



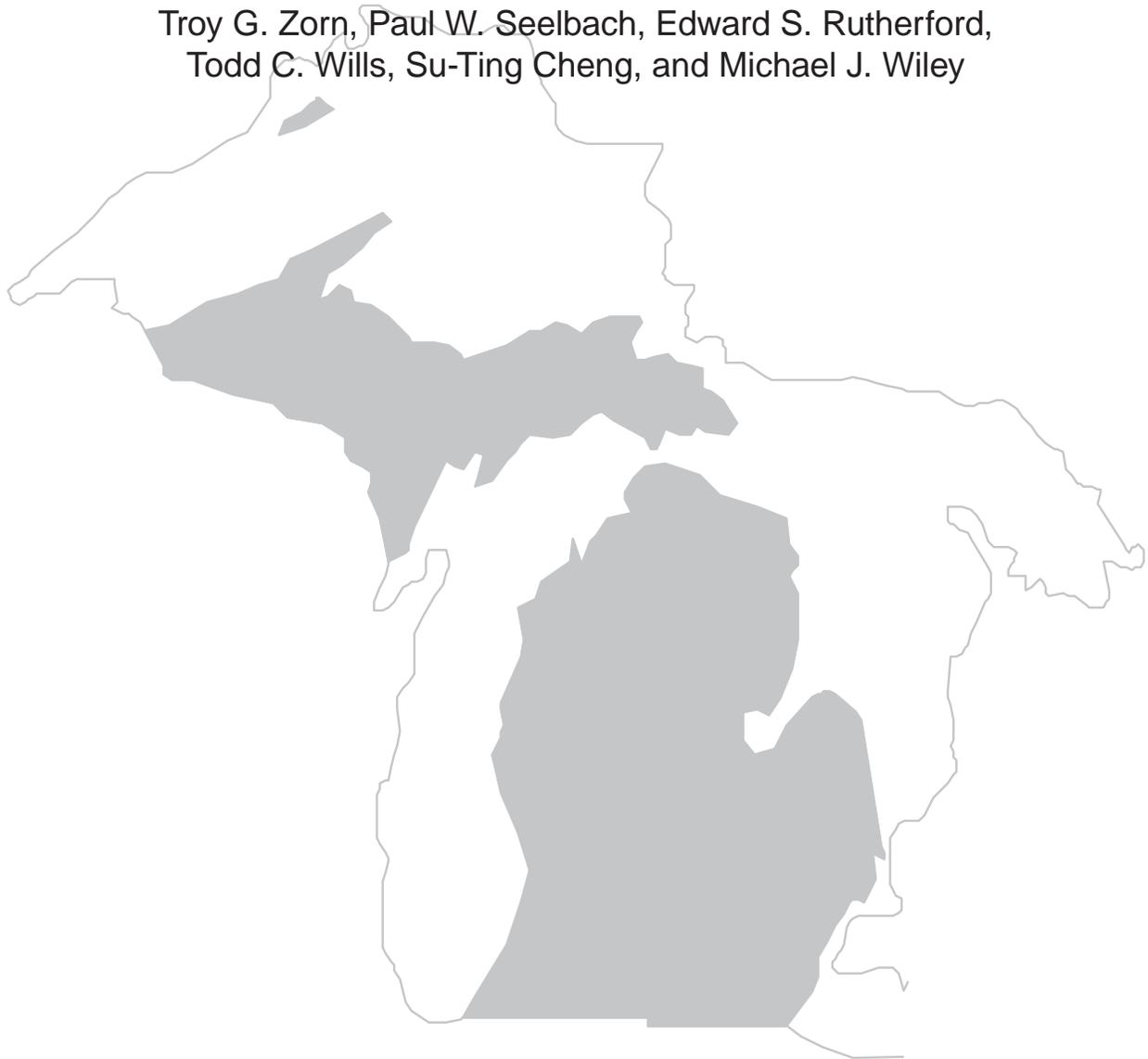
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Troy G. Zorn, Paul W. Seelbach, Edward S. Rutherford,
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A Regional-scale Habitat Suitability Model to Assess the Effects of Flow Reduction on Fish Assemblages in Michigan Streams

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Abstract.—Sound management and protection of the Great Lakes Basin's abundant freshwater resources requires the ability to predict local habitat conditions and fish communities across regional spatial scales. In response to concerns over increased use and potential diversion of its plentiful freshwater resources, the State of Michigan enacted legislation in 2006 that required creation of an integrated assessment model to determine potential for water withdrawals to cause an adverse impact to Michigan's waters or water-dependent natural resources. As part of this effort, we developed a model to predict how fish assemblages in different types of Michigan streams would change in response to decreased base flows. The model uses habitat suitability information from Michigan (catchment size, base flow yield, July mean water temperature) for over 40 fish species to predict assemblage structure and characteristic fish assemblages in individual river segments under a range of base flow reductions. River segments were classified into eleven strata based upon catchment size and July river temperature, and fish assemblages were predicted for each category. By synthesizing model runs for individual fish species at representative segments of each river type, we developed curves describing how typical fish assemblages in each type respond to flow reduction. The strata-specific, fish response curves can be used to identify streamflow reduction levels resulting in adverse resource impacts (ARIs) to characteristic fish populations. Our model provides a framework for evaluating impacts of flow withdrawals on biotic communities across a diverse regional landscape.

Introduction

Increasing use and potential diversion of the abundant freshwater resources of the Great Lakes Basin have generated alarms regarding water depletion and associated aquatic habitat degradation. The Great Lakes states and provinces responded in 1985 by signing the Great Lakes Charter (Anonymous 1985) which called for a common regional commitment to managing large water withdrawals and providing information about water use. The 2001 Annex to the Great Lakes Charter (Anonymous 2001) further committed the states and provinces to protect water resources in several

ways. Resource managers were challenged to develop a simple, efficient water management system that protects, conserves, restores, and improves the waters and water-dependent natural resources of the Great Lakes Basin. The 2001 Annex defined Great Lakes waters to include the Great Lakes and all basin streams, rivers, lakes, channels, and tributary groundwater. It also committed management agencies to develop and implement a common, resource-based conservation standard of “no significant individual or cumulative adverse impacts on the quantity and quality of the waters and water-dependent natural resources of the Great Lakes basin”, and to apply this standard to new water withdrawal proposals. It also called for improved sources and applications of information on impacts of water withdrawals to aquatic ecosystems.

In response to the 2001 Annex, the State of Michigan enacted Public Act 33 of 2006 (2006 PA 33; Michigan Legislature 2006), which required creation of an integrated assessment model to determine potential for water withdrawals to cause an adverse impact to the waters or water-dependent natural resources of the state. This new legal conservation standard stated that river flows should not be decreased “such that the stream’s ability to support characteristic fish populations is functionally impaired.” Thus, the water conservation standard was based upon both relationships between streamflow and the river’s fauna, and on key processes that determine critical aspects of aquatic habitats (e.g., temperature, flow stability, substrate, sediment transport, dissolved oxygen, or dilution of pollutants). The selection of fishes as the indicator of stream health acknowledged that fishes are widely accepted as stream indicators (Fausch et al. 1990; Simon 1999), and are also known and appreciated by the public. By integrating ecological and societal needs for water, Michigan’s legislation was consistent with current recommendations for implementation of ecologically sustainable water management (Petts et al. 1999; Baron et al. 2002; Richter et al. 2003, 2006; Annear et al. 2004). The Groundwater Conservation Advisory Council (GWCAC), a 17-member body comprised of industry, agriculture, water supply, conservation, and state agency representatives, was charged with development of the assessment model. A technical subcommittee of the GWCAC provided oversight to the work reported here.

Michigan is not alone in development of environmentally-sensitive, regional standards for flow management. Similar efforts are underway in Connecticut, Massachusetts, New Jersey, Pennsylvania, Tennessee, and Washington (Apse, C., personal communication, The Nature Conservancy, Portland, Maine; Kennen et al. 2007); and specific guidance for development of regional standards is emerging in the international scientific literature (Arthington et al. 2006; Apse et al. 2008). These efforts recognize that fixed targets for streamflows are inadequate because structure and function of river ecosystems are dictated by patterns of temporal variation in river flows (Poff et al. 1997; Annear et al. 2004). To protect freshwater biodiversity and maintain ecological functions and services of rivers, variability in natural flow regime (magnitude, frequency, timing, duration, rate of change, and predictability) must be maintained. Although intensive studies can define relationships between flow variability and ecological characteristics for specific well-studied or important rivers (Baron et al. 2002; Richter et al. 2003, 2006), site-specific biotic and hydrologic data and models do not exist for most rivers across a given region. To allow regional management agencies to develop meaningful flow standards (Annear et al. 2004), Arthington et al. (2006) advocated an approach that is intermediate between simple hydrologic rules of thumb and detailed, river-specific environmental flow assessments. They suggested estimating ecologically relevant indicator flows for river classes from models based on regional data, and then using regional relationships between indicator flow reduction and biotic impairment to develop environmental flow standards for each class.

We developed a framework for developing regional environmental flow standards for application across Michigan rivers, which was parallel to one currently advocated by an international team of scientists (Arthington et al. 2006; Anonymous 2008). Our process involved 3 steps: 1) building a regional database of monthly streamflow estimates representing baseline (current) conditions for river segments through Michigan; 2) classifying river segments based upon similarity of ecologically relevant attributes; and 3) developing flow alteration-ecological response relationships for each river

type. This last step, using regional survey data to develop biological benchmark or impact levels that reflect flow-ecology relationships, has been recently advocated by several scientists (Davies and Jackson 2006; Apse et al. 2008), and is essentially the development of habitat suitability indices (HSIs; Terrell et al. 1982) using regional survey data and landscape-scale habitat measures.

We selected summer base flow (defined in 2006 PA 33 as the August 50% exceedence flow, typically the lowest flow month during summer in Michigan) as our hydrologic indicator flow and used a statewide model to estimate this for each Michigan river segment (Hamilton et al. 2008). Most instream flow studies elsewhere in North America have occurred on hydrologically-unstable, high-gradient streams whose thermal characteristics depend upon elevation and snow-melt runoff. In contrast, many Michigan streams are low gradient, sand and gravel, hydrologically-stable environments with temperatures governed principally by groundwater inputs that can be quantified as base flow yields (Seelbach et al. 1997; Wehrly et al. 2006). Habitat conditions during summer base flows limit fish distributions as water temperatures peak during this time period and have a dominant effect on fish physiology, growth, and survival (Zorn et al. 2002; Wehrly et al. 2006; Whitley et al. 2006). Reductions in base flow may also significantly alter other habitat variables (e.g., dissolved oxygen or flow velocity) and critical ecosystem functions (e.g., sediment transport or channel maintenance). We recognize the ecological importance of high flows during other seasons, but for this application chose to focus exclusively on fish responses to summer base flow reduction, reflecting this critical biological period and the current wealth of survey data and models developed to classify stream habitats.

Research efforts in Michigan over the last 20 years have defined patterns and relationships among landscape scale habitat features, stream segment types, base flows, temperatures, and fishes (Seelbach and Wiley 1997; Zorn et al. 2002; Wehrly et al. 2006; Seelbach et al. 2006; Zorn and Wiley 2006; Brenden et al. in press). We leveraged this knowledge to classify Michigan rivers according to catchment size and water temperature (strong predictors of fish assemblages), and modeled reference fish assemblages and dose-response (base flow reduction versus fish assemblage structure) relationships for each river type.

Our overall goal was to develop ecologically-based, base-flow criteria to guide review of water withdrawals across Michigan waters. Our specific objectives were to:

1. Complete an ecological spatial framework (GIS database and classification) for Michigan rivers to provide meaningful spatial units for stream base flow estimation, habitat classification, and application of fish modeling results.
2. Develop a model to predict how fish assemblages degrade in response to decreasing base flows for each of the major river segment types in Michigan.
3. Use the model to describe how specific fish assemblages respond when flow reduction results in an adverse resource impact (ARI).

Methods

We combined a variety of traditional and novel methods and components to assemble the assessment model (Figure 1). Inventory databases representative of key hydrologic, thermal, and fish population attributes were critical for tailoring a series of spatial and ecological models to Michigan's rivers. Classification allowed the distillation of complex ecological relationships between river flows and biota into a relatively simple and understandable suite of outputs.

Ecological Spatial Framework and Habitat Classification

We delineated ecological valley segments as the spatial units for river habitat classification and for application of the model of flow reduction effects on fish populations. These ecological segments shaped the database framework for the statewide model; each segment represented one record (row) in the database, and various segment attributes were the fields (columns). When classified into segment ‘types’ using two key habitat attributes, these types served as the strata for development of specific reference fish populations and fish population response curves. Our final delineation and classification of ecological river segments was the product of an initial statistical analysis followed by several iterative expert reviews. Delineation of the segments defined the spatial scale at which we applied the impact assessment model to Michigan’s rivers.

Segment delineation.—We built the segment data system in a GIS environment using National Hydrography Dataset (NHD, USGS 2000) river ‘reaches’ (i.e., headwater-to-confluence or confluence-to-confluence river arcs). We used the extensive database of river and catchment attributes developed by Brenden et al. (2006) as reach-specific attributes. Segments were delineated by aggregation of ecologically similar, contiguous reaches using a river network analysis tool developed by Brenden et al. (2008). The analysis tool examined similarities among attributes of contiguous reaches, including catchment area, base flow yield, July mean water temperature, and catchment surficial geology. With this tool we aggregated Michigan’s ~34,000 unique reaches into ~9,000 ecological segments. Mainstem river segments were linear aggregations of neighbor reaches, and headwater segments were typically branched aggregations.

Segment classification.—The first step was to develop a multivariate classification and regression tree that categorized Michigan’s ecological river segments into habitat types based on how catchment area and July mean water temperature correlated with measured abundances of diagnostic fish species (Brenden et al. in press). Earlier statewide analyses indicated these two key variables best explain distributions and abundances of riverine fishes in Michigan (Zorn et al. 2002, 2004). The catchment area of each segment was delineated using GIS tools. The July mean water temperature for each segment was predicted using a combination of regression modeling and geostatistical kriging of water temperature data from 830 stream sites across Michigan (this model explained 70% of the variation in observed July mean water temperature; T. Brenden, personal communication, Michigan State University, East Lansing).

We used water temperature categories proposed by members of the Great Lakes Regional Aquatic GAP science team (J. Lyons, Wisconsin Department of Natural Resources, personal communication; Anonymous 2003) in our classification. The four categories are well-supported by the recent classification of Brenden et al. (in press), as well as several previous analyses of relationships of river temperatures and fishes in Michigan streams (Zorn et al. 2002; Wehrly et al. 2003; Wang et al. 2003):

- Cold = July mean water temperature $\leq 63.5^{\circ}\text{F}$ (17.5°C). The fish community is nearly all coldwater fishes; small changes in temperature do not affect species composition.
- Cold-transitional = July mean water temperature $> 63.5^{\circ}\text{F}$ (17.5°C) and $\leq 67^{\circ}\text{F}$ (19.5°C). The fish community is mostly coldwater fishes, but some warmwater fishes are present; small changes in temperature cause significant changes in species composition.
- Cool (or warm-transitional) = July mean water temperature $> 67^{\circ}\text{F}$ (19.5°C) and $\leq 70^{\circ}\text{F}$ (21.0°C). The fish community is mostly warmwater fishes, but some coldwater fishes are present; small changes in temperature cause significant changes in species composition.
- Warm = July mean water temperature $> 70^{\circ}\text{F}$ (21.0°C). The fish community is nearly all warmwater fishes and is not affected by small changes in temperature.

Since the temperature ranges for transitional categories are relatively small, and the predicted temperatures for the valley segments had an error range of similar magnitude, we initially assigned segments with temperature estimates at the warmest edge (>75th percentile) of the cold category to the cold-transitional class, and coldest edge (<25th percentile) of the warm category to the cool (warm-transitional) class.

Review of thermal classes.—Brenden et al. (in press) noted that the largest concern with their classification framework is the use of model-predicted river temperatures, and the possible effect that even small, inaccurate predictions may have on classification accuracies (Brenden et al. 2007). Therefore, as a second step we conducted an expert review of the segment temperature assignments to correct possible mistakes resulting from modeling or database inaccuracies. After reviewing the temperature assignments, we also reviewed and adjusted the initial river segment boundaries to ensure that thermally-similar, contiguous reaches were grouped at a spatial scale adequate for the predictive power of the water withdrawal models (i.e., that segment catchments were not unreasonably small relative to the resolution of model input data).

Since groundwater inflow is a critical factor influencing stream temperature in glaciated areas of the upper Midwest, four reviewers with knowledge of the geomorphology, hydrology, and ecology of Michigan rivers began the review process by examining map themes of the proposed ecological segment river temperature attributes, earlier versions of Michigan's valley segment thermal attributes (Anonymous 1981; Baker 2006; Seelbach et al. 2006), and predicted groundwater delivery potential (Baker et al. 2003) in a GIS. The synthetic geography of groundwater delivery potential was especially useful; this was created using a novel statewide spatial model of Darcy's Law of groundwater movement through a porous medium. The model used mapped surficial geology to infer transmissivity, and a digital elevation model to infer hydraulic head for the neighborhood of each map raster (Baker et al. 2003). Each watershed was reviewed from its upstream to downstream end. Individual NHD reaches created to delineate a continuous flow path through lakes ("lake reaches") were ignored. During review, the river temperature assignment of each reach in the valley segment database was visually checked against the earlier segment assignments, and also against the predicted groundwater deliveries to its local catchment and along the local river network. We also considered information from available MDNR Fisheries Division fish population surveys. When the proposed temperature class was not supported by these auxiliary information sources, it was changed to the next most appropriate category (e.g., from cool to warm) based upon the reviewers' judgment. Individual watersheds were checked at least twice (once by two separate reviewers) to ensure consistency in the process. Discrepancies in agreement between reviewers were noted and resolved through group discussion. During this review of the temperature assignments, we also evaluated and adjusted the valley segment boundaries to incorporate any changed temperatures; this was important mostly for headwater segments. Through this review step we reduced the ~17,000 segments to ~11,000.

Segment consolidation.—Application of our models only to catchments large enough to support the spatial scale of our hydrologic analyses was the primary technical recommendation of an expert panel called to review our approach (Beecher et al. 2006). In consultation with state and federal hydrologists, we felt that catchments ~1 mi² (2.6 km²) were unreasonably small, while catchments ~5 mi² (13 km²) were acceptable. We examined the frequency distribution of catchment sizes of our ~11,000 reviewed segments and chose to further aggregate all warm and cool (warm-transitional) segment catchments ≤3 mi² (7.8 km²) into the nearest larger segment catchment if the small catchment in question was of a similar temperature class to the larger neighboring catchment. We did not aggregate the smaller catchment if it represented a unique temperature class relative to nearby catchments in order to preserve local habitat diversity. Also, we did not aggregate the smaller catchments for cold and cold-transitional segments because they are often individually recognized

and highly valued by society. This additional aggregation process reduced the ~11,000 segments to ~9,000.

Next, we assigned river size categories to each river segment using criteria from habitat suitability models developed for Michigan fish species (Zorn et al. 2002), and supported by the size criteria found by Brenden et al. (in press). River valley segments were assigned to one of the following three size classes:

- Stream = Segment catchment area ≤ 80 mi² (207 km²).
- Small river = Segment catchment area > 80 mi² (207 km²) and ≤ 300 mi² (777 km²).
- Large river = Segment catchment area > 300 mi² (777 km²).

Our final classification was a cross-tabulation of the 4 river temperature classes (cold, cold-transitional, cool, and warm) with the 3 catchment size classes (stream, small river, and large river). Each of the ~9,000 valley segments in Michigan were assigned to one of the resulting 11 temperature-size categories (no valley segments were classified as “cold large river”).

In order to complete a GIS classification theme with a coherent, continuous flow path through ponds and lakes, the remaining unclassified lake reaches were assigned a temperature class using an Arc Macro Language (AML) script. We assigned the temperature class of the next downstream segment to lake reaches, with the exception of reaches flowing through drowned river mouth lakes. These reaches were assigned the temperature class of the next upstream segment. Lake reaches that occurred within a continuous valley segment were then assigned the valley segment number of the surrounding segments; lake reaches that fell on the break between different valley segments retained their own unique segment number.

Modeling Fish Assemblage Response to Base Flow Reduction

Choice of season.—Our modeling focused on effects of water withdrawal on fish during summer for several reasons. Streamflows are usually lowest during summer and water use is expected to be highest due to heightened demands for irrigation, cooling, etc. Stream temperature conditions during summer low-flow periods can be stressful to many fish species (e.g., trout and sculpin species), and water temperature elevation resulting from water withdrawal could potentially be highly detrimental to aquatic fauna. Summer months represent the main growing season for most fishes, and changes to stream conditions (e.g., temperature) affect fish metabolism, feeding, and growth (Brett 1979; Elliott 1981; Zorn and Nuhfer 2007). Nearly all fisheries surveys of Michigan streams occur during summer months, so linkages between streamflow, temperature, and fish assemblages are most direct during this time. Finally, relationships among flow, temperature, habitat conditions, and the distribution, growth, and abundance of Michigan fishes have been most extensively studied and are best understood for summer months (Zorn et al. 2002; Wehrly et al. 2003; Zorn et al. 2004; Seelbach et al. 2006; Wehrly et al. 2006; Zorn and Wiley 2006; Wehrly et al. 2007; Zorn et al. in press).

Fish data sources.—Data from fish surveys at 1,720 sites were used in the analysis, with 1,389 surveys covering the entire fish assemblage and 331 surveys targeting salmonids. Over 99% of the surveys occurred between 1980 and 2006, and over 97% of surveys occurred from May through October. Data were collected primarily by MDNR Fisheries Division with additional surveys conducted by the United States Forest Service (USFS) Hiawatha National Forest (HNF) (C. Bassett, USFS, unpublished data) and University of Michigan crews under the Michigan Rivers Inventory project (Seelbach and Wiley 1997). The database represented a joining of information previously compiled by P. Steen (University of Michigan, unpublished data) and T. Zorn, with data from HNF surveys being added to supplement the sample of rivers in Michigan’s Upper Peninsula (UP). The resulting database provided excellent coverage of most stream types (Figure 2), though data were

limited for much of the UP and for small streams (especially non-trout streams and those in coastal areas). In addition, coldwater species occurred more frequently than might be expected from a random sample of surveys of Michigan streams owing to greater management interest in coldwater fisheries. This was evident in the list of most frequently occurring species; white sucker (948 occurrences), creek chub (872), brown trout (761), johnny darter (649), brook trout (642), and central mudminnow (623).

Electrofishing (backpack or tow barge) was used to sample most sites, though rotenone was used on 158 sites, most of which were large, marginally wadeable or nonwadeable, cool (warm-transitional) or warm rivers. Seelbach and Wiley (1997) provided further details on sampling methods. Catch data were represented as numbers of fish per lineal foot of stream. Data from rotenone surveys, 43 UP multiple-pass depletion surveys, and 60 mark-recapture surveys were corrected for sampling efficiency (Seelbach et al. 1994) or effort to make them comparable with the single-pass electrofishing surveys conducted elsewhere.

Model development and evaluation.—The lack of intensive studies documenting long-term changes in stream habitats and fish assemblages due to water withdrawal in Midwestern states necessitated our use of statistical models to infer potential impairment to fish assemblages in Michigan’s diverse set of rivers. Lacking data on temporal changes in specific fish assemblages, we examined variation in species’ density along gradients of key habitat parameters across Michigan rivers. From these relationships, we developed a model to predict how the density of each species (and collectively the fish assemblage) at a site would respond to changes in habitat conditions resulting from water withdrawal. The model is based on the hypothesis that water withdrawal from a site would change the fish assemblage to resemble the fish assemblage at an otherwise similar site in Michigan that shared its lower discharge and associated hydrologic characteristics (e.g., water temperature, current velocity, or depth).

Our modeling process involved the following six steps: 1) Identifying “optimal” habitat conditions for each species; 2) Scoring the potential density for each species at a site based on similarity between habitat conditions at the site and optimal habitat values for each species; 3) Evaluating the relationship between predicted species scores and observed fish densities; 4) Predicting changes in habitat and overall species scores at sites for successive 10% increments of base flow reduction; 5) Identifying key fish populations for monitoring in segments and summarizing findings at the fish assemblage level; 6) Summarizing fish assemblage responses to water withdrawal for Michigan river types from model runs in representative segments. Below we provide further details on these steps.

1. Identifying optimal habitat conditions (mean and standard deviation) for each species. In a manner analogous to previous instream flow studies that characterized species microhabitat preferences as Habitat Suitability Indices (HSIs, e.g., Terrell et al. 1982; Raleigh et al. 1986), we identified optimal riverine habitat conditions for individual fish species using values of key habitat parameters from sites in Michigan where we observed the highest densities of each species. We focused on three important habitat variables, catchment area (CA), July mean water temperature (JMT), and base flow yield (BFY) which we defined as the August 50% exceedence flow (the definition of ‘index flow’ in 2006 PA 33; Anonymous 2007) divided by CA. These parameters have been previously identified in national and Michigan studies as indexing many variables important to fish metabolism, survival, reproductive success, distribution, and abundance (e.g., Poff and Ward 1989; Seelbach et al. 1997; Zorn et al. 2002; Wehrly et al. 2003; Zorn et al. 2004; Zorn et al. in press). These landscape-scale variables were also useful because they could be estimated for any river segment throughout the state. Methods for determining values of CA and JMT were described under ‘segment classification’. Statewide statistical models were used to predict values of BFY from catchment landscape attributes (Hamilton et al. 2008). Explicitly relating fish abundance to

BFY was particularly helpful to water managers as it provided a direct linkage for communicating effects of base flow reduction on fish assemblages.

Habitat conditions where numerical densities of a given species were highest in the state were considered “optimal” for that species. The top 20% of sites for each species were defined as optimal sites in Michigan. From the set of optimum sites identified for each species, we computed mean and standard deviation of JMT and \log_{10} -transformed BFY and CA values. We assumed a normal distribution of habitat conditions within the range of sites where species occurred. For each species, the mean defined the peak of the “normal curve”, and the curve’s width (i.e., breadth of a species tolerance for a habitat variable) was described by (or proportional to) the standard deviation. Examination of coefficients of variation for these variables suggested that a species’ mean and standard deviation values might be biased if they were computed from 10 or fewer sites. So, optimal values were computed for species only when 10 or more optimal sites were identified; rarer species were excluded from the analysis.

Due to the large number of occurrences of many species, we computed one set of optimal values for species that was specific to rivers in the southern Lower Peninsula (SLP) and another set specific to rivers in the northern Lower Peninsula and Upper Peninsula (NLP–UP). The line separating the SLP and NLP–UP regions was represented by the section boundary delimited by Albert et al. (1986) that divides the northern and southern ecoregions of the Lower Peninsula. Use of region-specific optima (in essence, regionally stratifying the model) resulted in greater precision when describing optimal conditions for each species (i.e., lower CV’s for 2 of 3 habitat variables summarized), and was expected to result in a more realistic model for each region. The regional optima led to a model that produced predictions for 43 species in the SLP and 33 species in the NLP–UP (Table 1).

2. Scoring the potential density for each species at a site. The model works by comparing how similar BFY, CA, and JMT conditions for a given reach were to each species’ optima for streams in the region. Habitat variables (BFY, CA, and JMT) for the reach were scored for each species based on the number of standard deviations (SD) that each was away from the optimal value for the species. If the site’s value was within 0.5 SD from the optimal value, the score was 4; if from 0.5 to 1.0 SD from the optimal value, the score equaled 3; if from 1.0 to 1.5 SD, the score was 2; if from 1.5 to 2 SD, the score equaled 1; and if >2 SD from optimal value, the score was 0. So, for example, if a Southern Lower Peninsula stream reach had a JMT of 66°F and the brook trout optimal JMT value (and standard deviation) for Southern Lower Peninsula streams was 63°F (standard deviation of 2.5°F), the reach would score as 2 for brook trout. We expected the potential of the site to be limited by the suitability of any of the three habitat variables because each indexed aspects of fish habitat important to fish metabolism, survival, and reproductive success (e.g., temperature, dissolved oxygen, current velocity and aeration, depth, permanence of habitats, etc.). Since we expected the lowest of the three habitat scores to limit the species density at the site, we identified it as the species’ score.
3. Evaluating the relationship between predicted species scores and observed fish densities. An important underlying assumption of our approach was that density for any given fish species was distributed normally around optimal BFY, JMT, and CA values. Recall that we had identified the mean and the limits of the data distribution but then had simply assumed a normal curve. We predicted 7,166 species scores at 183 sites where fish surveys occurred. We compared the predicted scores to measured fish densities to assess the level of empirical support for our modeling assumptions, particularly concepts of scores distributed normally around statistically-defined habitat optima (mean and SD values); use of the lowest score as the limiting score; and our eventual use of scores of 2 and 3 as thresholds for defining

characteristic and thriving fish assemblages. To allow pooling of results for different fish species to produce an overall evaluation, we standardized fish densities for each species, because each species has its own distinct density distribution within the state. Species' density at a site was standardized by dividing it by the median density for the species across all sites, with the resulting value being labeled relative density. Relative densities for each score value (i.e., 0 through 4) were averaged across species and sites, and plotted to examine the overall shape of this relationship (Figure 3a). For each species, we knew that relative densities would be highest at score 4 and lowest at score 0, however it was not clear how densities would fall between these endpoints (e.g., convex, linear, or concave pattern); nor was it clear how the pattern would look when data for multiple species were averaged as an assemblage response.

4. Predicting changes in habitat and overall species scores at sites for successive 10% increments of base flow reduction. The model was run for each 10% increment in BFY reduction (0% to 90%) to assess the influence of water withdrawal on the fish assemblage at a site. The value for CA was constant for each model run at a site. As BFY was incrementally reduced, fish scores for the BFY and JMT variables sometimes changed, causing the limiting fish score to change.

For each reduction in BFY, the predicted JMT often changed in response, because the stream's temperature could more rapidly equilibrate to ambient air temperature conditions. The rate at which the segment's JMT approached ambient air temperature increased as flow, depth, and velocity declined, and as the disparity between air and water temperature values increased, as per Newton's Law of Cooling. Therefore we added a second stage to the water temperature estimation process to account for this increased warming rate. A detailed description of this component of the model occurs in Appendix A. Statewide July air temperature data (Oregon State University-Spatial Climate Analysis Service, 2004), and depth and velocity predictions from hydraulic geometry regressions (T. Zorn, unpublished data, Michigan Department of Natural Resources, Marquette) were used with CA, BFY, and JMT data to predict changes in JMT resulting from water withdrawal. Mean July air temperature values were adjusted upward because they were obtained from a cooler period (ca. 1960–1980) relative to when water temperatures were estimated (ca. 1990–2005). The extent of adjustment was 2°F (1.1°C) based upon differences between JMT and air temperature values at warmwater streams in the database. Air temperatures for large river sites were increased by 3.5°F (2.0°C) due to a greater discrepancy between JMT and air temperature values.

The increased warming rate that results from flow reduction typically does not produce dramatic, localized increases in JMT. Instead, effects of increased warming rates are manifested further downstream after the river has had more time to equilibrate with ambient air temperature. Such effects were demonstrated by Nuhfer and Baker (2004) in a Michigan trout stream (Hunt Creek) where 90% water withdrawal caused slight thermal impacts within the 0.64 km study reach, but warming rates increased nearly ten-fold. They showed that increased warming rates could lead to significant losses of trout habitat downstream unless additional groundwater enters the channel.

We modeled downstream effects of flow reduction on JMT to help address these concerns. Because downstream warming effects on coldwater streams might be more pronounced when model predictions are allowed to extend further downstream, it was important to decide how far downstream to model. We limited the distance over which we assessed downstream warming so: 1) it would be no greater than the average valley segment length (i.e., 4.3 mi [6.9 km]); 2) that with a baseline (0% flow reduction) warming rate, there would be a 90–95% correspondence between species scores at mile 0 (where initial JMT predictions occurred)

and mile X (the distance downstream over which warming effects occurred). The latter criterion helped to ensure correspondence between species scores at the downstream (warmed) portion of the reach and the upstream part where initial JMT predictions were targeted and fish surveys occurred. Since species scores at the upstream portion would be compared to fish survey data to evaluate the model, we wanted initial conditions of the model runs to be tied to scores used in model evaluations rather than reflecting a substantially different, downstream fish assemblage due to baseline warming. For each stream type, we assessed correspondence between fish assemblage at the site and further downstream (at different downstream warming distances) to determine how far downstream to project warming. These exploratory assessments led us to select the following distances over which downstream warming was modeled. The distances, by river size and JMT class (cold, cold-transitional, cool or warm-transitional, and warm) were: streams (1, 1, 0.5, and 0.1 mi or 1.6, 1.6, 0.8, and 0.2 km); small rivers (4, 3, 3, and 2 mi or 6.4, 4.8, 4.8, and 3.2 km); and large rivers-(4 mi or 6.4 km for all classes). The JMT values predicted downstream were assigned scores in the model.

5. Identifying key fish populations for monitoring in segments and summarizing findings at the fish assemblage level. Examination of correspondence between species scores and observed densities (Figure 3) informed us about how model predictions for a segment could be used to describe fish species' responses to water withdrawal. Relative densities for fishes scoring 3 or 4 were generally two or more times higher than the median density. We defined Thriving Species at a segment as those with abundance scores of 4 or 3 (i.e., all habitat scores within 1 standard deviation of optimal values). Thriving means that BFY, JMT, and CA for that segment were near optimal for the species, and we expected the species to show high abundance, multiple age classes, and good reproduction. We also defined a broader group of species at a segment, Characteristic Species, as those whose three habitat scores were all within 1.5 standard deviations of the species' optimal values. In other words, their scores for each of the three variables were 2, 3, or 4. Characteristic Species were expected to be abundant at that segment compared to other segments with less suitable habitat conditions. Relative density values for Characteristic Species (i.e., those scoring two or higher) were generally higher than 1 indicating that observed densities were above the median value for the species (Figure 3). Based on these data and the intent of recently enacted streamflow protection legislation, we decided that assessment of the effects of water withdrawal should involve tracking the modeled "status" of species initially classified as Characteristic or Thriving in each type of river segment.

We created three fish assemblage response curves to help show effects of base flow reduction on Characteristic and Thriving species in the fish assemblage at a segment. Summaries computed at each level of BFY reduction were relative to values calculated at 0% flow reduction (i.e., baseline condition). The Thriving Species (Thriving) curve described the proportion of Thriving Species (those scoring 3 or 4) that remain at their original score (i.e., no decline in score) at each level of flow reduction. We viewed this curve as an early-warning indicator of assemblage response to base flow reduction. The Characteristic Species Remaining curve described the proportion of Characteristic Species that remained at characteristic abundance levels (i.e., scores ≥ 2) during each increment of BF withdrawal. The Characteristic Species Abundance curve described the sum of abundance scores for fishes identified as characteristic at 0% flow reduction, following these species through each level of base flow reduction. Thus, the latter two curves tracked responses of Characteristic Species, particularly in regards to species composition and overall population abundance. Though they measured different fish community aspects and differed in calculation, the Characteristic Species Remaining and Characteristic Species Abundance curves showed very similar responses to water withdrawal for all stream types. To reflect this, and facilitate

further flow policy negotiations, their values were averaged to produce a single curve describing proportional changes in Characteristic Species Remaining and Characteristic Species Abundance at different levels of water withdrawal (Figure 4). We refer to this composite curve as the Characteristic Species curve. We viewed the Thriving Species and Characteristic Species curves as best descriptors of fish assemblage responses to flow reduction. Together, these modeling summaries were intended to address the specific need of Michigan's GWCAC, namely, to support interpretation of when base flow reduction might impair a river's ability to support its characteristic fish populations.

6. Summarizing fish assemblage responses to water withdrawal for Michigan river types from model runs in representative segments. For each river type, we generated one set of response curves by averaging response variable values from individual model runs at a representative set of stream reaches (usually 15–20 reaches). Representation of sites from the two regions (i.e., SLP and NLP–UP) in the simulations for a river type was proportional to their occurrence in Michigan. For example, if 70% of Michigan's cold streams were in the NLP–UP, then 70% of the reaches used to simulate water withdrawal effects on cold streams were from the NLP–UP. When very few or no species were predicted to be characteristic at a site, the site was excluded from summaries for that type. This sometimes occurred for sites whose BFY or CA values were at the edges of the distribution of the data used in defining species optima. Fewer simulations were used for cold-transitional segments, which responded distinctly from other segments of their type and were separated from the type being studied. This resulted in a set of curves for the three size classes and four thermal classes. Because first-cut boundaries for cold-transitional classes were iteratively identified during the fish modeling process, their thermal bounds (along with those of adjacent cold and cool classes) were formally defined (and sometimes slightly adjusted) during classification. Thus, final temperature boundaries for all classes were not always available beforehand when defining the sampling pool for modeling each class.

Responses of Fish Assemblage and Species Metrics to Base Flow Reduction

The Michigan GWCAC used the fish assemblage response curves as a template for determining what level of base flow reduction would likely result in an ARI. Their desire was to apply a consistent conceptual decision rule to the curves for each of the 11 river types, thus determining a percentage base flow reduction threshold for each river type. They examined the rate of decline in the curves, while considering a series of narrative criteria provided by Davies and Jackson (2006) for interpreting ecological degradation. These narrative criteria suggested that there were five identifiable degradation stages, ending with total loss of ecological structure and function. Through collaborative discussions that reflected diverse perspectives on water uses, the GWCAC decided that an ARI (as determined by fish assemblage response) would correspond with degrading the assemblage past Davies and Jackson's (2006) first stage (declining density of existing species) and second stage (some loss of sensitive species and some beginning increase in tolerant species). They further suggested that this point corresponded with the point on the Characteristic Species curve, where that metric had declined by 10% (on the Y-axis in Figure 4). The Thriving Species curve was used to identify earlier stages of degradation due to flow reduction that might trigger other precautionary management actions.

We described recurring patterns in species composition and response to flow reduction for each stream type. More specifically, for each stream type we identified species that commonly occurred at characteristic or thriving levels. We applied the GWCAC's definition of ARI to each of the 11 river types; and for each type, we identified species that were commonly thriving under normal base flows but declined to characteristic or lower levels (i.e., scores ≤ 2) at reduced base flows. We also noted

species whose abundance score declined past 2, suggesting that they may no longer be common in the reach.

Results

Delineation and Classification of Ecological River Segments

We defined ~9,000 ecological river segments for Michigan, and created a database housing key attributes that describe river and catchment conditions related to the downriver point of each segment. Attributes included catchment area, index flow, estimated July mean water temperature, river type, and base flow threshold indicating an ARI. A summary of segment attributes describes Michigan's riverine resources (Table 2). Streams comprise 87% of the state's total river miles, and are fairly evenly split among cold (including cold-transitional), cool, and warm types. Taken separately, cold-transitional streams make up a small proportion of the total stream miles. Larger rivers have increased water temperatures, and a predominance of cool and warm types. The most flow-sensitive thermal type, the cold-transitional, makes up 8% of the state's total river miles. The thermal types show regional geographic patterns but there are some local exceptions also (Figure 5). Catchment area summaries per thermal type were predictable, as they were defined beforehand (Table 2). Stream catchment areas are of particular interest, as smaller catchments are by definition most susceptible to water abstractions. Stream catchment areas varied according to particular drainage network features, spanning from 1 mi² to 58 mi², and average values for the thermal types ranged from 9 mi² to 16 mi².

Modeling Fish Assemblage Response to Base Flow Reduction

We developed a model for predicting fish assemblage response to water withdrawal that was applicable to all types of Michigan rivers. Fish abundance scores were estimated for 33 species in the NLP-UP rivers and 43 species in the SLP rivers. Optimal conditions ranged widely among species and regions, reflecting the array of habitat conditions in Michigan (Table 1). For example, JMT optima ranged from 62.2°F (16.8°C) for brook trout to 73.9°F (23.3°C) for greenside darter. Catchment area optima ranged from 11 to 1,561 mi² (28.5 km² to 4043 km²), and BFY optima values differed nearly eight-fold among some species.

We observed a positive linear relationship between predicted species' scores and average relative densities observed for all species and sites, suggesting good correspondence at the fish assemblage level (i.e., for all species combined; Figure 3a). Higher mean relative density values associated with higher scores provided support for assemblage labels (i.e., Characteristic or Thriving) and for how species were treated when summarizing results at the fish assemblage level. Mean relative density values higher than 1 indicated that observed densities were above the state median value for the species, which supported our definitions of Characteristic Species (Figure 3a). Relative densities for Thriving Species (scores of 3 or 4) were generally two or more times higher than the state median relative density. Mean relative densities for fish scoring 0 or 1 were below the state median, with relative density values approaching zero for species scores of zero. These findings supported our hypothesis that declines in a species score would likely reflect a real decline in its density, and that a species might be considered lost from the reach as its score approached zero.

There was also much variability underlying the straight-line shape we observed in the averaged data. Zorn et al. (2002) examined the structure of Michigan stream fish assemblages and likewise reported a strong pattern in central tendencies but also a great deal of variability. We observed variability in the shape of the score-relative density relationship among individual species, as well as variation among sites in relative densities associated with a particular score's value (Figure 3b). Both

findings suggested that model predictions based on fish assemblage level responses are more robust than solely relying on predictions for individual species or at individual sites.

Fish assemblage structure, as indicated by the Characteristic and Thriving species identified, differed among river segments according to temperature category and river size. Fish assemblages tended to be more species-rich as temperature or size increased. To describe typical fish assemblages in each stream type, we identified species that were most commonly found at Characteristic or Thriving levels and describe them below (Tables 3–5). In small coldwater streams, typical Characteristic Species included salmonids (4 species), sculpins (mottled sculpin and slimy sculpin), a few cyprinids (central mudminnow, blacknose dace, and redbelly dace), northern brook lamprey, and burbot (Table 3a). Typical Characteristic fish species composition differed slightly in small cold-transitional streams compared to cold streams, with loss of species having the narrowest tolerance for reduced BFY's (slimy sculpin and brown trout), and addition of longnose dace, white sucker, creek chub and brook stickleback (Table 3a). Compared to small cold-transitional streams, cool (warm-transitional) streams had no northern brook lamprey, brook trout, coho salmon, northern redbelly dace, or longnose dace, but added rainbow darter, golden shiner, largemouth bass, green sunfish, and johnny darter (Table 3b). Differences in Characteristic Species common in small warm streams relative to cool (warm-transitional) streams included loss of mottled sculpin and rainbow trout, and addition of many species including cyprinids (central stoneroller, hornyhead chub, and common shiner), blackside darter, longear sunfish, northern pike, pirate perch, and black bullhead (Table 3b). Similar changes in fauna were evident across temperature categories within small and large rivers (Tables 4a-c, 5a-b). Some lacustrine species (e.g., yellow perch and bluegill) were often at low abundance in many stream types, due to frequently-occurring connections between inland lake and stream habitats. As a result, they appeared to have broad tolerances to habitat conditions and were predicted to be Characteristic Species in many stream types.

Fish assemblages structure, as indicated by which species were commonly at “Characteristic” levels of abundance, also differed among river sizes within a temperature category. The greatest difference in Characteristic Species was between streams and small rivers within the cold, cold-transitional, and cool (warm-transitional) temperature categories. For example, 3 Characteristic Species in coldwater streams were not Characteristic of small coldwater rivers, and 8 Characteristic Species in small coldwater rivers were not Characteristic in coldwater streams (Tables 3a and 4a); 11 of 15 Characteristic Species in cold-transitional streams were not Characteristic of cold-transitional small rivers (Tables 3a and 4a); five of 12 Characteristic Species in cool (warm-transitional) streams were not Characteristic of small cool (warm-transitional) rivers (Tables 3b and 4b); and 5 of 20 Characteristic Species of warmwater streams were not Characteristic Species in small warmwater rivers (Tables 3b and 4b). Differences in fish assemblages were generally smaller between small and large rivers within temperature categories: 5 of 16 Characteristic Species of cold-transitional small rivers were not Characteristic Species in large cold-transitional rivers (Tables 4a and 5a); 6 of 21 Characteristic Species of small cool (warm-transitional) rivers were not Characteristic of large cool (warm-transitional) rivers (Tables 4b and 5a); and 12 of 23 Characteristic Species of small warm rivers were not Characteristic of large warm rivers (Tables 4c and 5b). In addition, even more Characteristic Species of the larger waters were not Characteristic Species of smaller waters of the same thermal class. For example, 8 typically Characteristic Species of cold small rivers were not similarly identified with cold streams (Tables 3a and 4a), and 10 species were usually Characteristic of warm small rivers but not of warm streams (Tables 3b and 4c).

Two fish assemblage response curves (a Thriving Species curve and a Characteristic Species curve) were developed for each river type and provided useful descriptors of fish assemblage response to water withdrawal (Figure 4). By showing when abundances of Thriving Species started to decline, the Thriving Species curve was useful in tracking initial stages of degradation, and helpful in setting triggers for preliminary management actions. The Characteristic Species curve was used in defining the limits to assemblage degradation (i.e., an ARI) because it represented changes in overall

abundance and species composition for Characteristic Species in waters subject to flow reduction. Each curve represented the average response for the set of sites analyzed for that river type; however there was typically substantial variation among the responses for individual sites (Figure 6). In all, we developed sets of response curves for 11 river types (Figure 7). We saw a range of responses across the state's river types, reflecting differences in their base flow yields, Characteristic Species, and resulting sensitivities to base flow reduction. As expected, the cold-transitional streams and rivers showed high sensitivity to base flow reduction, due to the declines in coldwater fishes described above. Somewhat surprising was the insensitivity shown by the cold streams and small rivers.

Individual Species Responses to Base Flow Reductions thought to cause an ARI

In colder stream types (all sizes), certain species showed consistent declines in response to water withdrawal. We noted species changes occurring at the first 10% flow reduction increment beyond the ARI level for each type. Within coldwater streams, 5 of 7 species that thrived at most (>50%) sites often declined to Characteristic or lower abundance levels, with four species declining to sub-Characteristic levels (i.e., score ≤ 1) more than 20% of the time (Table 3a). Brown trout, brook trout, coho salmon, and northern brook lamprey declined most notably and consistently, while northern redbelly dace commonly declined but to a lesser degree. Though it was not initially Thriving at as many sites as the aforementioned species, slimy sculpin also consistently declined with flow reduction, often to the degree that it was considered lost from the reach (Table 3a). We saw a similar response in small cold rivers, where 9 species dropped from Thriving to Characteristic or lower levels at >40% of sites, and 6 of these species declined to below median abundance levels at >20% of sites. In these streams, brown trout, brook trout, chinook salmon, northern brook lamprey, American brook lamprey, and johnny darter were consistently vulnerable to flow reductions (Table 4a). None of the typically Characteristic Species in cold-transition, large rivers consistently showed declines in response to flow reduction (Table 5a). However, four commonly Thriving Species in these rivers (blackside darter, northern pike, rainbow darter, and smallmouth bass) declined consistently and substantially when flow was reduced (Table 5a). In large cool (warm-transitional) rivers, 4 of 12 Thriving Species (i.e., rosyface shiner, smallmouth bass, walleye, and yellow bullhead) dropped to Characteristic or lower abundance levels (i.e., scores less than 3) at >40 % of sites, with smallmouth bass and rosyface shiner declining to below median levels at >20% of sites (Table 5a). Smallmouth bass was the only species sensitive to flow withdrawals in all temperature categories of large rivers (Table 5).

The species that declined in response to flow reduction varied among sites for stream and small river types that were not cold. With the exception of grass pickerel and warmouth in cool (warm-transitional) small rivers, no species were identified as consistent "decliners" for a river type. However, the lack of species that consistently declined does not mean that few or no species declined in abundance when flow was reduced. Since changes were studied at the first flow reduction level below the ARI level, the overall abundance of Characteristic Species had declined by 10%, and 10% of Characteristic Species had declined to less than their median abundance level or a score of one (and could be considered "lost" or locally extirpated from the site). Therefore, a lack of consistent "decliners" indicated that the list of species declining varied among sites within a type to the extent that no particular species were consistently driving fish community changes for the type. This reflects the heterogeneous nature of fish assemblages within these types, and how they differ with CA, BFY, and JMT conditions of each river segment.

Discussion

River Habitat Classification

Implementation of the statewide river habitat classification allowed the state's 48,655 river miles to be assigned among useful ecological types, each having characteristic geography, hydrology, fish populations, and sensitivity to water removal. This simplified typing system, along with the resulting map of the state's entire riverine resource, has helped enable common understanding and meaningful discussions of hydrology and ecology among Michigan's diverse suite of natural resource policy leaders. Our river classification builds upon substantial previous Michigan work (Seelbach and Wiley 1997; Seelbach et al. 1997; Zorn et al. 2002; Wehrly et al. 2003; Baker 2006 ; Seelbach et al. 2006; Brenden et al. 2008; Brenden et al. in press), and is strongly aligned with other current regional river classification efforts (Anonymous 2003; Higgins et al. 2005; Brenden et al. 2006; Sowa et al. 2007). Our component thermal classification is based on a similar strong history of development across Michigan and Wisconsin (Wehrly et al. 2006; Wehrly et al. 2007; Brenden et al. in press; T. Brenden, Personal Communication, Michigan State University, East Lansing; J. Lyons, Personal Communication, Wisconsin Department of Natural Resources, Madison). The Ecological Limits of Hydrologic Alteration (ELOHA) Workgroup has recommended classification based on a suite of hydrologic properties (Arthington et al. 2006; Anonymous 2008). While our classification was based on thermal attributes informed by fish assemblages, we expect that our system would closely align also with hydrologic character. Creque et al. (2002) created a physical habitat classification that included a base flow yield attribute for rivers in Michigan that was very similar to the initial ecological classification of Seelbach et al. (2006), and subsequently to ours.

Approach to Modeling Fish Population Responses to Base Flow Reduction

Our model represents a blend of existing and novel approaches to the assessment of water quantity needs, and is firmly rooted in large, regional datasets and models. Given our need for statewide targets, we developed a form of habitat suitability indices that related population abundance to key landscape-scale habitat measures (BFY, JMT, CA) at many rivers throughout the state, rather than using the more traditional approach of developing indices based on use of locally-measured microhabitat variables (e.g., depth, velocity, substrate, cover, temperature) by individual fish in one or a few rivers (Terrell et al. 1982). These regional-based indices, when combined with measured or modeled landscape-scale habitat data (e.g., CA, BFY, JMT) for individual reaches, provide an empirical basis for setting standards (*sensu* Annear et al. 2004) for acceptable water withdrawals throughout Michigan. Such a regional approach is currently championed by experts in environmental flow standards (Arthington et al. 2006; Anonymous 2008). This approach has several important strengths: the empirical identification of base flow optima and lower limits defining fish species distributions; representation of the fauna and river types of the region; and a simple river typing system that allows comprehensive regional mapping and linkage to hydrologic information.

The landscape-scale variables we chose indexed many site-scale variables important to Michigan stream fishes (Zorn et al. 2002, 2004). Our model deviates somewhat from the traditional HSI approach in that our curves were based on statistical features of each species distribution (i.e., mean and standard deviation of optimal conditions) as opposed to interpolating values from a curve fit to the upper edge of the data distribution. Nevertheless, results from evaluation of the correspondence between model scores and relative densities of fish supports the development and application of the HSI's at the regional scales of statewide fish population databases and GIS-based habitat models. The model evaluation results support several key aspects and assumptions of our modeling including how we characterized assemblage optima, and how we defined and interpreted assemblage abundance scores.

We chose the mean flow of a low-flow month as our natural flow index and a proportional increment of this mean as the allowable take. Agencies have historically used a lower drought flow statistic, often the 7Q10 (7 day, 10-year low flow), but this extreme and brief event is not clearly relevant to biotic conditions, whereas the average conditions experienced by organisms during the entire low flow season are thought to more routinely shape assemblage structure and are well indexed by a monthly mean (Richter et al. 1997; Annear et al. 2004; Kennen et al. 2007). Agencies employing a natural flow regime approach often use monthly means as index flows (Hatfield et al. 2003; Kennen et al. 2007). Similarly, we avoided the pitfall warned by Annear et al. (2004) of establishing a minimum flow target, or “floor”. By using an increment of the monthly mean, we are maintaining the natural flow regime (reduced only by this increment).

Finally, in contrast to traditional Instream Flow Incremental Methodology (IFIM) studies, which focused on one or a few species, our approach enabled us to model flow responses of all the common fish species in Michigan’s lotic assemblages to provide a broad approach to protecting river ecosystems. Our subsequent challenge was to synthesize individual population responses for 33 or more species into a few simple curves that could be used as a basis for policy discussions and legal definitions. Our efforts to synthesize model results using Thriving Species and Characteristic Species curves will hopefully serve as building blocks for efforts to develop better models for flow protection in other regions.

Model Findings

Base flow yield and temperature both had powerful effects on species’ distributions and abundances. Although BFY, JMT, and CA were all important in determining initial abundance scores for species, once water flow reductions began, BFY had the dominant influence on declines in species scores. An examination of model predictions for a small sample of streams revealed that declining BFY caused about 80% of score declines, compared to about 20% for increasing JMT. There are several possible explanations why BFY had a dominant influence on fish scores. First, BFY not only provides a measure of the amount of groundwater in a river’s drought flow, it also indexes many key aspects of river habitat, such as summer and winter water temperatures, hydrologic flashiness, current velocity, substrate conditions (i.e., presence of fines), dissolved oxygen conditions, depth, and permanence of instream habitats. (Poff and Ward 1989; Power et al. 1999; Zorn et al. 2002; Wehrly et al. 2006; Zorn and Wiley 2006). Our comparative model predicted that BFY reductions would change fish communities to reflect those of streams having lower BFYs and their associated biophysical characteristics. Thus, BFY can potentially influence species distribution and abundance in many more ways than JMT. Second, because warming effects resulting from flow reduction are manifested further downstream, the limited downstream distances used in our model predictions of downstream JMT warming often resulted in the occurrence of relatively little warming. So, unless stream temperature initially was thermally marginal for a species, the magnitude of warming resulting from water withdrawal was often not dramatic enough to change a species’ score. Nuhfer and Baker (2004) noted that withdrawing 90% of the flow in a northeastern Michigan trout stream increased summer warming rates by 9-fold downstream of the study area, which would likely have negatively impacted growth or survival of salmonids. Such a change could lead to major effects on downstream fish populations unless additional groundwater entered the channel. Our warming module could not replicate the magnitude of warming actually observed by Nuhfer and Baker (2004). Further refinements to the warming module, and studies of downstream warming and its effects are needed. Finally, the tremendous variation (roughly 100-fold) in BFY across Michigan relative to that of JMT resulted in our treating these data differently in the model (i.e., geometric means vs. arithmetic means) which may also have contributed to its greater influence on species abundance.

Our models indicated that 20 to 50% of the summer base flow could be removed without serious adverse impact to fish assemblages in all river types except the cold transitionals (and these are sensitive by definition). This finding indicates that habitat suitability distributions are broad, likely due to both habitat plasticity in stream fishes and the high variability that always exists in fish assemblage survey data (Zorn et al. 2002). Few comparable quantitative studies exist, and reviewers agree that depicting biotic responses to flow withdrawals remains a primary challenge (Hatfield et al. 2003; Arthington et al. 2006; Kennen et al. 2007). Richter et al. (1997), in a paper titled “How much water does a river need” suggested that in the absence of applicable flow-biotic relationships, a common sense rule of thumb might be to manage for keeping flow conditions within the 25th and 75th percentiles for any given flow metric. The idea behind this range was to allow some management accommodation for human water uses while also providing a reasonable degree of protection to the river ecosystem. They also proposed that a more restricted range, 40th to 60th percentiles, could be applied to the most valued rivers. For comparison, we examined five cold and five warm Michigan rivers, and found a reduction in index flow (i.e., the August 50% exceedence flow) down to the 25th percentile level would equate to an average reduction of 24% of index flow (range 10–50%). The GWCAC recommended ARI flow-reduction thresholds for the 11 river types averaged about 30% of index flow (range 10–50%; Anonymous 2007), a similar result to Richter et al.’s (1997) rule of thumb.

Pennsylvania developed a map-based screening tool designed to flag proposed withdrawals that pose enough risk to trout stream habitats to warrant implementation of further, detailed planning review (Stuckey 2008). They arbitrarily chose acceptable habitat reductions of 5–15%, depending on the initial river type (habitat quality), and examined results from a large set of site-hydraulics habitat models to determine an increment reduction in base flow that would trigger further action. Their base flow metric was the 7Q10, a drought flow that is lower in magnitude than our August median flow. They determined that action threshold withdrawals would be 30–50% of the drought flow metric, again depending on trout river type. For comparison, we examined a sample of Michigan cold rivers and streams and found that 50% of the 7Q10 is equivalent to 40% of our August median index flow, indicating the action thresholds for both states are surprisingly close.

Several authors have alternatively developed quantitative relationships or rules of thumb focused on allowable proportions of annual flow totals or means. It is not clear how these relate to our analyses of reductions in base flows, although in some cases more protection was granted during low flow periods. Xenopoulos and Lodge (2006) created a similar, simpler response relationship between mean annual flows and coarse data on fish distributions in warm and cool Midwestern rivers, and found a more sensitive response; a 20% reduction in the mean annual flow resulted in the loss of 2–3 fish species. Petts et al. (1999) developed empirical habitat suitability relationships for trout and several invertebrate species found in British groundwater-dominated rivers and streams (similar to our cold types). For one example river, they determined that a shift from “optimum” to “desirable” conditions occurred with a reduction in total annual flow of ~30%, and a shift from “optimum” to “acceptable” occurred with a reduction of ~50%. Hatfield et al. (2003) applied a rule of thumb approach to a set of British Columbia rivers and determined that on average, 22% of flow could be diverted without causing an impact to fish habitats.

The vulnerability of species to water withdrawal sometimes appeared to vary by river type. For example, brook trout are characteristic of both coldwater and cold-transitional streams, though assemblages in the latter seem much more vulnerable to flow reduction based on their ARI levels (Figure 7). In cold streams, our modeling suggested that nearly half of the flow could be removed before substantial declines in populations of Characteristic Species were apparent. In contrast, some Characteristic Species declined in the more species-rich, cold-transitional streams at flow reductions as small as 10%. These declines were often initially seen in non-salmonid species, though adverse effects on brook trout were typically apparent at 20% flow reduction.

Why can trout in cold streams tolerate more withdrawal than trout in cold-transitional streams? The answer is related to the effects of flow reduction on stream temperatures, and how close the baseline temperature is to stressful temperatures for each fish species. Since most coldwater streams were near the thermal optima for trout (and some might even be a little colder than their optima), a fair amount of water withdrawal is possible before temperature shifts to the extent that it becomes stressful. For example, little response in brook trout populations occurred when up to 90% of summer flow was diverted in Hunt Creek, a highly groundwater-fed tributary in northeastern Michigan (Nuhfer and Baker 2004). Hunt Creek has baseline temperature far below a level that is thermally stressful to trout (July mean temperature of 14.5°C), so thermal effects on brook trout were not evident. Also, the study reach was relatively short (602 m), so while the warming rate of the stream increased dramatically, warming effects had little chance to reach levels problematic to brook trout before the diverted water returned to the de-watered channel (Nuhfer and Baker 2004). For similar reasons, flow reductions up to 50% in this same study reach were expected to have little effects on invertebrate habitat for most taxa present, and 50% flow reductions caused no significant declines in any observed invertebrate abundance metrics (Wills et al. 2006). However, withdrawals of 90% exposed some riffle habitats and resulted in significant declines in densities of mayflies, caddis flies, and all insects combined.

The transitional stream types have baseline JMT values around 66–68°F (19–20°C), near the edge of thermal tolerance levels for coldwater fishes such as trout (Wehrly et al. 2007). With reductions in base flow, these streams warm quickly and abundance of coldwater fishes drops precipitously. These effects likely occur with any fish species that reaches its maximum thermal tolerance limit in Michigan rivers, but are most pronounced in cold-transition streams due to the steep declines in coldwater fish populations that occur at particular temperature thresholds. Thus, these streams are most likely to change due to warming from water withdrawal or other factors, including climate change. Warming due to water withdrawal is also expected to increase populations of warmwater fishes in streams on the cold end of species' tolerance limits. Fish communities in cold-transitional streams and rivers had the steepest responses to base flow reduction, indicating the need for caution in setting limits on withdrawal and suggesting that these communities will be especially sensitive to future climate warming (Figure 2). In contrast, response curves for cold streams and small rivers had flatter slopes, suggesting communities in these river types are buffered by an abundant supply of groundwater and relatively robust cold temperatures.

Despite their initially flat slopes, curves for fish assemblages in cold river types showed precipitous declines (similar to those of cold-transitional types) once water withdrawal thresholds were reached (Figure 7). At these water withdrawal thresholds, cold river types essentially become cold-transitional river types, with their fish communities changing dramatically with further water withdrawals. Cold and cold-transitional fish assemblages in Michigan (more so than their warmwater counterparts) are also at increased risk from climate warming that is expected to occur.

Fish community response curves also varied within stream types. According to the model, populations in some streams responded at lower thresholds of base flow reduction, while some responded at higher thresholds (Figure 6). Within each stream type, the model curves are averages of a sub-sample of 15–20 representative streams. The types provide strata to control for variation within a type while allowing for description of fish community responses across the array of Michigan streams. Theoretically, each stream segment would have its own unique set of response curves, but the need for spatially and temporally extensive physical and biological data and models makes the development of accurate, stream-specific curves infeasible. We averaged responses within each stream type to increase sample size and ensure our predictions of fish assemblage response to water withdrawal were accurate and robust.

Comparison with Site-scale Studies

Our model predictions of species response to base flow reduction were consistent with previous studies and simulations in Michigan and elsewhere of fish species responses to flow reduction and temperature increase. We stress that all the various modeling approaches have inherent assumptions and limitations, and are best used in concert to see whether and where results converge. Our regional-scale empirical models accurately describe observed optimal habitat and habitat limits, but do not contain mechanistic or geographic detail. In contrast, typical site-scale hydraulic models estimate certain habitat changes accurately but are predicated on the assumption that fish populations will respond directly to these habitat measures; however this assumption has been very difficult to validate in the field (Zorn and Seelbach 1995; Nuhfer and Baker 2004).

Our model predicted changes in density of salmonids and other coldwater fishes with base flow reduction in cold small streams and rivers that were similar to modeling results in studies of various salmonid species and life stages (e.g., Jager et al. 1997; Van Winkle et al. 1997). Declines in these species are attributable to changes in both flow and temperature. For some species, the reduction in density with base flow is more likely a response to temperature changes, especially as temperature nears species' tolerance limits, while for others it may be more a response to flow changes.

While the Hunt Creek study did not show demonstrable effects of flow reduction on brook trout (see reasons mentioned above), it demonstrated that water withdrawal can have significant downstream effects on stream temperatures, and can lead to potentially lethal conditions for coldwater fishes, including trout and salmon species. Warming in Hunt Creek was notable at 50% reduction in flow (the lowest reduction in their study), and increased exponentially as flow reductions approached 90% (Nuhfer and Baker 2004). Water withdrawals increased the warming rate in the study reach up to 28 times or more (9 times on average), which would likely have negatively impacted growth or survival of salmonids in downstream reaches, a finding that prompted our addition of a downstream warming module. Further study of downstream warming effects is warranted as the magnitude of Hunt Creek observations could not be replicated with our downstream warming model (Appendix A). This uncertainty further supports a conservative approach to setting ARI thresholds for cold and cold-transitional river types.

A hydraulic modeling study of a cold-transitional stream in southern Michigan predicted that trout and invertebrate habitat availability would decline steadily with incremental summer base flow reductions, in essentially a 1:1 ratio (Gowan 1984). This finding supports our model prediction of high sensitivity for cold transitional river types, however the approach used differed from ours in that increases in water temperature were not considered.

Our empirical model predicted that base flow reductions would cause declines in abundances of cool and warm water species including smallmouth bass, rainbow darter, blackside darter, burbot, common shiner, logperch, northern hogsucker, northern pike, and pumpkinseed. Whitley et al. (2006) found that base flows influenced distribution and abundance of smallmouth bass. Even in rivers with very low natural base flows, spatial patterns in fish abundance have been shown to reflect the geography of groundwater inputs (i.e., localized base flow yields; Wall and Berry 2006). Several empirical studies suggested flow reductions actually may improve habitat for some pool-dwelling species, especially in the short term, and this may help explain why assemblage declines did not occur until withdrawals reached 25–50% of base flow in some cool and warm river types (Moyle and Baltz 1985; Schlosser 1985; Zorn and Seelbach 1995).

Though most studies of flow reduction have looked at effects on gamefish species, further work should focus on its influence on abundance and structure of entire fish assemblages. Previous studies suggest that responses to water withdrawal will vary by species, habitat-use guilds, and reproductive guilds (Annear et al. 2004), with the most varied responses being expected for rivers providing diverse habitat conditions and fish communities (e.g., moderate-gradient, warm or cool streams).

Limitations and Areas for Future Work

Our ability to make predictions of fish communities in some areas and types of lotic systems is limited by the availability of field survey data for use in model development. Fish assemblage data were lacking for certain waters, most notably small, warm streams in glacial lakeplain areas (e.g., Saginaw Bay, Lake Erie, and UP lakeplain areas) and UP rivers. Further work is needed to increase our information base and predictive power for these areas. In addition, results for large rivers were assumed to extend to non-wadeable rivers because comparable fish survey data were unavailable for these systems. We think this is a reasonable extrapolation since physical conditions and fish communities of large, marginally-wadeable rivers (typically surveyed using rotenone) are fairly comparable to larger, non-wadeable systems. We recognize that other taxa or physical criteria may have provided a more sensitive indicator of adverse impact to stream health than fishes but data were not readily available for modeling on a regional basis. For example, some macroinvertebrate families were somewhat more sensitive than trout to experimental water withdrawals in a Michigan trout stream (Nuhfer and Baker 2004; Wills et al. 2006). Abundance of macroinvertebrate populations is inherently variable among sites, seasons and years, and macroinvertebrate abundance estimates for Michigan streams are limited. However, spatial coverage of macroinvertebrate surveys in Michigan may be sufficient to allow modeling of macroinvertebrate communities in a manner analogous to the fish models used in this study (i.e., substituting spatial variation and gradients for temporal variation).

One weakness of our regional-scale HSI approach is that although we were able to describe the central tendency of fish-base flow relationship for each river type, we also identified considerable variation around this for individual species and sites. Our simple model is useful for setting regional flow standards but certainly does not account for all the complex mechanisms that affect fish abundances at specific sites. Our approach, which involves looking across spatial gradients of BFY reduction, lacks the resolution and mechanistic insight that can come from studies tracking responses of individual streams through time. Site-scale models can bring greatly enhanced accuracy and mechanistic realism; however it is impractical to do enough of these to provide comprehensive regional coverage. Also, the required assumptions about modeled habitat changes indexing actual fish population changes have rarely been validated, thus the empirical confidence in many HSI studies is low. However, correspondence between model scores and measured fish densities in this study provides empirical support for our HSI-based approach. As both regional and site-scale modeling approaches have somewhat complimentary strengths and weaknesses, we recommend conducting a targeted series of site-scale studies across a range of Michigan river types for comparison with the regional results.

Our modeling only addressed summer fish assemblage changes resulting from water withdrawal. Rivers and their fish communities are dynamic, changing seasonally with climate, flow levels, and as fish move between reproduction, growth, and refuge habitats (Schlosser 1993; Gowan et al. 1994). We focused on the summer period because it represents a major period of water use, is the major growing period for fish, and is the only period for which we have extensive fish survey data. However, since the groundwater inputs that support summer base flows also provide thermal buffer to harsh thermal conditions during winter low flow periods (Seelbach 1987; Power et al. 1999), our analysis may also be relevant to these. Channel-shaping and floodplain modification processes that occur during periods of higher flow are also important, and would be expected to continue at current frequencies and magnitudes, because allowable water withdrawal amounts are based on proportions of summer base flow and typically would represent only a minor proportion of flows during high-water periods. However, we need to better characterize the entire spectrum of natural flows for Michigan rivers to guide future policy discussions of holistic flow management as envisioned by Richter et al. (2003) and recognized by the GWCAC (Anonymous 2006).

Our ability to assess downstream warming effects on fish communities was limited by the spatial scale and structure of our models. We exerted considerable care to determine how far downstream we

should model withdrawal effects on stream warming, and explored the consequences of modeling further downstream on our predictions. Future efforts could examine alternate ways to model downstream warming, in particular ones that utilize topologic information in the valley segment data layer. In addition, our warming module was not able to reproduce the high warming rates observed in Hunt Creek (Nuhfer and Baker 2004). Further empirical study of relations between base flow and temperature warming rates would help refine our model and thus increase the overall predictive power of the fish model.

Since river classification and modeling were iterative, concurrent projects, the fish modeling scenarios did not always involve the exact stream type boundaries, particularly the temperature boundaries for the transitional classes. In addition, some response curves were based on fewer than 20 river segments per stream type because the transitional classes were typically broken out of adjacent cold or cool classes. Future model runs should incorporate the final boundaries, and explore the appropriate number of sites to model for developing response curves for each stream type.

We developed and used species optima values based on summaries for two geographic areas, the SLP and NLP-UP. We think these led to better predictive models because, for most species, they resulted in tighter descriptions of species optima (based on coefficients of variation for statewide-versus regional-based species optima values for CA, JMT, and BFY). However, limited sampling or other factors may have resulted in the regional data producing biased descriptions of optima for some species (e.g., slimy sculpin in NLP-UP). Future modeling efforts should determine the appropriate spatial scales for defining species optima.

More work is needed to explore and ultimately validate fish and habitat responses to base flow reductions. Dynamic simulation models that relate effects of incremental changes in water withdrawal to a stream's physical and chemical habitat variables, and its suitability for biota, exist for only a few Michigan river reaches. For selected river types, such models should be employed to evaluate a range of base flow reductions, with response variables including physical/chemical habitat (e.g., flow velocity, depth, wetted area, temperature, dissolved oxygen) and biological assessment metrics (e.g., algal biomass and production, photosynthesis, respiration, macroinvertebrate Ephemeroptera Plecoptera Trichoptera [EPT] index). The resulting habitat characteristics should be compared with threshold habitat suitability levels for fishes and macroinvertebrates, and metrics of stream physical processes (e.g., channel forming, sediment loading, etc.). Large-scale and long-term adaptive management experiments will be needed to examine actual responses of entire fish assemblages across a variety of river types.

Our development of curves depicting responses of fish assemblages to base flows is a promising step for river management; however healthy river habitats depend on wise maintenance of all the dimensions of flow variability (Poff et al. 1997; Richter et al. 2003). These flow aspects are typically outlined as magnitude, frequency, duration, timing, and rate of change; and must be understood across the entire annual period. Future efforts need to explore relationships between all of these aspects and fish assemblages in Michigan rivers.

Our effort to quantify base flow reductions resulting in ARI's in various stream types supported the use of the biological condition gradient (Davies and Jackson 2006) for a consistent, ecologically relevant interpretation of response of aquatic biota to stressors. At low levels of stress, there is no or minimal change in structural, functional or taxonomic integrity of biotic communities, and ecosystem function is maintained. With increasing levels of stress, there are evident-to-moderate changes in structure of the biotic community, with minimal changes in ecosystem function. Some sensitive species may be replaced by more tolerant taxa, while reproducing populations of other taxa are maintained. Further stress from water withdrawals can be expected to cause large-scale replacement of characteristic fishes by tolerant species and severe alteration of the stream's ecological structure and function. Our modeling identified species sensitive to water withdrawal in each stream type, and suggested that they should be closely watched in monitoring studies.

Long-term plans for sustainable use and protection of Michigan's streams must consider impacts of climate change and land use. Climate change may affect volume, timing and intensity of precipitation, and affect warming rates of rivers, with negative implications for larval fish survival and river connectivity (Gibson et al. 2005). A suite of the dynamic simulation models discussed above will be required to explore alternate futures for all Michigan river types.

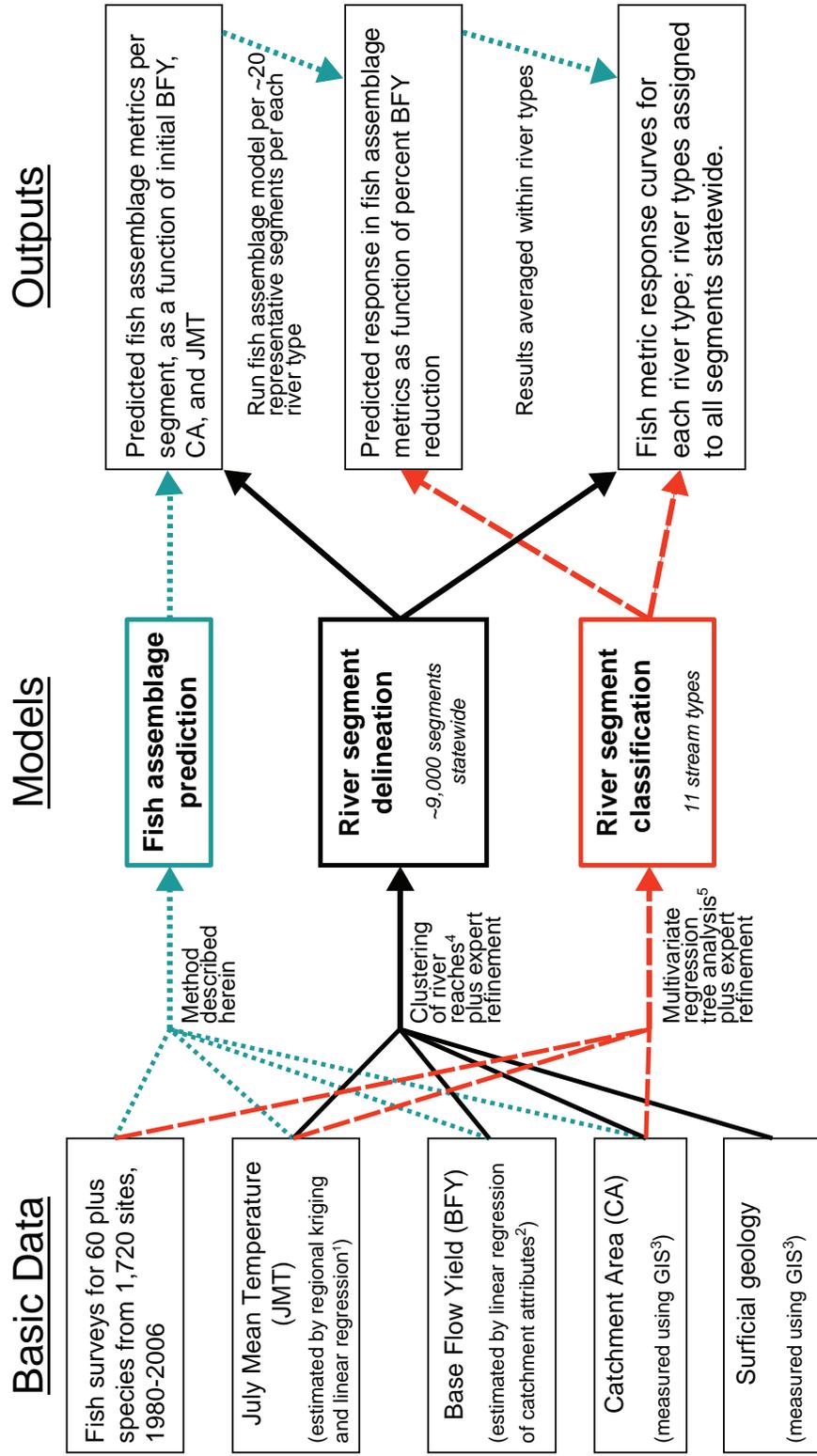
Management Implications

The curves defining fish response to base flow reductions in Michigan's river types can be used to guide and constrain policy discussions of water resource goals and water withdrawal thresholds. By plotting the curves together, a continuum of impacts to Characteristic and Thriving species is apparent as base flow is incrementally reduced. For example, the ARI line represents the threshold at which the stream's capacity to support Characteristic Species is likely to be adversely impacted. Zones to the left of the ARI line show a gradation of potential risks of water withdrawal on the fish community. Policy makers can use this information to identify threshold withdrawal levels that might trigger various management actions. For example, the GWCAC has proposed that certain management actions (e.g., increased engagement and responsibilities in water management by users) should be initiated at withdrawal levels above those that are expected to cause declines in abundance scores for 10% of Thriving Species (Anonymous 2007; Figure 7).

The GWCAC made it clear that this proposed Water Withdrawal Assessment Process and its component models (including this fish response model) represent the beginning of a major adaptive management effort that must include regular, iterative testing and refining (Anonymous 2007). These fish habitat suitability and interpretive response models are likewise only a first step towards improved ecological water management for Michigan. Targeted improvements to regional survey data, field experiments, and simulation modeling can all help to refine these tools. We expect our future efforts to foster continued alignment with, and convergence towards, the process for developing environmental flow standards recommended by the ELOHA workgroup (Anonymous 2008).

Acknowledgments

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¹ Brenden, personal communication
² Hamilton et al. 2008
³ Brenden et al. 2006
⁴ Brenden et al. 2007b
⁵ Brenden et al. 2008

Figure 1.—Flow chart of the flow-fish response assessment model showing major data, model, output components, and linkages.

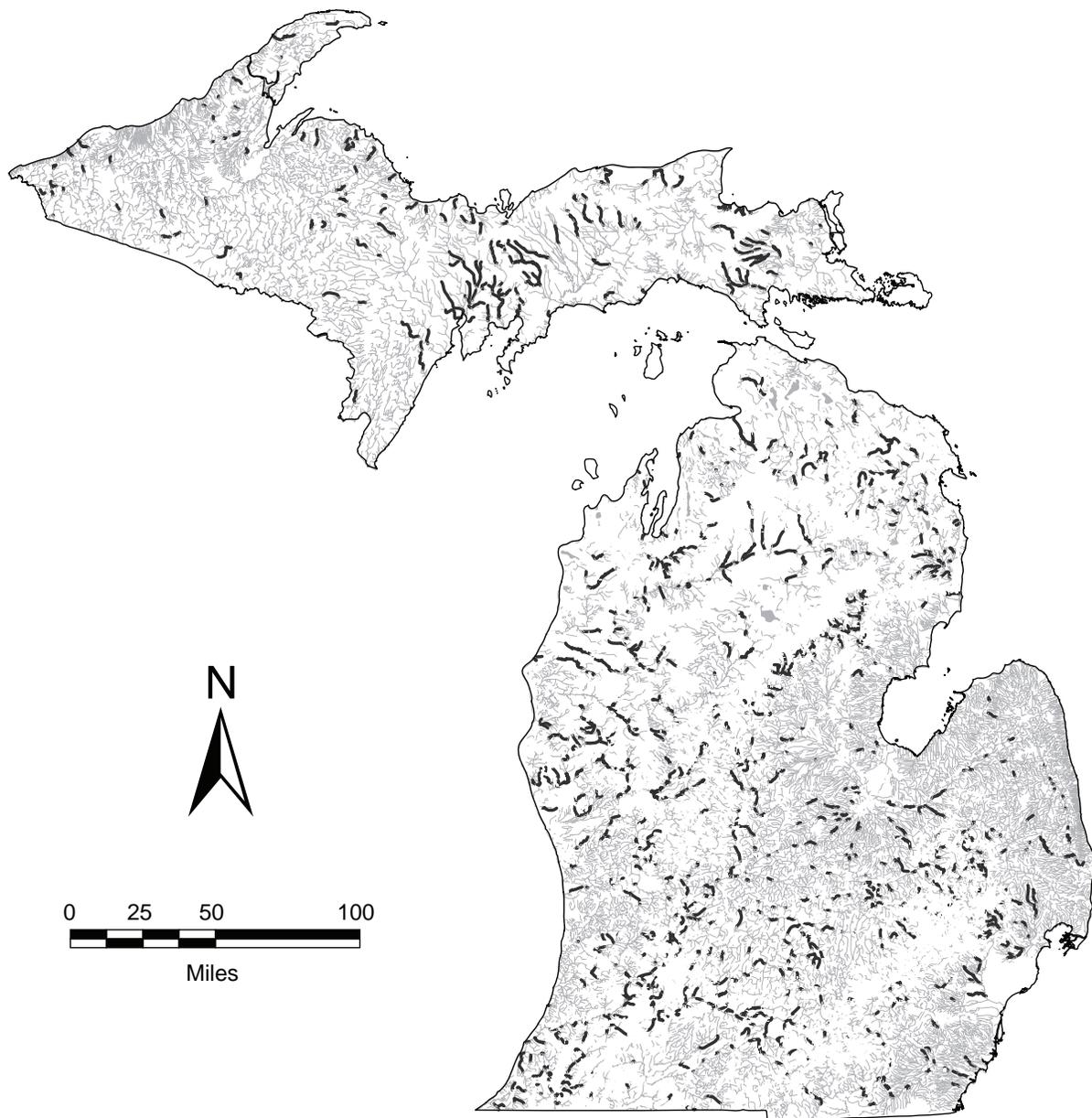


Figure 2.—Stream reaches with fish surveys (N= 1,720) shown in black and displayed on Michigan's drainage network.

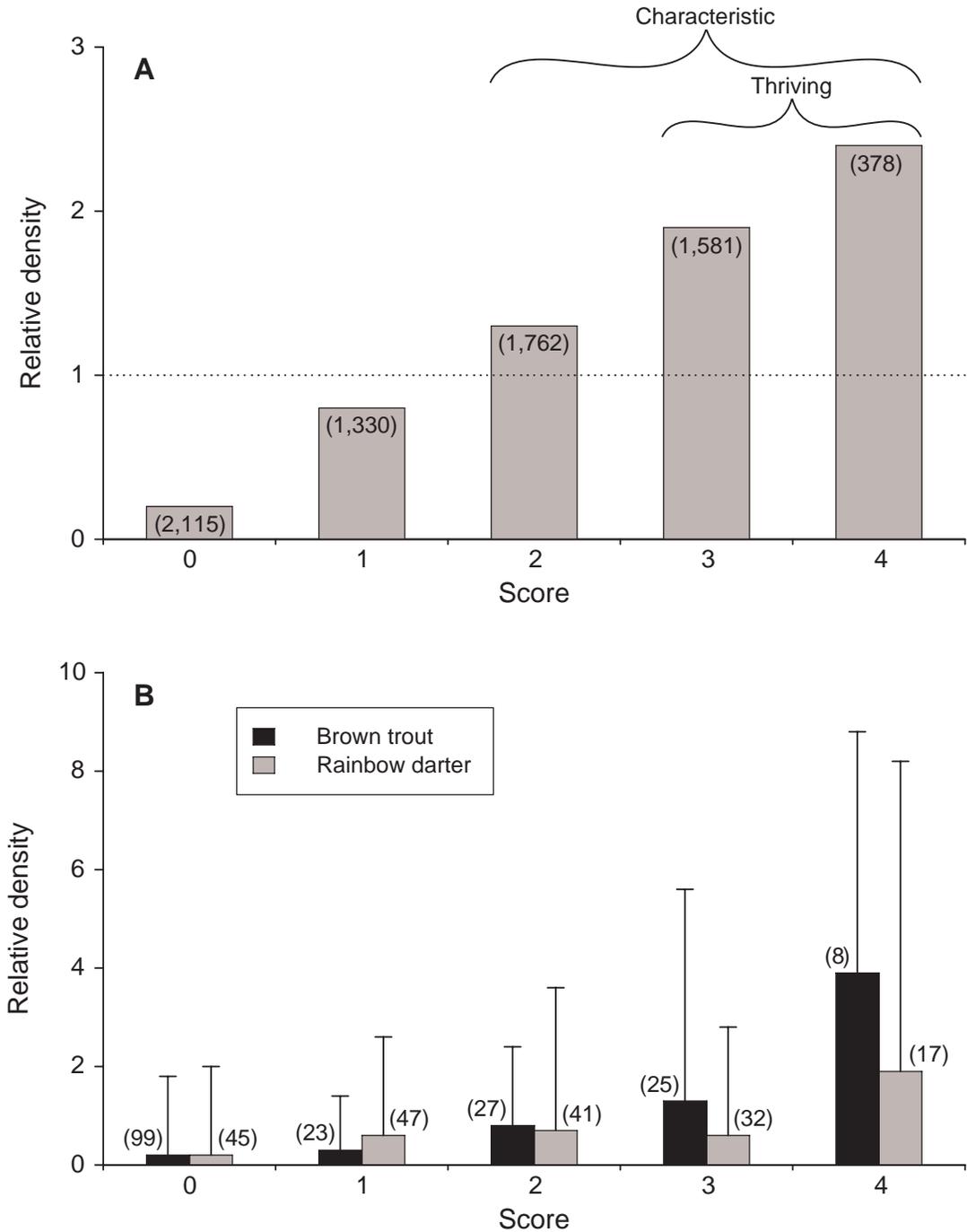


Figure 3.—A) Relationship between fish species' scores and species' relative densities, averaged across all species at 183 sites on Michigan rivers (7166 individual species scores were predicted). Relative density values were defined as the observed density of the species at a site divided by the median density for the species in the statewide data. Dashed line at relative density value of 1 marks the median density for each species. Relative densities of Characteristic Species (scoring from 2 to 4) were above the median value, while those of Thriving Species (scores 3 and 4) were roughly two or more times higher than median values. B) Relationships between score and average relative density for two example fish species, brown trout and rainbow darter, illustrating: 1) variation in the score-density relationship between species; and 2) variation in fish densities among sites for each score (whiskers equal two standard deviations).

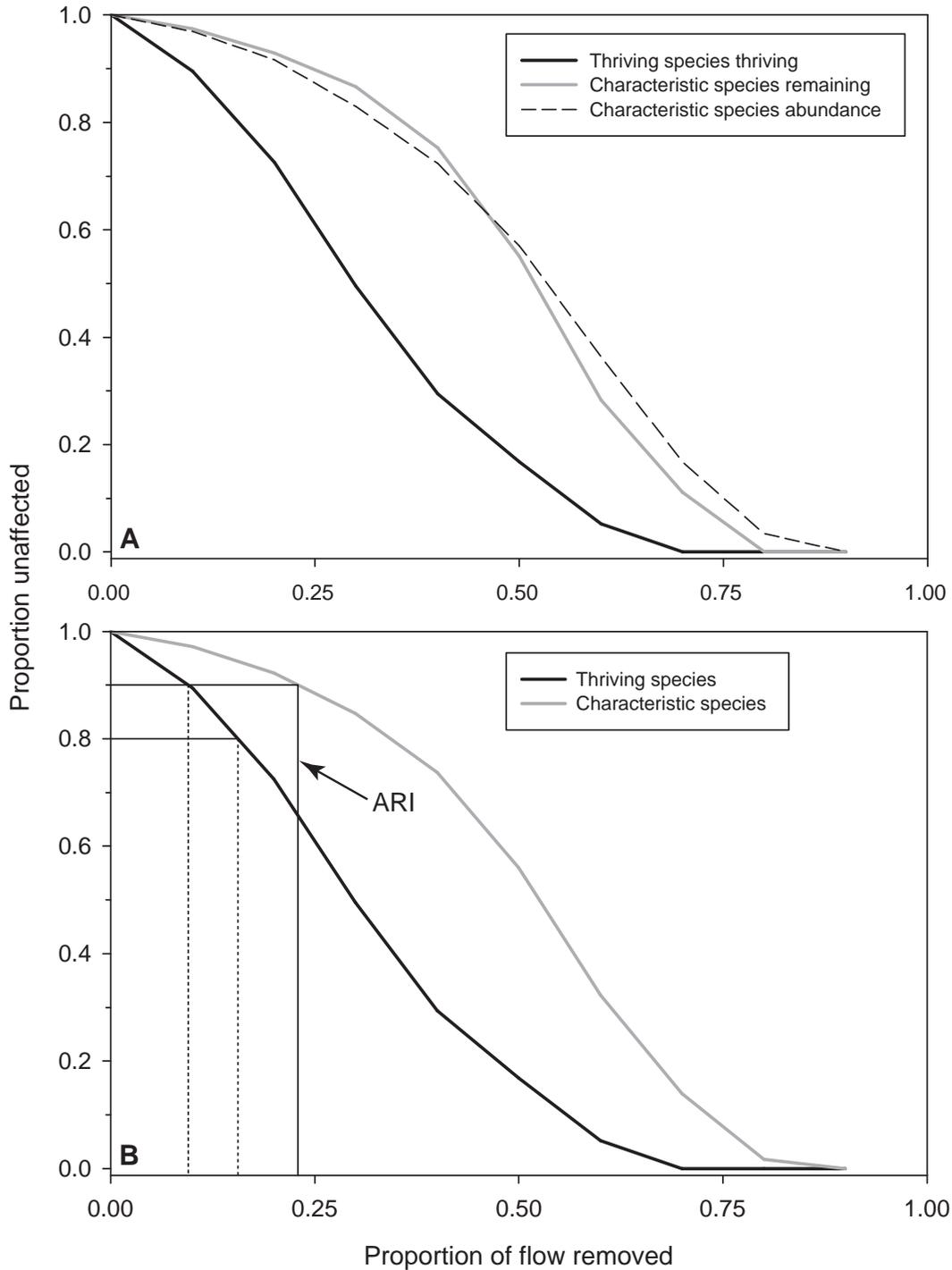


Figure 4.—Fish community response curves used in determining when water withdrawal was causing an adverse resource impact (ARI) to fish assemblages; the example here is for large, warm rivers. Three curves were developed for all stream types (A), but two “similarly-behaving” curves (Characteristic Species Remaining and Characteristic Species Abundance) were averaged for simplicity (B). The Michigan Groundwater Conservation Advisory Council recommended that an ARI, defined by fish assemblage response, is expected when the proportion of flow removed causes a 10% decline in Characteristic Species metric. Other precautionary management actions may be triggered at 10% and 20% drops in the Thriving Species metric.

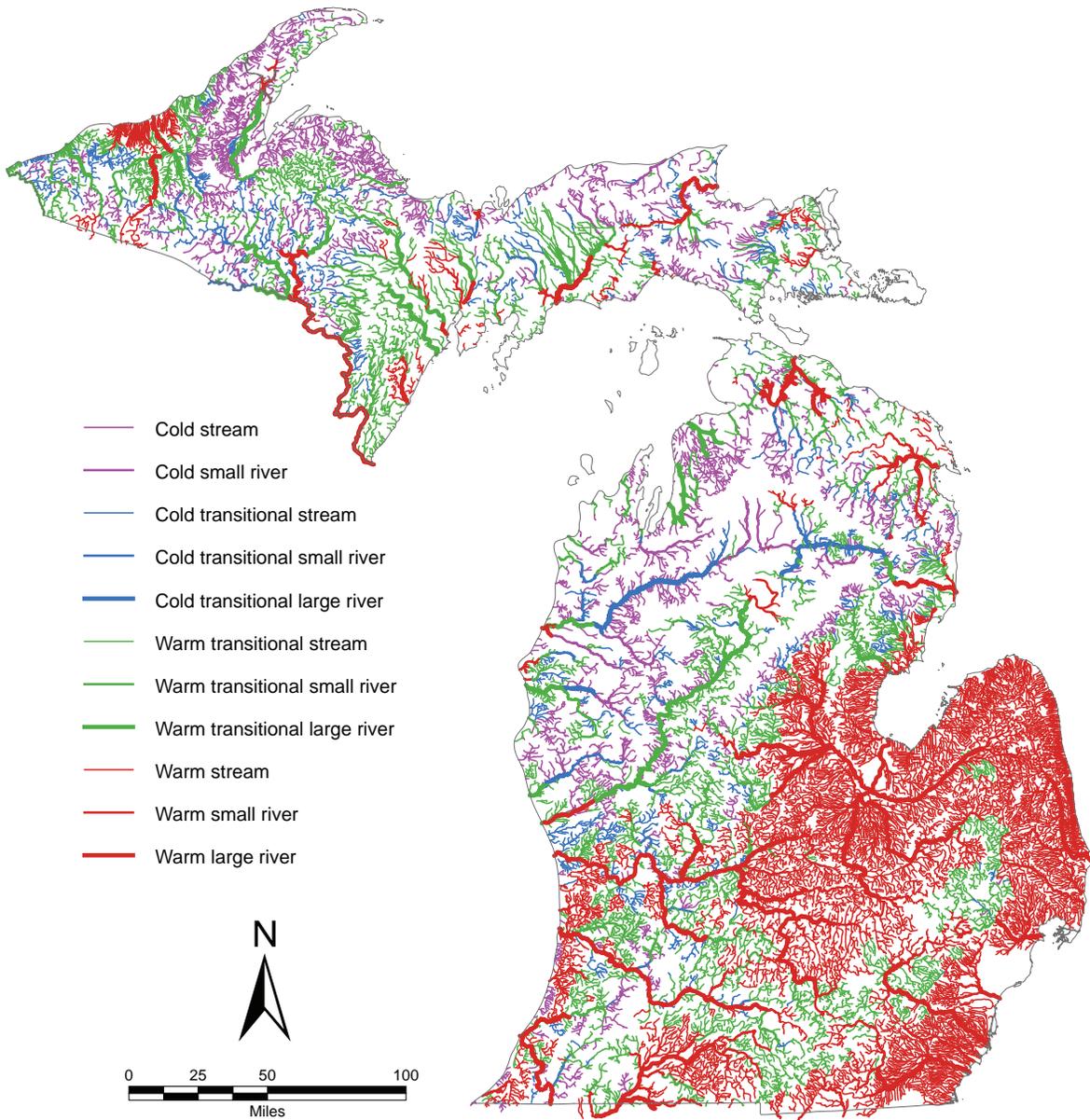


Figure 5.—Thermal and fish assemblage based classification of streams, small rivers, and large rivers in Michigan. This classification was completed in 2008 for use in the Water Withdrawal Assessment Tool and was based on the concepts presented by Seelbach et al. (2006), the foundational analyses of Brenden et al. (2008) and Brenden et al. (In Press), and a new thermal classification by Lyons (J. Lyons, Personal Communication, Wisconsin Department of Natural Resources, Madison) and colleagues.

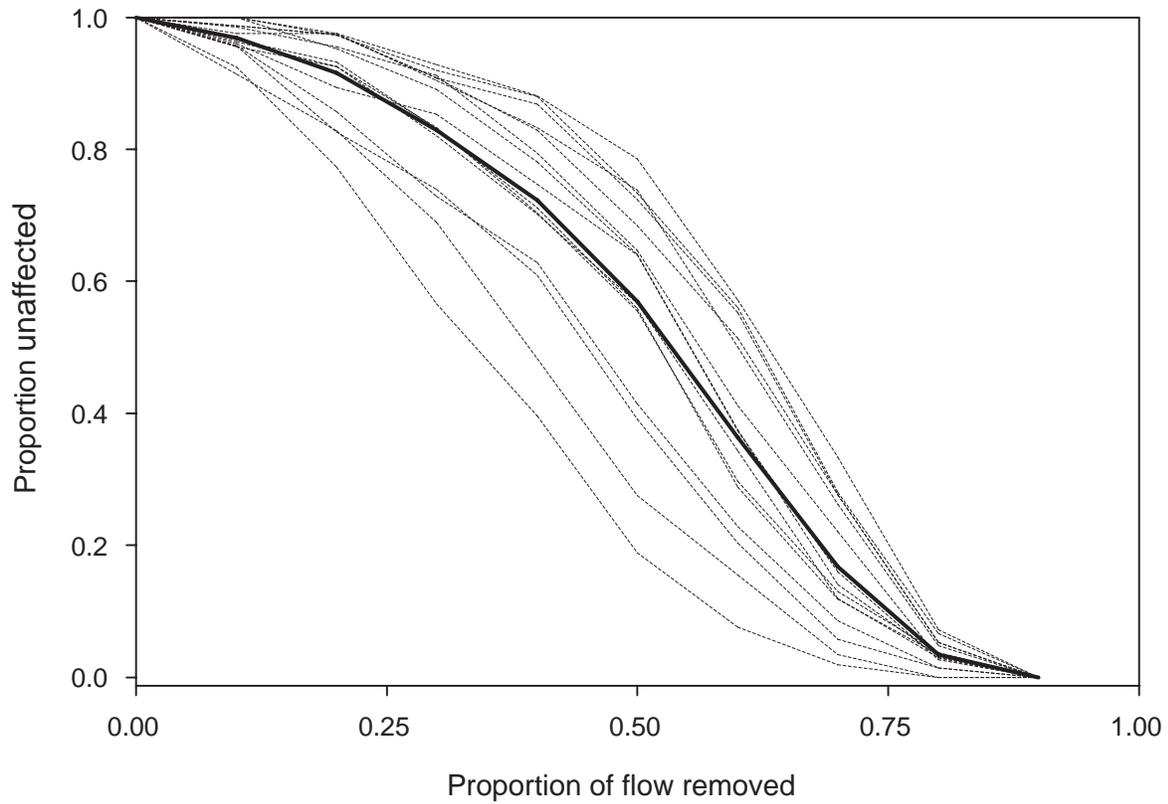


Figure 6.—Proportional changes in Characteristic Species Abundance metric versus flow reduction in representative large, warm rivers, calculated for a sample of 15 river reaches. The thick black line shows the average response of these representative reaches and defined the response for this river type.

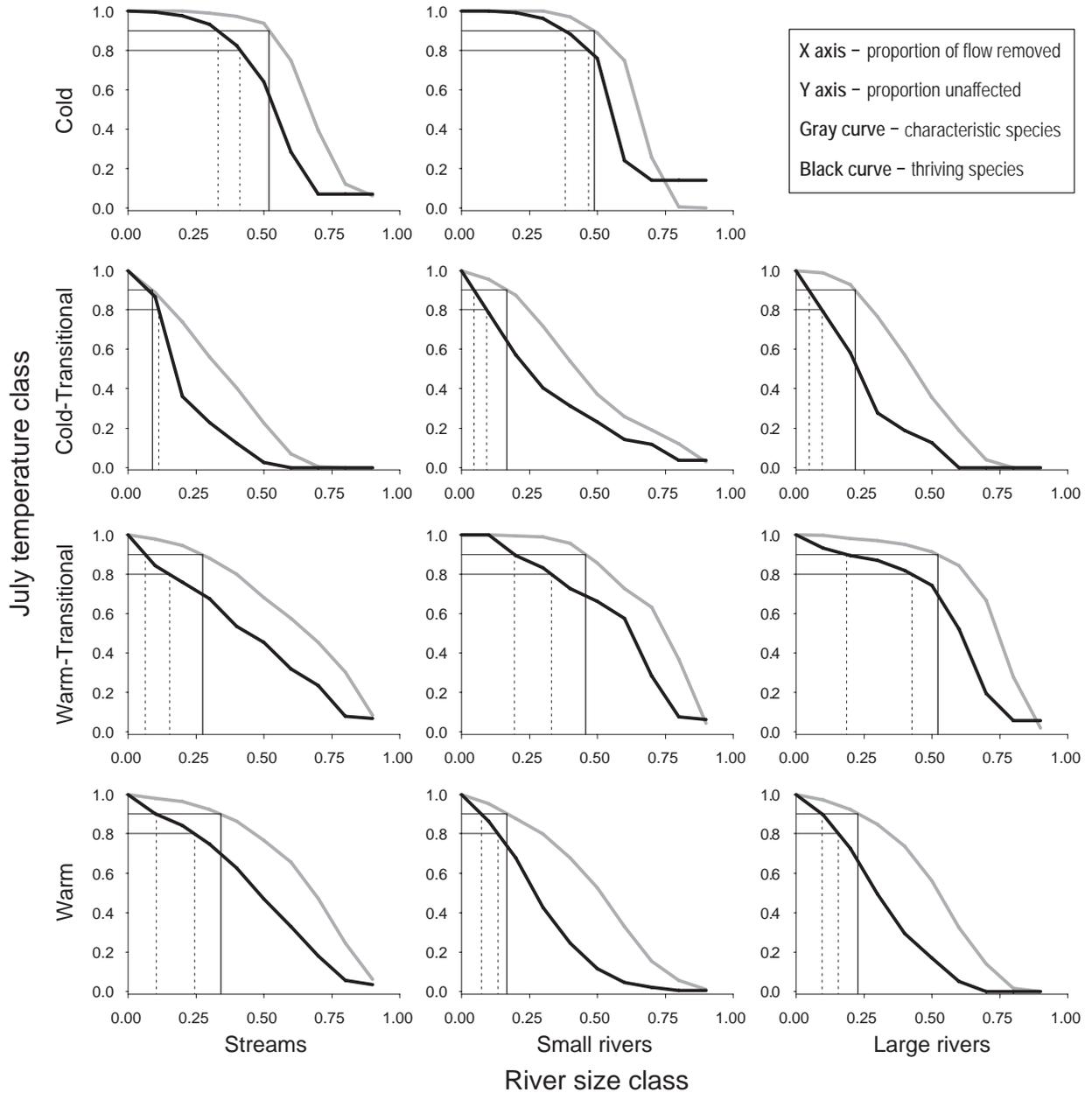


Figure 7.—Curves describing fish community responses to water withdrawal for Michigan’s 11 river types, as defined by size and July temperature characteristics. Axes are identical to those in Figure 4b. The black curve describes the proportion of Thriving Species thriving at each increment of flow reduction. The gray curve quantifies the proportional change in Characteristic Species Remaining and Characteristic Species Abundance metrics, and is an average of their values at each level of water withdrawal. The right-most vertical line in each plot identifies the flow associated with an ARI, while other vertical lines identify water withdrawal levels associated with undefined management actions to be taken in anticipation of the river BFYs approaching the ARI level.

Table 1.—Number of optimal sites (N) and optimal values of catchment area (CA), base flow yield (BFY), and July mean water temperature (JMT) for fish species in the northern Lower Peninsula and Upper Peninsula (NLP–UP), and southern Lower Peninsula (SLP) of Michigan. Species are sorted by ascending JMT. Optimal values for each species were the average values for these parameters at top 20% of sites for each species (based on species' numerical abundance at sites).

NLP–UP					SLP				
Species	N	CA (mi ²)	BFY (cfs/mi ²)	JMT (F)	Species	N	CA (mi ²)	BFY (cfs/mi ²)	JMT (F)
brook trout	114	74.5	0.668	62.2	brook trout	14	11.3	0.314	62.6
coho salmon	16	46.8	0.711	62.8	rainbow trout	25	47.0	0.390	65.2
mottled sculpin	74	59.8	0.590	62.9	brown trout	71	44.7	0.430	65.8
slimy sculpin	14	62.0	0.688	63.0	mottled sculpin	30	35.6	0.348	66.9
brown trout	81	108.6	0.743	63.4	central mudminnow	63	40.0	0.251	67.8
Chinook salmon	13	78.0	0.656	63.7	blacknose dace	50	35.2	0.250	67.8
northern redbelly dace	16	64.0	0.642	63.8	warmouth	11	116.9	0.356	68.3
brook stickleback	20	26.0	0.430	63.9	creek chub	93	58.7	0.189	68.5
northern brook lamprey	13	84.1	0.642	64.2	brook stickleback	15	18.7	0.129	68.7
rainbow trout	62	122.7	0.597	64.2	grass pickerel	36	163.6	0.318	69.0
blacknose dace	68	81.6	0.52	64.4	johnny darter	76	69.7	0.182	69.1
central mudminnow	60	49.7	0.518	64.7	rainbow darter	36	130.9	0.289	69.3
creek chub	80	62.7	0.465	64.8	white sucker	106	171.0	0.223	70.0
American brook lamprey	12	128.0	0.708	65.1	golden shiner	14	277.0	0.269	70.2
longnose dace	42	184.2	0.515	65.1	pirate perch	12	92.3	0.160	70.3
bluntnose minnow	21	129.6	0.600	65.2	black bullhead	15	108.9	0.164	70.4
yellow perch	22	243.0	0.594	65.5	central stoneroller	24	135.1	0.094	70.5
white sucker	86	164.5	0.548	65.6	hornyhead chub	31	223.6	0.234	70.6
hornyhead chub	12	65.0	0.521	65.6	largemouth bass	46	360.7	0.199	70.6
largemouth bass	19	103.3	0.554	65.8	bluegill	53	291.0	0.183	70.7
burbot	30	205.1	0.581	66.2	common shiner	59	219.7	0.239	70.8
johnny darter	51	182.7	0.594	66.3	green sunfish	76	229.3	0.220	70.8
bluegill	17	121.6	0.542	66.3	longear sunfish	11	221.5	0.190	71.0
pumpkinseed sunfish	16	139.7	0.492	66.6	blackside darter	50	312.7	0.237	71.3
green sunfish	12	266.1	0.482	66.9	yellow perch	16	509.0	0.226	71.3
logperch	21	460.6	0.603	67.1	rosyface shiner	12	432.6	0.330	71.7
common shiner	42	275.2	0.502	67.6	yellow bullhead	30	425.3	0.240	71.9
northern pike	12	350.2	0.504	68.0	northern hog sucker	49	574.6	0.241	72.2
northern hog sucker	14	596.2	0.527	68.3	northern pike	36	532.2	0.195	72.2
rock bass	28	310.9	0.514	68.3	shorthead redhorse	12	421.0	0.269	72.5
blackside darter	26	350.0	0.533	69.1	logperch	15	462.3	0.253	72.6
rainbow darter	11	629.5	0.495	69.6	bluntnose minnow	49	388.3	0.168	72.6
smallmouth bass	17	503.6	0.490	69.7	black crappie	19	1418.7	0.242	72.7
					walleye	11	1561.5	0.294	72.9
					stonecat	26	505.5	0.208	73.0
					rock bass	56	423.6	0.171	73.0
					pumpkinseed sunfish	47	441.0	0.148	73.0
					common carp	37	1116.3	0.200	73.4
					spotfin shiner	40	577.3	0.218	73.5
					smallmouth bass	32	918.3	0.219	73.7
					golden redhorse	19	554.4	0.199	73.7
					channel catfish	14	1491.3	0.186	73.7
					greenside darter	11	517.7	0.160	73.9

Table 2.—Descriptions of Michigan river types (cross-tabulation of thermal¹ by size² groups) in the water management valley segment map theme. Summaries are based upon: number of segments, total miles, and percent of total miles in Michigan; and catchment areas for sites in each type as described by 5th percentile, mean, and 95th percentile for segments in each type. Thermal and size class assignments based on studies of relationships to fish assemblage structure in Michigan and Wisconsin (J. Lyons, Wisconsin Department of Natural Resources, personal communication; Zorn et al. 2002; Wehrly et al. 2003; Brenden et al. in press; Zorn et al. in press).

Thermal group	River size										Catchment area (mi ²)								
	Streams			Small rivers			Large rivers			Streams			Small rivers			Large rivers			
	Number	Miles	% of total	Number	Miles	% of total	Number	Miles	% of total	5 th	Mean	95 th	5 th	Mean	95 th	5 th	Mean	95 th	
Cold	2,160	8,994	18	56	515	1				1	9	41	83	153	265				
Cold-transitional	497	3,080	8	102	656	1	53	353	1	1	16	58	86	166	283	309	603	1,387	
Cool (warm-transitional)	1,560	11,653	24	219	1,471	3	104	854	2	1	14	55	86	164	272	313	903	2,394	
Warm	1,198	17,806	37	197	1,546	3	201	1,727	3	1	16	58	84	153	278	322	1,389	4,660	

¹Thermal groups: cold = predominantly coldwater fishes and JMT typically ≤63.5°F (17.5°C); cold-transitional = mostly coldwater fishes but some warmwater fishes and JMT typically >63.5°F (17.5°C) and ≤67°F (19.5°C); warm-transitional = mostly warmwater fishes but some coldwater fishes and JMT typically >67°F (19.5°C) and ≤70°F (21.0°C); warm = predominantly warmwater fishes and JMT typically >70°F (21.0°C).

²Size groups: streams = predominantly stream fishes and CA ≤typically 80 mi² (207 km²); small rivers = CA typically >80 mi² (207 km²) and ≤300 m² (777 km²); large rivers = predominantly large river fishes and CA typically >300 mi² (777 km²).

Table 3a.—Characteristic and Thriving species in Streams with cold (C) and cold-transitional (CT) temperatures¹, and effects of reducing base flows past Adverse Resource Impact (ARI) levels. Species initially characteristic at 70% or more of sites are listed with percentage occurrence. Species initially thriving at >50% of sites are indicated with an "X". Species in italics met the Thriving Species criteria only. Percentages are shown for initially Thriving Species that decline to characteristic or lower levels at ≥40% or more of sites at the first flow reduction level beyond ARI. Initially Thriving Species whose abundance score declines to 1 or lower at ≥20% of sites are indicated by "X".

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20 % of sites	No. of sites
C	brown trout	100	X	80	X	15
C	mottled sculpin	100	X			15
C	rainbow trout	100	X			15
C	brook trout	93	X	80	X	15
C	blacknose dace	93				15
C	bluntnose minnow	73				15
C	burbot	73				15
C	central mudminnow	73				15
C	coho salmon	73	X	73	X	15
C	northern brook lamprey	73	X	53	X	15
C	northern redbelly dace	73	X	47		15
C	slimy sculpin	73		47	X	15
C	yellow perch	73				15
CT	bluntnose minnow	100				5
CT	brook stickleback	100	X			5
CT	creek chub	100	X			5
CT	mottled sculpin	100	X			5
CT	northern redbelly dace	100	X			5
CT	yellow perch	100				5
CT	brook trout	80	X			5
CT	blacknose dace	80				5
CT	bluegill	80				5
CT	central mudminnow	80				5
CT	coho salmon	80	X			5
CT	longnose dace	80				5
CT	northern brook lamprey	80				5
CT	rainbow trout	80				5
CT	white sucker	80				5

¹Thermal groups: cold = predominantly coldwater fishes and JMT typically ≤63.5°F (17.5°C); cold-transitional = mostly coldwater fishes but some warmwater fishes and JMT typically >63.5°F (17.5°C) and ≤67°F (19.5°C).

Table 3b.—Characteristic and Thriving species in Streams with cool (warm-transitional or WT) and warm (W) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
WT	blacknose dace	95	X			20
WT	central mudminnow	95	X			20
WT	creek chub	90	X			20
WT	johnny darter	90	X			20
WT	white sucker	90				20
WT	green sunfish	85				20
WT	largemouth bass	85				20
WT	mottled sculpin	85	X			20
WT	rainbow trout	85	X			20
WT	rainbow darter	75	X			20
WT	bluegill	70				20
WT	golden shiner	70				20
W	longear sunfish	85	X			20
W	pirate perch	85	X			20
W	blacknose dace	80				20
W	central stoneroller	80				20
W	golden shiner	80	X			20
W	johnny darter	80	X			20
W	rainbow darter	80	X			20
W	black bullhead	75	X			20
W	bluegill	75	X			20
W	central mudminnow	75	X			20
W	common shiner	75	X			20
W	creek chub	75	X			20
W	green sunfish	75	X			20
W	hornyhead chub	75	X			20
W	largemouth bass	75	X			20
W	northern pike	75				20
W	white sucker	75	X			20
W	yellow perch	75	X			20
W	blackside darter	70				20
W	bluntnose minnow	70				20

¹Thermal groups: warm transitional = mostly warmwater fishes but some coldwater fishes and JMT typically >67°F (19.5°C) and ≤70°F (21.0°C); warm = predominantly warmwater fishes and JMT typically >70°F (21.0°C).

Table 4a.—Characteristic and Thriving species in Small Rivers with cold (C) and cold-transitional (CT) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
C	brook trout	100	X	67	X	15
C	brown trout	100	X	60	X	15
C	northern brook lamprey	100		47	X	15
C	northern redbelly dace	100	X			15
C	yellow perch	100	X			15
C	American brook lamprey	93	X	67	X	15
C	bluntnose minnow	93	X	53		15
C	johnny darter	93		47	X	15
C	logperch	93		47		15
C	mottled sculpin	93				15
C	rainbow trout	93		40		15
C	blacknose dace	87				15
C	bluegill	87				15
C	burbot	87				15
C	largemouth bass	87				15
C	longnose dace	80				15
C	common white sucker	80				15
C	chinook salmon	73		40	X	15
CT	common shiner	87	X			15
CT	green sunfish	87	X			15
CT	largemouth bass	87				15
CT	white sucker	87	X			15
CT	yellow perch	87	X			15
CT	blackside darter	80				15
CT	bluegill	80				15
CT	bluntnose minnow	80				15
CT	northern hog sucker	80	X			15
CT	logperch	73	X			15
CT	northern pike	73	X			15
CT	pumpkinseed	73	X			15
CT	rainbow darter	73				15
CT	rock bass	73	X			15
CT	<i>burbot</i>		X			15
CT	<i>johnny darter</i>		X			15

¹Thermal groups: cold = predominantly coldwater fishes and JMT typically ≤63.5°F (17.5°C); cold-transitional = mostly coldwater fishes but some warmwater fishes and JMT typically >63.5°F (17.5°C) and ≤67°F (19.5°C).

Table 4b.—Characteristic and Thriving species in Small Rivers with cool (warm-transitional or WT) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
WT	blackside darter	100	X			5
WT	common shiner	100	X			5
WT	logperch	100	X			5
WT	rainbow darter	100	X			5
WT	bluegill	80				5
WT	bluntnose minnow	80				5
WT	golden shiner	80	X			5
WT	grass pickerel	80		40		5
WT	green sunfish	80	X			5
WT	johnny darter	80				5
WT	largemouth bass	80	X			5
WT	northern hog sucker	80	X			5
WT	northern pike	80				5
WT	pumpkinseed sunfish	80				5
WT	rock bass	80				5
WT	warmouth	80	X	40		5
WT	white sucker	80	X			5
WT	yellow perch	80	X			5
WT	<i>hornyhead chub</i>		X			5
WT	<i>longear sunfish</i>		X			5
WT	<i>yellow bullhead</i>		X			5

¹Thermal group: warm transitional = mostly warmwater fishes but some coldwater fishes and JMT typically >67°F (19.5°C) and ≤70°F (21.0°C).

Table 4c.—Characteristic and Thriving species in Small Rivers with warm (W) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
W	longear sunfish	100	X			20
W	bluntnose minnow	100	X			20
W	rock bass	90	X			20
W	pumpkinseed sunfish	90	X			20
W	greenside darter	90	X			20
W	central stoneroller	90				20
W	black crappie	90	X			20
W	logperch	85				20
W	yellow perch	80	X			20
W	white sucker	80				20
W	rainbow darter	80				20
W	northern pike	80	X			20
W	northern hog sucker	80	X			20
W	largemouth bass	80	X			20
W	hornyhead chub	80	X			20
W	green sunfish	80	X			20
W	golden shiner	80	X			20
W	common shiner	80	X			20
W	bluegill	80	X			20
W	blackside darter	80	X			20
W	black bullhead	80				20
W	stonecat	75				20
W	yellow bullhead	70				20

¹Thermal group: warm = predominantly warmwater fishes and JMT typically >70°F (21.0°C).

Table 5a.—Characteristic and Thriving species in Large Rivers with cold-transitional (CT) and cool (warm-transitional or WT) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
CT	burbot	100				6
CT	johnny darter	100				6
CT	logperch	100	X			6
CT	yellow perch	100				6
CT	green sunfish	83				6
CT	rock bass	83				6
CT	<i>blackside darter</i>		X	50	X	6
CT	<i>northern pike</i>		X	50	X	6
CT	<i>rainbow darter</i>		X	50	X	6
CT	<i>smallmouth bass</i>		X	50	X	6
WT	logperch	100	X			14
WT	black crappie	93	X			14
WT	blackside darter	93				14
WT	common shiner	93				14
WT	golden shiner	93				14
WT	green sunfish	93				14
WT	longear sunfish	93				14
WT	northern hog sucker	93	X			14
WT	rosyface shiner	93	X	64	X	14
WT	walleye	93	X	57		14
WT	yellow perch	93				14
WT	bluntnose minnow	86	X			14
WT	yellow bullhead	86	X	64		14
WT	bluegill	79				14
WT	common carp	79	X			14
WT	largemouth bass	79				14
WT	northern pike	79	X			14
WT	pumpkinseed	79				14
WT	rock bass	79				14
WT	smallmouth bass	79	X	57	X	14
WT	spotfin shiner	79	X			14
WT	stonecat	79	X			14
WT	greenside darter	71				14
WT	shorthead redhorse	71				14

¹Thermal groups: cold-transitional = mostly coldwater fishes but some warmwater fishes and JMT typically >63.5°F (17.5°C) and ≤67°F (19.5°C); warm transitional = mostly warmwater fishes but some coldwater fishes and JMT typically >67°F (19.5°C) and ≤70°F (21.0°C).

Table 5b.—Characteristic and Thriving species in Large Rivers with warm (W) temperatures¹. Other details as in Table 3a caption.

Thermal group	Species	Initially characteristic (% of sites)	Initially thriving at >50% of sites	Decline to characteristic or lower (% sites)	Decline to ≤1 at >20% of sites	No. of sites
W	bluntnose minnow	100	X			20
W	longear sunfish	100				20
W	pumpkinseed	90	X			20
W	greenside darter	85	X			20
W	rock bass	80	X			20
W	black crappie	75	X			20
W	channel catfish	75	X			20
W	common carp	75	X			20
W	golden redhorse	75	X			20
W	logperch	75	X			20
W	northern hog sucker	75	X			20
W	northern pike	75				20
W	spotfin shiner	75	X			20
W	stonecat	75	X			20
W	walleye	70				20
W	yellow bullhead	70				20
W	<i>smallmouth bass</i>		X	55	X	20

¹Thermal group: warm = predominantly warmwater fishes and JMT typically >70°F (21.0°C).

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Appendix A.–Overview of the “rate of heating” model for the Groundwater Conservation Advisory Council by S. Cheng and M. J. Wiley.

Our model is based on basic physical relationships (i.e., the energy balance, Newton's Law of cooling/heating), with the heat transfer coefficient being determined by Su-Ting Cheng from field measurements throughout the Muskegon River system and from lab tests. Physical channel parameters were based on hydraulic geometry relationships for depth and velocity developed from a statewide database (Seelbach and Wiley 1997), and are approximate for any real place. This is not a regression model (although the hydraulic geometry for depth and velocity are based on one) and the temperature rate of change calculation is not based on fitting data from any particular spot. Ultimately, the model is based on the same thermodynamic principles as that used by Bartholow’s Stream Network Temperature (SNT) Model (Bartholow 1989), so they should theoretically give similar answers if groundwater accrual rates and hydraulic geometry are similar. Our calculation approach was quite a bit different though. Our model is a more general model of the dominant physical processes, with no site-specific inputs (e.g., riparian shading, groundwater inputs, land use, etc.).

Background theory:

Based on the full energy budget, the rate of water temperature change (dT_{water}/dt) is:

$$\begin{aligned} \frac{dT_{water}}{dt} &= \frac{A}{mc} \left(\frac{dq}{dt} \right) = \frac{A}{(A \times d \times \rho) \times c} \left(\frac{dq}{dt} \right) = \frac{1}{d \times \rho \times c} \left(\frac{dq}{dt} \right) \\ &= \frac{1}{d \times \rho \times c} (SR + LR - BR + Cv + Cd) \\ &= \frac{1}{d \times \rho \times c} [SR + \sigma(T_{air} + 273)^4 \epsilon_{air} (1 - R_L) - \epsilon \sigma(T_{water} + 273)^4 + h_c(T_{air} - T_{water})] \\ &= \frac{1}{d \times \rho \times c} [SR + 4 \times 273^3 \sigma \epsilon (T_{air} - T_{water}) + h_c(T_{air} - T_{water})] \end{aligned} \quad (1)$$

where dT_{water} is changes in water temperature ($^{\circ}C$), dt is changes in time (h), d is depth (m), ρ is water density (kg/m^3), and dq/dt is heat flux (heat transfer per unit surface per unit time) (J/m^2h), SR is heat flux from solar radiation at the water surface (J/m^2h), LR is heat flux from longwave radiation (J/m^2h), BR is heat flux of back radiation from the water (J/m^2h), Cv is heat flux of convection (J/m^2h), and Cd is heat flux of conduction (J/m^2h), σ is the Stefan-Boltzman constant¹ (W/m^2K^4), ϵ_{air} is emissivity of the atmosphere, R_L is the reflection coefficient, ϵ is emissivity of water, and h_c is heat transfer coefficient (1/mh).

Newton’s Law of Cooling – a simplified version of the full energy budget – states that the rate of change of an object’s temperature is proportional to the difference between its own temperature and ambient temperature. Applied to the rate of water temperature change it is:

$$\frac{dT_{water}}{dt} = k(T_{air} - T_{water}) \quad (2)$$

Given Equations 1 and 2, the heat exchange coefficient k (1/h) can therefore be expressed as:

$$k = \frac{\frac{SR}{(T_{air} - T_{water})} + (4 \times 273^3 \sigma \epsilon + h_c)}{d \times \rho \times c} \propto \frac{1}{d} \quad (3)$$

¹ $5.67 \times 10^{-8} W/m^2K^4$

Appendix A.–continued.

Based on field and lab measurements, and consistent with theory we use:

$$k = \frac{0.0085}{d} \quad (4)$$

By solving the first-order ordinary differential equation (Equation 2), with initial temperature T_i , the stream temperature can be derived as:

$$T_{water} = T_E + (T_i - T_E) \times e^{-kt} \quad (5)$$

where T_E = equilibrium temperature ($^{\circ}\text{C}$), and t = travel time of water in each stream segment (h).

Equations 4 and 5 are used as the basis for the excel model with k corrected for changing depth with flow reduction, and travel time adjusted for changing velocity.