abundances of individual species on LFY-CA axes showed differences among fishes in LFY and CA conditions where species occurred and were most abundant. These patterns supported the notion that stream fishes respond in an individualistic manner to stream conditions, and that species-specific models are needed to describe fish assemblage structure in streams. We used relations between LFY, CA, and fish abundances to describe longitudinal changes in stream conditions and fish assemblages both within streams, and among hydrologically different streams. These relations have also been used to characterize potential fish assemblages of stream valley segments. Relations between LFY, CA, and fish abundances that we described are specific to Lower Michigan streams, because relationships between LFY, CA, and stream temperature vary regionally. However, our approach could be used to develop similar models specific to other regions.

Study and management of river systems and their component fish assemblages should be conducted across the scales at which they operate (Wiley and Seelbach 1997; Levin 1992). Streams are products of the landscape, having properties that reflect both catchment-scale features of the landscape (e.g. geology and land use) and local features (e.g. valley character and riparian conditions) of the environments through which they flow (Seelbach et al. 1997). Fishes move throughout these systems during their lives (Schlosser 1991), being most abundant in areas where physical and biotic conditions are most suitable. However, until recently, few studies of stream fish ecology included analyses of reach or catchment-scale variables. New advances in remote sensing, computer, and Geographic Information System (GIS) technologies provided us the opportunity to focus on modeling complex, larger-scale stream processes (e.g. streamflow, temperature, and water chemistry conditions) using a comparative approach, i.e. by looking at many different rivers (Seelbach and Wiley 1997).

Comparative studies have much to offer stream ecologists. Contrasts of different systems can aid in identifying important ecological gradients that influence assemblage structure (i.e. species composition and relative abundance) of fishes and other aquatic organisms. Identification of these gradients or patterns is an important "first step" toward understanding the underlying processes that shape biological communities. An understanding of the diversity and types of stream systems within a region provides the context for describing individual systems. In other words, one will better know how a river compares to the "universe" of rivers within the region. Such perspective can aid fishery managers in evaluating a stream's potential, identifying problem areas, and in setting realistic management objectives. By placing a stream within this larger context one can better understand more specific issues, such as identifying the factors limiting fish abundance at a particular site.

We used a comparative approach to examine distribution patterns of fishes in Michigan's Lower Peninsula streams. The objectives of this study were two-fold. First, we were interested in identifying groups of fishes having similar spatial patterns in their distribution and abundance. Such groupings could simplify the process of describing fish assemblage structure, providing a useful "short-hand" for contrasting fish assemblages in Lower Michigan streams. Lower Michigan streams have diverse fish assemblages with over sixty species having been collected from individual river basins, and 30-40 species commonly occurring at individual sites (Towns 1987; Smith et al. 1981). Combining fishes having similar distributions into groups has never been done for stream fishes in Lower Michigan though it has been by researchers studying other regions (e.g. Smith and Fisher 1970; Rose and Echelle 1980; Hawkes et al. 1986; Matthews and Robison 1988; Halliwell 1989; Degerman and Sers 1992). However, it is important to understand the limitations of such coarse-scale descriptors (Strauss 1982). Therefore, we evaluated the groupings to determine: 1) how well they described the variation in species distributions across the state; and 2) whether they could serve as reliable predictors of abundances of their constituent species.

Our second objective was to identify relatively simple, habitat-based ordination axes for use in contrasting both streams and fish habitat preferences. Recognizing that streams integrate features of the landscape, we sought to identify landscape-scale, system-driving variables that indexed multiple, site-scale features of stream habitat (e.g., temperature, velocity, and depth) important to fishes. A landscape ecology approach (Risser et al. 1983; Turner 1989; Pickett and Cadenasso 1995) that explicitly examined the influence of landscape patchiness on stream environments was needed to describe linkages between catchment-, valley-, and site-level characteristics of streams and relate them to fish distributions. Through literature review and by modeling relations between variables across these different spatial scales (Seelbach and Wiley 1997), we identified descriptors of a stream’s size and hydrologic characteristics as the key variables that link the landscape to proximal habitat conditions important to fishes. These variables provided landscape-scale habitat axes (i.e. a "macro-template") for ordinating streams and the distributions of fishes within them. (Southwood 1977). The following discussion will briefly introduce these two axes.

Low-flow yield

We used low-flow yield (LFY), defined as the base- or 90% exceedence-flow discharge divided by drainage area, as the first major stream habitat axis. As a measure of the relative contribution of groundwater to streams, LFY captures much of the variation in water temperatures among streams glaciated Midwestern states such as Michigan (Hendrickson and Doonan 1972; Dewberry 1980; Wehrly et al. 1998). In his classification scheme for Midwestern streams, Dewberry (1980) initially proposed LFY as an index of the stability of stream discharge and temperature regimes, and used it as an axis for characterizing a continuum of hydrologically-different streams in Michigan. It is a measure of the level of groundwater loading to the stream, reaching its highest levels in basins with highly permeable soils and steep topography (Hendrickson and Doonan 1972).

Temperature has been identified as one of the major factors affecting growth (Brett 1979), survival (Matthews and Styron 1979; Smale and Rabeni 1995a), and distribution (Magnuson et al. 1979; Shuter et al. 1980; Legendre and Legendre 1984; Bowlby and Roff 1986; Meisner et al. 1987; Meisner et al. 1988; Staso and Rahel 1994; Smale and Rabeni 1995b; Peterson and Rabeni 1996) of fishes. Not surprisingly, temperature has been identified as a key variable in many classifications of stream fishes (e.g. Huet 1959; Smith and Fisher 1970; Dewberry 1980; Zalewski and Naiman 1985; Hawkes et al. 1986; Matthews and Robison 1988; Lyons 1989; Rahel and Hubert 1991; Degerman and Sers 1992; Lyons 1996). However, the importance of temperature is not limited to distinguishing between the traditional warm- and cold-water fish categories. Studies describing differences in thermal preferences among fishes within these broad categories continue to accumulate (e.g. Matthews and Styron 1979; Matthews 1987; Staso and Rahel 1994; Smale and Rabeni 1995a; Smale and Rabeni 1995a).

In addition to indexing a stream’s thermal regime, LFY is correlated with a stream’s current velocity conditions during the growing season, and its hydrologic stability or “flashiness” (Hendrickson and Doonan 1972). Summer streamflow (current velocity) conditions influence fish behavior at the individual level (e.g. Kalleberg 1958; Bachman 1984; Godin and Rangeley 1989; Zorn and Seelbach 1995). At the guild level, hydrologically stable (high-LFY) Midwestern streams generally favor fishes characterized as streamlined, piscivorous, intolerant of turbidity and silt substrates, and preferring moderate velocities (Poff and Allan 1995). As an index of hydrologic stability, LFY can be thought of as part of a habitat template (sensu Southwood 1977) favoring particular life history strategies

(Poff and Ward 1989; Poff and Ward 1990; Schlosser 1990) and influencing lotic assemblage structure through time (Starrett 1951; Moyle and Li 1979; Poff and Ward 1989; Bailey and Li 1994).

Catchment area (CA)

We used the upstream catchment area (or CA) for each site, a correlate of discharge and an index of stream size, as a second major axis along which fish assemblage structure changes. We used CA to measure stream size, rather than stream order or width, because it is readily measured in the lab and provides a uniform understanding of stream size regardless of the scale of topographic maps or permanence of streams (Hughes and Omernik 1983).

Numerous early studies described changes in stream environments and communities primarily along a longitudinal gradient from cold, headwater streams to large, warmwater streams, while others looked at upstream-downstream patterns in warmwater streams (e.g. those in Hynes 1970; Hawkes 1975). Distinctions between biotic zones in streams have been attributed to various factors that often change predictably in a downstream direction such as current velocity, substrate, stream discharge, temperature, dissolved oxygen, dissolved nutrients, and biotic interactions (factors cited in various combinations by: Huet 1959; Kuehne 1962; Smith and Fisher 1970; Hawkes 1975; Horwitz 1978; Vannote et al. 1980; Rose and Echelle 1981; Zalewski and Naiman 1985; Hawkes et al. 1986; Matthews and Robison 1988; Lyons 1989; Wiley et al. 1990; Rahel and Hubert 1991; Degerman and Sers 1992; Lyons 1996). Longitudinal changes in the temporal stability of stream environments may also contribute to downstream changes in fish assemblage structure (Horwitz 1978; Vannote et al. 1980; Ward and Stanford 1983; Wiley et al. 1990). For example, CA, as a measure of stream volume, indexes the mean and daily variation in temperature during the growing season, both of which are important to stream fishes (Wiley et al. 1990; Gordon et al. 1992; Wehrly et al. 1998).

Methods

Michigan Rivers Inventory Data

We obtained data for this study from the Michigan Rivers Inventory (MRI) databases; these contain catchment-based characterizations of 672 sites in Lower Michigan (Seelbach and Wiley 1997). Types of data available for MRI sites included: general catchment characteristics (e.g. geology, climate, land use, topography); various reach- and site-scale habitat features; measured and predicted exceedence flows; measured and predicted July temperatures and water quality values; and fisheries survey data (Seelbach and Wiley 1997). For each MRI site, CA was measured and LFY was calculated by dividing a site's predicted 90% exceedence flow by its CA.

Fish assemblages at MRI sites were characterized by individual surveys conducted during the summer. Fish abundance data from rotenone and multiple-pass electrofishing depletion surveys done between 1982 and 1995 were obtained for 225 MRI sites. Seelbach and Wiley (1997) and Seelbach et al. (1988) provide greater detail regarding fish sampling techniques and computation of abundance estimates. Mark-recapture electrofishing surveys conducted between 1960-95 provided abundance information for key species (namely salmonids, smallmouth bass, and rock bass) at 82 additional sites. Presence-absence data were used to characterize species composition at sites where abundance data were not available. No fisheries data were available for 105 MRI sites.

We considered the quality of fish abundance estimates in the MRI database as somewhat coarse for several reasons. These data represented only a snapshot of the assemblage at a given time, because each site was only sampled once. Weight per area data from the rotenone surveys probably represented only about 75% of the actual standing crops of fishes because of sampling inefficiency (Seelbach et al. 1994). To make abundance estimates of all species captured at electrofishing depletion sites (Zippen 1958), we assumed equal catchability of all species. There was undoubtedly variation in catchability among species. Nonetheless, we felt that while any individual sample may not perfectly represent the "typical" fish assemblage structure of a site over time, our having fish samples from many similar streams allowed us to better characterize fish assemblage structure for a given type of stream. In addition, we expected patterns at the state-wide scale to be dramatic enough (e.g. contrasts of high versus low versus zero abundance levels) that these sampling-induced biases would not significantly alter our findings.

While the MRI sample sites provided a good representation of Michigan streams, fish assemblage data were lacking for a few stream types (Figure 1). This is largely because fish surveys were mostly done by (or in cooperation with) management agencies whose interests targeted larger streams, particularly those with sport fisheries. Consequently, small streams in general were under-sampled. Small coldwater streams were especially under-represented because abundance data were typically not collected for non-salmonid species. Also, lower reaches of large rivers (i.e. those having $\log_{10}$ CA values greater than 3.5 km^2) were somewhat under-represented in the fish data, because of various sampling difficulties.

Though somewhat coarse, fish abundance data reported in this study have considerable heuristic and practical value. Relatively few longitudinal zonation studies (e.g. Larimore et al. 1952; Gard and Flittner 1974; Balon and Stewart 1983; Rahel and Hubert 1991) have documented changes in fish abundances and assemblage structure, and each of these studied patterns witnin an individual stream or river system. The MRI data provide the opportunity to look at patterns both within a stream and across a variety of hydrologically different streams.

We expected plots of fish abundances on axes of LFY and CA to provide insight into ecological relationships and processes that are often difficult to see with presence-absence data. Dramatic changes in assemblage structure between sites that may be readily apparent in abundance data are often unnoticeable when only presence-absence data are available. Abundance data allow for distinction between conditions where species or groups of species thrive and those where they merely exist. This is especially true for species that may be very widespread in terms of presence, but are only abundant in limited areas. For example, largemouth bass and bluegill are widely distributed in Michigan streams due to the presence of lakes and ponds in drainage networks, but are only abundant in warmwater, lentic environments.

Grouping Fishes

Identifying clusters.–We used cluster analysis to group fishes whose standing crops at sites were correlated with one another. We performed the cluster analysis for 225 MRI sites that had abundance data for the entire fish assemblage at a site (Seelbach and Wiley 1997). Fish standing crops at sites were calculated by dividing each species' biomass by the area sampled. We used only relatively common species in the cluster analysis to reduce our chances of obtaining spurious clusters. Each species had to either occur at 9 or more sites, or have a total abundance in the dataset of at least 7.0 kg/ha, to be included in the analysis. This resulted in 69 species being included in the cluster analysis. We will refer to the hybrid sunfish as a "species" for the sake of simplicity. We used SPSS statistical software (SPSS, Inc. 1993) for all statistical analyses. The data were standardized (Z-distribution, mean=0, standard deviation=1) by species so that all species would be weighted equally in the clustering process. The complete linkage clustering method and Pearson correlation distance measure (recommended for clustering variables) were used. We identified seventeen clusters of fishes from the cluster analysis for use in subsequent analyses (Table 1). An unmodified dendrogram from the cluster analysis is shown in Appendix A.

Evaluating clusters.–We used ANOVA techniques to gain insight into how well the seventeen clusters explained species' distributions within the entire dataset. For each of seventy randomly selected sites, we calculated the amount of variation in species' abundances (standardized as Z-scores) explained by the clusters. Using cluster membership as the grouping variable for species at each site, we calculated the proportion of variance explained by the clusters (R^2) by dividing the between-groups (i.e. between clusters) sum of squares by the total sum of squares. This produced an R^2 value for each of the seventy sites. The average of all the R^2 values reflected the overall fit of the clusters to the dataset.

We then evaluated whether a measure of the abundance of a cluster could be used to represent the abundances of its constituent species. For each of the seventeen clusters, we calculated a fish cluster score at each MRI site where abundance data were available for at least half of the cluster members. The fish cluster score was simply the average of the Z-scores for the cluster members at the site, and reflected the relative abundance of the fish cluster there. We hypothesized that if the cluster abundance adequately represented abundances of all of its constituent species, then equal slopes would exist for simple linear regressions between a cluster's abundance (the independent variable) and the abundances of each of its constituent species. For each cluster, we computed a set of regression equations between the z-scores for the cluster and those of its constituent species, and noted when at least two slopes differed within the set of equations at a P-value of 0.05.

We did not consider the latter evaluation a very conservative test of a cluster's predictive power, since each cluster score was initially calculated from member species' z-scores. Thus by definition, the cluster and species scores should be correlated. However, it provided some initial indication as to whether a cluster could equally represent its constituent species.

Stream Ordination Axes

Plotting clusters on LFY-CA axes.–The fish abundance data allowed us to more accurately describe the quality of stream habitats for each fish cluster. We identified sites where each cluster was most abundant (i.e. having a cluster score greater than or equal to 0.5 standard deviations above the mean cluster score for all MRI sites), and characterized them with summary statistics (means and standard deviations) for $\log_{10}$ LFY and $\log_{10}$ CA. The logarithmic transformation helped distribute cluster data evenly along the ordination axes. The mean LFY and CA values were then used as coordinates for plotting the clusters on LFY-CA ordination axes.

Exploratory data analyses indicated that the MRI hydrology models (Wiley and Seelbach, unpublished data) under-predicted LFY's for some small trout streams, and that these streams should not be included in subsequent analyses. Examination of data from United States Geological Survey gaged streams in Michigan showed that substantial populations of salmonids did not occur in streams with a LFY of less than 0.10 cfs/km^2 (unpublished data). Therefore, sites with predicted LFY values of less than 0.10 cfs/km^2 (35.31 cfs = 1.0 cms) and substantial trout populations (z-scores for brook and brown trout clusters > 0.5 standard deviations above the mean for all MRI sites) were considered outliers and discarded.

Physical and biological parameters on LFY-CA axes.–We generated surface plots to show patterns in physical characteristics, fish clusters, and fish abundances for Lower Michigan streams on axes of LFY and CA by subsampling sites from the MRI dataset that met particular LFY and CA criteria. We developed a sampling matrix, with sites grouped into cells according to their LFY and CA values (Figure 2). Average values for various physical and biological parameters were calculated from MRI data available for sites in each cell, and plotted on LFY and CA axes. Parameters included: stream gradient; substrate; mean July weekly temperature characteristics (predicted by Wehrly et al. 1998; including weekly mean and range—indicative of diurnal range; Hynes 1970); proportion of coarse glacial deposits (i.e. outwash sand and gravel, post-glacial alluvium, ice-contact outwash sand and gravel, coarse-textured glacial till, and end moraines of coarse-textured till) in the catchment (Farrand and Bell 1982); fish species and cluster abundances; total fish standing crops; and fish species richness.

We think that plots of fish abundances on LFY and CA axes may reflect long-term average population levels, since abundances were averaged from many similar sites sampled during different years. Population estimates from individual fish surveys may differ considerably from these values, because of natural fluctuations in population levels. For example, replicate rotenone samples available from a few warmwater stream sites showed up to three-fold differences in abundance levels of the more commonly collected species, i.e. those having abundances >10 kg/ha (unpublished data). Wiley et al. (1997) suggested that fifteen to twenty years of population estimate data may be needed to accurately characterize the long-term mean and variance of trout populations in hydrologically-stable (groundwater-fed) Michigan streams. Since such long-term data do not exist for most Michigan streams, pooling similar sites allowed us to develop initial estimates of the mean and variance in fish populations associated with different stream types.

Results

Grouping Fishes

Cluster Analysis.–Several interesting groupings can be seen at various levels within the cluster hierarchy (Figure 3). Table 1 shows species membership in the seventeen clusters identified at level C in Figure 3. The first split (A in Figure 3) appears to generally separate small stream fishes from those more typical of larger downstream reaches. The clusters identified at level B in Figure 3 appeared to reflect the thermal and stream-size requirements of individual species. For example, clusters containing species typical of small- to medium-sized coldwater streams (brook trout, brown trout, and burbot clusters), those having species typical of small- to medium-sized cool streams (hornyhead chub and rock bass clusters), and those having species typical of medium to large, warmwater streams (tadpole madtom, freshwater drum, logperch, pirate perch, and black bullhead clusters) are grouped at this level.

We selected the seventeen clusters identified at level C for further use. We thought the clusters identified at this level had fairly distinctive habitat requirements, and might be useful in a management context. However, either fewer or more clusters could have been identified from this analysis. As at level B, membership of species in clusters at level C also appeared to reflect similarities in habitat requirements among species, in particular those relating to stream temperature and size conditions (Table 1). For example, headwater fishes that are often most abundant in runoff dominated streams (creek chub cluster) were separated from those more typical of streams with some groundwater inputs (blacknose dace cluster). Brook trout and slimy sculpin, fishes characterized as being most typical of very small, highly groundwater-fed streams were grouped at level C. Species typical of large-sized warmwater streams were grouped into several clusters (e.g. freshwater drum, logperch, and silver redhorse clusters). Membership of fishes in some clusters seemed to reflect shared preferences for specific habitats such as wetlands (northern redbelly dace cluster), vegetated floodplains (pirate perch cluster), and Great Lakes access (freshwater drum cluster).

Cluster Evaluation.–The proportion of variation in fish collections at seventy sites explained by species membership in the seventeen clusters ranged from 0.11 to 0.96, with an average of 0.39, and standard deviation of 0.19. By accounting for roughly 40% of the variation in the data matrix, the clusters provided a reasonable, albeit simplified picture of general associations of fishes in Lower Michigan streams. However, considerable variation within the data (about 60%) remained unexplained.

Regressions of cluster scores against constituent species' z-scores suggested that a single measure of cluster abundance should not be used to predict abundances of a cluster's constituent species. There were significant differences in regression slopes among cluster members for 11 of the 17 clusters examined (Table 1). The absence of significantly different slopes among the other six clusters could result from member species sharing similar abundance patterns, or be related to the small size of these clusters and the potentially greater influence of member species' abundances on the cluster score. Only in clusters having three or fewer species were member species' slopes not significantly different (Table 1).

Stream Ordination Axes

Cluster Plots on LFY-CA axes.–The seventeen fish clusters were distributed in a biologically-meaningful pattern when their LFY and CA optima (defined as mean LFY and CA conditions of highest cluster abundance) were plotted on axes of LFY and CA (Figure 4). For example, coldwater fishes (e.g. brook trout and brown trout clusters) were generally restricted to small (low-CA), high-LFY streams, and fishes typical of warm headwaters (e.g. creek chub and brook stickleback clusters) were found in the small, low-LFY portion of the graph. Small streams with intermediate LFY conditions supported coolwater fishes, such as those in the blacknose dace and hornyhead chub clusters.

Cluster optima were closer together on the LFY axis as stream size increased. Still, there appeared to be separation of clusters, with those containing mostly coolwater fishes (e.g. burbot and rock bass clusters) having optima in higher LFY streams, and more lentic clusters (e.g. black bullhead and pirate perch clusters) having optima in low-LFY streams (Figure 4). Low-flow yield optima for clusters of fishes most abundant in larger streams (i.e. logperch, tadpole madtom, smallmouth bass, yellow perch, and silver redhorse clusters) fell within an even smaller range of LFY values. This reflected both the reduced range in LFY values among streams of this size (Figure 1) and the relative scarcity of fish assemblage data for large, high-LFY streams, such as the lower AuSable and Manistee rivers.

We plotted the mean LFY and CA conditions where each cluster was most abundant, plus or minus one standard deviation, to gain insight into the discreteness of the clusters (Figure 5). Considerable overlap in distributions occurred among most clusters; however, little or no overlap occurred among those at the extremes of LFY and CA, such as those typical of small- versus large-sized streams (Figure 5). The extent of overlap seemed indicative of how frequently individual species from different clusters would co-occur. In our surveys, members of the blacknose dace cluster occasionally, commonly, and rarely occurred with respective members of the brook trout, brown trout, and walleye clusters. While these data suggested that cluster members occurred over a relatively broad range of LFY-CA conditions, combination of species (some having different LFY-CA preferences) into a cluster may also have increased variation about the cluster's mean LFY and CA conditions.

Physical variables on LFY-CA axes.–Surface plots of various physical factors demonstrated relations between LFY, CA, and physical characteristics of Lower Michigan streams. Low-flow yield provided an index of the geologic characteristics of catchments. Streams with high LFY's drained catchments having high percentages of coarse glacial deposits (Figure 6). Small, high-LFY streams also had the highest stream gradients (Figure 7). Sand and silt substrates were most common at small, low-LFY stream sites, and coarser substrates were more common in larger streams and those with higher LFY's (Figure 8). This pattern may reflect the positive association between LFY and the coarse substrates typical of end moraines, or the increased ability of high-velocity streams to transport fine particles (e.g. silt) during low-flow periods.

Meaningful patterns in predicted summer stream temperature variables appeared when plotted on LFY and CA axes. The estimated July weekly mean temperature increased with CA, but declined as LFY values increased (Figure 9). The estimated July weekly temperature range was highest in small, low-LFY streams, and decreased with increases in stream size (CA) or groundwater input (LFY) (Figure 10).

Fish assemblage attributes and species' abundances.–Patterns in fish assemblage-level characteristics emerged when plotted on axes of LFY and CA. Total standing crops of fishes generally increased as CA increased and LFY declined (Figure 11). Fish species richness increased with CA (Figure 12). In streams of comparable size, species richness was generally higher in low-LFY streams than high-LFY streams. This effect seemed more apparent as CA increased. These patterns may reflect the influence of LFY and CA on the thermal environment of streams. For example, total standing crops of fishes and species richness appeared to be limited by July weekly mean temperatures, or variables indexed by stream temperature (Figures 13 and 14).

Plots of the abundance of individual species on axes of LFY and CA (Figure 15) demonstrated relationships between these variables and species' distributions and standing crops in Lower Michigan streams. Distinct peaks in the abundance of each species occurred under particular LFY-CA combinations. These peaks represented what could be considered "optimal" conditions for each species relative to the types of stream habitats available in Michigan's Lower Peninsula. For example, brown trout occurred in small- to moderate-sized streams with fairly high LFY's, being generally most abundant at smaller sites (having $\log_{10}$CA values < 2.3). Blacknose dace and creek chub often co-occurred with brown trout in streams receiving moderate groundwater inputs, but their abundance peaks occurred in streams (poorly suited to brown trout) that received primarily surface runoff (Figure 15). Walleye were most abundant in large, cool streams, and occasionally occurred with brown trout in medium-sized streams, where relatively low abundance levels were recorded for both species (Figure 15).

Comparisons of cluster versus member species abundances on axes of LFY and CA (e.g. Figure 16) showed that clusters provide a general picture of abundance patterns, but with limited resolution relative to similar plots of member species. For example, members of the silver redhorse cluster showed differences among species in the range of LFY-CA conditions of occurrence and greatest abundance. Here, golden redhorse and greater redhorse appeared to have the broadest and narrowest LFY-CA "niches", respectively, of the three species, while silver redhorse had a peak abundance under the highest LFY levels. Differences between species in the range of LFY-CA conditions over which they are abundant suggests the potential use of such plots in characterizing species as habitat generalists or specialists in relation to stream size and hydrology.

Discussion

Grouping fishes

Description of clusters and comparison with other studies.–Membership of fishes in clusters at level C often appeared to reflect similarities in habitat preferences among species (Table 1). Somewhat similar clusters of species might have been expected based on descriptions of species' habitat requirements mentioned in life history accounts (e.g. Trautman 1981 or Becker 1983). Different headwater clusters seemed to correspond to thermally different stream types (Table 1). For example, species in the brook trout cluster occurred in spring-fed coldwater streams; those in the blacknose dace cluster in streams with some springs but considerable through- and surface-flow inputs; and those in the creek chub cluster in runoff-fed, low-velocity, warmwater streams. Species membership in other clusters also appeared to reflect their requirement for streams varying in size, temperature, and current velocity conditions (Table 1).

Fish clusters identified at level C seemed to characterize stream types identified in other classification studies. For example, Ricker's 1934 classification (in Hawkes 1975) of Ontario streams separated streams into groups based upon their size (width greater or less than 3 meters) and thermal conditions (warm versus cold). Many of the characteristic fishes (dace, trout, bass, pickerel, catfish) used in classifying Maryland streams in Van Dusen's 1954 study (in Hawkes 1975) are similar to clusters we identified. Correspondence analyses of stream fishes in Wisconsin (Lyons 1989) identified water temperature, stream gradient, substrate composition, and shoreline vegetation as being important in determining species associations. General associations among fishes in Lyons' study included: trout, dace, and sculpin; northern redbelly dace and brook stickleback; sunfishes and bullheads. Halliwell (1989) grouped Massachusett's fishes into groups that seemed to reflect shared preferences among species for particular temperature, stream size, and current velocity conditions. He identified the following five associations: 1) small, upland coldwater fishes including natural reproducing salmonids; 2) a marginal trout community with a few large trout, blacknose dace, and longnose dace; 3) a coolwater group including smallmouth bass, rock bass, and darters; 4) a warmwater lentic group containing sunfishes and bullheads; and 5) a lowland assemblage containing pickerel and chubsucker.

While our findings seemed to generally corroborate other studies, it is difficult to make direct comparisons of cluster membership with studies from other areas (Kuehne 1962; Hynes 1970; Hawkes 1975; Rose and Echelle 1981; Strauss 1982; Aadland 1993). Studies differ in the numbers and types of streams studied, and in the available species pools. Consequently each set of clusters produced are unique to that particular analysis. For example, the combination of brook trout, brown trout, and slimy sculpin into a single cluster by Strauss (1982) may reflect both some commonality in habitat requirements among these species and a lack of streams in his study area (the Susquehanna River drainage of Pennsylvania) with extremely high groundwater contributions. Enough of these streams apparently exist in Lower Michigan that brook trout and slimy sculpin were placed into a separate, very high-LFY cluster, while brown trout were grouped with rainbow trout and chinook salmon (Table 1). Still, the brook trout and brown trout clusters join at level B in the dendrogram (Figure 3). Management activities such as stocking might also influence clustering results.

Evaluation of clusters.–Our findings suggest that though the fish clusters explained considerable variation within the MRI dataset, their usefulness may be limited to coarse-scale descriptions of fish assemblage structure. The seventeen clusters identified in this study explained about 39% of the variation in fish distributions among the 225 MRI sites, and characterized several meaningful groupings of fishes. However, the biological reason for assignment of some species (especially those typical of medium- to large-sized, low-velocity, warmwater streams) to one cluster or another was not always clear.

Analyses of regression slopes demonstrated that measures of a cluster's abundance often did not equally represent the abundance of its constituent fishes (Table 1). This rather liberal test of a cluster's predictive ability showed differences in slopes among species within clusters for 54 of the 69 species (or 11 of 17 clusters) studied. Similarly, only 27 out of 43 fishes used in Strauss' (1982) analysis of Pennsylvania streams were included in statistically significant clusters. We recommend the use of quantitative techniques such as those described here for objectively evaluating the ability of species clusters to explain patterns in species' distribution and abundance.

Our experience with generating clusters also suggested that membership of some fishes in clusters should be viewed as tenuous. In general, cluster membership was more stable for headwater fishes than for fishes typical of larger streams. We found that cluster membership could change slightly in response to relatively small modifications of the dataset (e.g. addition or removal of data from a single site), and mention that the species clusters identified here (though often biologically informative) were chosen somewhat arbitrarily from the dendrogram (Appendix A).

More troublesome is the fact that ecologically-meaningful information at the species level is lost when fishes are combined into a cluster. In some cases, the ecological requirements of species in a cluster may differ such that habitat characteristics considered optimal for the cluster are not optimal for any of its constituent species. For example, optimal LFY conditions for the blacknose dace cluster ($\log_{10}$ LFY = -0.82 cfs/km^2) differ from those of either of its constituent species, blacknose dace and mottled sculpin, having respective $\log_{10}$ LFY values of –1.15 and –0.74 cfs/km^2. In addition, when species are combined into clusters species-specific information (e.g. zoogeographic range, or specific life history or habitat needs) cannot be readily used to explain patterns in species' distributions. Species-specific data would be preferred for studies of fish assemblage structure, because clusters cannot provide the most accurate information for the species of interest.

The utility of fish clusters versus individual species will depend upon the specific situation and audience. Fish clusters are useful as general descriptors of fish assemblage structure. The clusters identified in this report, and their relations to stream size and hydrology, have already been used to characterize potential fish communities of valley segments in an ecological classification of Michigan streams (Seelbach et al. 1997). The use of fish clusters or groups may lessen the focus on individual species, and foster a more holistic (fish assemblage-oriented) approach to stream protection and management. An individual species approach, however, has the advantage of being more straightforward and explainable due its lack of statistical manipulations. It is more biologically defensible because species, unlike clusters, are discreet biological units.

Biases associated with clusters.–Species clusters identified in this study were generated from field surveys conducted under summer conditions. Consequently, the clusters represent groups of species whose abundance during the growing season were correlated. Different species clusters might have been identified if fish abundance data from other seasons were included in this analysis because of seasonal differences in movement and habitat use among species. For example, if data from spring surveys were included in this analysis, species that make upstream spring spawning migrations may have been characterized as being small stream species, rather than characteristic of larger habitats.

Clusters probably reflected co-occurrences of adults (that often make up the bulk of the biomass) and habitats occupied by larger individuals during the growing season, because we clustered species based upon their biomass at sites. Clustering fishes based on numbers rather than weights would likely generate different results, particularly for fishes demonstrating major ontogenetic shifts in habitat use (e.g. young of year occupying creeks but adults living in lakes or big rivers). In this case, groupings would be based upon the more numerous young fish (rather than the fewer older fish that make up the majority of the biomass) and might be influenced by randomly-produced strong year classes. Clustering based on numeric abundance would also produce less-meaningful clusters if juvenile fishes exported from optimal habitats into nearby marginal habitats were clustered with resident fishes in these same habitats.

Stream Ordination Axes

LFY as a macro-habitat axis.–While the importance of stream size has been well documented, our findings demonstrate the additional value of LFY as a macro-habitat variable for characterizing stream environments and aquatic communities. In glaciated areas like Michigan, characteristics of streams; such as flow stability, temperature, substrate, riparian, and land use conditions; largely reflect the glacial history of their basins (Hendrickson and Doonan 1972; Richards et al. 1996; Seelbach and Wiley 1997; Wehrly et al. 1998). As a hydrologic variable, LFY integrates the effects of landscape-scale differences in geology, landform, and soil characteristics among catchments and indexes many variables important to fishes. These features of the landscape largely determine how precipitation is routed to streams (via groundwater, throughflow, or surface runoff) through their effect on water infiltration and percolation rates through subsurface soil layers. For example, catchments dominated by coarse-textured end moraines and their associated outwash deposits generally have coarser-textured soils containing higher proportions of gravel, cobble, and boulder than those draining areas of finer-textured till or lacustrine plains. Coarse-textured soils enhance the infiltration of precipitation and its percolation through subsurface soil layers, producing hydrologically stable (usually high-LFY) streams (Figure 6). The higher elevations and hydraulic head associated with end moraines, in combination with high infiltration and percolation rates of outwash soils, allow for the relatively rapid downslope movement of groundwater to nearby streams (Hendrickson and Doonan 1972; Dunne and Leopold 1978). Consequently, high-LFY streams in Lower Michigan usually also have high stream gradients (Figure 7). Interestingly, the occurrence of coarse stream substrates and high gradient reaches (Figures 7 and 8) may reflect the presence of local-scale geologic features that do not show on larger-scale maps, such as kames and other rocky deposits. Stream gradient has often been suggested as a key variable for stream classification (Trautman 1942; Dewberry 1980; Zalewski and Naiman 1985; Lyons 1996); LFY and CA to some degree index this variable for Lower Michigan streams. Although generally correct, it must be noted that the relationships between baseflow, and catchment geology and slopes pictured in Figures 6 and 7, were to some degree artifacts of our use of predicted flows in the analysis; as data on catchment geology and slope were important components of models used in predicting 90% exceedence flows (Wiley et al. 1997).

Low-flow yield is also correlated with landscape characteristics that influence the nutrient status and structural characteristics of stream habitats. For example, low organic content of the coarse-textured soils and the relatively steep topography of many northern Michigan landscapes makes their catchments better suited to forestry than agriculture (Albert et al. 1986). Streams draining forested landscapes typically have more extensively wooded riparian corridors, higher amounts of woody debris in the channel, and lower nutrient levels, than those draining ground moraines in agricultural regions (Wiley 1990; Kleiman 1995). Higher channel gradients and summer streamflow conditions produce relatively high current velocities during the growing season that favor some fishes over others (Poff and Allan 1995). High velocities, in combination with coarser substrates and abundant woody debris, produce turbulent flows along much of the stream bottom and favor development of well-defined riffles and pools.

Because it reflects summer (growing season) conditions, LFY is correlated with other proximal variables that have energetic importance to fishes including mean temperature (Figure 9), diel temperature variation (Figure 10), and dissolved oxygen levels (Hendrickson and Doonan 1972; Brett 1979; Wiley 1990). Such variables however, may also be strongly influenced by local-scale factors. For example, stream temperature is affected by local factors including riparian shading; local groundwater inputs; or the presence of upstream wetlands, lakes, or impoundments (Wehrly et al. 1998). It should be noted that the relationships shown in Figures 9 and 10 were also partially artifacts of our analysis, since CA and variables correlated with LFY were included in models used to predict July temperatures (Wehrly et al. 1998).

As a measure of the relative contribution of groundwater to streams, LFY provides a general index of the disturbance regime of the stream environment, with the magnitude and frequency of drought and flood events generally increasing as LFY declines (Hendrickson and Doonan 1972; Dewberry 1980). Several studies (e.g. Starrett 1951; Schlosser 1985; Coon 1987; Schlosser 1987; Strange et al. 1992; Nuhfer et al. 1994) have demonstrated the effects of flow conditions on temporal variability in species abundance. The importance of abiotic versus biotic factors in controlling fish assemblage structure through time is affected by the stability of a stream's hydrologic regime, with the role of biotic factors generally diminishing as LFY declines and conditions become harsher (Poff and Ward 1989; Bayley and Li 1994; Strange et al. 1992). Variability and predictability of a stream's hydrologic regime form part of a habitat template within which species' life histories must fit if they are to persist (Southwood 1977; Winemiller and Rose 1992).

Low-flow yield has additional appeal because it is a measurable quantity that can be expressed in real units. Many stream classifications use statistically defined, multi-variate factors which can be cumbersome to work with and difficult to explain. Low-flow yield, however, is a relatively simple parameter that can be readily quantified and explained. Dewberry (1980) suggested that a single measurement of low-flow discharge could adequately describe a stream's 90% exceedence flow. Catchment areas can be readily measured using GIS technologies, and development of predictive equations for exceedence flows using available streamflow gage data is becoming a fairly routine procedure. Such models presently exist for all streams in Lower Michigan (Wiley et al. 1997).

LFY and CA as temperature axes.–The observed relationships between aspects of stream temperatures, and LFY and CA (Figures 9 and 10), suggested that the LFY--CA template could be thought of as an index of the summer thermal environments available to stream fishes in Lower Michigan. Small CA streams with high LFY's would typically have a cold daily mean temperature with modest diurnal variation. Small CA streams with low LFYs would have a cool mean with high variation (mean July weekly range can be as high as 16° C; Wehrly, unpublished MRI data). Large CA and low LFY rivers would be expected to have a warm mean with little variation.

Many authors have documented the energetic importance of temperature to ectotherms and its influence on species' life history (Vannote and Sweeney 1980), behavior (Reynolds and Casterlin 1978; Tracy and Christian 1986; Staso and Rahel 1994), and distribution (Magnuson et al. 1979; Shuter et al. 1980; Matthews 1987; Smale and Rabeni 1995b; Peterson and Rabeni 1996). We also see evidence that thermal patterns structure fish communities in Lower Michigan streams and rivers. Different fishes are found in distinct portions of the available thermal niche space (Figure 17; Wehrly, unpublished MRI data). It appears important to consider both the daily mean and diel variation as temperature descriptors because habitats that have the same mean but different daily ranges seem to represent distinct thermal habitats for fishes (Figure 17). This may relate to the amount of time a stream provides optimal thermal conditions for a given species. Further research is needed to explore relations between different aspects of stream temperature and patterns in fish distribution and abundance.

Cluster optima plotted on LFY-CA axes.– The distribution of fish cluster "optima" (LFY and CA conditions where clusters were most abundant) on axes of LFY and CA suggested that assemblage structure changed along both axes. Optima were most widely spaced on the LFY axis in small streams, but converged with increasing CA (Figure 4). This seemed to reflect physical (hydrologic and thermal) characteristics of streams, many of which reached extremes of stability or instability in headwater reaches (CA values generally < 2.3). High-LFY headwater streams were dominated by coldwater stenothermic fishes in the brook and brown trout clusters. Species more tolerant of warm, physically variable, low-velocity pool environments, as represented by the brook stickleback, creek chub, and white sucker clusters, were most abundant in low-LFY headwater streams.

A variety of factors may explain why most headwater species were not abundant further downstream (Figure 5). Reductions in abundances of coldwater fishes may reflect their intolerance to warmer conditions downstream, and/or competition with (or predation from) species better adapted to larger or thermally different stream environments (Waters 1983; Larson and Moore 1985; Staso and Rahel 1994). However, high tolerances of some headwater fishes for extreme temperature and dissolved oxygen conditions (Matthews and Styron 1981; Smale and Rabeni 1995a; Smale and Rabeni 1995b) suggest that they should also thrive in the relatively benign conditions of downstream reaches. Biotic interactions may prevent these fishes from being abundant in larger streams. Some examples of thermally tolerant, headwater species mentioned in the literature as being susceptible to predation or being inferior competitors include central stoneroller (Power et al. 1985), fathead minnow (Becker 1983), creek chub (Becker 1983), and white sucker (Schlosser 1987). A lack of deeper pool habitats or the presence of other physical conditions unsuitable for adult piscivores may allow such fishes to thrive in headwater environments (Schlosser 1987).

Convergence in the physical characteristics (Figure 1) and fish assemblages (Figure 4) of Lower Michigan streams appeared to occur with increasing stream size. In many cases, this attenuation of differences may result from the accumulation of many hydrologically-different patches of glacial drift as streams (and their catchments) grow in size. Streams draining the smallest catchments, where "pure" deposits of the most permeable or least permeable soils occur, represent the physical and temporal extremes of hydrologic stability or instability. But as catchment size increases, hydrologically different patches of drift are often added to the catchment and their hydrologic effects blend together. This "blending" effect generally results in decreased variation in physical conditions and associated fish communities, and would explain the "funnel-shaped" distributions of many variables when plotted against CA. Also, in large streams, discharge volume itself becomes an important variable influencing the stability of habitat characteristics (Gordon et al. 1992).

Cluster overlap and implications for community assembly.–Distribution of species clusters on LFY-CA axes (Figure 5) provided insight into how stream fish communities are organized. Plots of optimal conditions for each species cluster show differences in LFY and CA conditions where cluster abundance scores were highest. However, considerable variation about the each cluster's LFY and CA optima, and differences among species within a cluster (Table 1), suggest that the actual combination of clusters (or species) at a stream site varies with LFY and CA conditions. This overlap and the tenuous nature of the fish clusters identified in this study implied that species respond individually to their environment, rather than as a group. Studies of the responses of species to variables such as temperature show similar patterns (Smale and Rabeni 1995a and Smale and Rabeni 1995b), with species having both overlapping ranges of tolerance and different extremes of tolerance. Our results suggest that stream fishes coexist in "open" communities (often distinguished by the name "assemblages") in which fishes respond individually (sensu Gleason 1926) to changing abiotic and biotic conditions, rather than in "closed" communities of inter-dependent species. The view that North American animal and plant communities generally have open structures is also emerging through paleoecological studies of community structure over longer (10^1-10^6 year) time scales (Delcourt and Delcourt 1991; Pielou 1991).

Assemblage-level patterns.–Patterns in fish standing crops and species richness also seem to corroborate the "open" view of assemblage structure, in that highest overall standing crops and species richness occur under LFY and CA conditions suitable for the most species, i.e. showing the most overlap among clusters (Figures 11 and 12). Wedge-shaped patterns in plots of total fish standing crops against estimated July weekly mean temperature (Figure 13), suggested that summer temperature conditions (or variables indexed by temperature conditions) may potentially limit total standing crops of stream fishes (Terrell et al. 1996; Thomson et al. 1996). We saw similar patterns between species richness and July weekly mean temperatures (Figure 14). Relatively low standing crops and species richness in coldwater streams may also relate to the generally lower productivity of these systems, the existence of relatively few coldwater-adapted fishes, or other factors.

Plots of individual species' LFY-CA optima on axes of LFY and CA could also be used to identify stream conditions where fish species richness would be expected to be unusually high (local richness "hotspots"). Whiteside and McNatt (1972), Gorman (1986), and Osborne and Wiley (1992) noted that larger streams served as sources for increasing fish species richness in adjacent smaller streams. We suggest that increased species richness would be expected at the confluence of streams whose CA and LFY values place them far apart in LFY-CA space. For example, species richness of a coldwater stream would increase when a low-LFY tributary enters it. For Michigan streams, connections to inland lakes or the Great Lakes may also enhance fish species richness. Juvenile largemouth bass and bluegill were actually the fishes found at the most survey sites (MRI, unpublished data), indicating frequent connections between stream sites and nearby lakes or ponds.

Longitudinal zonation patterns in Michigan.–Streams in glaciated areas such as Lower Michigan often do not display the typical longitudinal patterns (cold, high-gradient creeks grading into warm, low-gradient rivers) described by many authors (Hawkes 1975; Vannote et al. 1980). This region contains various types of glacial deposits and soil textures in a patchwork that seems to preclude description of streams using a single generalized pattern of longitudinal zonation. These features include end and ground moraines containing particles ranging in texture from clay to boulders, glacial outwash plains and channels consisting of coarse sands and gravels, and flat glacial lakebeds of clay. Consequently, some streams have warm headwaters and cool lower reaches, others are cold upstream and warm downstream, and others alternate between thermal states depending upon characteristics of the landscape. We use the LFY-CA axes as a map of the "universe" of Lower Michigan streams, to demonstrate this point and show how stream conditions and fish assemblages change with LFY and CA along a stream's course (Figure 20).

Many coldwater tributary streams draining coarse-textured end moraines in northeast Michigan flow northeast into the Thunder Bay and Cheboygan River catchments, streams which in their lower reaches become increasingly warm. For example, Gilchrist Creek is a small groundwater-dominated stream that drains coarse-textured moraines. It then joins the Thunder Bay River, a larger, still predominantly groundwater-fed stream that is warmed somewhat by lakes and impoundments within its upstream catchment. The fish assemblage of Gilchrist Creek is dominated by coldwater species, including salmonids and cottids. A coolwater assemblage containing hornyhead chub, brown trout, rock bass, and burbot is present in the Thunder Bay River. Fish species richness may be somewhat higher near the confluence of these two dissimilar streams due to exchange of cold- and warm-water species (see gap in Figure 20). Moving downstream, the Thunder Bay River grows in size as it receives water from runoff-fed tributaries that drain finer-textured deposits (medium-textured glacial tills, peat, and muck). Consequently, stream conditions and fish communities increasingly typify those of large coolwater rivers.

In contrast, many streams originate in lakes and marshes within outwash plains in northcentral Lower Michigan; initially providing warmwater conditions, then cool- to cold-water conditions due to groundwater accrual as their valleys descend through the outwash plain and among coarse-textured moraines, only to warm again as they flow across former glacial lakebeds before reaching the Great Lakes. For example, the North Branch of the Au Sable River begins as a warmwater stream, flowing through lakes and wetlands on a high outwash plain, but rapidly accrues groundwater from adjacent coarse-textured moraines along its course until it reaches the groundwater-dominated Au Sable River (Figure 20). The Au Sable River continues to gain groundwater inputs as its valley cuts through outwash deposits and moraines along its course to Lake Huron. Common species in fish communities from the headwaters of the North Branch of the Au Sable River to the mouth of the Au Sable River change from warm- and cool-water species (such as common shiner, blacknose dace, and rainbow darter), to cool- and cold-water fishes (including brown trout, hornyhead chub, and mottled sculpin), to large-river, coolwater species (such as burbot, walleye, shorthead redhorse, and logperch). Interestingly, the North Branch never has a LFY that would identify it as a trout stream using our template, however the rapid accrual of LFY shown in Figure 20 indicates a very large local groundwater influx to the lower reaches, resulting in a coldwater regime and excellent trout populations.

An opposite pattern exists for several southeast Michigan streams, namely the Raisin, Huron, Rouge, and Clinton rivers. These originate as small, cool streams in interlobate deposits of coarse-textured glacial tills, and outwash sands and gravels. These streams then cut through end moraines, receiving additional cool-water tributaries in the process. Finally, they accrue much runoff and LFY declines as they drain fine-textured lakeplain clays in the lower parts of their catchments. Agricultural drainage activities and urbanization have further enhanced runoff contributions in these areas. Changes in the Raisin River are shown in Figure 20. The general progression of most common species in fish communities in these streams would be from small-stream, coolwater fishes (such as blacknose dace, mottled sculpin, and hornyhead chub), to coolwater species (including smallmouth bass, stonecat, and rock bass) in medium-sized reaches, to warmwater fishes (such as freshwater drum, carp, channel catfish, and black crappie) more typical of larger, runoff-dominated streams.

Variation in longitudinal changes in fish communities suggests that distance downstream (or CA) alone does not provide an adequate model for predicting changes in fish assemblages in Lower Michigan streams. Other variables important to fishes, such as temperature and current velocity, differ among similar-sized streams and are not solely influenced by CA. Several authors (Balon and Stewart 1983; Wiley et al. 1990) have challenged the idea that all streams show similar longitudinal patterns in stream characteristics and fish assemblage structure. Wiley et al. (1990) suggested that empirical models incorporating key variables that drive ecosystem processes are needed to explain distributional patterns of biota in streams. In this study, the use of LFY and CA as ordination axes provided a useful coarse model, or macro-template, for displaying general patterns in stream characteristics and fish assemblage structure along a stream's entire course. Species-specific models that incorporate the most pertinent variables would better explain abundance patterns of stream fishes.

Application of LFY-CA classification.–The patterns described in this study have a variety of applications. Relations between LFY, CA and fish abundances can provide the an initial model for predicting fish assemblage structure in Lower Michigan streams. The difference between a site's LFY and CA and a species' LFY-CA optimum would serve as an index of the expected abundance of the species at the site. The fish assemblage structure at a site would be predicted by repeating this process for the entire species pool. Such a model has been used to develop site-specific target fish communities for a rehabilitation effort on the Rouge River, an urban stream in southeast Michigan (Wiley and Seelbach 1997). The model could likewise be used to predict assemblage structure at any unsampled site, providing a benchmark against which actual survey data could be compared. Wright (1995) developed such a system for predicting and interpreting invertebrate distributions in British streams.

Relationships between fish abundance and a site's LFY and CA values can be used to graphically evaluate the potential of a stream reach for supporting game and non-game fishes, allowing managers to identify more realistic and attainable fishery management goals. This can be done by locating a site's LFY and CA values on a surface plot for the species of interest (e.g. Figure 17). We are in the process of using such relationships to describe species-specific, ecological distributions of Michigan stream fishes.

Limitations of LFY-CA classification.–We think the approach of using LFY and CA as ordination axes for contrasting streams and displaying fish abundance patterns is widely applicable. These axes should be especially useful in geologically patchy regions, such as glaciated areas. At the spatial scale of Lower Michigan, LFY and CA axes appear to work well because they explain much of the variation in stream temperatures in the region. Empirical relations between LFY, CA, and fish abundances that we describe, however, are specific to Lower Michigan because air and groundwater temperatures (and resulting stream temperatures) vary regionally. For example, two streams, one in Michigan's Upper Peninsula and the other in southern Ohio, might have identical LFY and CA characteristics but quite different stream temperature conditions and fish assemblages. Still, the LFY-CA approach could be used to develop models specific to other regions (e.g. states) that relate fish abundances to LFY and CA.

The LFY-CA stream classification has limited usefulness for identifying specific mechanisms behind observed abundances of fishes at sites. The LFY and CA axes integrate many features of stream habitats important to fish, but do not distinguish which particular feature may be limiting abundances in a particular situation. In addition, LFY and CA do not account for local factors that may influence stream conditions and fish assemblage structure at sites. Such factors would include local groundwater inputs, rocky outcrops, woody debris, dams, and lakes. Nevertheless, the LFY-CA axes provide a useful framework for describing individual streams within a geographically broader context; characterizing a stream's potential; and suggesting large-scale constraints upon a system.

Future Directions

We are working to develop a more detailed understanding of the processes involved in shaping fish assemblage structure in Michigan streams. Our findings support the view that fish communities have "open" structures, and suggest a species-specific approach to predicting their assembly. The fish clusters and large-scale variables, LFY and CA, are useful for describing general patterns in fish assemblages in Lower Michigan, but their level of resolution is too coarse to provide a more detailed, site-scale, understanding of stream fish assemblage structure. The community at any site reflects an assembly of species- and population-level responses to historical and contemporary processes (abiotic and biotic) occurring within the stream environment (Tonn 1990). We are currently developing species-specific models that use these types of information to explain abundance patterns of common fishes in Lower Michigan streams. This effort will use data on fish abundances and habitat characteristics at MRI sites, and attempt to incorporate pertinent information on each species' present distribution, life history requirements, and susceptibility to biotic interactions.

Acknowledgments

Many people contributed to this project. Field survey data used here were collected by Michigan Department of Natural Resources Fisheries Division field crews over the last several decades, and more recently by crews based out of the University of Michigan and Institute for Fisheries Research. J. Fay (the University of Michigan GIS Lab) obtained summaries of catchment characteristics for modeling. K. Wehrly provided predicted temperatures. J. Warner (University of Michigan Center for Statistical Consultation and Research) suggested the ANOVA technique for evaluating the cluster analysis, and R. Lockwood provided helpful advice regarding linear regression techniques. J. Gapczynski helped build the initial fish databases. A. Sutton provided superb technical and graphics assistance. R. Clark provided useful editorial suggestions.

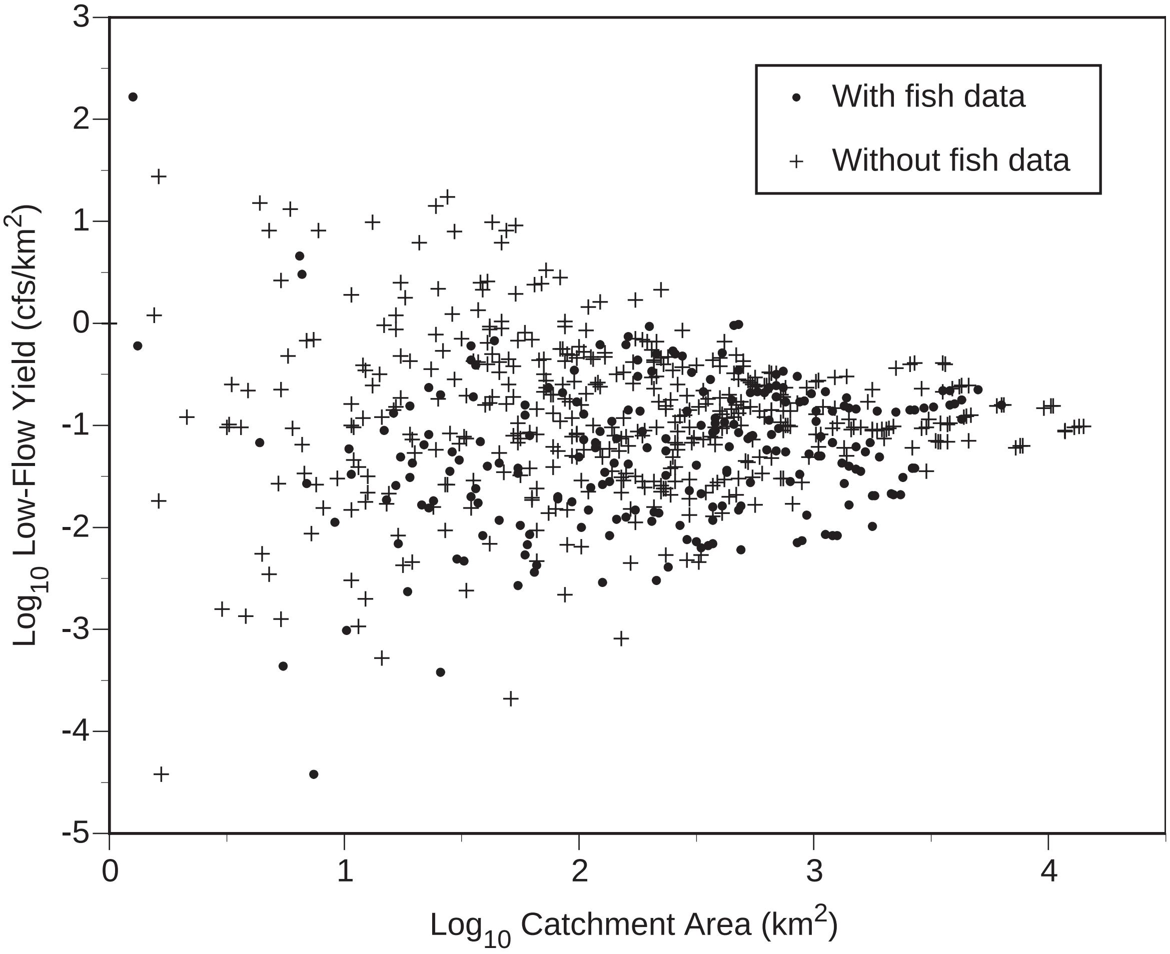

Figure 1.–Low-flow yield and catchment area values for: a) 675 sites in the Michigan Rivers Inventory; and b) 225 Michigan Rivers Inventory sites with abundance data for all fishes at sites.

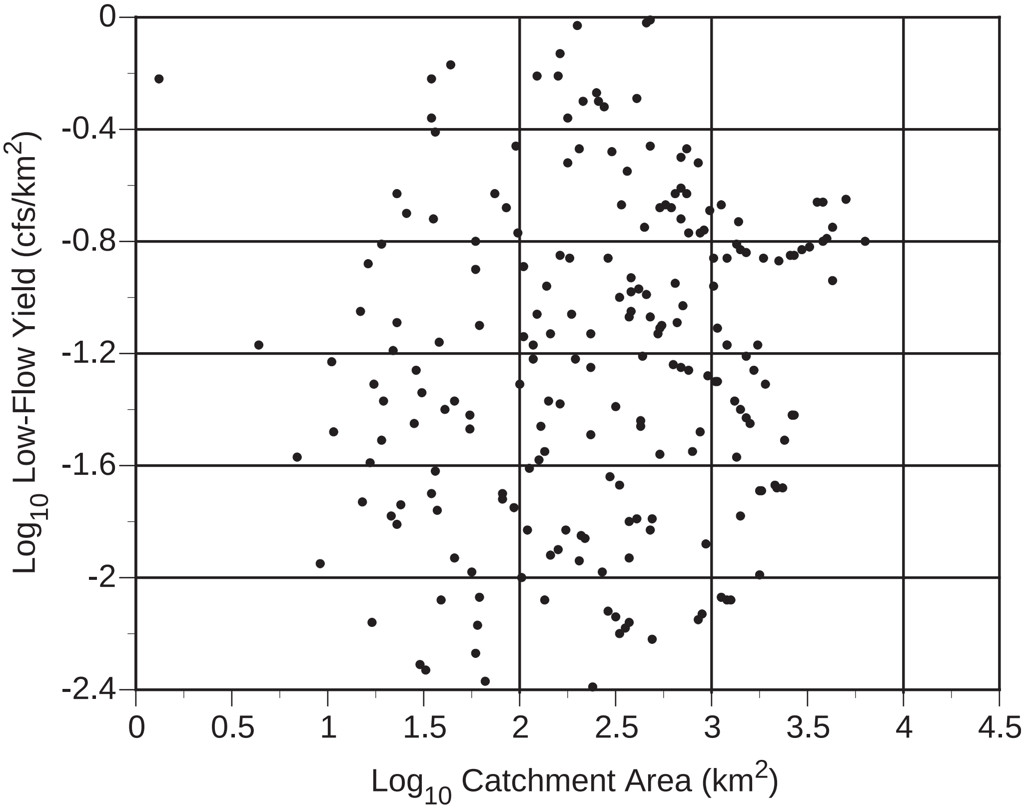

Figure 2.–Sub-sampling grid for obtaining summary statistics (means and standard deviations) from Michigan Rivers Inventory sites meeting various LFY and CA criteria. Lines indicate the low-flow yield and catchment area boundaries of each cell. Cut-points for the x-axis are <2, 3, 4, and >4, and for the y-axis are >-0.4, -0.8, -1.2, -1.6, -2.0 and <-2.0. Spots show Michigan Rivers Inventory sites with fish assemblage data.

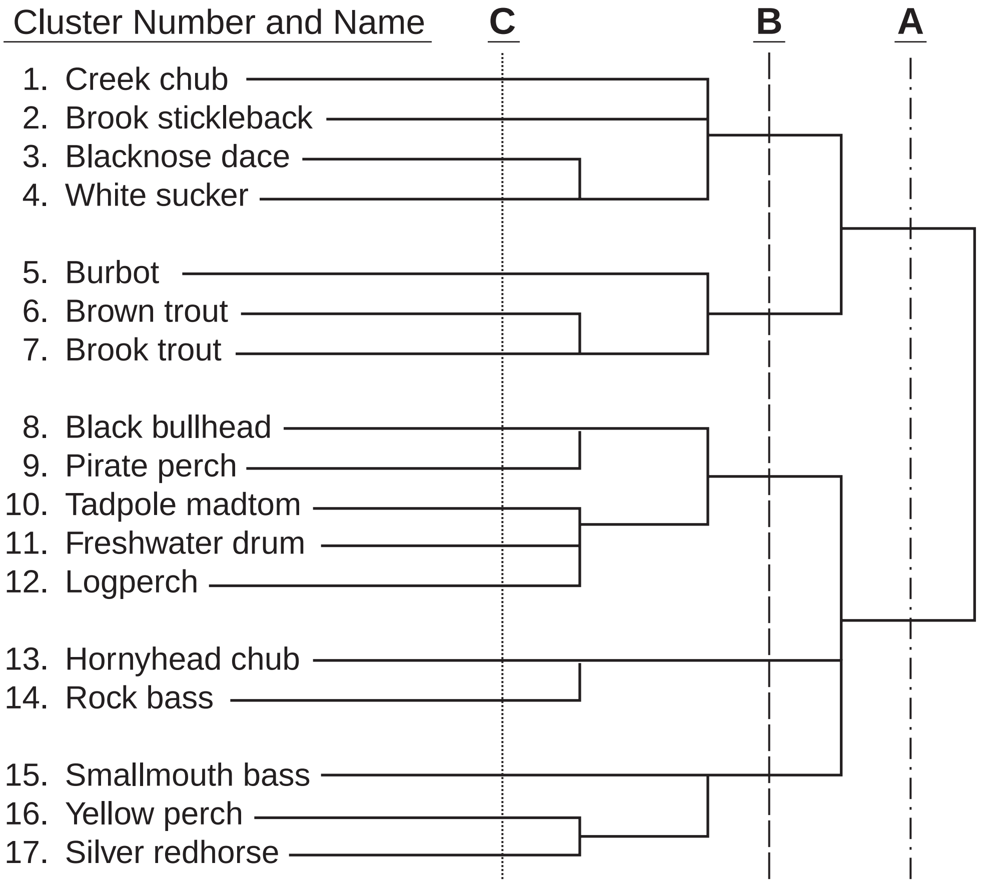

Figure 3.–Clusters of fishes obtained from hierarchical clustering of fishes at 225 Michigan Rivers Inventory sites with fish assemblage data. Letters identify cutpoints for clusters discussed in text. Numbers and species names refer to clusters identified at cutpoint “C” in the dendrogram and are used in the text and subsequent figures. Raw cluster analysis output is shown in Appendix A.

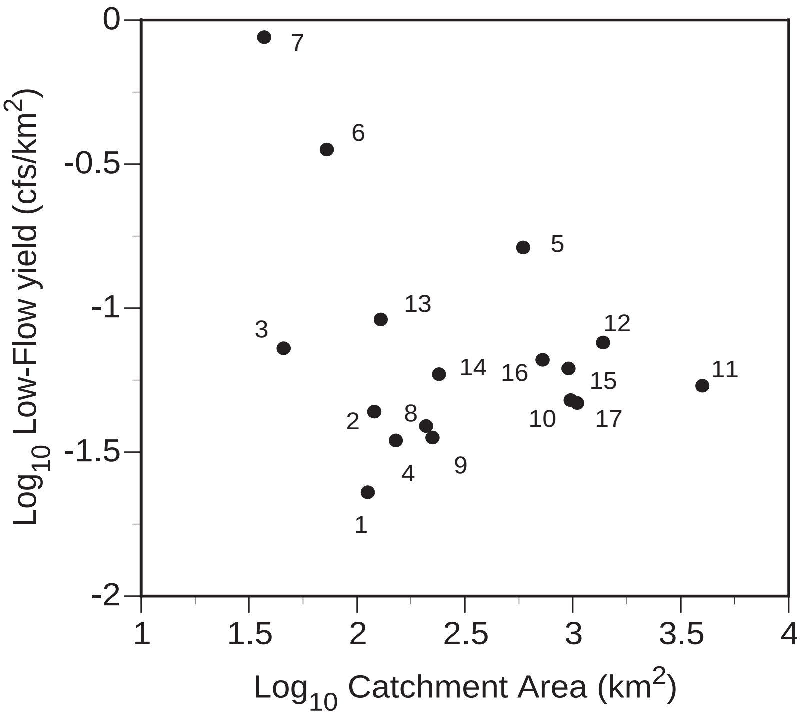

Figure 4.–Mean LFY and CA conditions of sites on Lower Michigan streams where each cluster was most abundant (i.e. sites having cluster z-scores ≥0.5 standard deviations above the mean cluster score for all sites) plotted on LFY-CA axes. Cluster numbering scheme is from Figure 3.

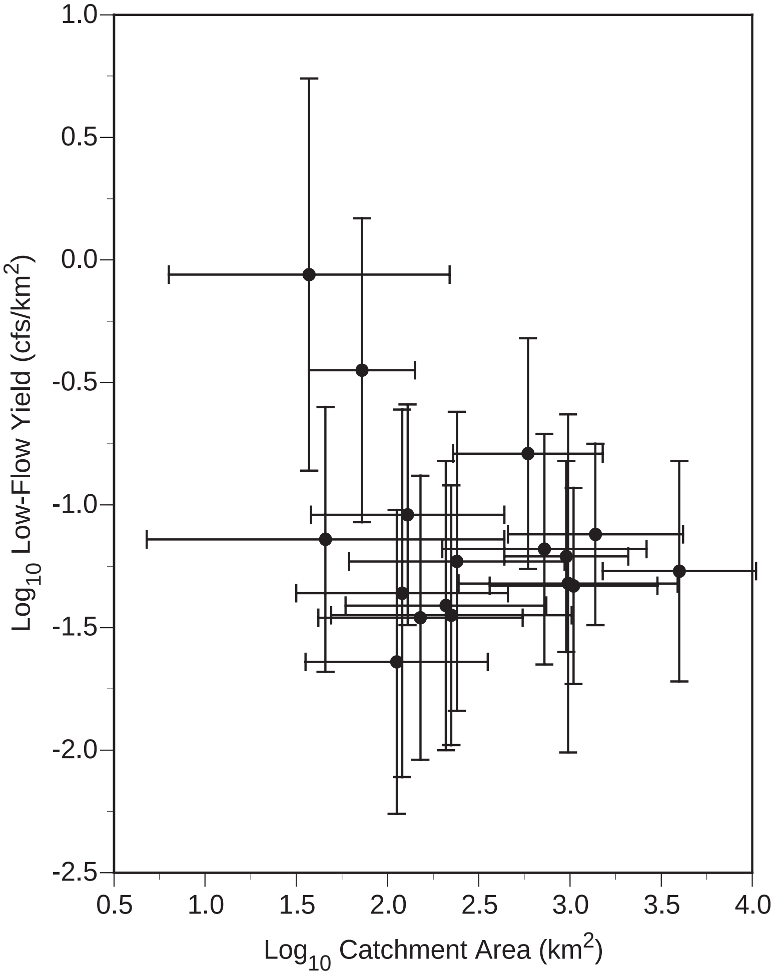

Figure 5.–Mean and standard deviation of LFY and CA conditions of sites on Lower Michigan streams where each cluster was most abundant (i.e. sites having cluster z-scores ≥0.5 standard deviations above the mean cluster score for all sites) plotted on LFY-CA axes.

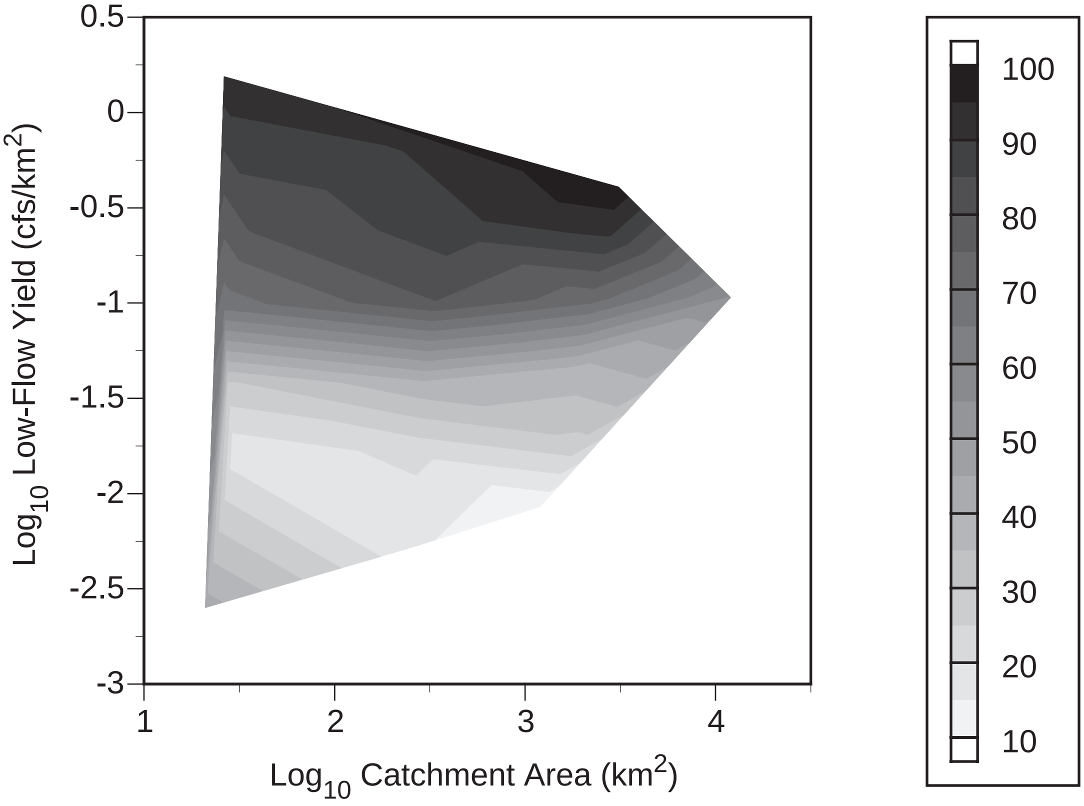

Figure 6.–Percentage of coarse-textured glacial deposits (i.e. outwash sand and gravel, post-glacial alluvium, ice-contact outwash sand and gravel, coarse-textured glacial till, and end moraines of coarse-textured till) in Lower Michigan catchments varying in CA and LFY.

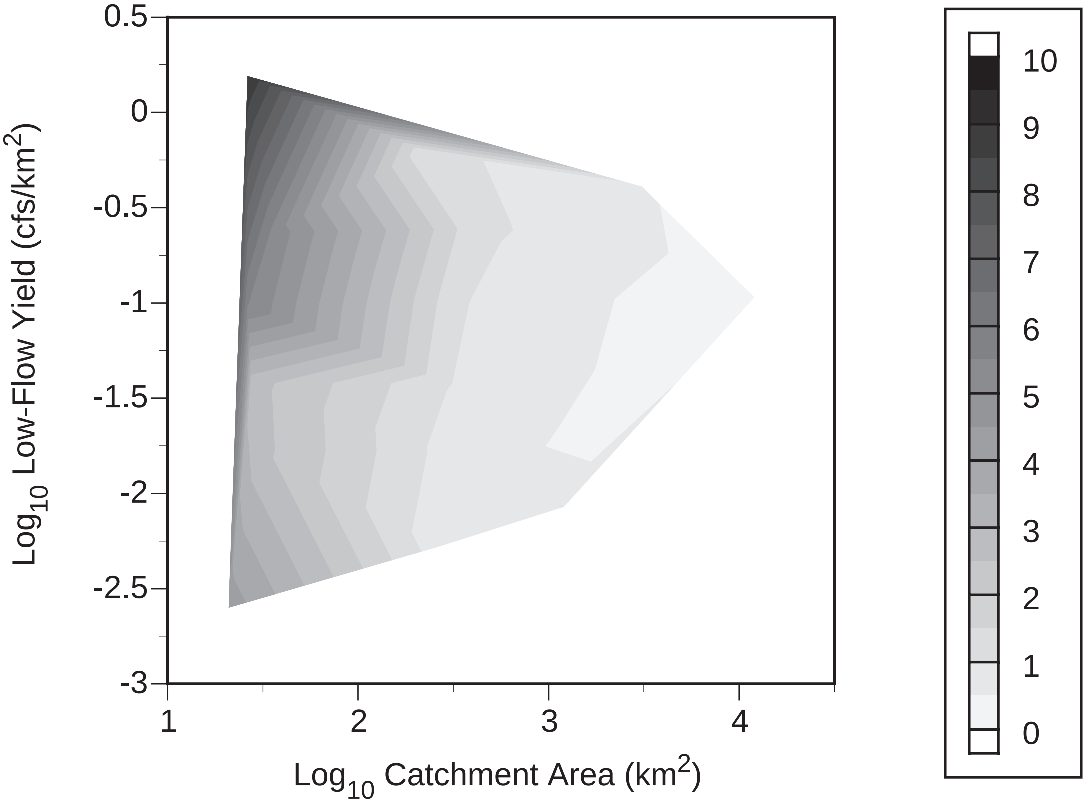

Figure 7.–Average stream gradient (m/km) for reaches of Lower Michigan streams varying in LFY and CA.

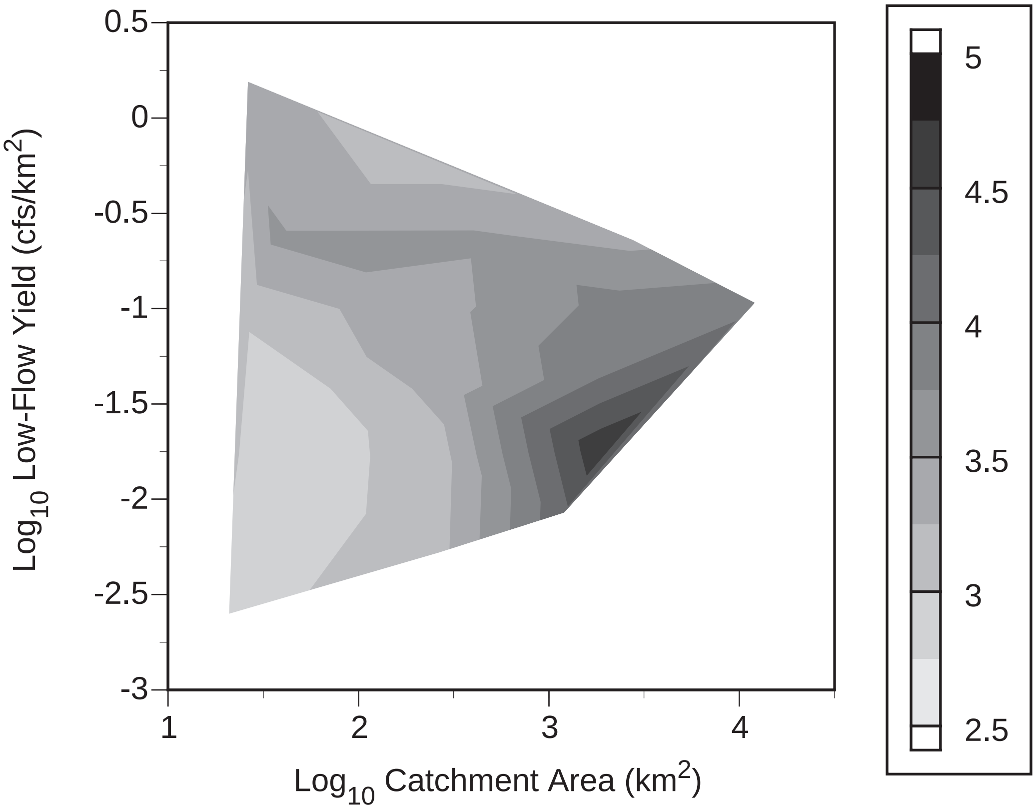

Figure 8.–Average substrate size for Lower Michigan streams varying in LFY and CA. Values represent a weighted average of the percent composition of different-sized substrates at sites. Substrate codes are 2=silt, 3=sand, 4=gravel, and 5=cobble.

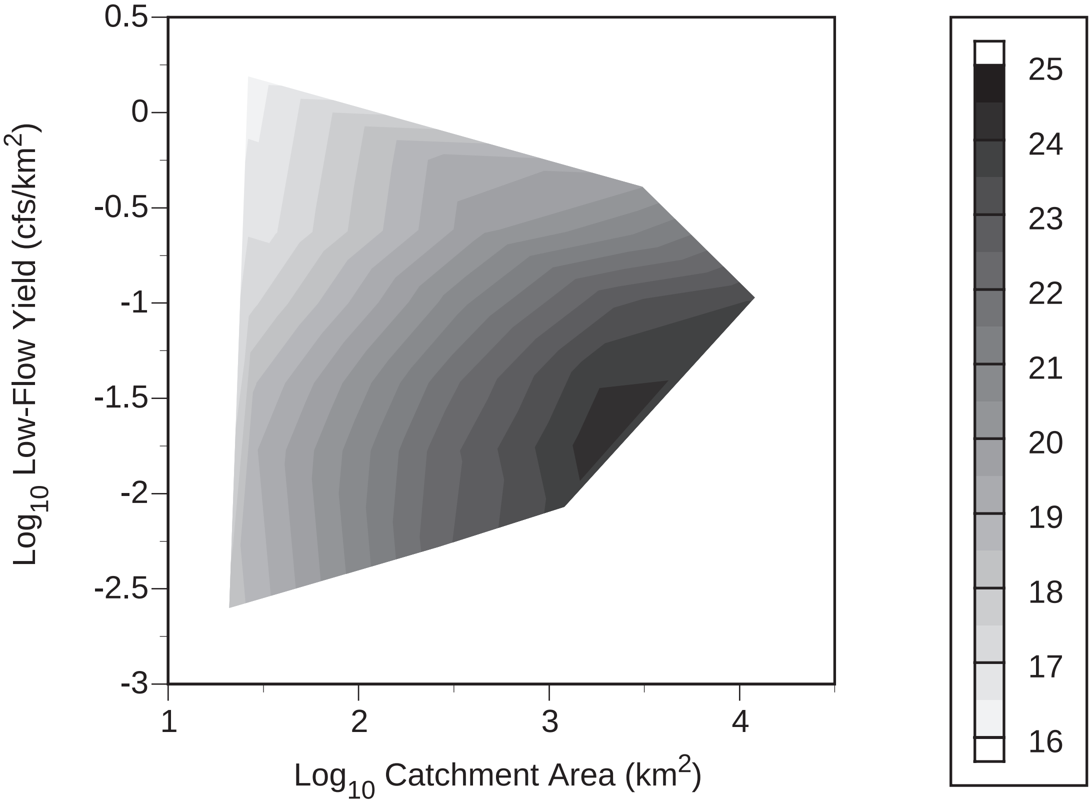

Figure 9.–Predicted July weekly mean temperature (°C) of Lower Michigan streams varying in LFY and CA.

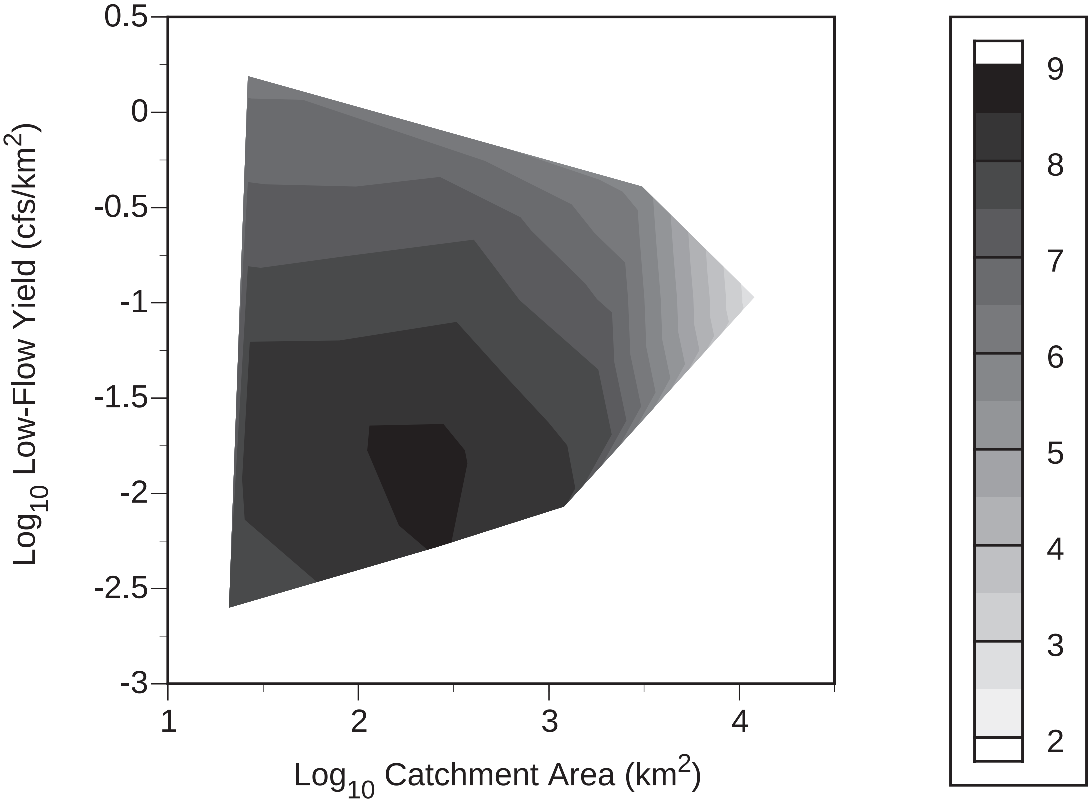

Figure 10.–Predicted range in July weekly temperature (°C) of Lower Michigan streams varying in LFY and CA.

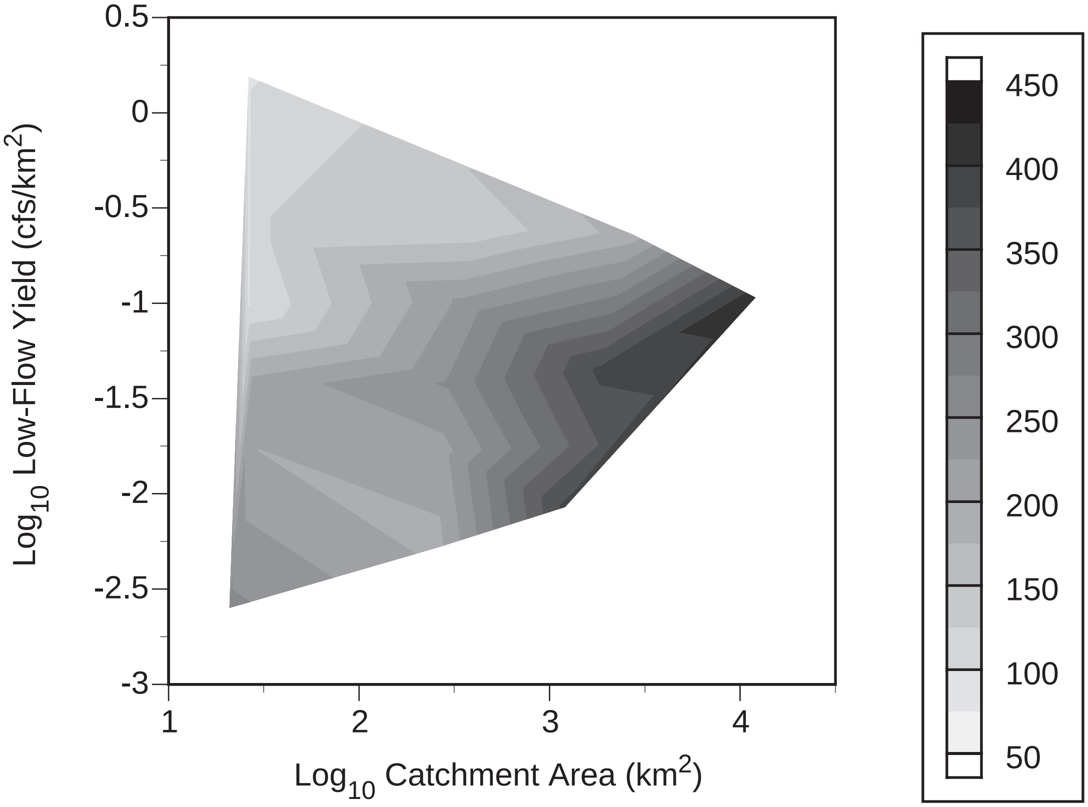

Figure 11.–Average values of total fish standing crops (kg/ha) in Lower Michigan streams varying in LFY and CA.

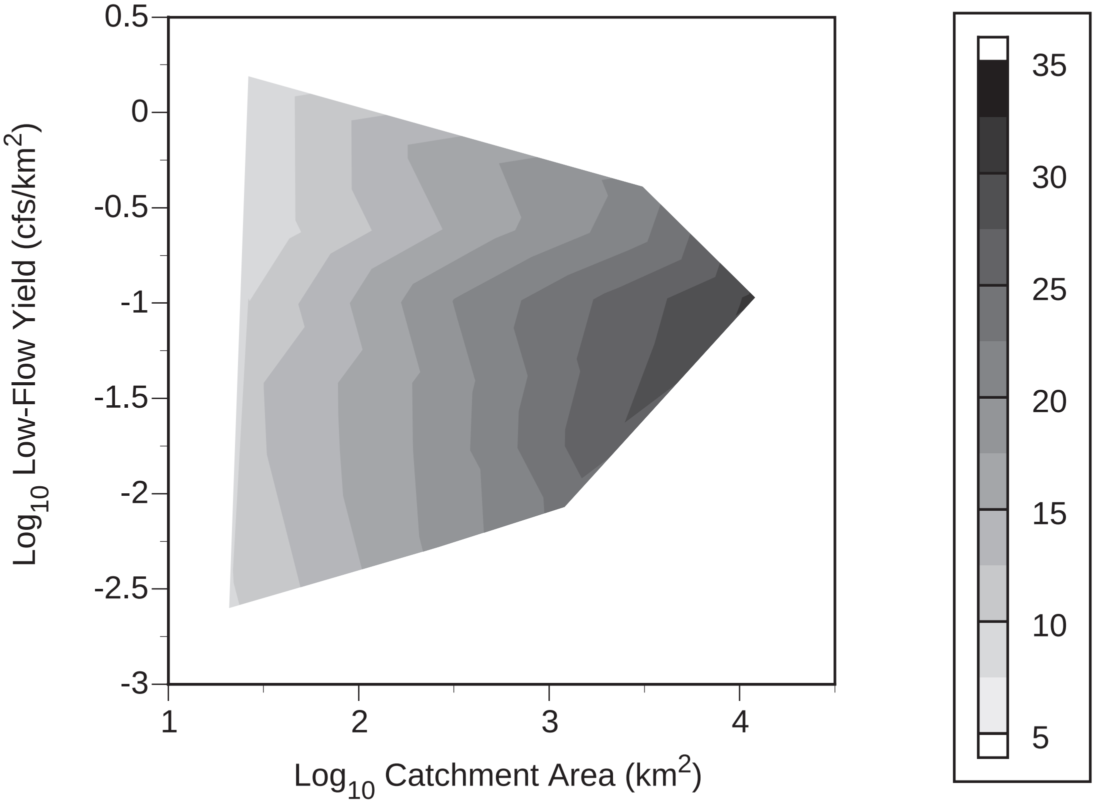

Figure 12.–Average number of fish species at sites in Lower Michigan streams varying in LFY and CA.

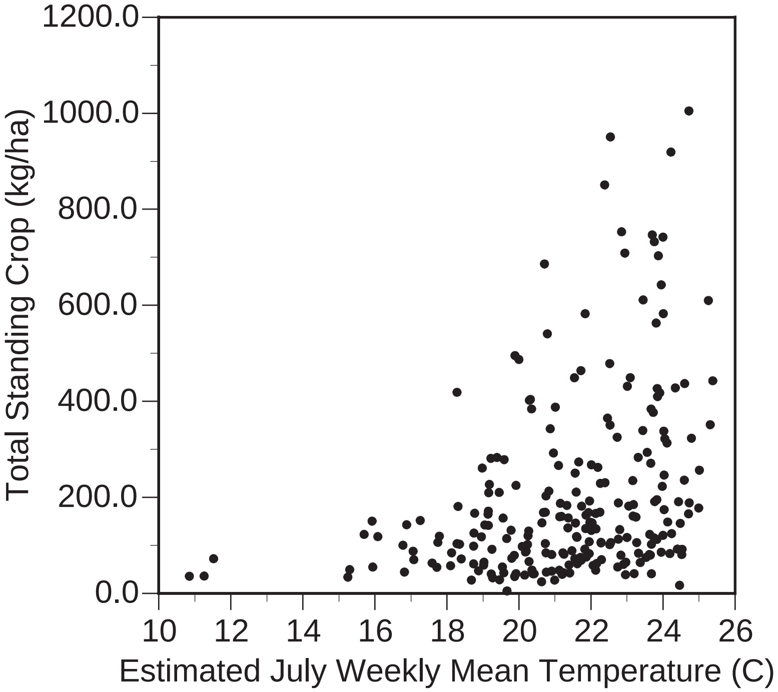

Figure 13.–Total standing crop of fishes at Lower Michigan stream sites plotted against predicted July weekly mean temperature.

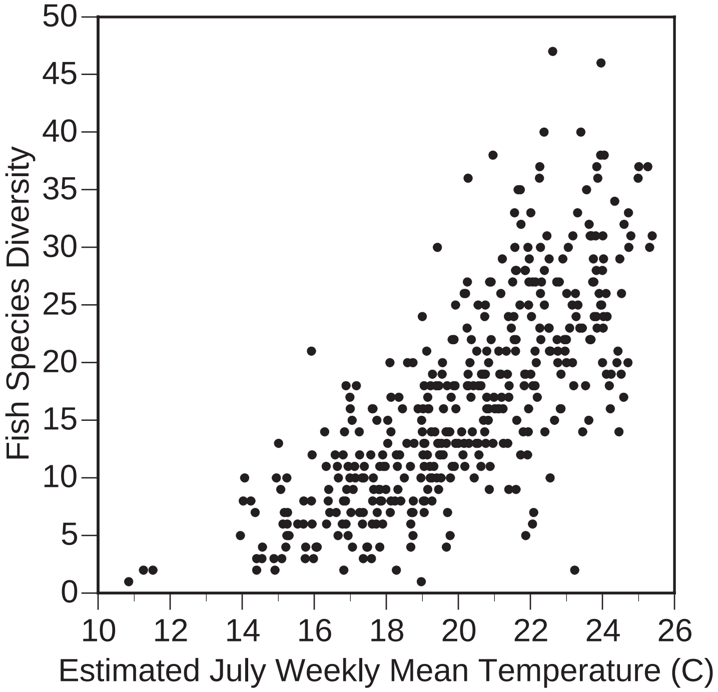

Figure 14.–Fish species richness (i.e. number of species at sites) in Lower Michigan streams plotted against predicted July weekly mean temperature.

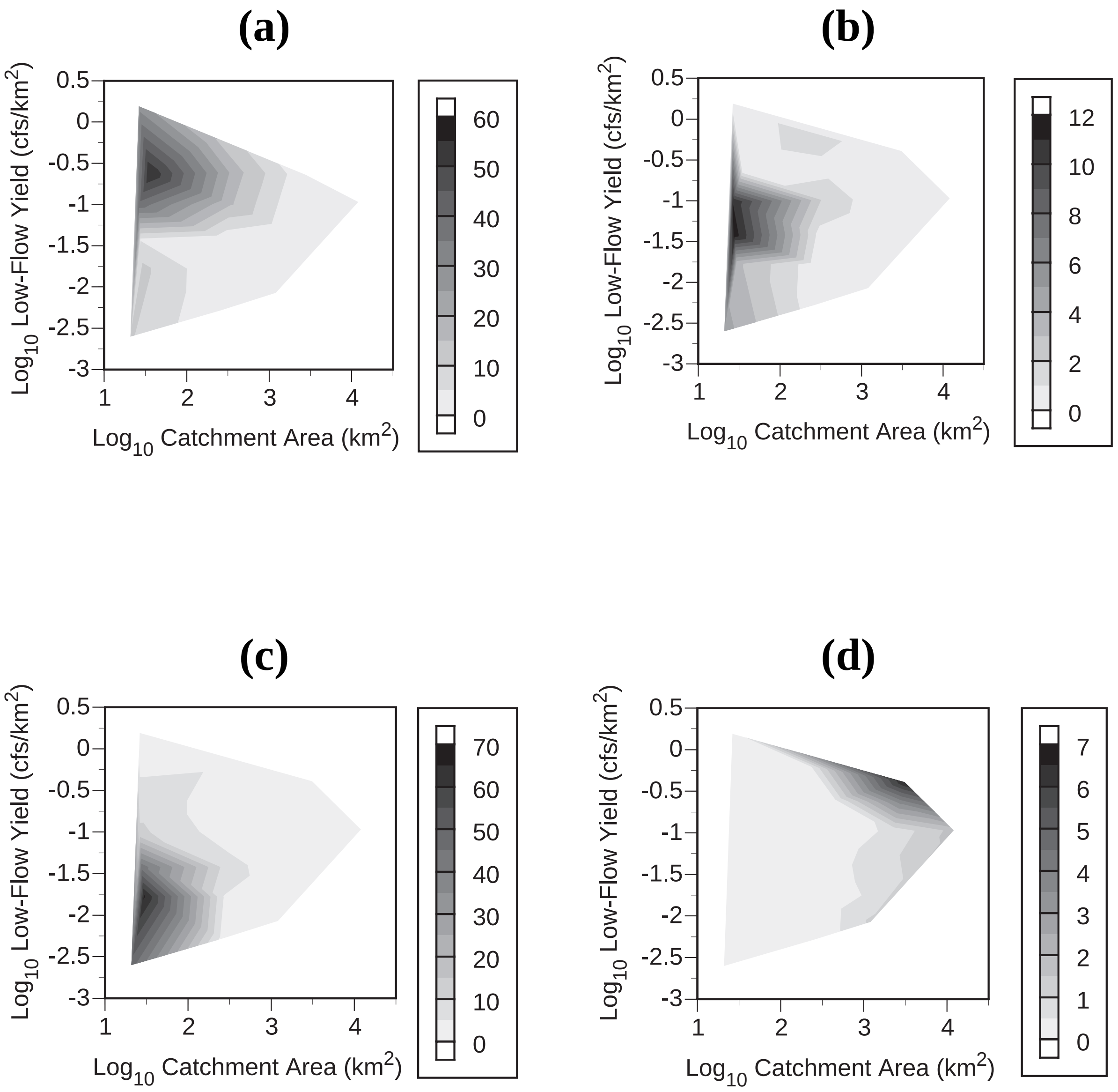

Figure 15.–Average abundances (in kg/ha) of brown trout (a), blacknose dace (b), creek chub (c), and walleye (d) in Lower Michigan streams varying in LFY and CA.

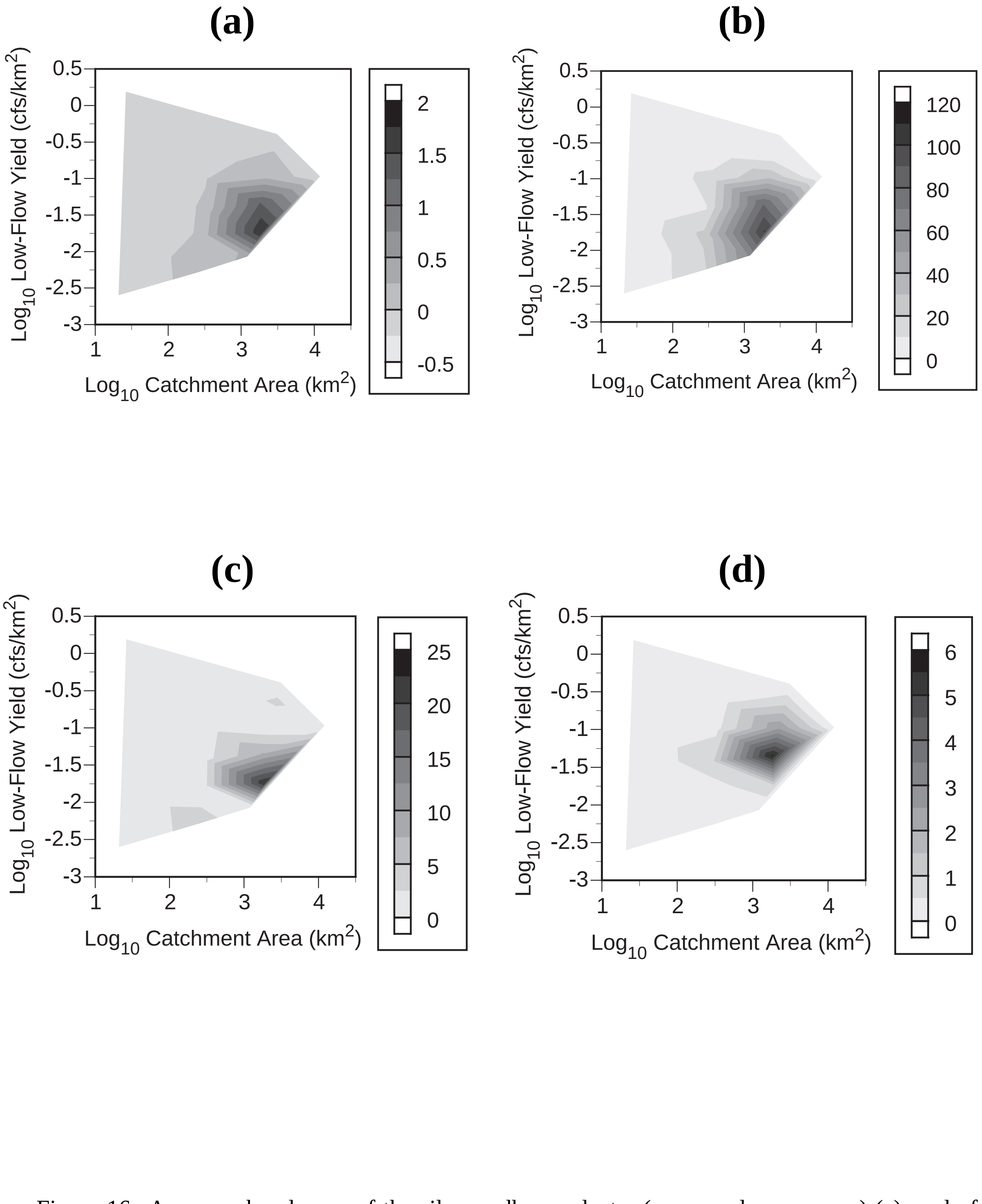

Figure 16.–Average abundances of the silver redhorse cluster (expressed as z-scores) (a), and of constituent species (in kg/ha): golden redhorse (b), greater redhorse (c), and silver redhorse (d) in Lower Michigan streams varying in LFY and CA.

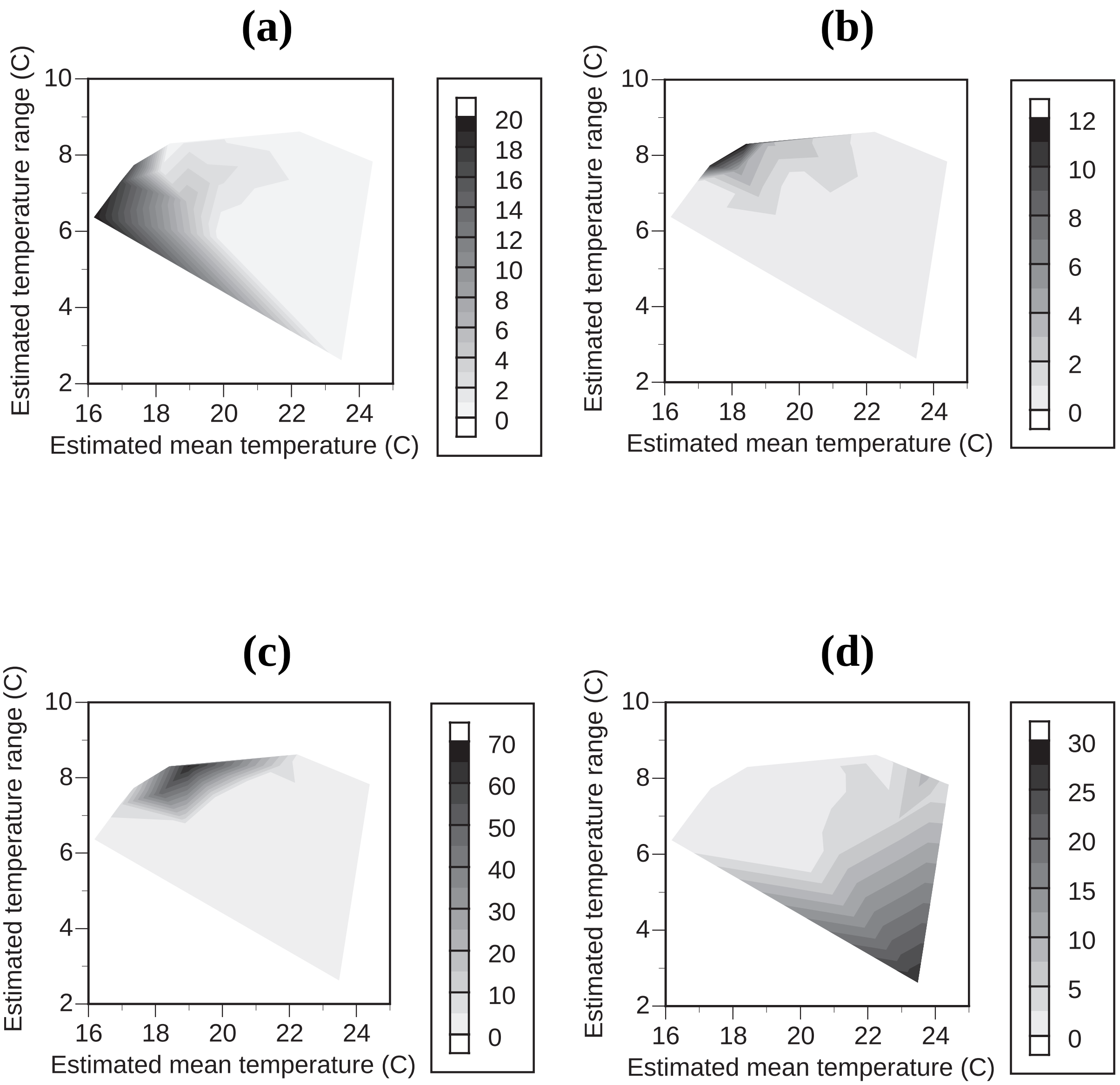

Figure 17.–Average abundances (in kg/ha) of brook trout (a), blacknose dace (b), creek chub (c), and channel catfish (d) on axes of predicted mean and range in July weekly temperature.

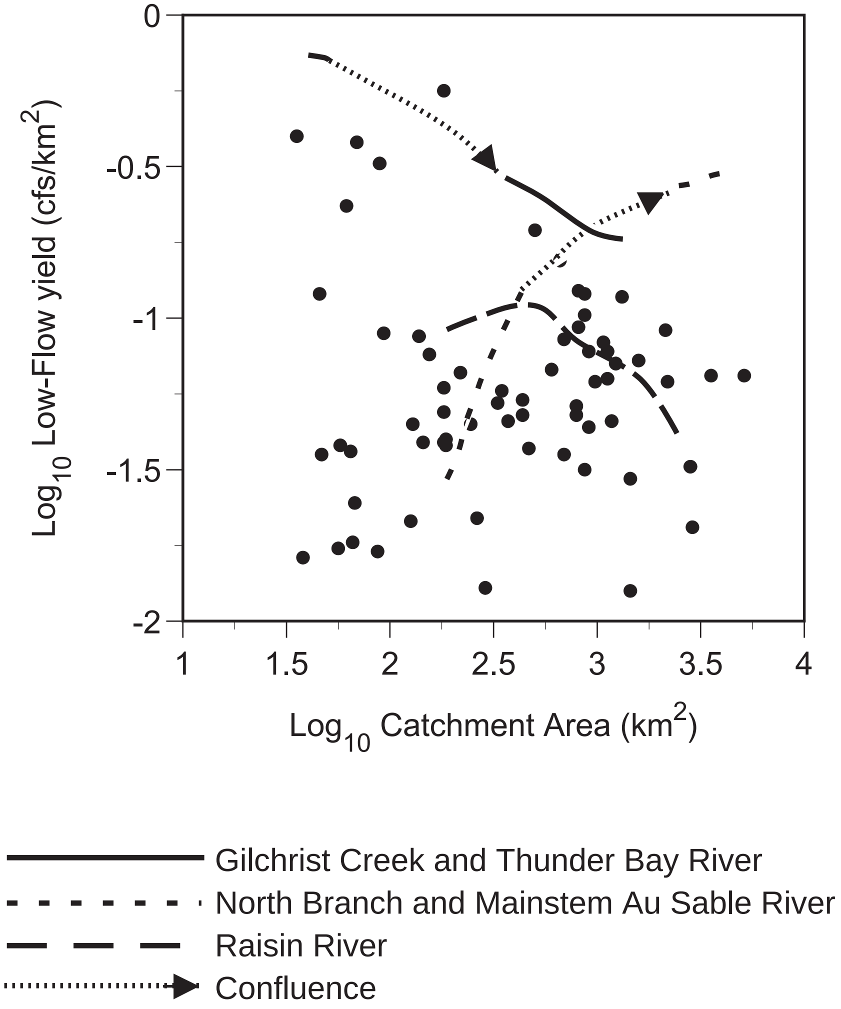

Figure 18.–Longitudinal trajectories of three Lower Michigan streams as they change in LFY-CA characteristics along their course. Dots represent mean LFY and CA conditions of stream sites where fishes in this study were most abundant (i.e. sites where the species' z-score was ≥0.5 standard deviations above the species' mean z-score for all sites). Downstream changes in distances between a stream's LFY-CA value and the LFY-CA optima of fishes suggest changes in fish community structure. Also, note the abrupt change that occurs at the confluence of tributary and mainstem reaches.

Table 1.–Clusters of fishes from Lower Michigan streams identified by hierarchical cluster analysis. Number and species name in bold type are used to identify clusters in the report text and figures. An asterisk indicates clusters whose members had significantly different (P = 0.05) slopes for regressions of species z-scores against the cluster score. Scientific names are shown in italics.

1. **Creek chub** * *Semotilus atromaculatus*
   Redfin shiner *Lythrurus umbratilis*
   Central stoneroller *Campostoma anomalum*
   Common shiner *Luxilis cornutus*
   Bluntnose minnow *Pimephales notatus*
   Johnny darter *Etheostoma nigrum*

2. **Brook stickleback** * *Culea inconstans*
   Hybrid sunfish
   Northern redbelly dace *Phoxinus eos*
   Bluegill *Lepomis macrochirus*

3. **Blacknose dace** *Rhinichthys atratulus*
   Mottled sculpin *Cottus bairdi*

4. **White sucker** * *Catostomus commersoni*
   Fathead minnow *Pimephales promelas*

5. **Burbot** *Lota lota*
   Longnose dace *Rhinichthys cataractae*

6. **Brown trout** * *Salmo trutta*
   Rainbow trout *Oncorhynchus mykiss*
   Chinook salmon *Oncorhynchus tshawytscha*

7. **Brook trout** * *Salvelinus fontinalis*
   Slimy sculpin *Cottus cognatus*
   Coho salmon *Oncorhynchus kisutch*

8. **Black bullhead** *Ameiurus melas*
   Yellow bullhead *Ameiurus natalis*
   Green sunfish *Lepomis cyanellus*

9. **Pirate perch** * *Aphredoderus sayanus*
   Central mudminnow *Umbra limi*
   Bowfin *Amia calva*
   Pumpkinseed *Lepomis gibbosus*
   Golden shiner *Notemigonus crysoleucas*
   Northern pike *Esox lucius*
   Blackside darter *Percina maculata*

10. **Tadpole madtom** * *Noturus gyrinus*
    Flathead catfish *Pylodictis olivaris*
    White crappie *Pomoxis annularis*
    Common carp *Cyprinus carpio*
    Black crappie *Pomoxis nigromaculatus*
    Spotted sucker *Minytrema melanops*
    Walleye *Stizostedion vitreum*

11. **Freshwater drum** *Aplodinotus grunniens*
    Quillback *Carpoides cyprinus*
    Gizzard shad *Dorsoma cepedianum*

12. **Logperch** * *Percina caprodes*
    Channel catfish *Ictalurus punctatus*
    Spotfin shiner *Cyprinella spiloptera*
    Brook silverside *Labidesthes sicculus*
    Mimic shiner *Notropis volucellus*
    Shorthead redhorse *Moxostoma macrolepidotum*
    Sand shiner *Notropis stramineus*

13. **Hornyhead chub** * *Nocomis biguttatus*
    Grass pickerel *Esox americanus*
    Lake chubsucker *Erimyzon sucetta*

14. **Rock bass** * *Ambloplites rupestris*
    Brown bullhead *Ameiurus nebulosus*
    Longear sunfish *Lepomis megalotis*
    Largemouth bass *Micropterus salmoides*
    Rainbow darter *Etheostoma caeruleum*

15. **Smallmouth bass** * *Micropterus dolomieu*
    Black redhorse *Moxostoma duquesnei*
    Striped shiner *Luxilis chrysocephalus*
    River chub *Nocomis micropogon*
    Northern hog sucker *Hypentelium nigricans*
    Stonecat *Noturus flavus*
    Greenside darter *Etheostoma blennioides*

16. **Yellow perch** *Perca flavescens*
    Rosyface shiner *Notropis rubellus*

17. **Silver redhorse** *Moxostoma anisurum*
    Greater redhorse *Moxostoma valenciennesi*
    Golden redhorse *Moxostoma erythrurum*

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Appendix A.–Unmodified output from cluster analysis of 69 common fishes in Lower Michigan streams. Species abundances were standardized to a z-distribution (mean = 0 and standard deviation = 1). Complete linkage clustering method and Pearson distance measure were used.

```
                       Rescaled Distance Cluster Combine

                    0         5        10        15        20        25
Species             +---------+---------+---------+---------+---------+

Redfin shiner       -+---------------+
Central stoneroller -+               +---+
Common shiner       -----------------+   +-----------------+
Creek chub          ---------------------+                 +-----+
Bluntnose minnow    ---------------+-----------------------+     I
Johnny darter       ---------------+                             I
Brook stickleback   ---------+---+                               I
Hybrid sunfish      ---------+   +---------------------+         I
Northern redbelly dace ----------+                     +---------+-+
Bluegill            -----------------------------------+         I I
Blacknose dace      -------------------------+-----------------+ I I
Mottled sculpin     -------------------------+                 +-+ I
Fathead minnow      -----------------------------+-------------+   +-+
White sucker        -----------------------------+                 I I
Burbot              -------------------------------------+-------+ I I
Longnose dace       -------------------------------------+       I I I
Brown trout         -------------------------+-------------+     +-+ I
Chinook salmon      -------------------------+             +---+ I   I
Rainbow trout       ---------------------------------------+   +-+   I
Brook trout         -------------------+---------------------+ I     I
Slimy sculpin       -------------------+                     +-+     I
Coho salmon         -----------------------------------------+       I
Black bullhead      ---------------+---------+                       I
Yellow bullhead     ---------------+         +-----------------+     I
Green sunfish       -------------------------+                 +-+   I
Mudminnow           ---------------------------+-------------+ I I   I
Pirate perch        ---------------------------+             +-+ I   I
Bowfin              -------------+---------------------+     I   I   I
Pumpkinseed         -------------+                     +-----+   I   I
Golden shiner       ---------------+---------+         I         I   I
Northern pike       ---------------+         +---------+         I   I
Blackside darter    -------------------------+                   +-+ I
Flathead catfish    ---------------+-----+                       I I I
White sucker        ---------------+     +---------+             I I I
Carp                ---------------------+         +---------+   I I I
Black crappie       ---------------------+---------+         +-+ I I I
Tadpole madtom      ---------------------+                   I I I I I
Spotted sucker      -----------------------------------+-----+ I I I I
Walleye             -----------------------------------+       +-+ I I
Freshwater drum     -------------------------+-------------+   I   I I
Quillback           -------------------------+             +---+   I I
Gizzard shad        ---------------------------------------+   I   I I
Channel catfish     -------------------------+---------------+ I   I I
Spotfin shiner      -------------------------+               I I   I I
Brook silverside    ---------+-------------+                 +-+   +-+
Mimic shiner        ---------+             +---------+       I     I
Logperch            -----------------+-----+         +-------+     I
Shorthead redhorse  -----------------+               I             I
Sand shiner         ---------------------------------+             I
Grass pickerel      -----------+-----------+                       I
Lake chubsucker     -----------+           +-------------------+   I
Hornyhead chub      -----------------------+                   I   I
Brown bullhead      -----------------+-----------+             +---+
Longear sunfish     -----------------+           +-----------+ I   I
Largemouth bass     ---------------------+-------+           +-+   I
Rock bass           ---------------------+                   I     I
Rainbow darter      -----------------------------------------+     I
Black redhorse      -------------------+-----------+               I
Striped shiner      -------------------+           +---------+     I
River chub          -------------------------------+         I     I
Northern hog sucker ---------------+-------+                 +---+ I
Smallmouth bass     ---------------+       +-------------+   I   I I
Stonecat            -----------------------+             +---+   +-+
Greenside darter    -------------------------------------+       I
Rosyface shiner     -----------------------------+-------------+ I
Yellow perch        -----------------------------+             +-+
Golden redhorse     -----------------+-----------+             I
Greater redhorse    -----------------+           +-------------+
Silver redhorse     -----------------------------+
```