LANDSCAPE AND INCHANNEL FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF RIVERINE SMALLMOUTH BASS IN MISSOURI

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

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LANDSCAPE AND INCHANNEL FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF RIVERINE SMALLMOUTH BASS IN MISSOURI

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ABSTRACT

I developed a series of spatially-nested research objectives to identify habitat elements related to the distribution and abundance of riverine smallmouth bass *Micropterus dolomieu* in Missouri. The range of smallmouth bass was identified using a few natural-occurring landscape variables: coarse-textured soils within the watershed, watershed relief, and soil permeability. Relative abundance could be predicted for every stream segment within this range using natural-occurring landscape and stream segment variables: soil permeability, channel gradient, stream size, spring-flow volume, and local slope. Densities of smallmouth bass in stream segments depended on interactions between land use (forest, pasture, and urban) and particularly important natural-occurring features (coarse-textured soils and soil permeability). Higher relative abundances based on natural features related to higher densities in pasture watersheds whereas urban watersheds generally had the lowest densities of fish regardless of natural conditions. Young-of-year fish densities were higher in stream segments with high spring flows compared to low spring flows, but not for other age classes. All age classes used pools more than other habitats. Microhabitat temperature selection differed among age classes with young of year selecting warmer microhabitats than adults. Velocity was the most significant variable identifying microhabitats used by young of year whereas depth was important in small streams and stream segments classified by pasture land use.

This research shows how natural watershed conditions influence the magnitude of the effects of land use and relate to use of fine scale habitat elements.

Chapter 1

General Introduction

The term “habitat” embodies a central concept in ecology that not only encompasses the totality of an organism’s relation to its environment, but also serves as the focus for conservation, restoration and enhancement of biological populations and communities. Since early general ecological definitions, e.g., “the place where an organism lives” (Odum 1963), the concept has acquired a multitude of meanings, often specific to certain spatial scales (e.g., Johnson 1980), and by additional modifiers that often lack a specific meaning (e.g., critical habitat, essential habitat, or habitat type). A common theme associated with many definitions is that habitat relates an organism to aspects of the surrounding physical, chemical, and biological environment (Milner et al. 1985), and efforts of ecologists now focus on determining which of the innumerable aspects influence the fitness parameters of that organism (Hall et al. 1997). Different habitat characteristics may result in quite similar or different abundances of a species and those characteristics are influenced by a variety of terrestrial and aquatic characteristics. It is becoming ever more evident that “the place where an organism lives” (Odum 1963) provides a suitable environment for the organism, but causes for the realized environment might originate very far away.

Stream systems are inherently linked to the terrestrial landscape (Hynes 1975; Vannote et al.1980). There are many different interpretations of what actually constitutes a landscape, often related to a specific objective or management action, or to the study organism of interest. For example, what constitutes a landscape for a grasshopper is quite different than the landscape of a migratory bird. Definitions of "landscape" invariably include a heterogeneous land area that is hierarchically structured. I will consider a landscape an area that is spatially heterogeneous (with respect to habitat factors) with the watershed as the largest spatial extent, intended to be relative to an organism's perception and environmental scaling (Weins 1976). River ecology incorporates spatially nested factors (e.g., climate, geology) that influence abiotic and biotic structure at intermediate and fine spatial scales (Frissell et al. 1986). For stream management to be most effective, ecological studies and perspectives should be integrated across a broad range of spatial scales that include influences of the terrestrial environment.

Increasing stressors on aquatic systems coupled with habitat alteration have resulted in numerous instream and site-level management strategies, whereas, larger-scale processes that may contribute to habitat loss remain poorly addressed (Imhof et al. 1996). Landscape characteristics may act as confounding influences on local habitat conditions (Allan et al. 1997). Non-point source pollution from land-use alteration has resulted in cumulative effects on stream ecosystems (McDonnell and Pickett 1990; Richards et al. 1996). The importance of riparian vegetation in reducing non-source pollutants and determining abiotic and biotic characteristics of streams is well documented (*see* Castelle et al. 1994 for a review). However, management of riparian lands with little or no regard for coarser-scale landscape (e.g., watershed) influences may limit the effectiveness of intended management strategies. Increasingly, ecologists emphasize a landscape perspective intended to make stream management strategies more effective.

Conflicting conclusions regarding the relative importance of natural-occurring landscape factors (e.g., geology, soils) versus anthropogenic landscape attributes (e.g., secondary growth forests, urban areas, and pastures dominated by cool-season grasses) often occur because of spatial autocorrelation between land-cover classes and geographic regions. Relations between land-use attributes and stream biota could be explained by natural spatial factors that happen to covary with land cover (Allan 2004; King et al. 2005). Natural-occurring landscape factors influence the suitability of locations for agriculture and urban development (anthropogenic landscape attributes). Whenever anthropogenic land use is assessed without regard to natural environmental gradients, the influence attributed to anthropogenic land use can be overestimated if these land-use attributes covary (Allan 2004). Therefore, landscape studies should determine relations between biota and natural-occurring abiotic landscape factors a priori and study land-use effects within a framework that addressing significant natural factors.

There is growing impetus to elucidate the impacts of anthropogenic activities on fish populations. Anthropogenic alteration of the landscape often adversely affects stream ecosystems via numerous pathways and at multiple spatial scales. Habitat changes caused by economic development and water appropriations of freshwater resources have resulted in the decline of many fish species (Postel et al. 1996; Tilman et al. 2001). It is difficult to identify the specific attribute(s) of "habitat" that becomes degraded resulting in the decline of fish populations. Fishes are generally capable of being placid with respect to how they use habitat (i.e., under adverse conditions or the presence of predators, fish may use alternative habitats). However, to better manage stream fishes, we need to identify those coarse scale natural-occurring landscape features that interact with anthropogenic landscape attributes, and result in the decline in abundances rather than just differences in habitat use.

Few landscape studies have addressed the effects of anthropogenic land-use attributes within the framework of natural-occurring environmental features that influence a particular species of interest. Research lacking in this area is reflected in our current management strategies that fail to consider the natural-occurring conditions in a watershed and the influence these conditions have on the initial "potential" of the fishery in our streams. For example, smallmouth bass *Micropterus dolomieu* in streams located in the Ozark border region of Missouri have declined over previous decades, presumably as a result of anthropogenic changes in land use (Sowa and Rabeni 1995). Because abundances of fish were higher in previous decades, we might assume natural-occurring landscape conditions are adequate and anthropogenic landscape factors are related to the decline. Alternatively, smallmouth bass abundances in other streams located in watersheds altered by anthropogenic land use may be quite low because the natural-occurring landscape conditions are marginal to support higher densities. If these streams had not been sampled previously, managers would have no way to know if these streams would likely benefit from watershed restoration (i.e., managers would not be aware of the potential fishery that might exist in this locality). A better approach would be to first identify the natural conditions that relate to particular abundances and then determine how these abundances might change under different anthropogenic landscape conditions (e.g, urban landscapes). Before we can knowledgably address habitat restoration measures, we must understand how an organism is associated with its physical environment under a variety of natural (e.g., soils, geology) and altered (e.g., pasture, urban) landscape conditions. The overarching goal of this study was to investigate the effects natural-occurring and anthropogenic landscape and inchannel factors have on the distribution and abundance of riverine smallmouth bass in Missouri.

Smallmouth bass is an excellent study organism for this research because it is an ecologically important part (i.e., top-level predator) of streams in the east-central United States, including Missouri. Abundances of smallmouth bass in Missouri are thought to be declining as a result of habitat alterations (Pflieger 1997). Habitat alterations, including changes to physical habitat, temperature, and flow, are likely a result of substantial land-use changes that have occurred in Missouri over the past 100+ years. Researchers have indicated the influence channel morphology (e.g., percent of pool habitat) appears to have on the abundance of smallmouth bass (Sowa and Rabeni 1995; Dauwalter et al. 2007); however, no relation has been established between smallmouth bass and natural-occurring and anthropogenic landscape features. Considerable research has addressed the importance of inchannel habitat features (*see* references herein) to smallmouth bass but these relations have never considered within separated natural and anthropogenic coarse-scale constraints.

Land-use changes in Missouri over the past 100+ years have been substantial. Historically, Missouri was a mixture of prairie (approximately one-third of the state), savanna, woodland and forest (Nigh and Schroeder 2002). Most of northern and western Missouri was upland and wet prairie with woodlands (i.e., oak forests) occurring on steeper slopes. Prior to Euro-American settlement, woodlands began encroaching these areas due to the changing climate (e.g., wetter and cooler) and reductions in burning practices. Historically, much of the Ozark region was old-growth forest (predominately oak, but pine was co-dominant) with lesser tracks of savanna and prairie. Today, Missouri has largely been converted to secondary growth forest, cropland, pasture and urban areas, with small remnant tracks of native vegetation remaining (Nigh and Schroeder 2002). Native vegetation in prairie regions was altered to crops, cool-season grasses for pastures, urban areas, or secondary growth forest. Much of the current land cover relates to natural conditions (e.g., soils, geology) because the areas with fertile soils and appropriate topography were largely converted for farming and crops whereas pastures dominated regions with good soils, but steeper terrain (e.g., southwest Missouri). The eastern Ozark region remains the most forested, but reflects historic logging and fire-suppression practices because these areas are now secondary growth forests that are much denser than historically. Urban and agriculture in this portion of the Ozarks still exists, but is generally limited to alluvial bottoms and flatter uplands. The combination of land-use attributes currently existing on the landscape within Missouri and the diverse natural-occurring landscape features make Missouri an excellent canvas to study the interactive effects landscape and inchannel features have on the distribution and abundance of smallmouth bass at multiple spatial scales.

Objectives

In subsequent sections of this dissertation, I address the following objectives:

1. Determine which natural-occurring environmental factors at landscape and in-channel scales best predict the distribution and relative abundance of riverine smallmouth bass in

Missouri, (published and appropriately cited as: Brewer, S.K., C.F. Rabeni, S.P. Sowa, and G. Annis. 2007. Natural landscape and stream segment attributes influencing the distribution and relative abundance of riverine smallmouth bass in Missouri. North American Journal of Fisheries Management 27: 326-341)

2. Determine how smallmouth bass densities relate to natural and human-induced landscape variation and if land-use attributes or the interaction between land use and natural factors influence habitat use at smaller spatial scales,

3. Determine how densities (young of year, age 1, and age 2^{+}), length distributions (young of year), and channel unit habitat use by riverine smallmouth bass are influenced by spring flow and temperature in highly altered landscapes,

4. Determine microhabitat use by young-of-year smallmouth bass under different landscape constraints.

Each objective of this study builds on the previous objective (Figure 1). The first objective identifies the natural landscape and inchannel factors that influence the distribution and abundance of smallmouth bass. The significant factors identified in this objective were used to identify the potential (i.e., what the expected abundance of fish would be based on natural conditions alone) of a smallmouth bass fishery in every stream reach in Missouri (regardless of whether they have been sampled previously). My second objective builds on the first by identifying how anthropogenic land use in respective watersheds relate to changes in smallmouth densities, and the relative influence land use has on densities depending on the significant natural features within respective watersheds. My third objective identifies differences in densities of different age classes in relation to the significant natural landscape feature, spring flow. Additionally, I determine if spring flow influences the inchannel distribution (e.g., channel unit) of age classes and how their distributions relate to temperature at very fine spatial scales. My final chapter examines how young-of-year smallmouth bass use microhabitats under different anthropogenic land uses (i.e., pasture and forest) while continuing to hold significant natural-occurring features relatively constant (as with other objectives).

The management implications of this study will certainly vary by locality. Information specific to Missouri streams will provide tools for prioritizing conservation and management efforts across the landscape. Objective one provides the potential of thousands of stream kilometers to support a smallmouth bass fishery. Most of these stream segments have never been sampled, but this research will provide a starting point for appropriate management at un-sampled locations. Additionally, managers can further investigate why some stream reaches have fisheries significantly below their potential, whereas, others may be above their "potential" due to factors that have not been considered in this research. I expect the relation between these landscape and inchannel factors to differ outside of Missouri, but it seems likely that the underlying cause of the importance (e.g., runoff associated with soil groups with low infiltration rates) to remain unchanged once these causes have been identified. The second objective provides insight to likely changes that occur with particular anthropogenic land-use attributes within

Missouri watersheds and identifies watershed conditions that might benefit most from restoration strategies. The important implications drawn from objective three (spring flow associations) will likely be important to the management of smallmouth bass in the southern portion of their range and farther north as the effects of global warming intensify. My final objective will be important to the management of year-class strength because it provides information on microhabitat use under different anthropogenic land uses. This information is specific to Missouri streams, but comparisons are made to the findings of other studies to identify common patterns that may exist in other localities. Additional implications of this research are discussed in subsequent chapters relative to specific results.

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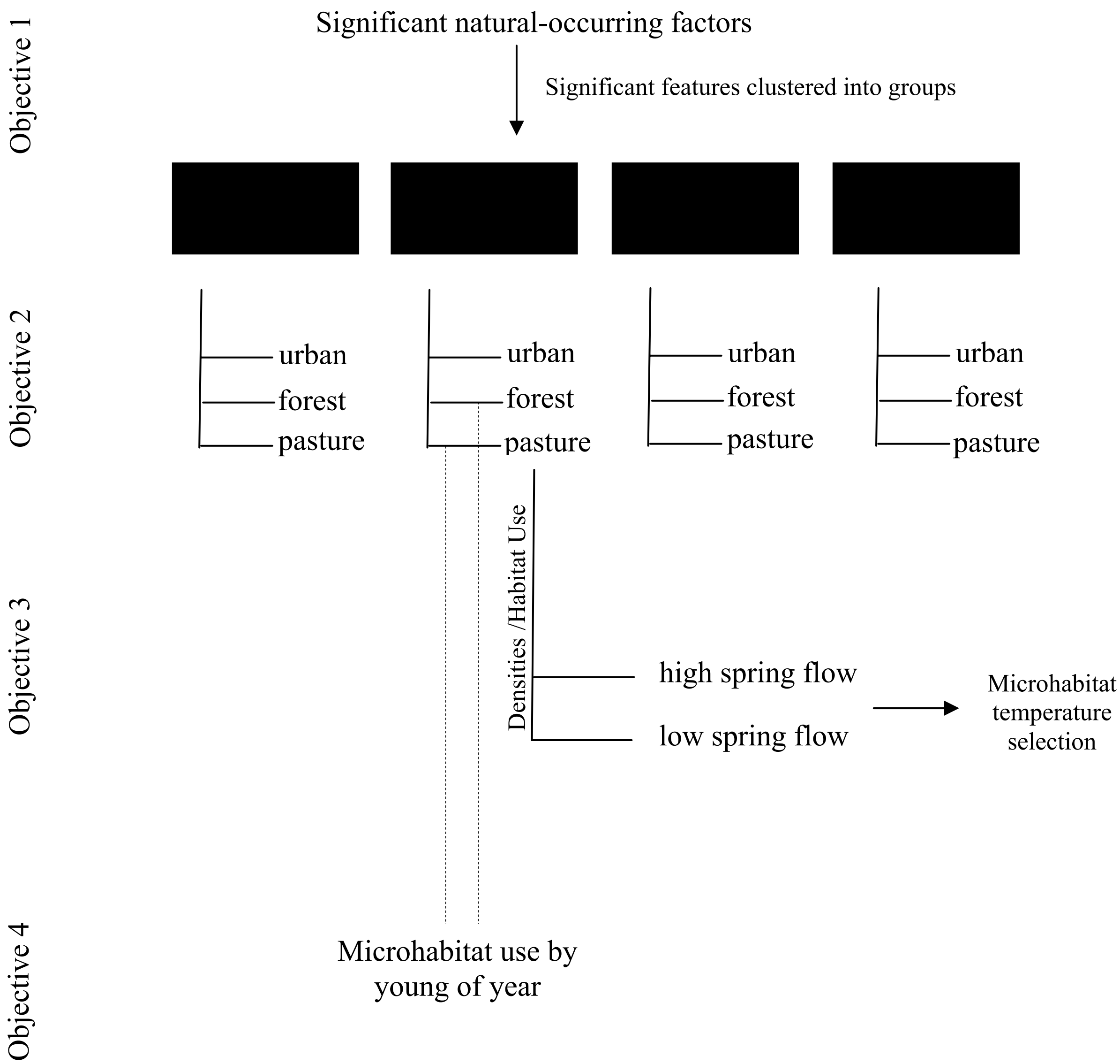

FIGURE 1.- Schematic showing the connection between objectives addressed in this study

Chapter 2

Natural-occurring landscape and in-channel factors affecting the distribution and relative abundance of riverine smallmouth bass in Missouri

Abstract.- Appropriate efforts for protecting and restoring fish populations cannot be achieved until the multi-scale factors responsible for the relative quality of a fishery are known. I spatially linked statewide historical fish collections to environmental features in a geographic information framework as a basis for modeling the importance of landscape and in-channel features related to a stream reach's potential to support a smallmouth bass population. Decision tree analyses were used to develop probability-based models to predict statewide presence and within-range relative abundances. Identifying the geographic range of smallmouth bass throughout Missouri and the probability of occurrence within that range was accomplished using a few broad landscape variables: the percentage of coarse-textured soils in the watershed, watershed relief, and the percentage of hydrologic soil group D (HSGD) in the watershed. The within-range relative abundance model included both landscape and in-channel variables. As with the statewide probability of occurrence model, soil permeability (HSGD) was particularly significant. The predicted relative abundance of smallmouth bass in stream segments containing low percentages of HSGD was further influenced by channel gradient, stream size, spring flow volume, and local slope. I assessed model accuracy using an independent data set, and good concordance was shown. A conceptual framework involving natural-occurring factors affecting smallmouth bass potential is

presented as a comparative model for assessing transferability and studying potential land use and biotic effects.

The condition of many Missouri streams is perceived by many anglers and biologists to be deteriorating and resulting in the widespread decline of sportfish populations, especially smallmouth bass *Micropterus dolomieu* (Pflieger 1997). Presently, fisheries managers have few tools to help monitor status and trends in smallmouth bass populations throughout their range, or to predict likely population changes due to habitat degradation or habitat restoration. Smallmouth bass are a valuable recreational and ecological asset in many Missouri streams. Existing sampling data for smallmouth bass cover a small fraction (< 1%) of the total stream kilometers in which this species likely occurs. Resource managers need spatially comprehensive information in order to prioritize conservation efforts beyond sampled locations. Considering there are over 175,000 kilometers of stream within Missouri, the only realistic way to generate such information is through predictive modeling.

Identifying habitat potential at multiple spatial scales would provide a basis for habitat management important for the persistence of sportfish populations. Whereas the importance of scale to fish-habitat relations is well recognized, the large-scale processes that account for many habitat conditions remain poorly understood or addressed (Allan et al. 1997). At the landscape scale, ultimate (e.g., geology) and intermediate (e.g., soils, land use) factors may limit fish distributions and abundances. However, within watersheds with appropriate landscape-level factors to support a viable fishery, reach-scale analysis may pinpoint habitat factors that may be improved upon through local management practices. Identifying landscape constraints would provide a basis for sound management expectations on a regional basis, a system for efficient prioritization of restoration or enhancement efforts, and the ability to plan specific conservation measures that are most appropriate to a particular location.

Efforts to understand the links between landscape and local factors and their influence on the distribution and abundance of fishes have become increasingly important and represent a central avenue of research (Jackson et al. 2001). Landscape models contribute to our understanding of fish-habitat relations at large spatial scales (Olden and Jackson 2002), but also provide a framework for studying habitat relations at finer scales. Landscape factors may act as confounding or constraining influences on the structure of aquatic communities (Allan et al. 1997), and directly and indirectly influence local habitat conditions (Schlosser 1995). By understanding the constraints imposed by landscape factors, we can then focus on local habitat conditions and the relative importance of these conditions to the fitness (e.g., growth, survival, and reproduction) of populations.

Appropriate efforts for protecting and restoring fish populations cannot be achieved until the multi-scale factors responsible for the relative quality of a fishery are known thereby providing the mechanistic understanding necessary to sustain or improve fish populations in a variety of geographic settings. Successful management of this species throughout its range is ultimately a three-step process. First we must understand and document those naturally occurring environmental factors associated with distribution and abundance. Secondly we need a better understanding of how anthropogenic activities interact with the natural environmental features to impact fish populations, and finally to make our conclusions more general by developing a mechanistic understanding of processes involved. The objective of this chapter concentrates on the critical first step, to determine which natural factors at landscape and in-channel scales contribute to the distribution and relative abundance of riverine smallmouth bass in Missouri. My approach was to spatially link historical fish collections (>2500) to environmental features in a geographical information framework as a basis for modeling the importance of landscape and in-channel features related to a stream reach's potential to support a smallmouth bass population.

Study Area

Community fish samples (*n* = 2664) were obtained from four biogeographic regions in Missouri: Central Dissected Till Plains, Osage Plains, Ozark Highlands, and the Mississippi Alluvial Basin (Nigh and Schroeder 2002). The Central Dissected Till Plains covers northern Missouri and is characterized by glaciated plains that become increasingly dissected as they near major drainages, especially the Missouri and Mississippi Rivers. The Osage Plains region occupies a large portion of west-central Missouri and is characterized by smooth plains with numerous bedrock outcroppings. Streams in the Central Dissected Till Plains and Osage Plains regions generally carry high sediment loads during periods of runoff, are low gradient, and highly meandering; however, numerous stretches of larger streams have been channelized. The Ozark Highlands region includes most of southern Missouri and is characterized by extensive geologic erosion which results in a highly dissected plateau. Carbonate bedrock and karst features are evident throughout the region. Many of the streams within the region are spring-fed and carry little suspended sediment except during periods of high runoff. The

Mississippi Alluvial Basin region includes only the southeastern tip of Missouri. This region was historically swampland but was drained and converted primarily to cropland. Streams in this region are characterized by low gradient and carry high suspended sediment loads; many of these streams have been channelized and leveed or serve as drainage ditches.

Methods

I created models to predict both the distribution and the relative abundance of smallmouth bass throughout Missouri. The model predicting the probability of smallmouth bass presence was created using samples distributed throughout the state. Once the geographic range of smallmouth bass in the state was defined, a subset of samples falling within this range was used to model factors associated with relative abundance. Both models were developed empirically using a suite of landscape (e.g., geology, soils, landform) and in-channel (e.g., gradient, flow) predictor variables that were generated, using GIS, for every stream segment within a 1:100,000 digital stream network of Missouri. Landscape variables were quantified for the entire watershed. Many of the landscape variables were also quantified for the immediate drainage of each stream segment (segmentshed). In-channel variables were quantified for specific stream segments. The resulting models were used to query the digital stream network and generate spatially-explicit maps depicting spatial patterns of smallmouth bass presence and relative abundance across Missouri. Model accuracy was assessed with independent data.

Fish Sampling Data.- Fish community data were obtained from the Missouri Department of Conservation. I used community fish samples for which relative abundance data were available (*n* = 2664). All original data (*n* = 2664) were used to model the probability of fish presence, whereas only a subset (*n* = 1994) was used to develop the relative abundance model. Using historical data limited the approach taken in the analysis. For example, sampling effort and gear type varied by collection; I could not separate out individual methodologies due to numerous gear types being used during a sampling event and only one sampling effort being recorded for that specific event. Thus, relative abundance of smallmouth bass was calculated to standardize the data. Relative abundance data were plotted to identify potential outliers. Six obvious outliers were identified and deleted. These observations had grossly inflated relative abundance values (>20%) for smallmouth bass, a top predator, that were inconsistent with ecological theory (e.g., Lindeman 1942). Relative abundances for the remaining samples were capped at 10% because there was a normal distribution within this range; eleven observations that were > 10% but < 20% were capped at 10%. All other data ranged between 0% and 10%.

Predictor Variables.- Riverine fishes are influenced by numerous landscape and in-channel factors and processes operating at multiple spatial and temporal scales. Of particular interest are those landscape factors operating within the overall watershed and immediate drainage of a particular stream segment and the local in-channel factors associated with that specific stream segment (Table 1).

Landscape Variables.- Principle landscape factors that interact to determine local instream habitat are geology, soils, landform, and land use (Hynes 1975). To account for these potential landscape influences I used a 1:100,000 digital stream network created by the Missouri Resource Assessment Partnership (Sowa et al. 2005). This coverage contains over 106,000 individual stream segments, each attributed with numerous landscape and in-channel habitat variables. Most landscape variables were quantified for the watershed and the immediate drainage of each stream segment, or segmentshed (Table 1). Percentages for five general lithologic classes were based on the 1:500,000 statewide digital geology data for Missouri (MDNR 1992). Percentages for four soil-surface texture and Hydrologic Soil Group classes were derived from data contained in the 1:250,000 STATSGO coverage for Missouri (USDA-NRCS 1994). The original sixteen soil-texture classes were condensed into four general classes based on dominant soil textures and similar soil characteristics. This was done to reduce the overall number of predictor variables and to more evenly distribute the number of predictor variables falling within each major variable class. Hydrologic Soil Group percentages (A, B, C, D) were used as a means of estimating runoff potential. Landform was characterized in two ways based on data generated from a 30-m digital elevation model (DEM) (USGS 2000). Maximum and minimum elevations (m) were calculated for each watershed. Minimum values were subtracted from maximum values to generate overall watershed relief. Mean slope (%) of all 30-m grid cells was also calculated for the immediate drainage of each stream segment.

Measures of spring flow volume per unit area and spring density were also included as predictor variables. These variables were computed for the watershed in the statewide digital stream network. A GIS coverage, developed by the Missouri Department of Natural Resources, that contains locations of 4,369 springs was used to generate these variables. Within this coverage there are 588 springs with known discharges. Discharges were added to an additional 54 springs using information from Vineyard and Feder (1982). Dicharges for the remaining 3,727 springs, which are primarily smaller springs, were estimated based on a computed median discharge value. I used data for 642 springs with known discharges to calculate this median discharge. First, I removed those springs having discharges greater than 2 standard deviations above the mean (> 1.56 m^3/s). I then computed the median value for the remaining springs (0.008 m^3/s), which was applied to all springs lacking discharge data. Spring density was calculated by dividing the total number of springs within the watershed by watershed area. Spring flow volume per unit area was calculated by dividing the sum of spring discharges within the watershed by the corresponding area. The resulting values were multiplied by 100,000 because the resulting numbers were so small they posed a problem for data management and analyses.

Local In-channel Variables.- Streams encompass an array of physical features and processes that tend to change in a longitudinal continuum (Vannote et al. 1980). Measures of drainage area or stream size have long been found to be an important predictor of the distribution and abundance of riverine biota (Moyle and Cech 1988). I used link magnitude (Shreve 1966) as my measure of stream size because it related more precisely to drainage area (Hanson 2001) than other commonly used measures (i.e., Strahler ordering system). Link magnitude was calculated for each stream segment using ArcView. Size discrepancy, a general measure of the position of a given stream segment within the broader drainage network, was also included and describes the difference in size between the segment of interest and the immediate downstream segment. A more precise measure of size discrepancy, D link, was also used as a predictor variable. This variable represents the link magnitude of the immediate downstream segment.

Two different binary variables were used to characterize the flow conditions within each stream segment. Specifically, each segment was classified as intermittent or perennial, which generally characterizes the base-flow conditions of each segment. Each segment was further classified as losing or not losing based on data from the Missouri Department of Natural Resources and the US Forest Service. As a result of the karst landscape of the Ozarks a number of larger streams or rivers in this region lose a substantial portion, or sometimes all, of their flow to the underlying groundwater system (Vineyard and Feder 1979). These so called "losing streams" may be completely dry or contain a series of isolated pools under normal baseflow conditions.

Stream gradient is associated with numerous abiotic and biotic factors within streams (Hack 1957; Knighton 1998; Nino 2002). Three measures of stream gradient were calculated for each stream segment using a 30-m DEM with ArcView. Segment gradient represents the local gradient of each stream segment as measured between the upstream and downstream confluences that mark the boundary of each segment. Channel gradient represents channel gradient measured over a much longer stretch of stream in order to provide a broader "gradient context" for each stream segment. Collectively, these two measures of stream gradient allow identification of situations in which the stream segment of interest has a relatively high gradient, yet is situated within a series of segments that have a relatively low gradient, or vice versa. To calculate each of these measures of stream gradient, the minimum stream elevation was subtracted from the maximum elevation, divided by the corresponding stream length, and multiplied by 1,000. The third measure of stream gradient, biogeographic gradient, is a relativized measure that categorizes each stream segment as being low, intermediate, or high gradient relative to stream size and biogeographic region. Biogeographic gradient categories account for, and largely remove, the significant association between gradient and drainage area in order to better identify local scale variations in substrate conditions, water velocities, and the availability of habitat types.

There is currently a lack of a detailed map of stream temperatures for Missouri. However, a coldwater streams datalayer, produced by the Missouri Department of Conservation was available. This datalayer is certainly not comprehensive and largely corresponds to those stream segments supporting naturalized trout populations or put and take trout fisheries. This datalayer was used to produce a binary variable that classified stream segments in the 1:100,000 digital stream network as either cold or warm.

Model Development.- Decision tree analyses were used to develop probability-based models to predict presence and relative abundance of smallmouth bass across Missouri. Classification and regression trees, such as those generated by decision tree analyses, are robust to the many data issues that confound traditional parametric models (Urban 2002) and are able to capture and model complex ecological data (Olden and Jackson 2002).

Additionally, classification trees may be used in conjunction with GIS to generate maps using coding provided by predictive models.

Answer Tree 3.0, an extension of SPSS statistical software package, was used to construct my decision tree models. This modeling package offers a choice of four algorithms (C&RT, QUEST, CHAID, and Exhaustive CHAID) that perform the same basic function, to examine predictor variables and find the one that gives the best classification of the target variable (i.e., presence or relative abundance) by recursively splitting the data into subgroups until the analysis is completed based on pre-defined stopping criteria (Answer Tree 3.0 User's Guide 2001). The Exhaustive CHAID algorithm was used because it does a more thorough job of examining all possible splits for each predictor variable and because it can produce more than two categories at any level in the tree (unlike C&RT and QUEST). Exhaustive CHAID is a modification of CHAID that was developed to improve the splitting capability by computing an adjusted-P value for the predictor that provides the strongest association with the target variable. In that manner, exhaustive CHAID finds the best split for each predictor and then subsequent splits within the tree by comparing the adjusted-P values.

The size of the tree (i.e., number of levels) Answer Tree 3.0 allows is determined a priori by the user. The chosen stopping criteria reduces the probability of overfitting the model, which is problematic when large datasets containing a large number of variables are used (Answer Tree User's Guide 2000). The maximum number of levels allowed in a model was set at ten; however, neither of the models reached this level. The minimum number of collections allowed in each node type (parent, child, and terminal) is defined by the user. The minimum number of collections allowed in a parent node (one that is further subdivided and links to one or more child nodes) was set equal to 10% of the total collections for that model. The minimum number of collections allowed in a child node (one that has a preceding level) was set to one. Terminal nodes are child nodes that have no further subdivision.

Growing criteria are based primarily on a selected alpha level. The alpha level was set at 0.10, and I used a Bonferoni adjustment to account for the increased likelihood of committing a type-1 error with multiple predictor variables. Whereas 0.05 is generally the standard alpha level chosen for statistical tests, a more liberal level was chosen for model building as 0.05 often results in highly restrictive models. Since my primary interest was to identify factors that relate to smallmouth bass distribution and abundance, use of a liberal cutoff was justified.

A statewide probability of occurrence model was created by inputting all landscape, segmentshed, and in-channel variables into Answer Tree 3.0. After this model was completed, a GIS map depicting the predicted presence of smallmouth bass was constructed using ArcView by querying the attribute table of the 1:100,000 digital stream network with the set of if/then statements that were prescribed by the model. Any 8-digit hydrologic unit that contained stream segments meeting the conditions set forth by presence model was used to define the potential geographic range of smallmouth bass. Collections that fell within this potential range were used as the input dataset for generating the relative abundance model. This model used the same predictor variables included in the probability of occurrence model, except I excluded the biogeographic gradient variable. A spatially-explicit GIS map of predicted smallmouth bass relative abundance was created using the same methods described for the probability of occurrence model.

Model Accuracy.- The accuracy of my models predicting smallmouth bass probability of occurrence and relative abundance was assessed using an independent data set obtained from the Missouri Department of Conservation’s Missouri Resource Assessment and Monitoring (RAM) Program. Standardized surveys conducted by the RAM Program use electrofishing and seining as collection methods. The independent data were collected in 2000-2003 and included 149 collections from 116 stream segments. Each of these 149 collections was spatially referenced to the 1:100,000 digital stream network and placed into one of six probability of occurrence categories and one of seven relative abundance categories from my models. This was done by working backwards from each child node (6 child nodes for presence model and 7 for relative abundance model) to include all the habitat features that contributed to the resulting probability of occurrence or relative abundance displayed for each child node. For example, if the percent of limestone geology in the watershed greater than 60 and gradient less than 6.78 resulted in splits prior to a child node, that category would include samples from stream segments with greater than 60% limestone geology and gradients less than 6.78 for the resulting probability of occurrence or predicted relative abundance displayed by the resulting child node. The subset of independent collection records falling within each of these categories was used to calculate an observed probability of presence and mean relative abundance. These values were compared to the probability of presence and relative abundance as predicted by my models.

Results

Statewide probability of occurrence model

The statewide model predicting the probability of smallmouth bass occurrence was dominated by landscape variables examined at the watershed level. (Figure 1). Particularly important was the percentage of coarse-textured soils. Stream segments in watersheds lacking coarse-textured soils had the lowest probability of possessing smallmouth bass, with a maximum probability of only 14% when watershed relief was high. Smallmouth bass are predicted to have limited success in these segments even when watershed relief is considered. Segments in watersheds with low to moderately rocky soils (1-57%) could achieve almost a 50% probability if Hydrologic Soil Group D ([HSGD] soils with low permeability and high runoff potential) was absent. Segments in watersheds with high amounts of rocky soils (58-92%) had the highest percentage of samples reflecting a presence response (46% and 60%, respectively). Segments in watersheds with >92% coarse-textured soils had a high probability of occurrence (45%); however, it was less than in the two categories previously described. The statewide model classified 75% (SE = 0.008) of the samples (n = 2664) correctly. Of the samples misclassified (n = 671), the majority (69%) predicted smallmouth bass to be absent when they were actually present (omission error).

Geographic range relative abundance model

The relative abundance model included watershed and in-channel variables (Figure 2). As with the statewide presence model, soil permeability (HSGD) was particularly significant. The mean relative abundance of smallmouth bass was predicted to be low (0.20) in segments with watersheds containing > 7% of HSGD. Segments in watersheds containing low amounts of HSGD (≤ 7%) were further divided on the basis of channel gradient. In segments with relatively high gradients (> 2.10 m/km), relative abundance can be as high as 0.82 if the stream is large (link magnitude > 7), whereas relative abundances are predicted to be very low if the stream is small (link magnitude < 7). Lower gradient habitats were further divided on the basis of spring flow volume and local slope. The highest relative abundance (1.73) occurred in habitats with high spring flow and high local slope. However, even in these habitats, there was a 40% chance that relative abundance would be zero.

Spearman correlation coefficients were significant ($P \leq 0.001$) between relative abundance and all predictor variables included in the geographic range relative abundance model except for channel gradient ($P = 0.05$). Because I had a large number samples ($n = 1994$), r values as low as (+/-) 0.07 were significant ($P \leq 0.001$) so the coefficient (r) values are reported for each variable rather than the significance level. Correlations between habitat variables included in my model and smallmouth bass relative abundance were (r value in parentheses): spring flow volume (0.42), slope (0.35), link magnitude (0.31), HSGD (-0.25), and channel gradient (-0.04).

Model Validation

My model predicting the probability of smallmouth bass occurrence statewide performed well when compared to the validation data (Figure 3). The predictive model and validation data followed the same trend of increasing or decreasing occurrence percentages for each of the six model-defined categories (Figure 4). The predicted and observed probabilities were off ≤ 3% in all but two categories. The remaining two categories where I predicted a 22% and 45% probability of occurrence underestimated the occurrence percentage by 11% and 25%, respectively.

The geographic range model predicting relative abundance also predicted well in most categories (Figure 5). The predictive model and validation data follow the same increase in relative abundance for six of the seven defined categories (Figure 4). The predictive model overestimated relative abundance in all but two categories. Predicted and observed relative abundances were off ≤ 0.35 in all but two categories. The remaining two categories where I predicted the highest relative abundances (1.04 and 1.73) were overestimated by 0.67 and 0.54, respectively.

Discussion

These results delineate the natural environmental constraints affecting the distribution and relative abundance of smallmouth bass throughout Missouri. This framework provides a holistic approach to view management options and a more complete understanding of the hierarchical structure of natural-occurring factors influencing smallmouth bass populations. The importance of these analyses can be illustrated by the different combinations of conditions that exist to allow smallmouth bass to persist (i.e., presence) and thrive (i.e., higher relative abundances). Often, authors pinpoint a few specific habitat conditions that are used by a species, but it may be more realistic to identify different sets of conditions that allow for successful populations. Different large-scale factors may produce the same local effects that translate into appropriate habitat conditions for a species. Realizing what these conditions are will provide an important first step in making management strategies more effective.

Understanding the biological potential of an individual stream segment is a critical first step to effective fisheries resource management because it provides the foundation for realistic management expectations (Frissell et al. 1986). The maps and associated GIS coverages I have generated provide fisheries managers in Missouri with spatially-explicit information on smallmouth bass fishery potential for every stream reach in the state. Such data can be used to establish harvest regulations specifically suited to the fishery potential of a given stream. They can also be used to educate private landowners, interest groups, and fisherman about the fishery potential of a particular stream or more generally explain the geographic patterns in fishery potential across the state. Most importantly, these maps and data can be used to identify those stream segments that are significantly below their potential. Once identified, managers can use the ecological understanding generated from this and previous studies to further identify those situations and management activities that are most likely to have the greatest benefit for improving the smallmouth bass fishery and overall stream health.

Statewide probability of occurrence model

Identifying the range of smallmouth bass throughout Missouri can be accomplished using a few broad habitat variables. Spatially, those areas near the Ozark border region delineate the northern and western range of smallmouth bass. Other studies have identified the role that large-scale factors play in determining fish-distribution patterns (see Argent et al. 2003 and references therein).

At the catchment level, geology is expected to play a major role in the distribution of fishes (Frissell et al. 1986). Geologic strata directly influence the characteristics of channel-bed material, discharge regime, and chemical composition of the water (Cannan and Armitage 1999). Whereas geologic variables were not significant in the distribution model, rocky soils were very important and significantly ($P < 0.001$) positively correlated with sandstone and igneous conditions (Spearman rank correlation: $r = 0.43$ and 0.32, respectively). Coarse-textured substrates may be created by several different geologic strata manifesting their importance through soil characteristics. Additionally, the resolution (i.e., 1:150,000 for geology and 1:250,000 for soils) of data used in model development likely had some effect on the relative importance of soils versus geology.

Riverine smallmouth bass are often associated with habitats that contain rocky substrates (Hubert 1981; Paragamian 1981; Pflieger 1997). The availability of coarse-textured substrates may facilitate growth and survival. Coarse-textured substrates create areas of reduced current (Hynes 1970) which reduce the energetic cost associated with maintaining position within a riverine system. The abundance of prey sources within rocky substrates may also influence use of these habitats. Smallmouth bass spent 90% of their foraging time over coarse-textured substrates in the Flat River, Michigan (Rankin

1986). Juvenile smallmouth bass exhibit higher feeding rates in habitats containing cobble than habitats dominated by vegetation and are less vulnerable to predation (Olsen et al. 2003). Paragamian (1981) reported a curvilinear response between the density of smallmouth bass and coarse-textured substrates in Iowa streams. Lyons (1991) found that rocky substrate was an important variable in predicting smallmouth bass presence in Wisconsin streams where catch-per-effort reached a maximum value in habitats containing approximately 70% rocky substrate. This is similar to the relation I found between the probability of occurrence and the percentage of rocky soils. The apparent decline in smallmouth bass occurrence in habitats containing > 92% rocky soils has several possible explanations. First, it is possible that extremely rocky habitats are not suitable for the invertebrate prey base important to smallmouth bass. Some invertebrates may require a certain amount of finer substrates to persist in rocky habitats. A second explanation may be due to reproductive fitness. The nest success of smallmouth bass was shown to decline in a Lake Erie population as substrate coarseness increased (Goff 1986). The decline in nest success was thought to be due to the accumulation of silt on nests located in extremely coarse substrates and the ineffectiveness of male fish fanning nests within these habitats. A third explanation for a decline in occurrence in extremely rocky habitats relates to sampling efficiencies. The sampling gears used by Lyons (1991) and this study are likely less effective in extremely rocky habitats. In fact, the greatest discrepancy between the probability of occurrence predicted by my model and the probability of occurrence observed using the validation data occurred in habitats with > 92% coarse-textured soils. I predicted a 45% probability of occurrence where a 70% probability of occurrence was observed; if the validation data holds true, the highest probability of occurrence would actually be in stream segments with the greatest amount of coarse-textured soils.

Stream segments in watersheds containing 1-57% rocky soils are further constrained by the presence of HSGD. The probability of smallmouth bass occurrence more than doubles when HSGD is absent from the watershed. Hydrologic soil group D represents soils with slow infiltration rates and therefore high runoff potential. The distribution of HSGD throughout Missouri borders the distribution of smallmouth bass, primarily in the northern and western Ozark border region. Since the 1940's smallmouth bass have been perceived to be declining in this region (Pflieger 1997). Increasing summer water temperatures and relative pool area resulting from land-use practices in the region were likely causes for the decline of smallmouth bass in this region (Sowa and Rabeni 1995). The changes in channel morphology due to land-use practices and high runoff potential associated with HSGD may be responsible for the decreased success of smallmouth bass in this region. Sedimentation is often suggested as a factor causing declines in fish populations due to urban and agricultural land-use practices (Lenat 1984; Scott et al. 1986). Mason et al. (1991) suggested that turbidity associated with chemical runoff due to land-use practices may be detrimental to smallmouth bass populations. However, the presence of a particular geologic or soil condition is likely important in determining the ecological impacts resulting from land-use practices.

Another condition resulting in an extremely low probability of occurrence is the absence of rocky soils; the probability of occurrence is increased minimally in streams with higher watershed relief. The relative success of fish occurring in habitats lacking rocky soils is limited; however, the increase in relief may produce velocities that help keep the substrate free from siltation to a degree that allows persistence in these areas.

Geographic range relative abundance model

The relative abundance model illustrates a hierarchical pattern with watershed factors initially delineating relative abundances and local in-channel factors increasing or decreasing relative abundances within these larger watershed constraints. The importance of soil permeability (HSGD) emerges as the primary split and follows reasonably from the presence-absence model (i.e., relative abundances of smallmouth bass are expected to be low with increasing percentages of this watershed characteristic). In watersheds containing low percentages of HSGD, channel gradient, link magnitude, spring flow volume, and local slope are contributing factors to higher or lower relative abundances. However, a strong relationship (Spearman correlation: $r = -0.72$, $P < 0.001$) was evident between link magnitude and gradient; the gradient split of 2.10 was generally associated with small rivers. For example, 95% of samples associated with gradients > 2.10 were classified as headwater streams and creeks whereas 80% of samples with gradients ≤ 2.10 were classified as small or large rivers. The importance of gradient to the distribution and abundance of smallmouth bass has been suggested by several authors (Trautman 1942; Bulkley et al. 1976) and discounted by Paragamian (1981); however, in this study, channel gradient and link magnitude appear to be representing the same environmental factor so I limited the discussion to the ecological significance of stream size. The Spearman coefficient describing the correlation between smallmouth bass relative abundance and channel gradient was insignificant (r = - 0.04, P = 0.05), but the association with link magnitude was significant (r = 0.31, P < 0.001), further justifying limiting my discussion to the importance of stream size.

The major determinant of environmental variability in streams is fluctuation in stream flow. Stream size emerges as an important predictor with higher smallmouth bass relative abundances expected in small and large rivers (i.e., link magnitude > 7 and most streams with channel gradient ≤ 2.10). Typical downstream changes in biological characteristics are predicted in response to geomorphic features and energy dynamics (Vannote et al. 1980). Fish populations are expected to shift from largely insectivorous species in low-diversity headwater streams to a more diverse community of piscivores and insectivores as stream size increases. Poff and Allan (1995) found that hydrologic variation was an important determinate in structuring Midwestern fish assemblages. Lower-order streams support lower diversity due to high environmental variability (Jackson et al. 2001). In larger streams, hydraulic variation is lower and habitat characteristics are more stable. Zorn et al. (2001) used cluster analysis to separate fishes typical of small streams with those typical of large streams; smallmouth bass were found to be significantly more abundant in larger streams. My results reflect the same association with smallmouth bass relative abundance increasing with stream size. Highly variable flows in smaller streams affect reproductive success and a lack of deeper-water habitats and other abiotic factors (e.g., temperature; Coutant 1975) may result in marginal conditions for adult piscivores to thrive in smaller streams (Schlosser 1987).

In relatively low gradient reaches or larger streams, the contribution of increasing spring flow increased the predicted relative abundance of smallmouth bass. Groundwater influences temperature regime and flow stability. Temperature has long been recognized to affect the distribution, abundances, and fitness (i.e., reproduction, growth, and survival) of stream fishes. Bioenergetics modeling suggests temperature is an important factor in determining reproductive success and survival of smallmouth bass in lakes particularly near their distributional limits (Shuter et al. 1980, 1989). Bioenergetics modeling on smallmouth bass in Ozark streams suggested increased temperatures from land-use activities resulted in decreased abundances (Zweifel et al. 1999). Coutant (1975) identified temperature as the most important factor determining the number of smallmouth bass offspring and subsequent year class strength. Stream systems with groundwater inflows provide refuge from extreme temperatures experienced during summer periods (Matthews and Berg 1997). This may be especially important in larger streams that benefit less from riparian shading than do smaller streams (Hynes 1970; Whitledge et al. 2006). High temperatures result in physiological stress and increased metabolic demand on fishes. This may result in slower growth, susceptibility to disease, and lower survival rates. Spring-fed systems also provide warm-water refuges during the winter months (Peterson and Rabeni 1996) which may increase overwinter survival, especially for young-of-year fishes. Significant groundwater contributions to a stream system may also ameliorate the effects of rapidly fluctuating discharge regimes resulting in lower environmental variability; an effect similar to that occurring in larger streams.

High local slope further increased the predicted relative abundance of smallmouth bass in spring-fed rivers. This is likely due to local slope being highly correlated with bluff-pool habitats. Bluff pools typically have steep outer banks (high slope), tend to remain stable because they are formed where the river channel meets resistant bedrock at angles promoting local scour, and contain large concentrations of boulders (Rabeni and Jacobson 1993). Numerous studies indicate the importance of this habitat unit to smallmouth bass. The amount of boulders in the Jack's Fork River, Missouri, was one of the most important predictors explaining variation in density and biomass of smallmouth bass; in this river, boulders occur almost exclusively in bluff-pool habitats (McClendon and Rabeni 1987). Todd and Rabeni (1989) found boulder habitats were used by smallmouth bass three times more often than other cover types during the winter in the same river. Adult and juvenile centrarchids used scour channel units (bluff pool, lateral pool, and obstruction pool) most often in two reaches of the Jack's Fork River (Peterson and Rabeni 2001).

Model Validation

The broad landscape variables used exclusively in my probability of occurrence model and which accounted for nearly half of the variables in my geographic range model are indicative of many coarse-resolution models. However, reliability of predictions made with coarse-resolution models is uncertain without proper validation (Heglund 2002). Lack of external testing is common and most often due to insufficient field data. When external data sets are available, the data are often constrained because collections are taken over limited spatial and temporal scales (Heglund 2002). I was able to obtain data from a statewide sampling program that alleviated two of the fundamental problems associated with model validation: time and space. My validation data set was collected over three years and was spatially diversified throughout the state.

My measure of choice for model validation was based on my objective of prediction. My presence model was off by ≤ 3% for four of the probability of occurrence categories and no more than 25% for the remaining two categories. This low level of error is surprising given that coarse landscape features cannot explain all the variation in local habitat features. My geographic-range model also predicted well, especially considering relative-abundance data were used. I expected the accuracy of prediction to be lower in the geographic-range model because of stochastic changes in fish abundances over time and chance encounters. A sample collected from a location containing a large school of cyprinids may significantly alter relative-abundance values. Also, fall collections include young-of-year fishes which are absent from samples collected during the spring. The accuracy of my predictions was reasonable and more importantly, made ecological sense. These validation results combined with the spatial and temporal extent of the validation data and ecological support (i.e., published literature) increase the predictive value of these models.

Conceptual Framework

The hierarchical organization of stream habitats is well established (Frissell et al. 1986; Tonn 1990; Poff 1997). This conceptual framework depicts multiple habitat filters, operating at different spatial and temporal scales, through which species must pass to occupy and persist in a given location. Coarse-scale filters (e.g., regional filters impacted by climate and geologic history) are thought to control lower-level assemblages, but anthropogenic effects (e.g., species introductions, land-use impacts) may cause filters to act in the reverse order (Tonn 1990). My results delineate natural-occurring factors, presumed to operate from coarse to fine spatial-scale filters, which illustrate the conceptual hierarchical pattern on smallmouth bass distribution and relative abundances.

I developed a hierarchical, conceptual framework by combining abiotic factors from my statewide probability of occurrence and geographic range models (Figure 6). The suite of habitat filters illustrate smallmouth bass potential at a given location starting with coarse, watershed factors scaling downward to local, in-channel factors. Each filter is associated with a GIS and ecological scale, which can be different (*see* discussion on improving predictions). Coarse-textured soils were the most important factor in determining the range of smallmouth bass and therefore define the primary filter. Soil permeability (HSGD) was the final variable used to define the range of the species and it was the most important variable in determining the relative success (i.e., higher relative abundance) of smallmouth bass within the defined range. This variable was defined as a watershed variable, but I believe in some instances it may be important as a segmentshed variable. A segmentshed variable may be especially important in areas acting as geographic transition zones (e.g., the Ozark border region). Stream size, inherently an in-channel variable, adds to the relative success of the species following appropriate soil and runoff potential. The influence of groundwater enters the model after stream size. Spring flow was defined as a watershed variable due to limitations in data, but I believe this variable would be ecologically significant at the in-channel scale. My final filter, local slope, is locally significant and possibly indicative of bluff-pool habitats.

This conceptual framework includes natural-occurring factors affecting the potential of a smallmouth bass fishery; however, it also provides a comparative model for studying future land-use and biotic effects that may change the structure and importance of environmental factors. For example, would a land-use practice change the potential (i.e., predicted relative abundance) of a population at the coarsest or finest filters? Does groundwater influence ameliorate the effects of land-use practices? In streams containing smallmouth and largemouth bass populations, do the local or finest filters change? I believe this conceptual model will promote a more holistic understanding of natural-occurring landscape factors that influence the distribution and abundance of smallmouth bass and initiate a starting point to generate a comprehensive understanding that anthropogenic effects may have on the relative quality of a fishery in a given location.

Improving Predictions

The ability to make accurate and ecologically meaningful predictions has been enhanced by the availability of analytical and spatial-modeling tools and large data sets. However, potential exists to increase our understanding of species-habitat relations by identifying the benefits, caveats, and data needs necessary to improve our predictions and our ultimate goal, ecological understanding. In this section, I identify the benefits and drawbacks of my approach, data needs for increasing our understanding of smallmouth bass habitat associations, the issue of transferability, and the benefits this study may provide to future research.

Classification and regression trees (e.g., Answer Tree 3.0) are valuable analyses in the context of ecological data. Huston (2002) argues that analyses should emphasize environmental factors that have the potential to be limiting to the abundance of a species because most species may be limited by one or more factors and likely all of these factors are not limiting in a synchronous fashion. Analytical procedures, such as classification and regression trees and generalized additive models, depict ecological data in a Hustonian manner because the data are partitioned into subsets on the basis of ecological constraints (i.e., classification and regression trees) or envelopes (i.e., generalized additive models) rather than correlates (O'Connor 2002). These models require large data sets that are typically unavailable in species-habitat studies. Therefore, data are gathered from various sources using numerous methodologies, often with different objectives in mind. This type of data is somewhat limiting because absolute numbers (i.e., abundances) cannot be used. It would also be useful, from a fisheries management perspective, to provide some insight as to the size structure of these populations. Unfortunately, these data are generally not available in quantities that would facilitate being broken into size classes or even life stages (i.e., juvenile and adult). Nonetheless, these models provide the first quantified understanding of the large-scale environmental factors influencing riverine smallmouth bass populations throughout Missouri.

Incorporating GIS technology in modeling approaches has its benefits and limitations. Geographic information technology has aided modeling efforts by allowing quantification of river segments, delineation of catchment boundaries, classification of river networks throughout a state or region, and allows for quantification of landscape and in-stream attributes. However, differences may exist between the spatial scale at which the data are collected and the scale at which ecological models operate (Goodchild 1997). This mismatch of scales can affect the perceived importance of a habitat feature. Another problem with geospatial data is that differences often occur in grain and extent

(Weins 2002). I used a 30-m DEM to develop geology and soils layers of differing resolutions, applied spring-flow data to streams based on known flows from a subset of springs, and used fish samples collected over stream reaches of varying lengths. The differences in re-scaling and the resolution among these data may have affected the outcome or perceived importance of a particular habitat feature; unfortunately, the effects of combining these data are unknown.

Results from this study re-emphasize the importance of sampling gear efficiencies to our perceptions of fish-habitat structure. For example, stream reaches predicted to have the greatest relative abundance of smallmouth bass may yield the highly unlikely scenario of zero relative abundance, 40% of the time. The importance of gear efficiencies for warm-water stream fish sampling has been recognized (e.g., Bayley and Peterson 2001; Peterson and Rabeni 2001), but long-term data sets which facilitate large-scale analyses usually lack efficiency estimates and perhaps more problematic, a way to delineate samples by gear type. Despite sampling shortcomings, patterns exhibited over large spatial and temporal scales are expected to be dramatic enough (e.g., contrasts of high versus zero relative abundance data) that sampling-induced biases would not significantly alter the results obtained.

Identifying the appropriate scale associated with habitat filters is a major challenge associated with predicting species occurrences or abundances (Poff 1997). Results presented in this study highlight the importance of watershed and in-channel filters. For many of these filters, the appropriate scale was easy to identify; for example, watershed characteristics are affected by soil properties, but the slope surrounding a stream segment is inherently local (in-channel). However, the intermediate, or segmentshed variables, were not significant in either model. This may be due to several reasons. Habitat variables were aggregated to simplify the number of variables for model-building trials. For example, the STATSCO soil classification system established for Missouri contains >100 categories. These categories were originally defined in GIS using 16 categories. Condensing these variables based on dominant soil-texture classes resulted in 4 general soils classes. Application of general soil classifications likely result in watersheds with homogeneous soils though they are really quite heterogeneous. The location of a stream segment where a fish is found is affected by everything upstream of that location. My geographic range model identified the association of increasing smallmouth bass relative abundance with larger streams. Because of this association, it may not be ecologically meaningful to define landscape variables at the segmentshed scale though it might prove to be important for species associated with headwater streams. Fish sampling occurred in a landscape affected by anthropogenic change which could affect the perceived importance of a particular scale. Wang et al. (2003) concluded that fish assemblages in landscapes with minimal agricultural and urban influences had stronger correlations with local environmental features than watershed features and suggested watershed-scale management would be most effective in highly altered landscapes. Other studies (Wang et al. 2001, 2002) have demonstrated that the effects of local-scale environmental features are less predominant than land-use features in highly altered landscapes. The influence of landscape condition on the perceived importance of spatial scales is further complicated by results indicating the importance of both scales in structuring fish assemblages (Richards et al. 1996; Allan et al. 1997). Accurate predictions and ecological understanding of fish-habitat relations depends on the appropriate resolution used to characterize the processes that create patterns of interest (Huston 2002). My geographic range model demonstrates the importance of spring flow defined at the watershed scale, but the importance of spring flow is manifested only in larger streams which inherently implies it is an in-channel variable. Information on heterogeneity was lost because a single value was used to characterize spring flow over an entire watershed. The availability of accurate spring-flow data for every stream reach in the state would likely increase the predictive ability of my model and provide information on the importance spring flow might have on smaller streams.

The transferability of general landscape models depends on the linkages established between habitat features at different scales (Poff 1997); understanding these linkages determines the type of filter (e.g., disturbance) that exists. It is difficult to provide direct evidence explaining the linkages that exist between different scales and habitat features. However, I may provide indirect evidence to support what I believe is the overarching theme in my results; that of hydrologic stability. The important (i.e., resulted in changes in relative abundance) environmental features included in my model were HSGD, stream size, and spring flow. I will use HSGD and correlates to illustrate my point. Hydrologic soil group D defines runoff potential based on soil characteristics. If I define HSGD as a disturbance filter, then its usefulness as a predictor depends on how well HSGD correlated with disturbance variables at lower spatial scales. Doisy et al. (2005) examined channel and reach-scale variables associated with sedimentation from 36 streams distributed throughout the geographic range of smallmouth bass in Missouri. A Spearman rank correlation matrix between the sedimentation variables (provided by Doisy et al. 2005) and numerous landscape and land-use variables indicated that sediment-size distribution variables were significant ($P \leq 0.05$) with one variable, the percentage of HSGD in the watershed. The variables that were significant included (r value reported in parentheses): percent of clay and silt within a stream reach (0.48), percent of sand within the reach (0.60), percent of all particles ≤ 2 mm within a reach (0.67), and percent embeddedness (0.41). These simple correlations provide evidence that HSGD has some influence on reach-scale habitat conditions. This does not imply that HSGD does not influence habitat features at other scales or that is does not interact between scales. I do not have the data to provide linkages with stream size and spring flow and lower spatial-scale factors but the influences (hydrologic stability and temperature) of these variables on fishes are well established (see geographic range discussion).

The predictive ability of these models when applied to areas outside Missouri will depend on how well linkages between spatial scales apply, if similar environmental conditions exist, if there are additional mitigating factors not included in my models, and if the spatial scales represented in my models are ecologically meaningful. I believe the ability to predict may be compromised when transferred to another location, but the importance of many of these environmental factors will remain. For example, rocky features are important to smallmouth bass in other Midwestern states (e.g., Wisconsin and Iowa) and I expect this to be the case in other locations though they may be manifested through different geology or soil groups. I also expect that habitat features affecting runoff potential would be equally applicable, though may not be created by HSGD. Other habitat features may not be important to smallmouth bass in other regions. For example, spring flow may be important in Missouri streams due to higher stream temperatures whereas it may not be as important for smallmouth bass in northern portions of the species range.

Predicting land-use impacts on fishes is an essential component of fisheries management. However, separating the impacts of land use from other landscape features is difficult. Streams adjust channel dimensions in response to changes in sediment supply and discharge (Dunne and Leopold 1998) which result from many land-use practices. Despite this knowledge, few studies have addressed the ecological effects of urbanization in streams (but see Scott et al. 1986; Gafny et al. 2000) though numerous studies have addressed some aspect of agricultural effects (e.g., Lenat 1984; Menzel et al. 1984; Richards et al. 1996). Mechanistic studies that address physical habitat, water quality, and food-web disturbances are less common (Suren 2000). Perhaps this is partially due to difficulties obtaining appropriate sampling localities (i.e., locations with varying percentages of a particular land use with otherwise similar natural conditions). Understanding the natural habitat features that affect the distribution and abundance of a population is prerequisite to understanding land-use impacts. This study provides the predicted relative abundances and associated habitat conditions necessary to increase our understanding of potential land-use impacts on smallmouth bass populations and a starting point for understanding the linkages between spatial-scale elements.

The purpose of this study was to identify natural-occurring factors that contribute to the distribution and abundance of riverine smallmouth bass in Missouri. Through prediction and validation I was able to apply estimates of fishery potential to every stream reach in Missouri. This information provides a framework to guide fisheries-management initiatives and a hierarchical and conceptual model for comparing future research. These findings may be used as a guide and comparative model to facilitate future research addressing anthropogenic effects on fishery potential at any given location. The effects of re-scaling and using data with differing resolutions are unknown, but future generation of more accurate data with compatible resolution will facilitate better predictions and choice of appropriate scale. Transferability of these models outside of the area for which they were developed is questionable until the appropriate linkages and filter types are identified. Developing these linkages will facilitate a mechanistic understanding of the processes involved and allow conclusions to become more general.

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TABLE 1.- Statistical descriptions (mean, standard deviation [Std dev], minimum and maximum) for landscape and in-channel habitat variables used in model development. Italics denote ordinal variables with the number of levels included in parentheses. Landscape factors were calculated for the entire watershed and immediate drainage of a particular stream segment (excluding slope: calculated for each stream segment and, spring variables: calculated for each watershed) whereas in-channel variables were quantified for specific stream segments

Variable Group	Model variable	Mean	Std dev	Minimum	Maximum
Landscape					
Geology (%)	Limestone_dolimite	74.02	31.14	0.00	100.00
	Sandstone	14.45	22.51	0.00	100.00
	Alluvium	5.16	20.54	0.00	100.00
	Clay	0.25	2.41	0.00	49.87
	Igneous	1.33	6.87	0.00	100.00
Runoff potential (%)	HSGA	0.92	6.36	0.00	100.00
	HSGB	42.38	34.53	0.00	100.00
	HSGC	39.47	33.90	0.00	100.00
	HSGD	11.97	25.46	0.00	100.00
Soils (%)	Loam_silt_clay	63.23	37.11	0.00	100.00
	Rocky	30.93	37.02	0.00	100.00
	Variable	0.25	3.78	0.00	99.88

Variable Group	Model variable	Mean	Std dev	Minimum	Maximum
	Sand_fine gravel	0.58	5.99	0.00	100.00
Landform	Watershed relief	131.89	92.49	0.00	427.00
	Slope (%)	8.79	4.73	0.67	21.76
Springs	Spring density	3.64E-04	9.5E-03	0.00	0.21
	Spring flow volume	8.26E-03	0.12	0.00	3.15
In-channel					
Flow	*Flow(2)*	1.07	0.38	0.00	2.00
	Losing (2)	0.02	0.14	0.00	1.00
Temperature	*Temperature (2)*	1.95	0.23	0.00	2.00
Stream size	*Size discrepency (11)*	0.45	1.43	0.00	10.00
	Dlink	52801	222702	0.00	1000000.00
	Link magnitude	45058	206760	0.00	1000000.00
Gradient	Segment gradient	2.72	5.19	0.00	116.40
	Channel gradient	2.68	4.97	0.00	116.40
	Biogeographic gradient (3)	1.50	0.89	0.00	3.00
Elevation	Minimum elevation	209.71	71.56	0.00	434.00

FIGURE 1.- Decision tree model showing the probability of smallmouth bass occurrence based on landscape-scale habitat variables. The predicted probability of occurrence (bold numbers) and sample size (in parentheses: the number of samples reflecting a presence response over the total number of samples) are shown for the entire data set and at each node. Child nodes are represented by circles. Hydrologic soils group D = HSGD

FIGURE 2.- Decision tree model showing the predicted relative abundance of smallmouth bass based on landscape and in-channel scale variables. The predicted relative abundance (bold numbers) and sample size (in parentheses) are shown for the entire data set and at each node. Child nodes are represented by circles. Hydrologic soils group D = HSGD

FIGURE 3.- The observed smallmouth bass occurrence percentage (validation data) as a function of the predicted probability of occurrence based on my model for each of the six respective probability categories.

FIGURE 4.- Maps showing the statewide distribution of probability of occurrence (top) categories (5) and within-range relative abundance (bottom) categories (7) predicted by decision tree models. Two categories (45% and 46%) predicting the probability of occurrence were collapsed because of similar values. The adjacent inserts show the detail provided by each map

FIGURE 5.- The observed smallmouth bass relative abundance (validation data) as a function of the seven predicted relative abundance categories predicted by my model

FIGURE 6.- Conceptual model of a stream reach's potential to support a smallmouth bass population. The suite of natural-occurring habitat filters is ecologically hierarchical scaling downward from watershed to in-channel features. Each filter has an associated ecological and geographic information system (GIS) scale which may differ in some instances because of limitations imposed by technology and available data. This conceptual framework serves as a comparative model for evaluating transferability and assessing potential land use and biotic effects thought to alter the importance of in-channel features

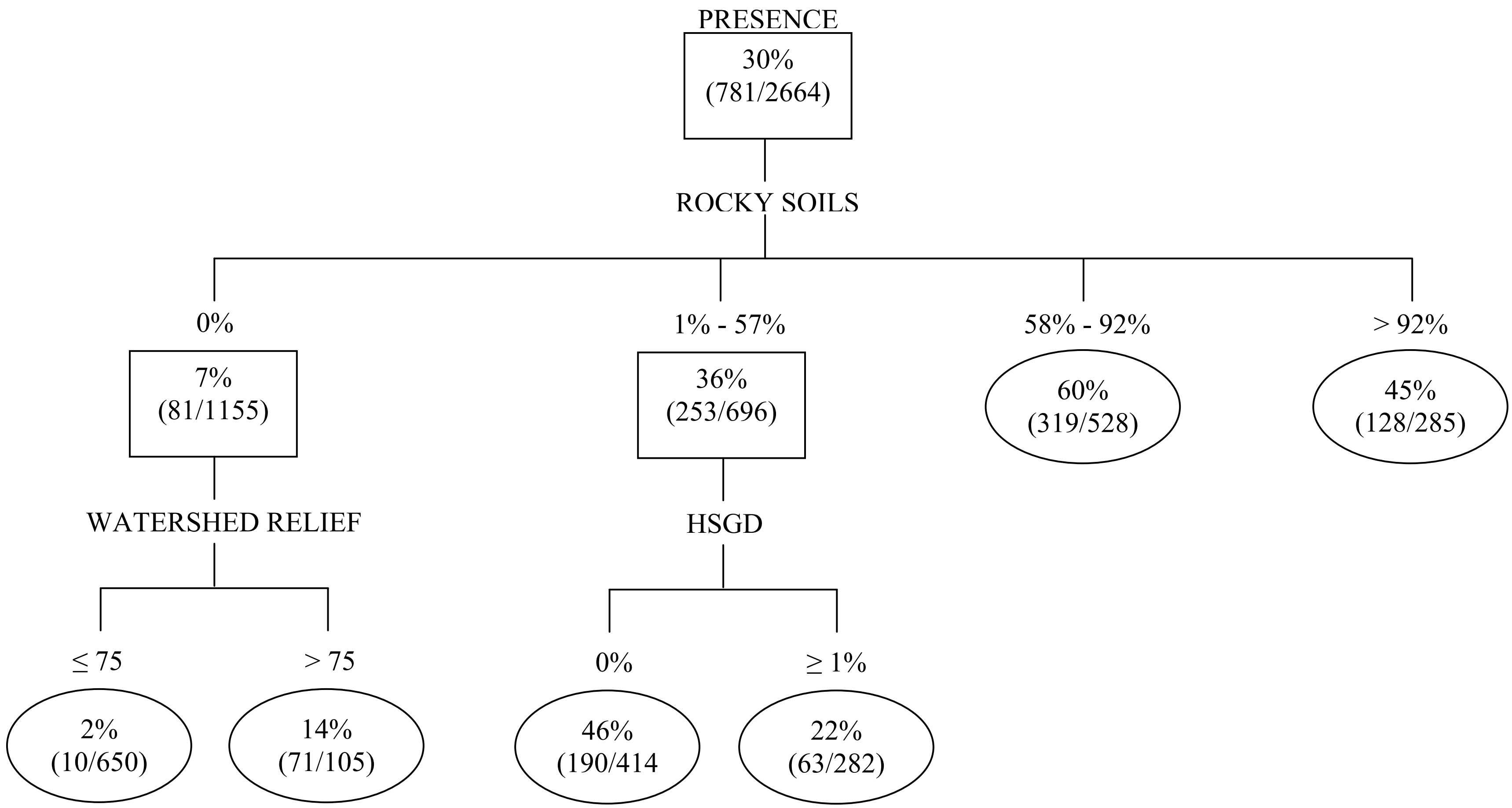
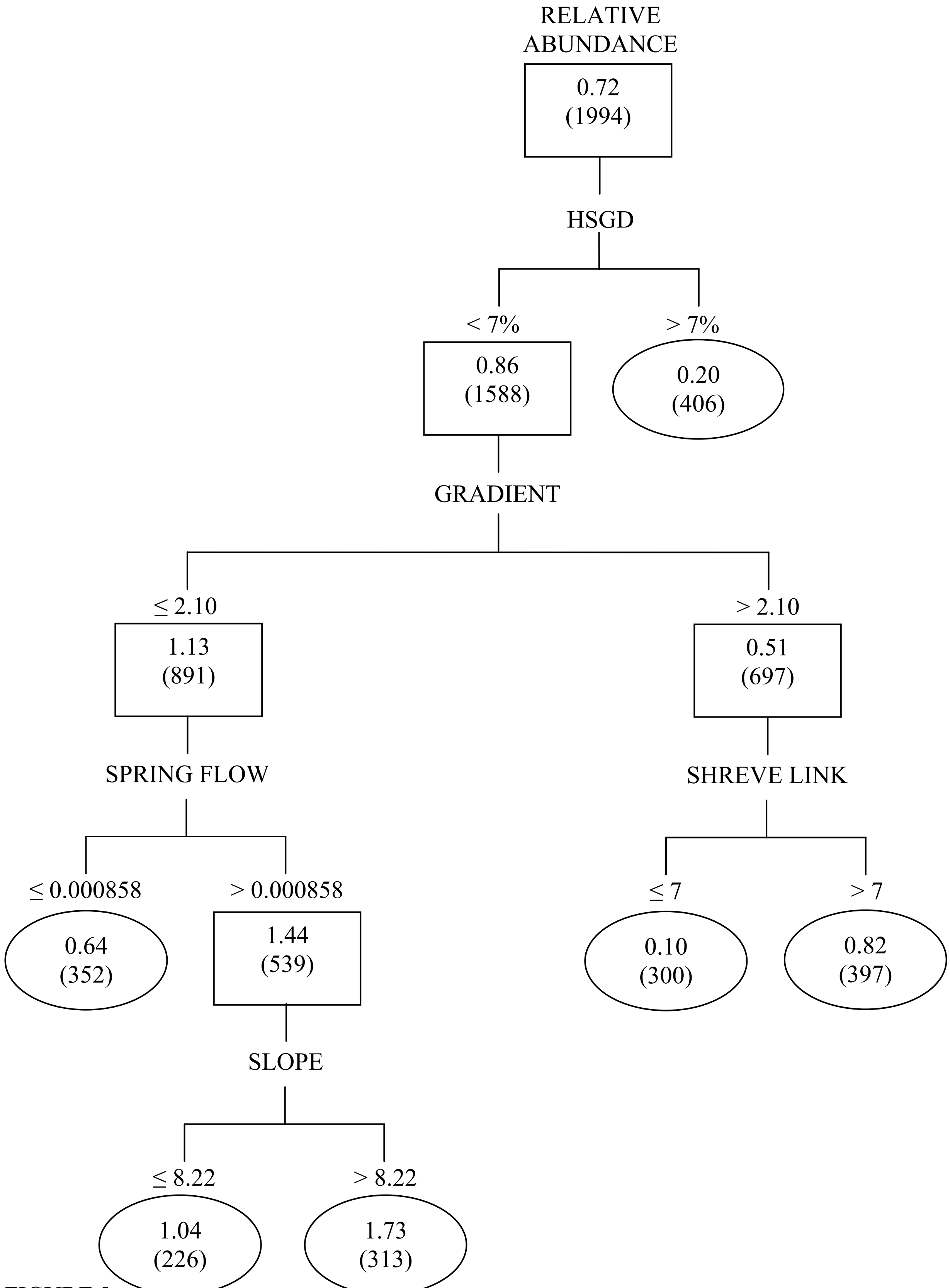

PRESENCE
30%
(781/2664)
ROCKY SOILS
0%
1% - 57%
58% - 92%
> 92%
7%
(81/1155)
36%
(253/696)
60%
(319/528)
45%
(128/285)
WATERSHED RELIEF
HSGD
≤ 75
> 75
0%
≥ 1%
2%
(10/650)
14%
(71/105)
46%
(190/414
22%
(63/282)

FIGURE 1.-


RELATIVE ABUNDANCE
0.72
(1994)
HSGD
< 7%
0.86
(1588)
> 7%
0.20
(406)
GRADIENT
≤ 2.10
1.13
(891)
> 2.10
0.51
(697)
SPRING FLOW
≤ 0.000858
0.64
(352)
> 0.000858
1.44
(539)
SHREVE LINK
≤ 7
0.10
(300)
> 7
0.82
(397)
SLOPE
≤ 8.22
1.04
(226)
> 8.22
1.73
(313)
FIGURE 2.-

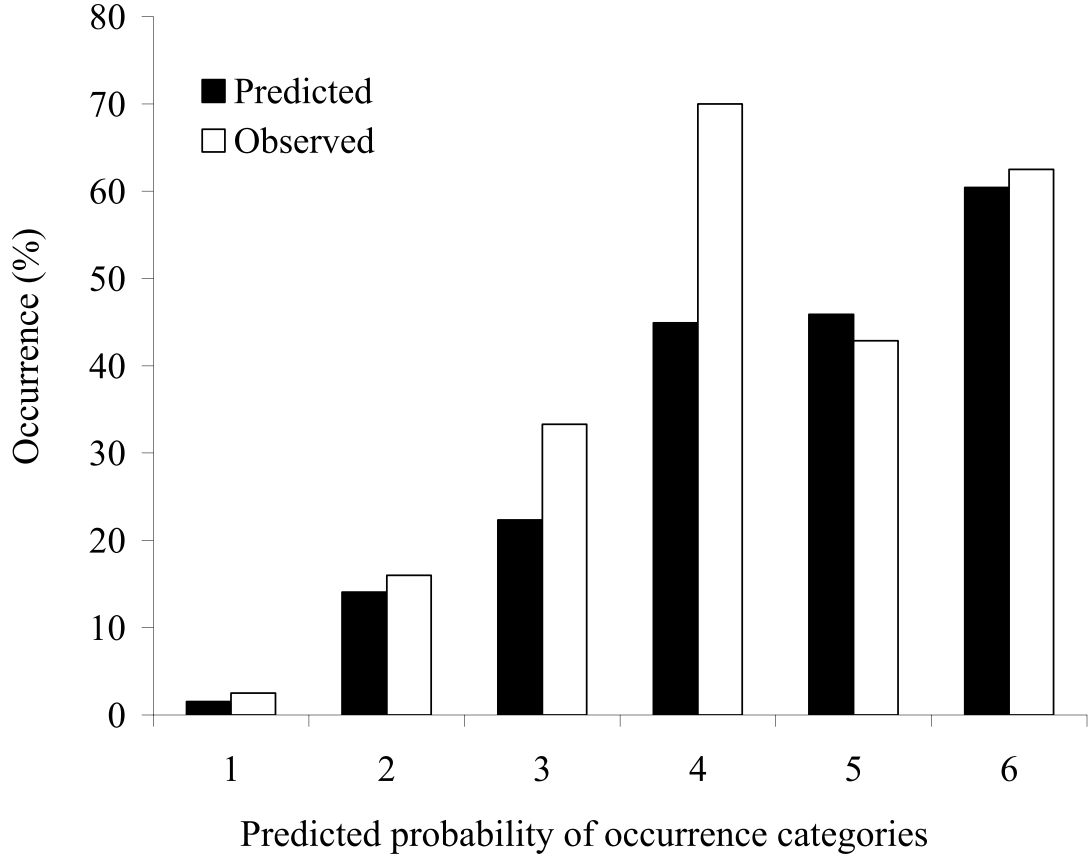
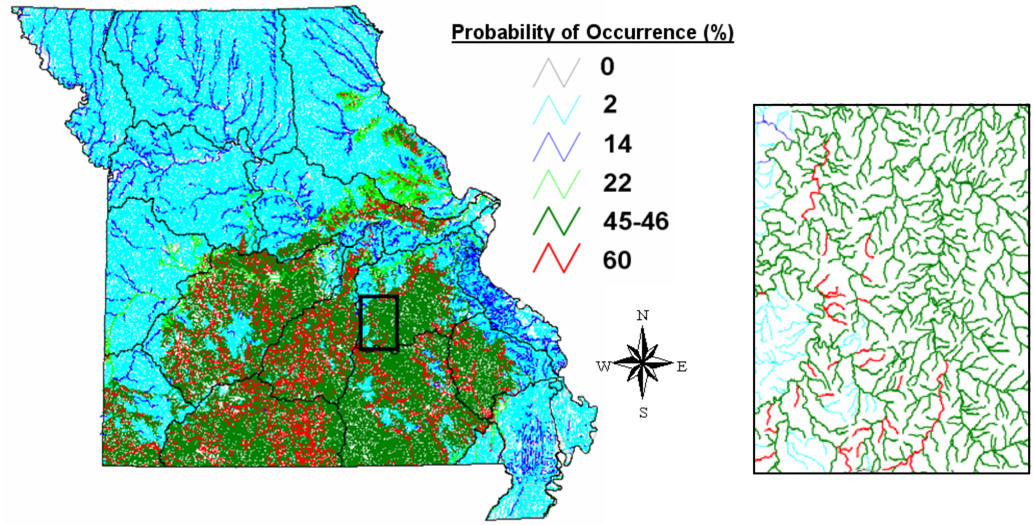

80
70
60
50
40
30
20
10
0
Predicted
Observed
Occurrence (%)
1
2
3
4
5
6
Predicted probability of occurrence categories

FIGURE 3.-


Probability of Occurrence (%)
0
2
14
22
45-46
60
N
W
E
S

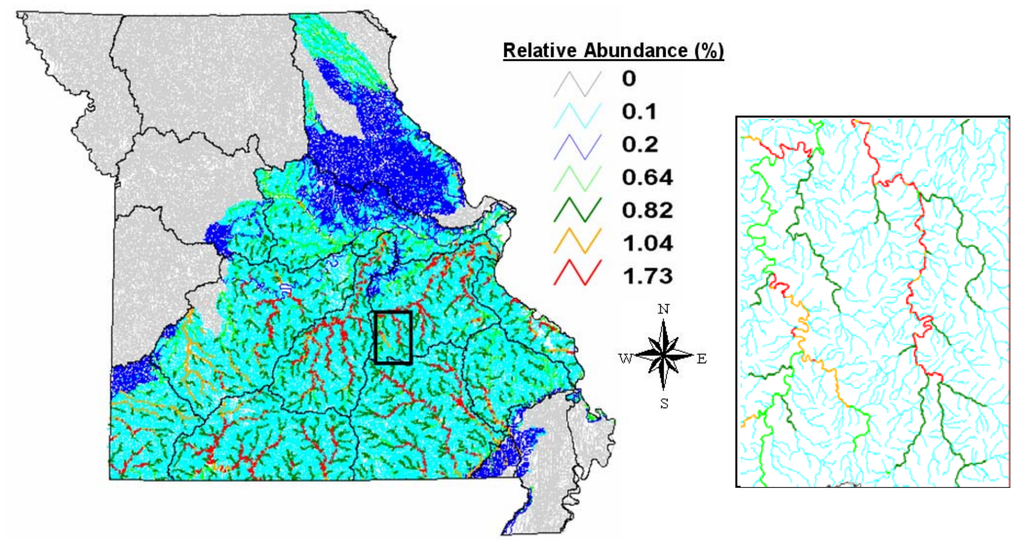
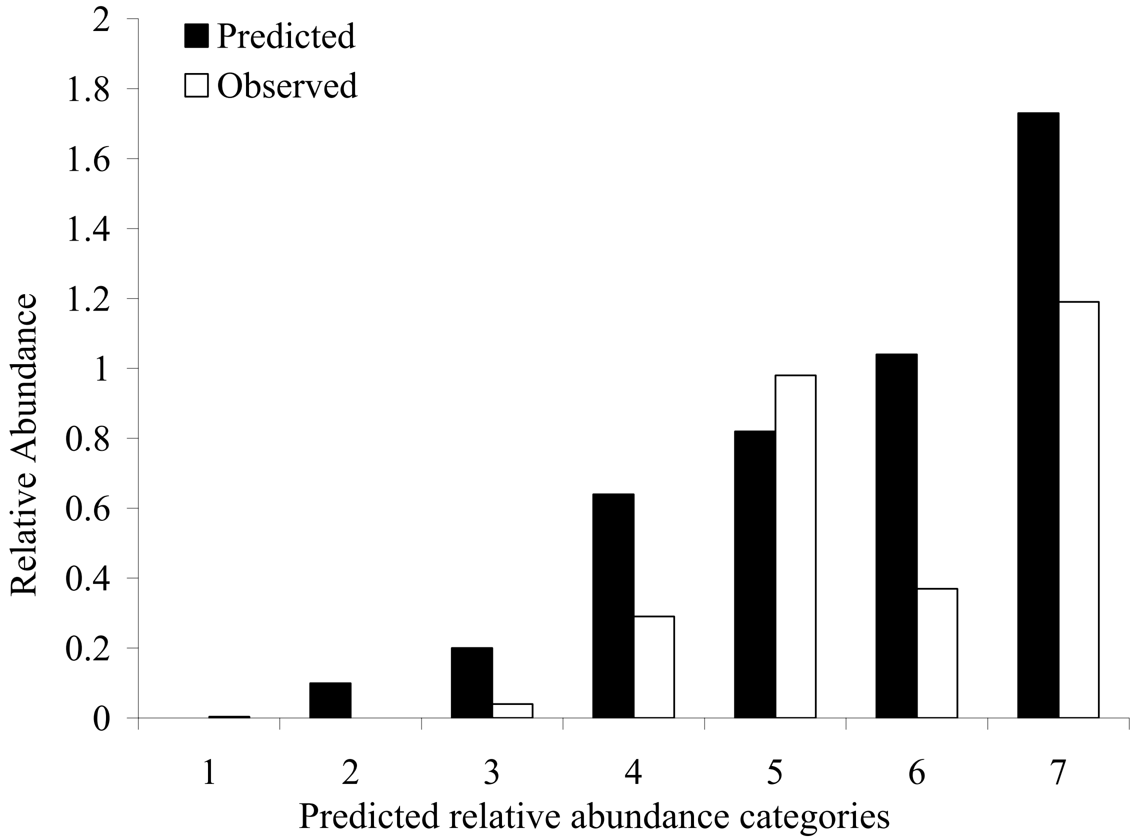

Relative Abundance (%)
0
0.1
0.2
0.64
0.82
1.04
1.73
N
W
E
S

FIGURE 4.-



Predicted
Observed
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Relative Abundance
1
2
3
4
5
6
7
Predicted relative abundance categories

FIGURE 5.-

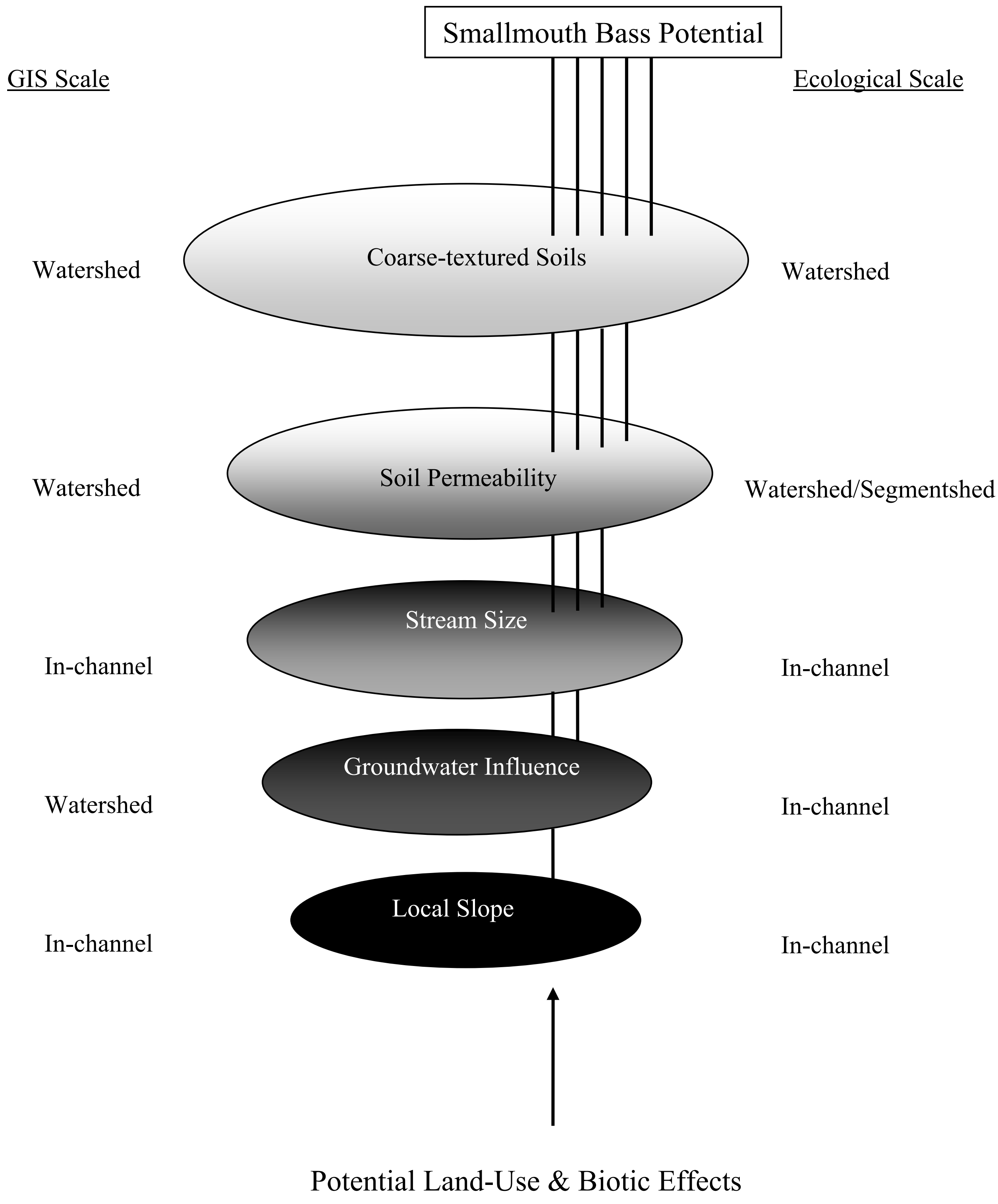

Smallmouth Bass Potential
GIS Scale
Ecological Scale
Watershed
Coarse-textured Soils
Watershed
Watershed
Soil Permeability
Watershed/Segmentshed
In-channel
Stream Size
In-channel
Watershed
Groundwater Influence
In-channel
In-channel
Local Slope
In-channel
Potential Land-Use & Biotic Effects

FIGURE 6.-

Chapter 3

Hierarchical land-use and in-channel influences on the distribution and abundance of riverine smallmouth bass

Abstract.- I examined whether the influence of watershed land use on the abundance of smallmouth bass *Micropterus dolomieu* in Missouri USA streams varied depending on the naturally occurring features of the watershed. An experimental design of replicated land uses (n = 3) within clusters (n = 4) of streams (n = 36) in watersheds with unique naturally-occurring factors (i.e., runoff potential and coarse-textured soils) was used. Decision tree models indicated landscape and in-channel variables were related to densities of smallmouth bass. Land use explained the most variation in my models and the in-channel features of temperature, flow and sediment, contributed significantly to the models, but explained less variation. Analyses of variance of densities indicated significant main effects of cluster and land use, and also interactive effects indicating densities depended on interactions between land use and natural conditions. Land-use category also determined the likelihood of smallmouth bass presence in channel units (analyzed by generalized linear models). I conclude this species has differing vulnerabilities to anthropogenic land-use attributes, with better natural conditions related to decreased proportional declines in densities when pasture land use is increased in each respective watershed.

Recognition of the vast extent and ecological significance of land-use changes worldwide (Turner and Meyer 1994) has resulted in an increasing number of studies examining effects of land-use changes on aquatic systems (e.g., Richards et al. 1996; Wang et al. 1997; Paul and Meyer 2001; Wang et al. 2001; Brazner et al. 2004; Chadwick et al. 2006). Landscape conversions from forest or prairie to urban, agriculture, or pasture affects aquatic systems via numerous pathways including altered hydrology, water chemistry, sediment dynamics, channel geomorphology, trophic resources, riparian stability, and local habitat complexity. Collectively, the relations established between these pathways and associated biota illustrate the influence anthropogenic activities have on aquatic systems.

Aquatic ecosystems are strongly influenced by their surroundings at multiple spatial and temporal scales (Schlosser 1991; Allen et al. 1997; Fausch et al. 2002). Ecological patterns observed at small spatial scales are the product of local habitat structure and constraints imposed at larger spatial and temporal scales (Frissell et al. 1986; Tonn 1990; Snelder and Biggs 2002; Brewer et al. 2007). In this context, the hierarchical influence of anthropogenic activities in a watershed may manifest at multiple spatial and temporal scales. For example, human activities at the landscape scale disrupt geomorphic processes that create and maintain habitat at finer spatial scales (Allen 2004). The relationship between spatial scales may influence the quality or quantity of habitat available to and used by fishes.

Our understanding of relations between anthropogenic activities in a watershed and the constraints imposed by natural-occurring landscape factors is limited. Anthropogenic activities in a watershed often covary with the natural-occurring conditions (i.e., geology, soils) that exist within those regions (Richards et al. 1996; Allen 2004; King et al. 2005). When the natural-occurring conditions within a region are ignored, the effects of land use may be unintentionally overstated (Allen 2004). Wang et al. (2003) demonstrated that land use was a minor driver in the relatively undisturbed Northern Lakes region. Likewise, regions almost entirely dominated by a particular land use may not reveal a strong relation between land use and the abundance of organisms; however, natural factors may be more important when anthropogenic influences are minor (Allen 2004).

Understanding land-use impacts on fishes is an essential component of fisheries management. Land-use changes over the past 100+ years in Missouri have resulted in substantial flow, temperature, and physical habitat changes which have likely profoundly affected riverine smallmouth bass *Micropterus dolomieu* populations. However, separating the impacts of land use from other landscape features is difficult. Understanding the natural habitat features that affect the distribution and abundance of a population is prerequisite to understanding land-use impacts. Coarse-textured soils and soils with low runoff potential (hydrologic soil group D) were identified as the most influential natural-occurring landscape features affecting the distribution and relative abundance of riverine smallmouth bass in Missouri via modeling procedures (Brewer et al. 2007). Combinations of significant percentages of these natural-occurring conditions were used in this study to develop clusters of similar stream segments and then integrate land-use attributes into each cluster with the goal of identifying the impacts of land use (watershed spatial scale) and in-channel features (stream segment and channel unit [CU] spatial scales) on the distribution and abundance of riverine smallmouth bass at multiple spatial scales. The objectives of this study were 1) to model the relation of land use and in-channel habitat features to densities of different age classes (young of year [YOY], age 1, and age 2^+) of smallmouth bass, 2) determine if densities of smallmouth differed depending on land-use attributes (forest, pasture, urban), natural-occurring features (combinations of coarse-textured soils and runoff potential), or more importantly, the interaction between land-use attributes and natural-occurring features in the watershed and, 3) determine the likelihood of smallmouth bass occurrence in respective CUs for stream segments in each land-use category, and whether CUs were used differently depending on land-use classification.

Study Area

Smallmouth bass occupy three biogeographic regions in Missouri: Central Dissected Till Plains, Osage Plains, and the Ozark Highlands (Nigh and Schroeder 2002). Sampling was conducted on 36 streams, located in all of these biogeographic regions (this encompasses the entire state excluding the southeastern lowland areas). The Central Dissected Till Plains covers northern Missouri and is characterized by formerly glaciated plains that become increasingly dissected as they near major confluences, especially the Missouri and Mississippi Rivers. Streams sampled in this region were limited to the northeastern section of Missouri, following the distributional limits of smallmouth bass (Brewer et al. 2007). The Osage Plains region occupies a large portion of west-central Missouri and is characterized by smooth plains with numerous bedrock outcroppings. Streams in the Central Dissected Till Plains and Osage Plains regions generally carry high sediment loads during periods of runoff, are low gradient, and highly meandering; however, numerous sections of larger streams have been channelized. The Ozark Highlands region includes most of southern Missouri and is characterized by extensive geologic erosion, carbonate bedrock, and karst features. Many of the streams within this region are spring-fed and have low suspended sediment loads except during periods of high runoff. Historically, all of these regions were a mixture of prairie, savanna, woodland and forest. Today, these regions have largely been converted to secondary growth forest, cropland, pasture and urban areas, with small remnant tracks of native vegetation remaining (Nigh and Schroeder 2002). In this study, I classified stream segments from forested watersheds as "forest" and stream segments from grassland watersheds as "pasture".

Methods

*Study design and site selection***.-** Thirty-six stream segments (Figure 1) were selected using criteria that allowed assessment of both natural and anthropogenic-induced variation in smallmouth bass abundance across Missouri. Criteria pertaining to natural variation in habitat conditions were based on watershed features having the strongest impact on smallmouth bass probability of occurrence and relative abundance (*see* Brewer et al. 2007 for complete description). Most of the variation in the predicted distribution and abundances of smallmouth bass throughout Missouri could be explained using two natural-occurring conditions in the watershed: the percentage of coarse-textured soils and the percent of hydrologic soil group D (indicative of soil permeability). Using these two environmental features, multivariate cluster analyses of over 150,000 stream segments resulted eighteen distinct clusters (*see* Doisy et al. 2005 for a complete description). Five clusters met the initial criteria used for varying abundances of smallmouth bass (based on natural-occurring features) and the four clusters chosen (Clusters 2, 3, 4, and 11) contained the highest frequency of stream segments, therefore, had the highest potential for achieving replication and interspersion (Table 1).

Once the clusters were established, additional criteria were used to select stream segments within each cluster. Stream segments within each cluster were queried to identify segments that were perennial, had similar drainage areas, and had a Shreve link of 10 - 250. Stream segments were then identified that had the highest percent of forest, pasture and urban land use within their respective watershed but were otherwise similar with regard to other human disturbances (i.e., mines, landfills). Within this pool of potential sites, stream segments were initially selected based on proximity to public lands or roads, condition of the riparian corridor (relatively intact), and proximity to one another. Attempts were made to intersperse forest, urban, and pasture sites (Figure 1).

Habitat Data.- Landscape variables (i.e., watershed area, land-use attributes) (Table 2) were derived from existing geospatial data. I used a 1:100,000 digital stream network created by the Missouri Resource Assessment Partnership (Sowa et al. 2005). This coverage contains over 106,000 individual stream segments, each attributed with numerous landscape variables. Land use was the variable of primary interest but I included watershed area in case my limitation on Shreve Link was not sufficient to account for stream size.

Several in-channel variables (e.g., % pool) were measured on site at the time of fish sampling (Table 2). I simplified the CU classification system proposed by Rabeni and Jacobson (1993) and used six CU types: pools, riffles, runs, vegetated edges, non-vegetated edges, and side-channel habitats (i.e., forewaters and backwaters). Each site was mapped prior to sampling so the relative percentages of CUs could be determined and flags could be placed as CU boundaries where necessary. Discharge was calculated using the velocity-area method (Gordon et al. 2004) at a minimum of two locations in each stream segment. Pool temperature (°C) was measured at mid-pool depth with a hand thermometer in a minimum of three pools or three pool sections (when pools were > 200 m in length) at each site.

Remaining in-channel variables (e.g., sinuosity) (Table 2) were obtained from a previous study (Doisy et al. 2005), conducted on the same sites in summer 2005, using the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) protocol. In-channel measures of sediment for the entire segment were based on measures from the sub-bank and embeddedness calculations of the EMAP protocol. Mean substrate size classes in all cross sections were: 1 = fines, 2 = sand, 2.5 = fine gravel, 3.5 = coarse gravel, 4 = cobble, 5 = small boulder, and 6 = large boulder. Specific variables were chosen from the EMAP data because I expected the variable to change due to land-use alterations (e.g., width:depth ratios) or the variables have been related to increased smallmouth bass densities or fitness (e.g., substrate, % fines) in other studies.

Fish sampling.- Multiple methods of sampling were used because fish were collected over three biogeographic regions and under a variety of landscape conditions. Sampling methods used a combination of snorkeling, seining, and above-water visual observation. The choice of method used at any point in time depended on water clarity and depth. Turbidity values indicate that these methods, though not equal in efficiency, are not expected to be biased against any one cluster or any particular land use (Figure 2). Snorkeling was my primary sampling method (approximately 60% of the time). Snorkeling was used when water clarity allowed observers to view the bottom of the stream in water a minimum of 1-m deep. Seining was used to cover the same area with approximately similar effort (time) when turbidity was high enough in particular CUs to prevent snorkeling. Seining was used in approximately 40% of the streams sampled, most of the time (approximately 80%) to sample < 20% of the stream segment. Seining was used in every cluster and land-use category (40% of the time in stream segments in forested watersheds) so the distribution of methods across treatments should prevent any bias in my results. Above-water visual observation was used when water clarity allowed observers to see the stream bottom in < 0.5-m deep stream sections if surface conditions did not impede observation. Visual observation usually occurred in edge-water habitats, run habitats of smaller streams, and extremely shallow pools. This method was incorporated because a pilot study I conducted revealed a compromise in my ability to detect YOY smallmouth bass while snorkeling versus above-water observation in shallow-water habitats. This method was used to sample a portion of CUs in every stream sampled.

Fish sampling was conducted in late summer (July - September) 2006. At each site, a minimum of 40 times the channel width was sampled. Beginning at the most downstream point of the stream segment, CUs were sampled independently throughout the site so densities of each age class (YOY, age 1 or age 2^+) of smallmouth bass could be determined for the entire stream segment (for objectives 1 and 2) and individual CUs (for objective 3). Whereas riffle habitats were mapped to calculate area, they were excluded from sampling because pilot sampling indicated these CUs were used only rarely in very small streams by young-of-year smallmouth bass (also *see* Chapter 4). I could not justify the amount of effort required to include this CU given it would not change densities obtained to any appreciable degree. To support this claim, 20 riffles were randomly selected and snorkeled and no smallmouth bass were identified in any of them.

Each sampling gear had a specific protocol. When snorkeling was used, 2-3 snorkelers (three snorkelers were used for the largest streams) would begin at the downstream end of the CU and moved upstream at a rate of approximately 5 m^2 min^{-1} to the end of the CU (either marked discretely with a flag or using natural features). Each snorkeler limited their observations to half (or a third if three persons were sampling) of the stream and covered their half (or third) by swimming in a zig-zag pattern. When a smallmouth bass was encountered, the snorkeler used a sweeping motion to encourage the fish to move downstream. Snorkelers reduced the possibility of double counting individual fish at the center of the stream by pointing out any fish counted in this area to the other snorkeler(s). The same approach was used for above-water visual observations by walking slowly through the CUs in a zig-zag pattern and communicating fish counted with the other observer(s). Exception to this approach occurred only when sampling edgewater habitats. In non-vegetated edge habitats, above-water observations were made by one observer on the bank and another streamside. In shallow vegetated-edge habitats, observers on each side would slowly look through the stands of vegetation (usually water willow, *Justicia americana*) working from the downstream to upstream end of the CU; if water depth permitted (≥ 0.25 m), the streamside observer would snorkel slowly along the outside band of the water willow. When turbidity prohibited snorkeling in any CU, a seine was used to cover the same amount of area (excluding major obstructions) in an amount of time nearly equivalent to snorkeling. Seining began at the downstream end of the CU and continuous passes were made throughout the CU until it was adequately covered. Fish were identified on site and released downstream of the sampling point.

Analyses.- Decision tree analyses were used to develop models to predict densities (number/m^2) of YOY, age 1, and age-2^+ riverine smallmouth bass based on a suite of continuous and categorical landscape and stream segment variables (Objective 1) (Table 2). Decision trees are well suited to ecological data because they consider complex interactions (e.g., nonlinear) (Olden and Jackson 2002) and are able to identify a variety of conditions that may result in similar or completely different outcomes. Density of smallmouth bass in individual stream segments was weighted by the proportional abundance of each CU in that segment. Scatterplots were constructed and used to identify one outlier (Cowskin Creek). Prior to model building, this outlier was removed because densities were artificially inflated (nearly five times greater than any other stream) due to extremely low flows that reduced this stream to intermittent pools where fish were restricted. Answer Tree 3.0, an extension of SPSS statistical software package, was used to construct my decision tree models ($\alpha \leq 0.10$). I used the Exhaustive CHAID algorithm to examine predictor variables to find the one that gave the best classification of the target variable by recursively splitting the data into subgroups until the analysis was completed based on my pre-defined stopping criteria. The Exhaustive CHAID algorithm was used because it does a more thorough job of examining all possible splits for each predictor variable and because it can produce more than two categories at any level in the tree (unlike C&RT and QUEST). Exhaustive CHAID was developed to improve the splitting capability by computing an adjusted-*P* value for the predictor that provides the strongest association with the target variable.

The size of the tree (i.e., number of levels) Answer Tree 3.0 allows is determined apriori by the user. The chosen stopping criteria reduces the probability of overfitting the model. The maximum number of levels allowed in a model was set at three. The minimum number of collections allowed in a child node was set to one and the minimum number of collections allowed in a parent node was set equal to 10% of the total collections.

After the tree was developed, I manipulated my data by +/- 5% and developed new models using the same established criteria. Because my sample size was relatively small (n = 36), I wanted to ensure the relations established between densities of smallmouth bass and habitat variables were strong enough to remain unchanged even if my data were manipulated to some degree.

Analysis of variance was used to determine if differences existed in densities (YOY, age 1 and age-2^+) of smallmouth bass between clusters, land-use categories, and the interactive effect of cluster and land use (Objective 2) ($\alpha \leq 0.10$). Data (n = 35 streams) were rank transformed because of failure to meet assumptions associated with ANOVA (i.e., normal distribution and equal variances). Rank transforming data results in loss of information, but approaches distribution-free nonparametric alternatives (Conover and Iman 1981). The test statistic for ranked data measures the difference between the weights of the groups instead of the differences in the original variables. Fisher's least significant difference (LSD) test was used to identify where differences in smallmouth densities occurred between clusters and land-use types. The power of multiple comparisons procedures for non-normal populations is greater when rank transformed data are used (Conover and Iman 1981).

Generalized linear models (proc genmod: SAS 2000) were created to determine the probability that smallmouth bass would be present (binomial distribution, logit function) rather than absent in streams segments located in watersheds with particular land-use attributes (i.e., forest, urban or pasture), in CUs, or particular CUs depending on land-use attribute ($\alpha \leq 0.10$) (Objective 3). All stream segments (n = 36) were included in these analyses because densities were not weighted therefore, there were no outliers. Likelihood ratio statistics were calculated for each treatment (land use, CU, and interaction) resulting in a single chi square for the entire data set. Likelihood ratio statistics test the null hypothesis that all coefficients in the data set are equal to zero (Allison 1999). The antilog of each logit estimate was used to calculate the odds [(P_p / 1 - P_p), where P_p is the probability of fish being present] of smallmouth bass being found versus not found in individual treatments (land-use categories or CUs) and the antilog of the difference between logit estimates, or odds ratio [(P_x / 1 - P_x) / (P_y / 1 - P_y) where x and y are different treatments and P is the probability of residing in that treatment], was used to calculate the likelihood of smallmouth bass being present in one treatment versus another. For example, if the logit estimate for smallmouth bass in stream segments located in forested watershed was -0.22 and in pasture watersheds was -1.24, then smallmouth bass would be more than twice as likely to occur in stream segments located in forested watersheds compared to urban watersheds (e.g., e^x (-0.22 - -1.24) = 2.77). Non-vegetated edges and side-channel habitats were excluded from the analysis on YOY because these habitats were extremely rare in my samples (i.e., side channels only occurred in two stream segments) or no fish were encountered in those CUs. Models created to determine age 1 and age 2^+ smallmouth bass probability of occurrence excluded non-vegetated edges, vegetated edges, and side-channel habitats due to limited samples or absence of fish. These exclusions were necessary as the algorithm will not converge when zeros exist in an entire unit (i.e., CU type in any land-use group).

Results

Predicting densities of smallmouth bass using land use and stream-segment features

The most important variable in my model predicting densities of YOY smallmouth bass was land use ($F_{2, 32}$ = 4.39, P = 0.02) (Figure 3). Densities of YOY were predicted to be nearly three fold higher in stream segments located in forested watersheds compared to those in watersheds classified by pasture and six fold higher than those stream segments classified by urban land use. Land use explained 23% of the variation in my data. Densities were predicted to more than double in stream segments located in forested watersheds when discharge was added to the model (> 0.47 m^3/s). Discharge accounted for an additional 21% of variation in my data ($F_{1, 10} = 16.35$, $P = 0.04$). Water temperature was significant in relatively smaller streams (discharge ≤ 0.47 m^3/s), nearly doubling predicted densities of YOY ($F_{1, 7} = 12.96$, $P = 0.08$). Overall, my model explained 62% of the variation in YOY densities. The same variables were significant to my decision tree after manipulating my data by +/- 5% and creating new models using the same input variables.

The only variable significant in my model predicting densities of age-1 smallmouth bass was land use ($F_{2, 32} = 3.27$, $P = 0.05$). Mean densities of age-1 fish were greatest in stream segments located in forested watersheds, followed by pasture watersheds and urban watersheds, respectively (Figure 4). This model only explained 17% of the variation in my data. Land use remained the only significant variable in my model after manipulating densities by 5%.

The most important variable in my model predicting densities of age-2^+ smallmouth bass was land use ($F_{2, 32} = 4.92$, $P = 0.01$) (Figure 5). Mean densities of age-2^+ were predicted to be three fold higher in stream segments located in forested watersheds than those in watersheds classified by pasture and more than fifteen fold higher than those stream segments located in watersheds classified by an urban landscape. Land use explained 23% of the variation in my data. Mean densities of smallmouth bass were predicted to more than double when discharge was added to the model (> 0.24 m^3/s). Discharge accounted for an additional 37% of variation in my data ($F_{1, 10} = 23.15$, $P = 0.01$). The percentage of fines in the channel was significant in stream segments located in watersheds classified by pasture land use ($F_{2, 9} = 51.33$, $P = 0.0003$), increasing predicted mean densities of age-2^+ fish by approximately five fold when percent fines ranged between 1.8 and 3.6%; however, when the percentage of fines present in the channel was greater than this range, mean densities of smallmouth bass were predicted to be much lower but similar to one another. Overall, my model explained 81% of the variation in age-2^+ densities. The same variables were significant to my decision tree after manipulating my data by 5% and creating new models using the same input variables.

Land use interactions with natural-occurring watershed features

The overall cluster by land use factorial ANOVA was significant for YOY smallmouth bass densities ($F_{11, 34} = 5.47$, $P = 0.0003$). The model was significant for the main effects of cluster ($P = 0.0003$) and land use ($P = 0.003$). Cluster three and four had significantly higher densities than the other clusters (Figure 6). In clusters two and three, densities were significantly higher in forested streams compared to other land-use categories within the same clusters (Figure 7). In cluster four, urban streams had significantly lower densities of YOY than streams in pasture or forested watersheds. There were no differences in densities between land-use categories in cluster eleven. Perhaps more importantly, the interactive effect cluster*land use was also significant ($P = 0.03$) indicating the effects of land use depend on the natural conditions within the watersheds. Clusters three and four had the highest densities of YOY in pasture watersheds (Figure 8). Cluster eleven had significantly lower densities than other clusters in forested watersheds. Densities of YOY were relatively low in all clusters in urban watersheds with cluster three obtaining the highest mean value.

Factorial ANOVA for densities of age-1 smallmouth bass was significant ($F_{11, 34}$ = 4.38, P = 0.001). The main effects of cluster (P = 0.002) and land use (P = 0.006) were significant. Cluster three had the highest densities of age-1 fish compared to other clusters (Figure 6). In clusters two and three, densities were significantly higher in forested streams compared to other land-use categories (Figure 7). In cluster four, urban streams had significantly lower densities of age-1 fish than streams in pasture or forested watersheds. Like other age classes, there were no differences in densities between land-use categories in cluster eleven. The interactive effect of cluster*land use was also significant (P = 0.06). There were no significant differences in fish densities between clusters in urban watersheds. More importantly, clusters three and four had the highest densities of age-1 fish in pasture watersheds (Figure 9). In forested watersheds, cluster eleven had the lowest densities when compared to all other clusters.

Factorial ANOVA for densities of age-2^+ smallmouth bass was significant ($F_{11, 34}$ = 4.50, P = 0.001). The main effects of cluster (P = 0.002) and land use (P = 0.007) were significant. Cluster three had the highest mean densities but only cluster eleven was significantly lower (Figure 6). In clusters two and three, densities were significantly higher in forested streams compared to other land-use categories (Figure 7). In cluster four, urban streams had significantly lower densities of age-2^+ fish than streams in pasture or forested watersheds. There were no differences in densities between land-use categories in cluster eleven. Like models for other age classes, the interactive effect of cluster*land use was also significant (P = 0.03). Clusters three and four had the highest densities of age-2^+ fish in pasture watersheds (Figure 10). Cluster eleven had significantly lower densities than other clusters in forested watersheds. There were no significant differences in fish densities between clusters in urban watersheds.

Viewing the models for each age class together, several important patterns emerge. First, regardless of age class, the highest densities of fish occurred in clusters three and four. In two of three models, forested streams had significantly higher densities in cluster four when compared to other clusters. Cluster three and four had the highest densities of fish in pasture watersheds whereas cluster two densities were almost zero in this land-use category even though densities were at modest levels in forested watersheds. Urban streams were highly impacted in most all cases as was cluster eleven, regardless of land-use attribute.

Smallmouth bass occurrence in channel units and the influence of land use

In the 36 streams I sampled, 710 individual CUs were examined: 37% pool habitat, 27% runs, 10% vegetated edges, 25% non-vegetated edges, and 1% side channels. In streams where smallmouth bass were present, I examined 457 CUs.

Young-of-year fish occurred in all the CU types examined and were only absent from a CU type in three stream segments. Young-of-year fish were present in 35% of the CUs examined and included in the analysis. Smallmouth bass were more likely to be present than absent depending on land-use category (forest, pasture, or urban) (Chi-square = 15.35, $P = 0.0005$) and CU (Chi-square = 23.18, $P < 0.0001$), but not the interaction between land use and CU (Chi-square = 4.85, $P = 0.30$) indicating CU habitat use did not change depending on land use in the watershed. Young of year were equally likely to occur in stream segments in urban watersheds as in stream segments in pasture watersheds but were two times more likely to occur in forested watersheds than urban watersheds (e.g., from Table 3: -0.22 + 1.24 = 1.02, e^x (1.02) = 2.77) or pasture watersheds (e.g., from Table 3: -0.22 + 1.13 = 0.91, e^x (0.91) = 2.48). Regardless of land-use attribute, YOY were three times more likely to occur in pools than runs or vegetated-edge habitats.

Age-1 smallmouth bass used a variety of CUs but were generally absent from edgewater habitats. Age-1 fish were present in 31% of CUs examined that were also included in the analysis. Smallmouth bass were more likely to be present than absent depending on land-use category (Chi-square = 12.28, P = 0.002) and CU (Chi-square = 21.44, P < 0.0001) but like YOY, not the interaction between land use and CU (Chi-square = 3.51, P = 0.17). Age-1 fish were two times more likely to occur in stream segments located in pasture watersheds than urban watersheds but four times more likely to occur in stream segments in forested watersheds than urban watersheds (Table 4). Regardless of land-use attributes in the watershed, age-1 smallmouth bass were four and a half times more likely to occur in pools versus run habitats.

Age-2^+ smallmouth bass used pool and run CUs more than other habitats, achieving their highest densities in pools. Age-2^+ fish were present in 30% of the CUs examined that were included in the analysis. Smallmouth bass were more likely to be present than absent depending on land-use category (forest, pasture, or urban) (Chi-square = 13.10, P = 0.001), CU (Chi-square = 48.82, P < 0.0001) and perhaps more importantly, the interaction between land use and CU (Chi-square = 5.27, P = 0.07) indicating CU habitat use differed depending on land-use conditions in the watershed. There was a greater chance of age-2^+ smallmouth bass being present in streams located in pasture watersheds than urban watersheds, but an even greater likelihood of fish being present in forested watersheds than pasture watersheds (Table 5). Regardless of land-use attribute, smallmouth bass were more likely to occur in pools than runs. Fish were equally likely to be present or absent from pool habitats in forested and urban streams whereas they were more likely to be present than absent in pools in pasture watersheds. Perhaps more importantly was the interactive effect where fish were much more likely to occur in run habitats in forested or pasture watersheds than in urban watersheds (Logit estimate = 23.22, Chi-square = 1113.0, $P < 0.0001$ and Logit estimate = 23.88, Chi-square 3247.7, $P < 0.0001$, respectively).

Discussion

Land use was the most significant variable in my decision tree models for each age class with forested watersheds resulting in the highest densities of smallmouth bass. Numerous other researchers have found a positive relation between forest cover and fish-assemblage structure and densities (Steedman 1988; Maret et al. 1997) whereas urbanization (Scott et al. 1986; Weaver and Garman 1994; Onorato et al. 2000; Walters et al. 2005) and to a lesser extent, pasture (Meador and Goldstein 2003) result in degraded community structure. Land use was the only variable significant in my age-1 model, whereas several natural in-channel features contributed to increases or decreases in densities of smallmouth bass. In my YOY and age-2^+ models, increases in discharge within forested watersheds resulted in ≥ four fold increases in densities. Smallmouth bass are expected to increase in density as stream size increases (Zorn et al. 2001; Brewer et al. 2007; Dauwalter et al. 2007). Generally, hydraulic variation is lower in larger streams and habitat characteristics are more stable. Highly variable flows in smaller streams affect reproductive success (Orth and Newcomb 2002) and a lack of deeper-water habitats and other abiotic factors (e.g., temperature; Coutant 1975) may result in marginal conditions for adult piscivores to thrive in smaller streams (Schlosser 1987). It appears this relationship is also applicable for YOY; however, as anticipated by the optimum temperature (29°) for YOY growth (Shuter and Post 1990), higher temperatures in smaller streams were important to this life stage. In watersheds classified by pasture land use, high percentages of fine sediments resulted in low densities of smallmouth bass. Excess fine sediments likely provide unsuitable habitat for important macroinvertebrate prey of smallmouth bass. Sedimentation due to agricultural (Lenat 1984) and rangeland (Meador and Goldstein 2003) land-use practices is indicated as a factor in fish population declines; likely, pasture land use has a similar impact. However, macroinvertebrate fauna may be enhanced with increasing amounts of pasture land use until some threshold is reached (Quinn and Hickley 1990; Quinn 2000) which may explain why densities of smallmouth bass increased with a slight increase in fine sediment and then declined as the percentage in the channel continued to increase.

Nonlinear responses to land use are expected when a species exhibits a threshold response to a particular stressor. Decision tree models are valuable in this context as they are amicable to nonlinear data and may aide in identification of thresholds. In my study, I retained the ordinal variable to describe land-use category (i.e., forest, pasture, or urban stream) because it explained more variation than using the percentage of forest in the watershed. However, in each case, if percent forest was used rather than the ordinal variable, it replaced the ordinal variable in the model and each split near 70%, resulting in a five fold increase in densities when compared to densities in streams located in watersheds with < 70% forest. I was unable to identify any noticeable threshold for the other land-use categories; however, in all but one case, urban streams had lower densities than streams classified in other categories indicating a disproportionate effect when considering the amount of urban land use in each watershed (the maximum amount of urban land use in any watershed was 22% but the mean of all urban streams was only 6%). Other researchers have identified significant changes in biota in watersheds with > 10% urban influence (*see* Paul and Meyer 2001 for a review). Mean densities of fish in pasture streams were intermediate in nature and more variable depending on the natural conditions in the watershed. It is difficult to make comparisons between my findings and others regarding the influence of pasture land use as many consider this part of agriculture whereas I distinctly separated pasture from row crops. However, Meador and Goldstein (2003) argue pasture agriculture has a reduced impact when compared to row crop agriculture.

Natural-occurring conditions in the watershed that resulted in the higher mean densities of smallmouth bass were > 50% coarse-textured soils (Clusters three and four). The importance of rocky substrates to smallmouth bass has been found by numerous other researchers (Hubert 1981; Paragamian 1981; Lyons 1991; Pflieger 1997). In a previous study (Brewer et al. 2007), I predicted the probability of smallmouth bass occurrence to nearly double when greater than 58% coarse-textured soils were in the watershed; it appears that mean densities also approximately double. More interesting are the changes that occur when land use is considered within the natural-occurring framework.

Each land-use category appears to have a unique effect when viewed in light of the natural conditions occurring in the watershed. In each cluster, except cluster eleven, forested streams had the highest densities of smallmouth bass. Two possible reasons exist for the situation in cluster eleven. First, it may be that the natural conditions within cluster eleven are such that increasing the percent of forest within those watersheds does little to improve conditions for smallmouth bass. Second, "legacy effects" (Allen 2004) from historical natural or anthropogenic disturbances (Harding et al. 1998) may inhibit smallmouth bass fitness in these regions where channel alterations may exist with an unknown recovery time. I cannot determine which scenario may be the case; however, the first scenario seems more likely given the spatial distribution of sampling sites within this cluster. These sites were not geographically clustered; however, these sites and the conditions within this cluster appear to follow the distributional limits of smallmouth bass in Missouri (*see* Brewer et al. 2007). Cluster two, on the other hand, has appreciable densities of smallmouth bass in forested watersheds, but other land-use attributes (i.e., urban or pasture) appear to have a strong negative effects on smallmouth bass abundance. Urban streams, regardless of cluster, have extremely low densities of fish. However, the amount of pasture in the watershed appears to have a larger impact on streams in cluster two (which had relatively low densities in forested watersheds) when compared to other clusters. I interpret this to mean the natural conditions within cluster two are marginal thus pasture influences largely decrease the potential of a smallmouth bass recreational fishery within these regions. It is unclear, given the amount of variation in streams located in pasture and forested watersheds in cluster four, whether there would be an impact on smallmouth bass densities due to watershed changes from forest to pasture. Whereas variation in densities within each cluster and land-use category is quite high, I argue the trends in the data are biologically meaningful. It appears the better the natural conditions are in the watershed for smallmouth bass, the more resilient these densities will be to land-use changes realizing that a threshold will likely exist where this will no longer be the case. This threshold, although unknown, is expected to be different because of the natural conditions that occur within each watershed. For example, the mean percentage of watershed in pasture land use is 82% for cluster two and 81% in cluster four but these similar percentages result in different effects.

Age-2^+ smallmouth bass use of CUs depended on land use in the watershed. The significant interactive effect was driven by the higher occurrence of smallmouth bass in run habitats in pasture or forested watersheds versus urban watersheds. This was likely due to the availability of run habitat in each respective land-use category. The mean percentage of run habitat was highest in forested watersheds (30%), followed by pasture watersheds (19%) and urban watersheds (11%). Alternatively, the amount of pool habitat was the lowest in forested watersheds (mean = 64%) compared to pasture and urban watersheds (mean = 79% and 76% respectively). Whereas it appears adult smallmouth are more likely to occupy pools than runs regardless of land-use activities in the watershed, the amount of run habitat appears to be important to the fishery. Age-2^+ smallmouth bass used run habitats more when they were available in appreciable amounts and the densities were higher in pool habitats (forested watersheds) with an increase in run habitat. Stream segments containing less percent pool when compared to other sampled segments in Oklahoma have also been found to have higher densities of smallmouth bass (Dauwalter et al. 2007). Sowa and Rabeni (1995) found a negative relation between smallmouth bass total density and percent pool area in Missouri streams. This indicates channel morphology exerts an influence over densities in individual CUs, especially within urban watersheds.

The interactive effect between land use and CU use was not significant to the younger age classes (YOY and age 1). Younger age classes appear, in this respect, to be more opportunistic than their adult counterparts. I describe them as opportunistic rather than generalists because they are clearly still affected by degraded habitats (i.e., lower densities in urban and pasture streams). However, they have the ability to use most all CUs though increases in velocity appear to limit their use of these habitats (i.e., reduce densities). Pert et al. (2002) review the discrepancies in habitat use by young-of-year smallmouth bass and distinguished between patterns observed between and among populations. In this study I examined among population differences in CU habitat use and results are in agreement with Pert et al. (2002) and others (Lobb and Orth 1991; Orth and Newcomb 2002; Deuwalter et al. 2007) who consider juveniles to be rather opportunistic in their use of local habitat. Regardless of their ability to use a variety of habitats, YOY and age-1 fish were still more likely to use pool habitats.

For management and restoration activities to be effective, we need a comprehensive understanding of the interactive effects between natural-occurring environmental conditions and anthropogenic influences. Here, I have identified changes in smallmouth bass densities that occur with different combinations of land-use activities in a variety of natural settings. To further address this issue, studies are needed that will examine the specific mechanisms that promote these changes. Additionally, work is needed to address how improvements in the landscape (usually defined as best management practices) affect these populations or if an alternative strategy is necessary. Nonetheless, the information presented here should help guide the location of improvements or types of improvements made. For example, it is unlikely that increasing the percentage of forest area in cluster eleven will increase smallmouth bass densities in this region. I argue that conditions in cluster eleven, signified primarily by high runoff potential, create naturally flashy stream conditions that will not be improved upon by increasing the percentage of forested habitat. These conditions occur outside of the state of Missouri and likely have the same implications for smallmouth bass management. The influence of the surrounding landscape clearly had an effect at multiple spatial scales but may be more complicated than expected due to prior anthropogenic activities (i.e., cluster eleven). Understanding the geomorphic connections between land-use attributes within natural settings and channel morphology may provide additional insight to the changes in biota occurring within these regions. Realizing the true connection between anthropogenic and natural settings is necessary to increase the effectiveness of conservation and management practices.

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TABLE 1.- Description of four strata established based on modeling results from Brewer et al. 2007. Natural-occurring conditions in each stratum were assigned based on the percentages of coarse-textured soils (CTS) and hydrologic soil group D (HSGD) in the watershed. Nine streams were assigned to each stream strata, three to each land-use category. The mean percentage of each land use is provided for each land-use designation

Stream stratum	Natural Conditions	Land-use designation	% Forest	% Urban	% Pasture
1	CTS < 50%	Forest	81	< 1	18
(Cluster 2)	HSGD < 7%	Pasture	16	< 1	82
		Urban	29	13	53
2	CTS < 50%	Forest	62	< 1	23
(Cluster 11)	HSGD > 7%	Pasture	20	< 1	46
		Urban	29	5	40
3	CTS 50-90%	Forest	62	< 1	37
(Cluster 4)		Pasture	18	< 1	81
		Urban	35	4	60
4	CTS > 90%	Forest	82	< 1	18
(Cluster 3)		Pasture	33	< 1	66
		Urban	31	2	66

TABLE 2.- Statistical descriptions (mean, standard deviation [Std dev], minimum, and maximum) for habitat variables used in model development. Italics denote ordinal variables with the number of levels included in parentheses. Landscape factors were calculated for the entire watershed and in-channel variables were quantified for specific stream segments

Variable spatial scale	Model variable	Mean	Std dev	Minimum	Maximum
Landscape	Watershed area (km)	254	171	53	795
	Land use (3)	N/A	N/A	N/A	N/A
In-channel	Discharge (m^3/s)	0.29	0.31	0	1.25
	Pool (%) in segment	70	23	21	100
	Temperature (°C)	24	4	16	31
	Channel sinuosity (m/m)	1.20	0.21	1.00	2.09
	Mean substrate size class (6)	3.2	0.43	2.4	4.4
	Fines (%)	6.23	5.41	0	20
	Riparian distance (m)	0.51	0.36	0	1.41
	Max residual depth in segment (cm)	122	60	29	351
	Mean width:depth (m/m)	36	9	21	63

TABLE 3.- Generalized linear model results for young-of-year smallmouth bass. Asterisks identify significant logit values (P < 0.10) indicating an unequal probability of presence versus absence. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

	Land use			
CU	Pasture	Forest	Urban	
	-0.42	0.33	-0.22	-0.10
Pool	(0.65)	(1.39)	(0.80)	(0.90)
	* -1.43	-0.15	* -2.08	* -1.22
Run	(0.24)	(0.86)	(0.13)	(0.30)
	* -1.88	* -0.87	* -1.09	* -1.28
Vegetated edge	(0.15)	(0.42)	(0.34)	(0.28)
	* -1.24	-0.22	* -1.13	
	(0.29)	(0.80)	(0.32)	

TABLE 4.- Generalized linear model results for age-1 smallmouth bass. Asterisks identify significant logit values ($P < 0.10$) indicating an unequal probability of presence versus absence. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

	Land use			
CU	Pasture	Forest	Urban	
Pool	* -0.72 (0.49)	0.09 (1.09)	* -0.57 (0.57)	* -0.40 (0.67)
Run	* -1.54 (0.21)	* -0.95 (0.39)	* -3.26 (0.04)	* -1.92 (0.15)
	* -1.13 (0.32)	* -0.43 (0.65)	* -1.91 (0.15)	

TABLE 5.- Generalized linear model results for age-2^{+} smallmouth bass. Asterisks identify significant logit values ($P < 0.10$) indicating an unequal probability of presence versus absence. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

	Land use			
CU	Pasture	Forest	Urban	
	* -0.56	0.33	-0.33	-0.19
Pool	(0.57)	(1.39)	(0.72)	(0.83)
	* -2.14	* -1.48	* -25.36	* -9.66
Run	(0.12)	(0.23)	(0.00)	(0.00)
	* -1.35	* -0.58	* -12.85	
	(0.26)	(0.56)	(0.00)	

FIGURE 1.- Map of Missouri, showing the distribution of sampling sites, by cluster and stream type (pasture, forest, and urban)

FIGURE 2.- Mean turbidity (NTU) +/- 90% confidence intervals for streams in each land use category by cluster

FIGURE 3.- Decision tree model showing the predicted densities (number/m^2) of young-of-year smallmouth bass based on landscape and in-channel scale variables. The predicted density (bold numbers) and sample size (in parentheses) are shown for the entire data set and at each node. Child nodes are represented by circles

FIGURE 4.- Decision tree model showing the predicted densities (number/m^2) of age-1 smallmouth bass based on landscape and in-channel scale variables. The predicted density (bold numbers) and sample size (in parentheses) are shown for the entire data set and at each node. Child nodes are represented by circles

FIGURE 5.- Decision tree model showing the predicted densities (number/m^2) of age-2^+ smallmouth bass based on landscape and in-channel scale variables. The predicted density (bold numbers) and sample size (in parentheses) are shown for the entire data set and at each node. Child nodes are represented by circles

FIGURE 6.- Mean density (number/m^2) of smallmouth bass (+/- 90% confidence intervals) in associated cluster. Different letters indicate significant differences (based on rank transformed values) in densities among clusters for individual age classes

FIGURE 7.- Mean density (number/m^2) of smallmouth bass (+/- 90% confidence intervals) by cluster and land-use type (young of year on top panel, age-1 on middle panel, and age-2^+ on bottom panel). Different letters indicate significant differences between land-use types within each cluster (based on rank transformed values)

FIGURE 8.- Mean density (number/m^2) of young-of-year fish (+/- 90% confidence intervals) by cluster and land-use type. Different letters indicate significant differences between land-use types between clusters (based on rank transformed values)

FIGURE 9.- Mean density (number/m^2) of age-1 fish (+/- 90% confidence intervals) by cluster and land-use type. Different letters indicate significant differences between land-use types between clusters (based on rank transformed values)

FIGURE 10.- Mean density (number/m^2) of age-2^+ fish (+/- 90% confidence intervals) by cluster and land-use type. Different letters indicate significant differences between land-use types between clusters (based on rank transformed values)

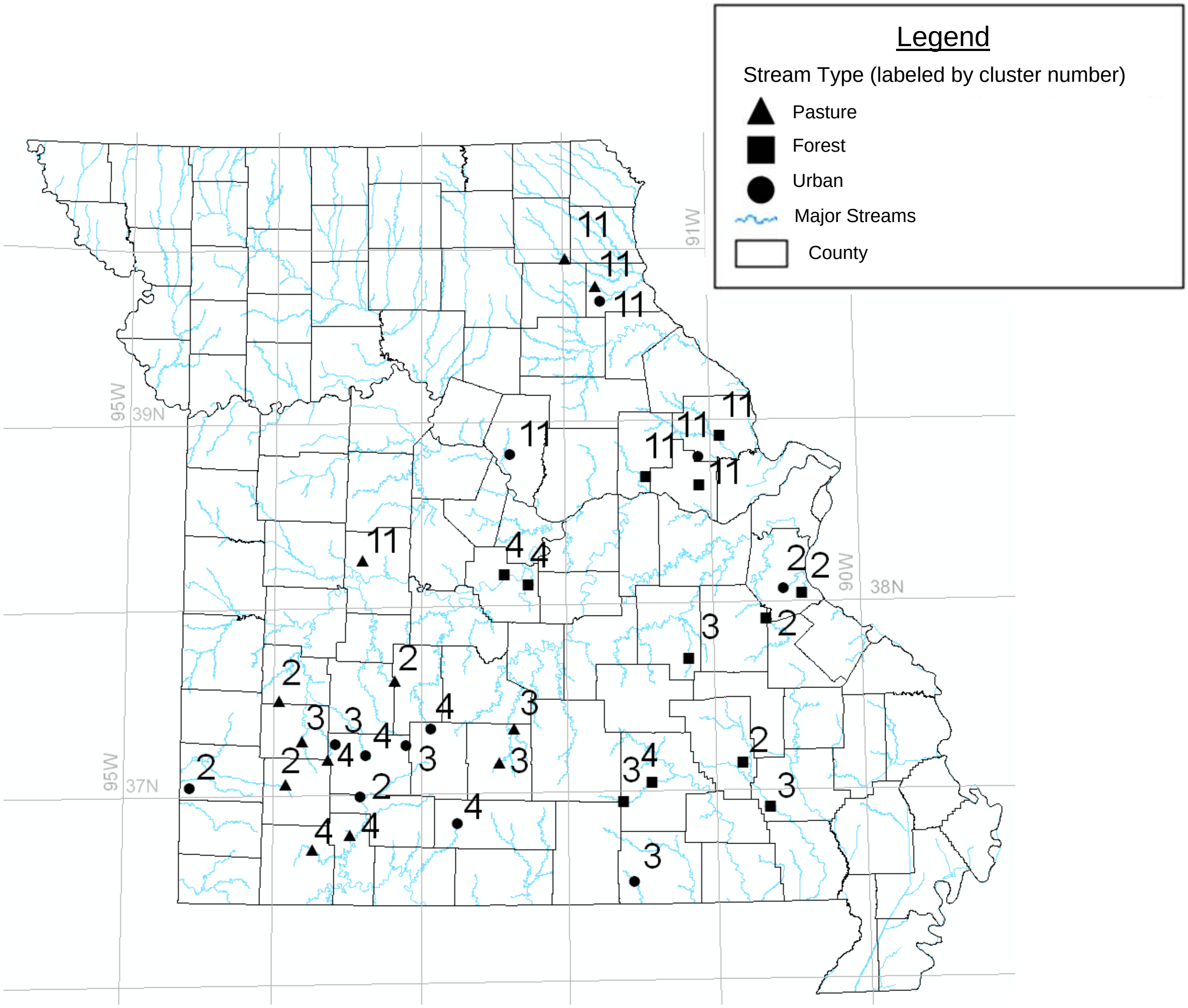
Legend
Stream Type (labeled by cluster number)
Pasture
Forest
Urban
Major Streams
County
91W
95W
39N
90W
38N
95W
37N

FIGURE 1.-

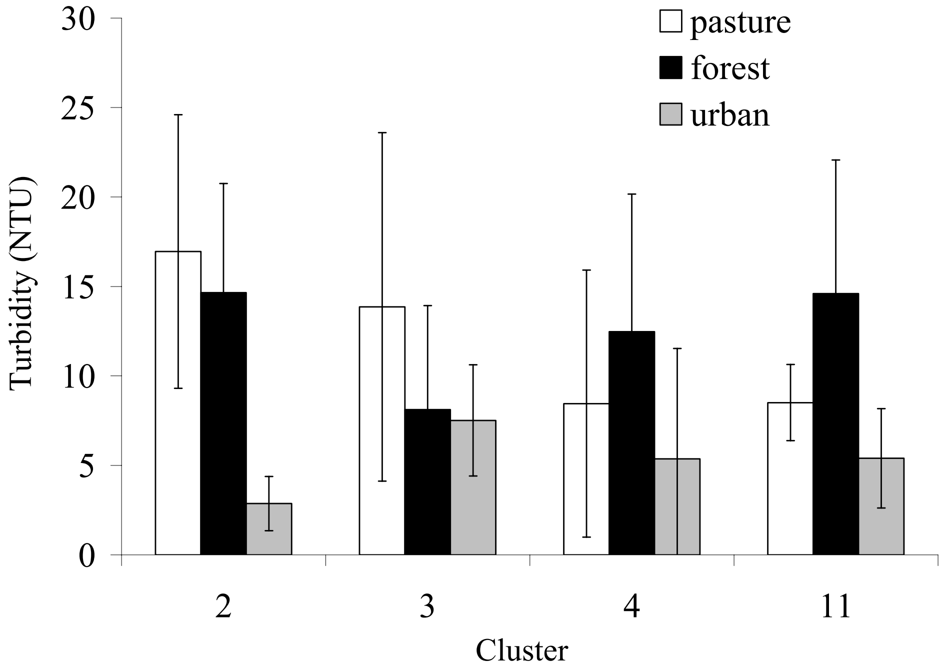
30
25
20
15
10
5
0
Turbidity (NTU)
pasture
forest
urban
2
3
4
11
Cluster

FIGURE 2.-

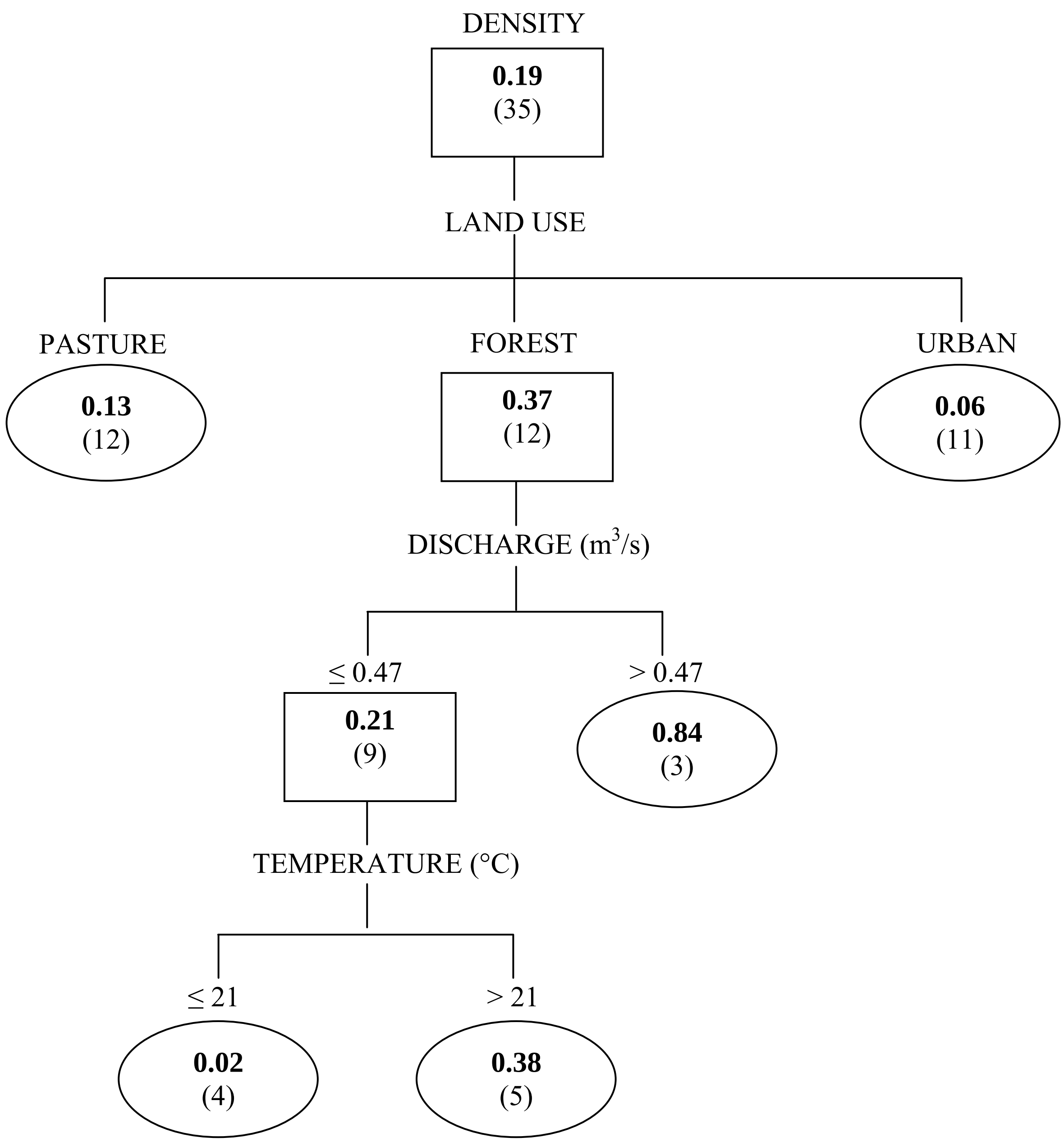
DENSITY
0.19
(35)
LAND USE
PASTURE
0.13
(12)
FOREST
0.37
(12)
URBAN
0.06
(11)
DISCHARGE (m3/s)
≤ 0.47
0.21
(9)
> 0.47
0.84
(3)
TEMPERATURE (°C)
≤ 21
0.02
(4)
> 21
0.38
(5)

FIGURE 3.-

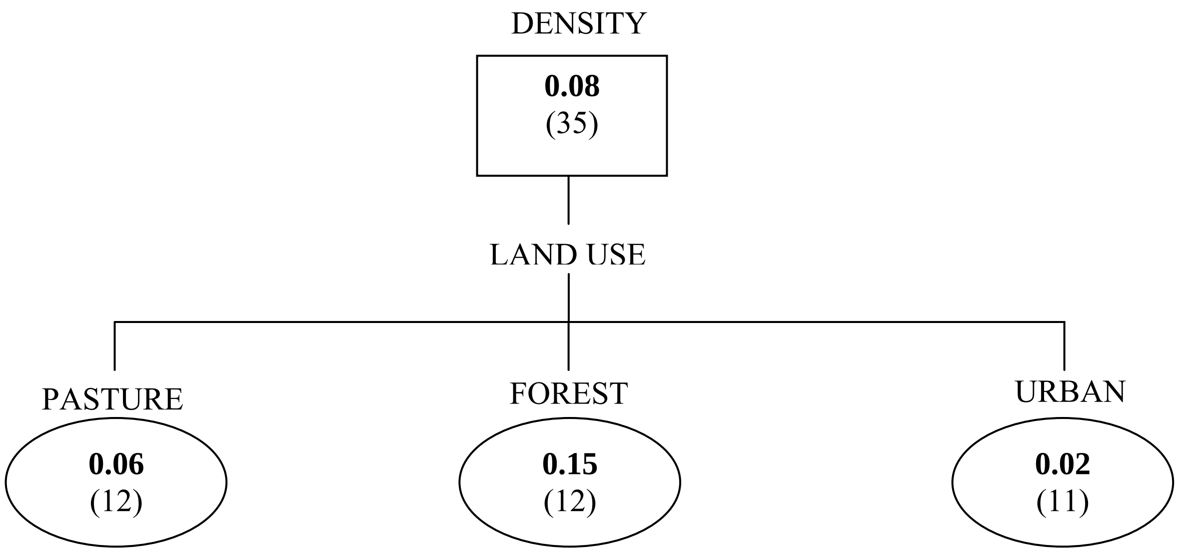
DENSITY
0.08
(35)
LAND USE
PASTURE
0.06
(12)
FOREST
0.15
(12)
URBAN
0.02
(11)

FIGURE 4.-

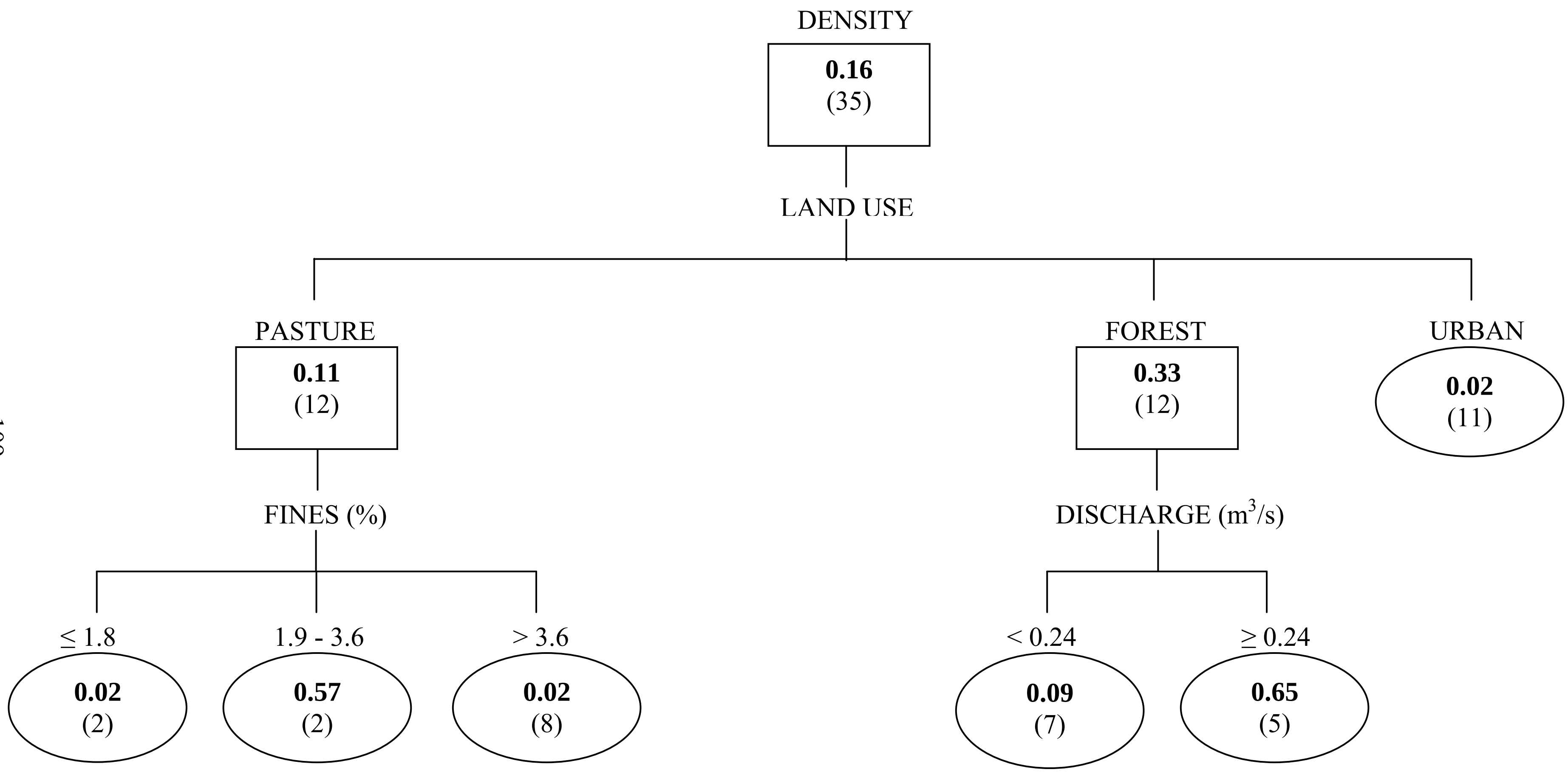
DENSITY
0.16
(35)
LAND USE
PASTURE
0.11
(12)
FOREST
0.33
(12)
URBAN
0.02
(11)
FINES (%)
DISCHARGE (m3/s)
≤ 1.8
0.02
(2)
1.9 - 3.6
0.57
(2)
> 3.6
0.02
(8)
< 0.24
0.09
(7)
≥ 0.24
0.65
(5)

FIGURE 5.-

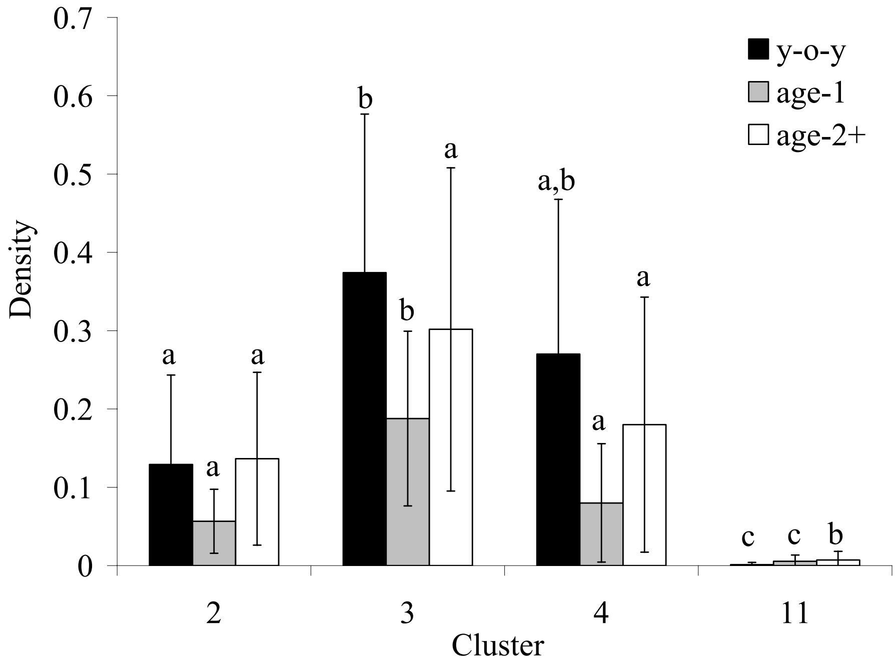
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Density
y-o-y
age-1
age-2+
b
a
a,b
a
b
a
a
a
a
c
c
b
2
3
4
11
Cluster

FIGURE 6.-

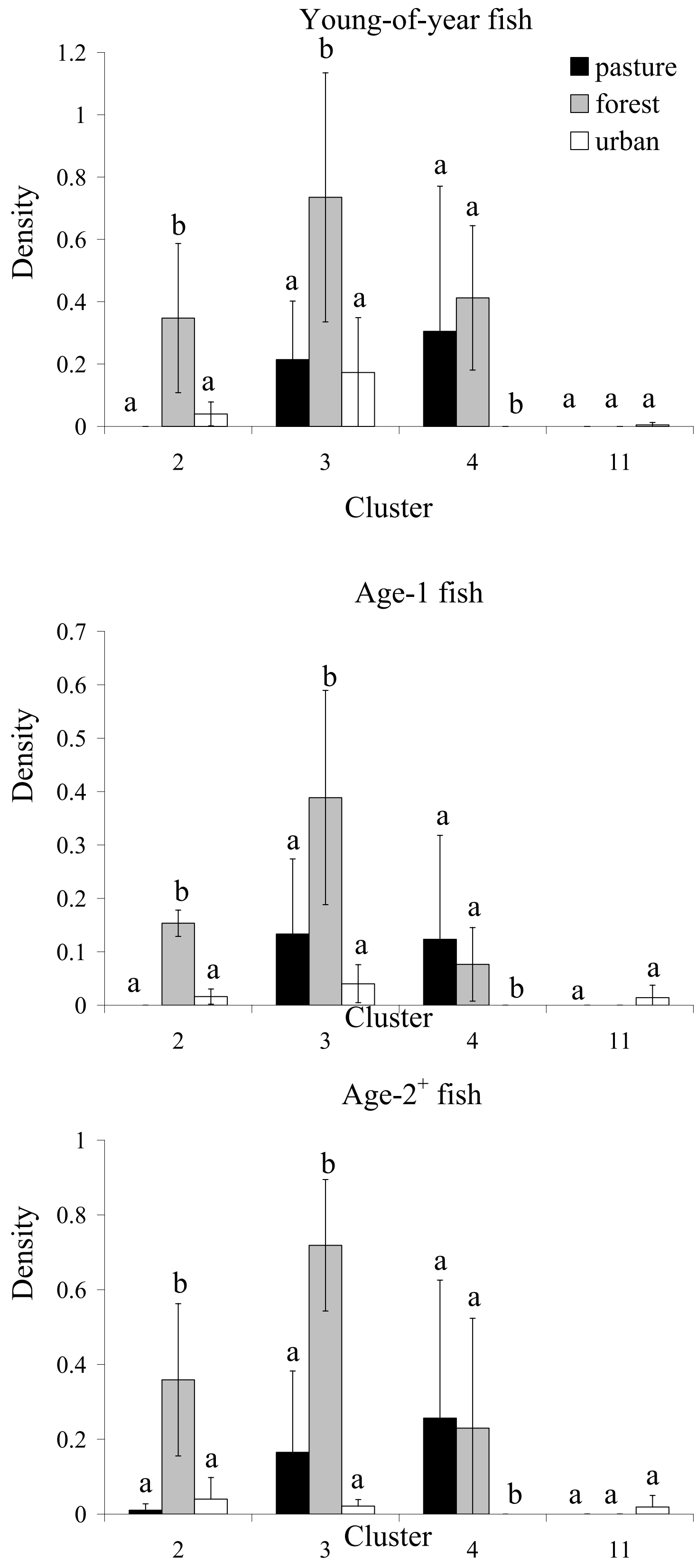
Young-of-year fish
pasture
forest
urban
Density
1.2
1
0.8
0.6
0.4
0.2
0
a
b
a
a
b
a
a
a
b
a
a
a
2
3
4
11
Cluster
Age-1 fish
Density
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
b
a
a
b
a
a
a
b
a
a
Cluster
2
3
4
11
Age-2+ fish
Density
1
0.8
0.6
0.4
0.2
0
a
b
a
a
b
a
a
a
b
a
a
a
Cluster
2
3
4
11

FIGURE 7.-

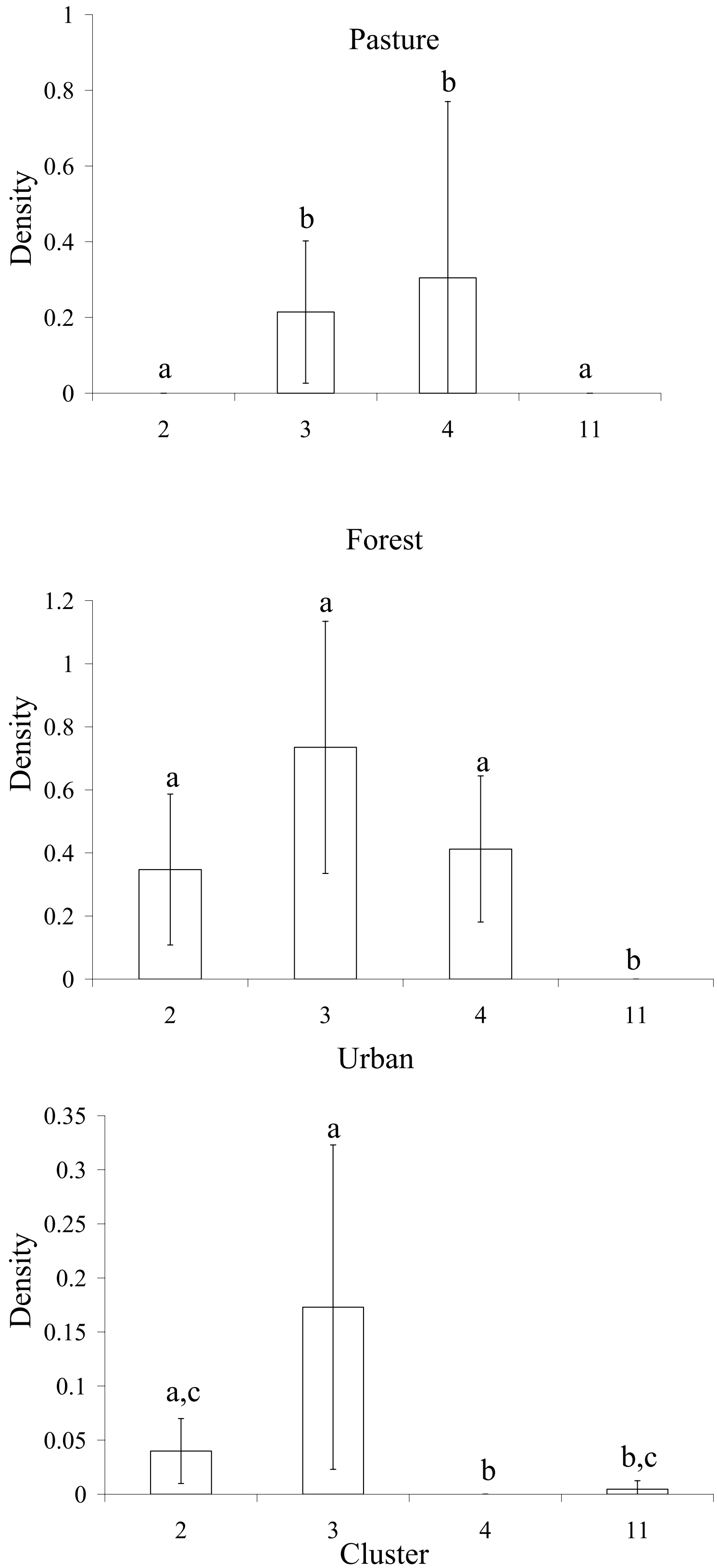
Pasture
Density
1
0.8
0.6
0.4
0.2
0
a
b
b
a
2
3
4
11
Forest
Density
1.2
1
0.8
0.6
0.4
0.2
0
a
a
a
b
2
3
4
11
Urban
Density
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
a,c
a
b
b,c
2
3
4
11
Cluster

FIGURE 8.-

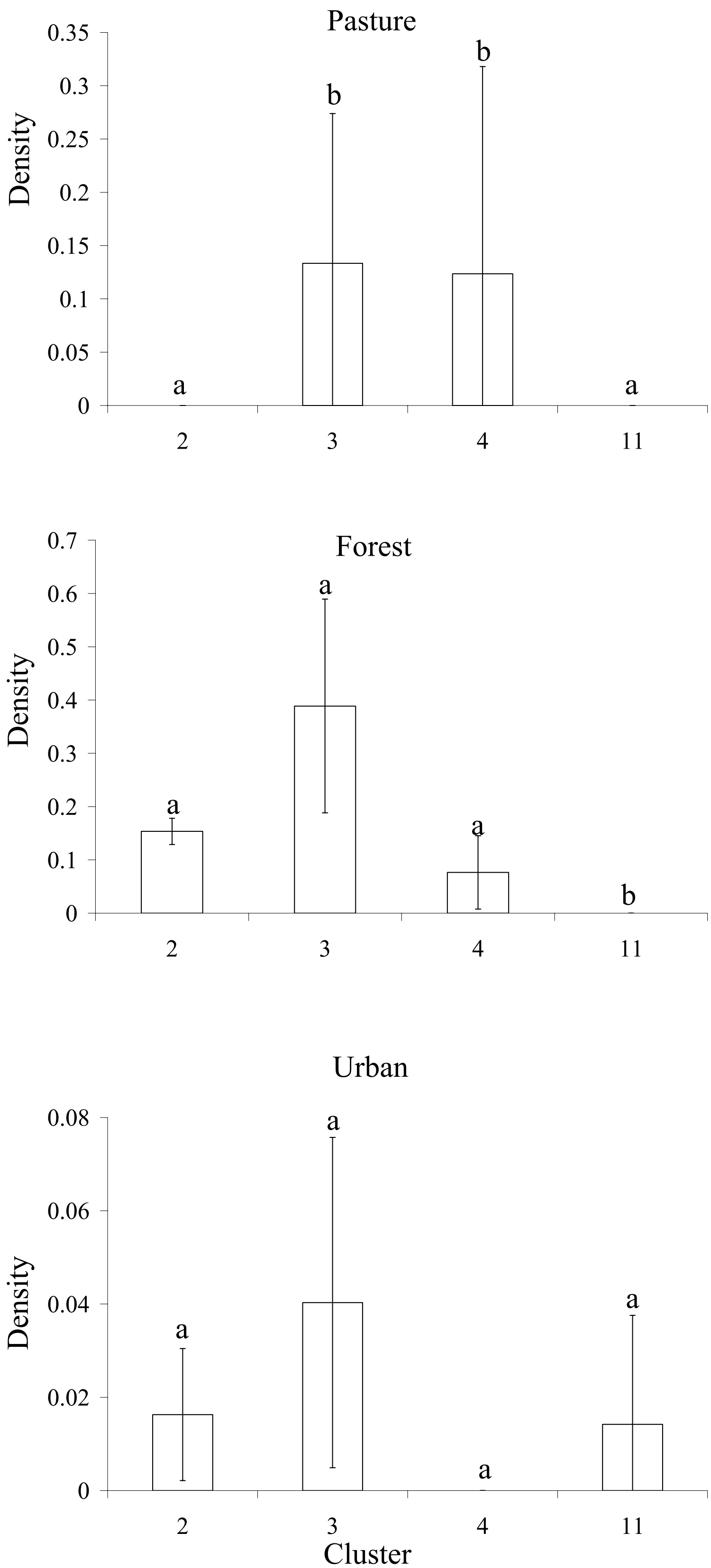
Pasture
Forest
Urban
Density
Cluster
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0.7
0.6
0.5
0.4
0.08
0.06
0.04
0.02
2
3
4
11
a
b

FIGURE 9.-

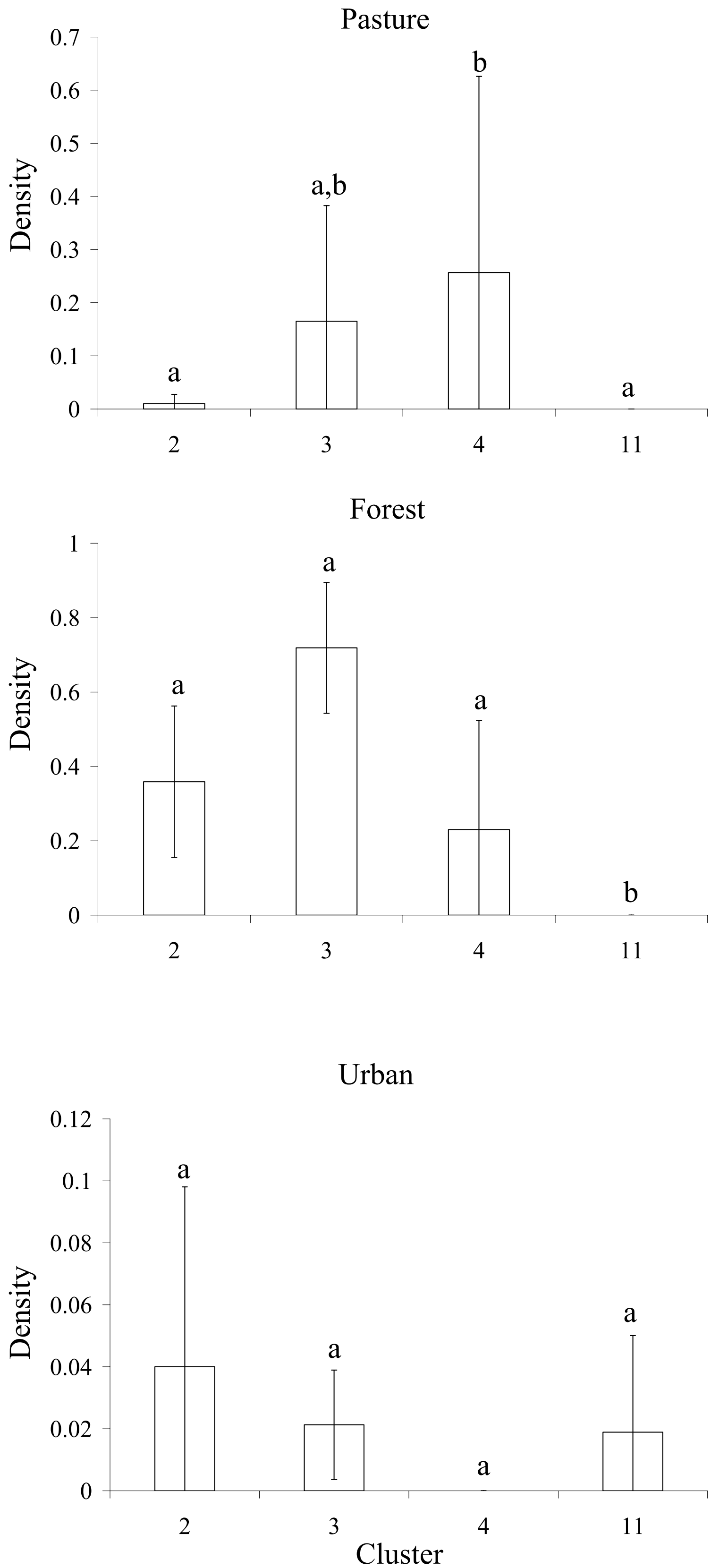
Pasture
Density
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
a,b
b
a
2
3
4
11
Forest
Density
1
0.8
0.6
0.4
0.2
0
a
a
a
b
2
3
4
11
Urban
Density
0.12
0.1
0.08
0.06
0.04
0.02
0
a
a
a
a
2
3
4
11
Cluster

FIGURE 10.-

Chapter 4

Groundwater influence on the distribution and abundance of riverine smallmouth bass, *Micropterus dolomieu,* in a highly altered landscape

Abstract.- This study examines how groundwater contributions to streamflow relate to the distribution and abundance of smallmouth bass *Micropterus dolomieu* in a highly altered landscape (predominately pasture) in Missouri USA. My objectives were to determine how smallmouth bass densities compared between streams with high (HSF) versus low (LSF) spring flow, determine which channel units (CU) were used by different age classes and if habitat use depended on spring-flow influence, determine if temperature selection occurred by different age classes at the microhabitat level and if the length-frequency distributions of young of year (YOY) differed depending on spring-flow influence. Mean densities of younger age classes were significantly higher in HSF stream segments. There was no significant difference in densities of age-2^+ fish. Young of year were more likely to be present than absent from CUs depending on spring-flow category and CU, but not the interaction between spring flow and CU. Older age classes were more likely to be present depending on CU but not spring-flow category or more importantly, the interaction between the variables. All age classes were more likely to be present in pools than other CUs. Microhabitat temperature selection differed among age classes. YOY selected warmer temperatures with a gradual shift toward cooler temperatures for older age classes. Total length of YOY was skewed toward larger individuals in streams classified by LSF whereas total length was skewed towards smaller individuals in stream classified by HSF. Significant groundwater influence appears to be

related primarily to increased hatch or survival of YOY and the availability of appropriate temperatures for adult smallmouth bass growth.

The influence of groundwater on fish habitat in warmwater streams can be considerable. Sufficient groundwater can modify the annual temperature regime to be cooler in summer and warmer in winter, and moderate the annual hydrograph to provide greater base flows and dampened flows during spates. Flow and temperature are both factors implicated in success of populations of riverine smallmouth bass *Micropterus dolomieu.*

Groundwater contributions provide stable hydrologic regimes. Poff and Allan (1995) suggested stable base-flow conditions were indicative of habitat persistence for fish assemblages. The effect of high flow on smallmouth bass has been reported most often as the interruption of spawning activity (Graham and Orth 1986; Lukas and Orth 1995) and the destruction of nests containing egg and wash out of fry stages (Pflieger 1975; Simonson and Swenson 1990). The positive relation of higher base flows to increased abundances of smallmouth bass has been predicted from models of Missouri streams (Brewer et al 2007).

Water temperature exerts a substantial influence on the abundance, growth, and survival of fishes. Temperature is critical to the timing of life-history events, especially reproduction (Fry 1971). Coutant (1975) identified temperature as the most important factor determining the number of smallmouth bass offspring and subsequent year class strength. High temperatures result in physiological stress and increased metabolic demand on fishes which may result in slower growth, susceptibility to disease, and lower survival rates. Summer temperatures in Missouri streams have been shown to regularly exceed optimum growth temperatures of smallmouth bass (Zweifel et al. 1999; Whitledge et al. 2006) Stream systems with groundwater inflows can provide refuge from extreme temperatures experienced during summer periods (Matthews and Berg 1997). This may be especially important in larger streams that benefit less from riparian shading than smaller streams (Hynes 1970; Whitledge et al. 2006). Spring-fed systems also provide warm-water refuges to smallmouth bass during winter months (Peterson and Rabeni 1996) which may increase overwinter survival, especially for young-of-year (YOY) fishes.

Land-use changes have and will continue to alter stream hydrology and water temperatures. Storm flows typically increase in frequency and magnitude in altered watersheds (Allan 2004). Increases in mean annual flows in the Kankakee River, Illinois were attributed to an increase in land clearing and urbanization (Peterson and Kwak 1999). Riverine smallmouth bass densities in the Kankakee River Basin were predicted to decline under the combined effect of changing climate and altered land use effects on both temperature and flow regimes (Peterson and Kwak 1999). Land use changes from natural conditions to agriculture not only increase peak flows, but also reduce base-flow conditions (Poff et al. 1997). Reductions in base-flow often result in increased areas of shallow-water habitat that are more susceptible to thermal increases (Richards et al. 1996). The loss of riparian and landscape vegetation increases stream temperatures due to increased exposure of the stream to thermal warming and the warming of surface runoff on the altered landscape (Paul and Meyer 2001), which may only be marginally mitigated by proper riparian management (Whitledge et al. 2006).

Significant groundwater contributions in a stream may mitigate the effects of anthropogenic activities. In a previous study (Brewer et al. 2007, *see* Chapter 2 herein), I identified spring flow as an important natural-occurring environmental feature in increasing the predicted relative abundance of smallmouth bass. This chapter concentrates efforts on understanding how this natural-occurring environmental feature (i.e., spring flow) and temperature relate to the distribution and abundance of smallmouth bass in a highly altered landscape. My objectives were to 1) determine how smallmouth bass densities of different age classes (young of year [YOY], age 1 and age 2^{+}) relate to spring flow, 2) determine if smallmouth bass were more likely to occur in particular channel units depending on spring-flow influence, 3) determine if temperature selection (where use is greater than availability) occurred at the microhabitat level from a subset of streams sampled and 4) determine if differences existed in the distributions of YOY total length depending on spring-flow classification (high versus low).

Study Area

Sampling was conducted on 13 streams (Table 1) located in the southwestern portion of the Ozark Highland biogeographic region of Missouri (Nigh and Schroeder 2002). The Ozark Highland region is restricted to southern Missouri and is characterized by extensive geologic erosion, carbonate bedrock, and karst features. Study streams were further restricted to the Central Plateau, Osage-Gasconade Hills, White River Hills, and Springfield Plains sections (Nigh and Schroeder 2002). Many of the streams within these sections are spring-fed and have low suspended sediment loads except during periods of high runoff. These sections also have a unique interspersion of streams with high and low spring-flow influence located in a highly altered landscape. This region is likely the most altered by human activities in the Ozark Highlands with native grasses, savannas, and woodlands having been converted largely to pasture agriculture for cattle (Nigh and Schroeder 2002). Remaining woodland areas are primarily restricted to the most dissected parts of these sections.

Methods

Study design and site selection.- Thirteen stream segments were selected using criteria that allowed assessment of spring-flow influence on smallmouth bass densities in highly altered watersheds. Geographic information system (GIS) was used to select an initial pool of stream segments. Criteria pertaining to natural variation in habitat conditions expected to influence smallmouth bass densities were kept relatively constant (*see* Brewer et al. 2007 for a complete description); hydrologic soil group D was < 7% in all watersheds and stream sizes were kept in the range of Shreve Link 50-150. Rocky soils are also related to the distribution and abundance of these fish but soils in this region are predominately rocky (but less than 90%) so this variable was not used to restrict my pool of stream segments. Stream segments were only included in my initial pool of sample sites if there was < 30% of forested land in the watershed. Stream segments in these highly altered watersheds were then classified into high spring flow (HSF) or low spring flow (LSF) groups. I added to an existing GIS coverage of spring-flow volume (588 springs) developed by the Missouri Department of Natural Resources using information on an additional 54 springs obtained from Vineyard and Feder (1982). Spring flows above 2 standard deviations (> 55 cfs) were removed and then a median flow (0.28 cfs) was calculated and applied to the remaining springs with unknown flows (primarily smaller springs). The mean spring-flow value was calculated for stream segments included in my initial sample pool and I assigned those segments with spring flows > 1 standard deviation above the mean to a HSF group and those segments with spring flows > 1 standard deviation below the mean to a LSF group. My final pool of potential sampling sites was made based on proximity to public lands or roads, condition of the riparian corridor (relatively intact), interspersion of high spring-flow and low spring-flow sites, and adequate flow conditions (not drying).

Fish sampling.- Multiple methods of sampling were used to balance my ability to detect younger age classes and adults: a combination of snorkeling and above-water visual observation. The choice of method used depended on water depth and surface agitation (i.e. wind conditions). Underwater observation (snorkeling) was my primary sampling method and was used when depths were > 0.5-m. Above water observation was used in depths were < 0.5 m if surface conditions did not impede observation. Above water visual observation was used in edge-water habitats, run habitats of smaller streams, and extremely shallow pools. This method was incorporated because a pilot study I conducted revealed a compromise in my ability to detect YOY smallmouth bass while snorkeling versus above-water observation in shallow-water habitats. This method was used to sample a portion of CUs in every stream sampled so any potential bias should be adequately dispersed across treatments.

Fish sampling was conducted in July - September 2006. At each site, a minimum of 40 times the channel width was sampled. Beginning at the most downstream point of the site, CUs were sampled independently throughout the site so densities of each age class (YOY, age 1 or age 2^+) of smallmouth bass could be determined for individual CUs in addition to the entire stream segment.

Each sampling gear had a specific protocol. When snorkeling was used, two snorkelers began at the downstream end of the CU and moved upstream at a rate of approximately 5 $m^2 \bullet min^{-1}$ to the end of the CU (either marked discretely with a flag or using natural features). Each snorkeler limited their observations to half of the stream and covered their half by swimming in a zig-zag pattern. Snorkelers reduced the possibility of double counting individual fish at the center of the stream by pointing out any fish counted in this area to the other snorkeler. The same approach was used for above-water visual observations by walking slowly through the CUs in a zig-zag pattern and verbally identifying fish counted with the other observer. Exception to this approach occurred only when sampling edgewater habitats. In non-vegetated edge habitats, above-water observations were made by one observer on the bank and another streamside. In shallow vegetated-edge habitats, observers on each side would slowly look through the stands of vegetation (usually water willow *Justicia Americana*) working from the downstream to upstream end of the CU; if water depth permitted (≥ 0.25 m), the streamside observer would snorkel slowly along the outside band of the water willow. Regardless of method used, when a smallmouth bass was encountered, the observer placed a lead-weighted fluorescent flag on the substrate at the location where the fish was observed and then used a sweeping motion (if snorkeling) to encourage the fish to move downstream.

Stream segment and channel unit habitat.- Discharge, wetted width, CU area, and pool temperature were measured on site at the time of fish sampling. Discharge was calculated using the velocity-area method (Gordon et al. 2004) at a minimum of two locations in each stream segment. Mean wetted width was determined for each stream by measuring wetted width every 20 m throughout the site. Each site was mapped prior to sampling so the relative percentages of CUs could be determined and flags could be placed as CU boundaries where necessary. I simplified the CU classification system proposed by Rabeni and Jacobson (1993) and used six CU types: pools, riffles, runs, vegetated edges, non-vegetated edges, and side-channel habitats (i.e., forewaters and backwaters). Pool temperature (°C) was measured at mid-pool depth with a hand thermometer in a minimum of three pools or three pool sections (when pools were > 200 m in length) at each site.

Temperature microhabitat.- A subset of stream segments (n = 4) was used to determine if temperature was selected for at the microhabitat scale. Transects, perpendicular to stream flow, were established in each CU at 10-m intervals to determine the availability of temperatures (°C). Temperature was measured at a minimum of three points along each transect with additional points located in areas where noticeable changes occurred. Temperature was also measured at each fish location by placing thermometers on the substrate surface of any location where a smallmouth bass was observed and then returning to retrieve the thermometers after each CU was sampled. Temperature was measured by holding a thermometer in the water column until the reading stabilized when fish were identified suspended in the water column (< 5% occurrence).

Young-of-year length distributions.- A subset of stream segments (n = 10) was used to determine if the distribution of fish lengths was significantly different between segments with HSF influence versus segments with LSF influence. Total length (TL) of each YOY smallmouth bass was visually estimated and recorded by each observer. Estimating TL of fish in the range encountered in YOY was relatively accurate after substantial practice. Observation and subsequent capture of 20 YOY in Rocky Creek (a tributary of the Current River, Shannon County, Missouri) indicated minimal error (mean +/- 95% confidence intervals: 1.8 mm +/- 0.63) associated with my visual estimations of TL.

Analyses.- Prior to analyses on stream segment or CU habitat use, I removed data collected from Big Sugar Creek due to significant local upwelling and cooling due to water transfer beneath gravel bars. Differences in mean discharge, turbidity, or temperature between the remaining stream segments (n = 12) assigned to either high or low spring-flow categories were assessed by conducing a Shapiro-Wilks test to determine whether data were normally distributed. Because data were normally distributed ($P > 0.05$), I used a t-test to determine if significant difference ($P < 0.10$) existed between the means of each stream segment descriptor (discharge, turbidity, or temperature) in each spring-flow category.

The Shapiro-Wilks test indicated stream segment density data were not normally distributed ($P < 0.05$) and could not be normalized using common data transformations (e.g., arcsin and square root). Therefore, I used a Wilcoxon-Mann-Whitney to assess whether mean densities of each age class (YOY, age 1, and age-2^+) were statistically different ($P < 0.10$) depending on spring-flow category.

Generalized linear models (proc genmod: SAS 2000) were created to determine the likelihood that smallmouth bass would be present (binomial distribution, logit function) in streams segments with HSF influence versus stream segments with LSF influence, in particular CUs, or particular CUs depending on spring-flow influence ($\alpha < 0.10$) indicating CU habitat use depended if spring-flow influence was high or low. Likelihood ratio statistics were calculated for each treatment (spring-flow influence, CU, and interaction) resulting in a single Chi square for the entire data set. Likelihood ratio statistics test the null hypothesis that all coefficients in the data set are equal to zero (Allison 1999). The antilog of each logit estimate was used to calculate the odds of smallmouth bass being present (P_p / 1 - P_p), where P_p is the probability of fish being present. An odds ratio ($[(P_x / 1 - P_x) / (P_y / 1 - P_y)]$ where x and y are different treatments (e.g., different CUs or spring-flow categories) and P is the probability of residing in that treatment, calculated by taking the antilog of the difference between logit estimates, was used to determine the likelihood of smallmouth bass presence in one treatment versus another (e.g., more likely to be present in pools versus runs). For YOY smallmouth bass, all CU were included in the analysis. Age-1 smallmouth bass were only present in one vegetated edge and one non-vegetated edge habitat and occurred in two riffles; therefore, those CUs were excluded from the analysis. The model created to determine age-2^+ smallmouth bass probabilities excluded edgewater habitats and riffles due to the absence or limited number of occurrences (once in a riffle) in those habitats. These exclusions were necessary as the algorithm will not converge when zeros exist in an entire unit (i.e., CU type in either spring-flow group).

Frequency-of-use and availability histograms were constructed to examine temperature used and temperature available to YOY smallmouth bass in a subset of stream segments (n = 4). The number of fish located at each available temperature was scaled to 100% to represent a frequency. A specific temperature was considered to be selected when the frequency of temperature use was greater than temperature availability.

A two-sample Kolmogrov-Smirnov test was used to determine if the probability distributions of YOY total lengths differ between HSF stream segments and LSF stream segments ($P < 0.10$). A two-sample Kolmogrov-Smirnov test is sensitive to all types of differences (e.g., center or the tails of the distributions) that may occur between two distributions (Daniel 1990). Descriptive statistics (e.g., quantiles) were calculated to provide further information on length distributions.

Results

There were no statistical differences between mean turbidity ($t = -0.61$, $P = 0.56$) and mean discharge ($t = -0.70$, $P = 0.50$) conditions at the time of sampling in HSF and LSF stream segments (Figure 1). T-test revealed significant differences in mean water temperature between streams classified as HSF versus LSF ($t = 5.84$, $P = 0.0002$).

Relation between smallmouth bass densities and spring flow

The Wilcoxon-Mann-Whitney 2-group test revealed significant differences between densities of younger age classes between spring-flow classifications but not for the age-2^+ fish. Mean densities of YOY ($z = 2.16$, $p = 0.03$) and age-1 ($z = 1.68$, $p = 0.09$) smallmouth bass were statistically significantly higher in streams segments classified as HSF (Figure 2). Mean densities of age-2^+ fish were higher in streams classified as HSF (0.06 in HSF compared to 0.02 in LSF) but these differences were not statistically significant ($z = 0.72$, p 0.47).

Relation between channel unit habitat use and spring flow

I sampled 205 individual CUs: 20% pools, 31% runs, 22% riffles, 4% vegetated edges, 16% non-vegetated edges, and 7% side-channel habitats. Young-of-year fish occurred in all CU types sampled whereas, age-1 fish only occurred one time in each edge-water habitat and twice in riffles and age-2^+ fish never occurred in edge-water habitats and only occurred once in a riffle habitat.

Young of year occurred in 49% of the CUs sampled. This age class was more likely to be present than absent depending on spring-flow category (high or low) (Chi-square = 4.29, $P = 0.03$) and CU (Chi-square = 61.95, $P < 0.0001$), but not the interaction between spring-flow category and CU (Chi-square = 4.63, $P = 0.46$) This result indicates CU habitat use did not depend on spring-flow influence. Young of year were twice as likely to be present in stream segments classified by HSF than stream segments classified by LSF (Table 2: HSF logit estimate 0.46 - LSF logit estimate -0.41 = 0.87, e^x (0.87) = 2.4). Fish were more likely to be present in pools than all other CU types (6-70 times more likely). Young of year were five to fourteen times more likely to use any CU other than riffles.

Age-1 fish occurred in 66% of the CUs included in the analysis (n = 119). This age class was more likely to be present than absent depending on CU (Chi-square = 18.64, $P < 0.0001$), but not spring-flow category (high or low) (Chi-square = 1.86, P = 0.17) or the interaction between spring-flow category and CU (Chi-square = 0.34, P = 0.84). Fish were four times more likely to occur in pools than runs and eighteen times more likely to occur in pools than side channels, but four times more likely to be present in runs than side-channel habitats (Table 3).

Age-2^+ fish occurred in 47% of the CUs included in the analysis (n = 119). This age class was more likely to be present than absent depending on CU (Chi-square = 29.77, $P < 0.0001$), but not spring-flow category (Chi-square = 0.43, P = 0.51) or the interaction between spring-flow category and CU (Chi-square = 0.05, P = 0.97). Fish were eight times more likely to occur in pools than runs and fifty-three times more likely to occur in pools than side-channel habitats, but six times more likely to be present in runs than side channels (Table 4).

Microhabitat temperature selection

Temperature selection patterns were similar among rivers and age classes of smallmouth bass. A wider range of temperatures were available in streams with significant groundwater contributions but the pattern of younger fish selecting warmer temperature remained. The coolest temperatures were generally found in pool habitats where adult fish most often occurred, but when cool temperatures were available in other CUs with sufficient available depth they were also used by adult fish. A pattern of adult fish using cooler water temperatures and younger fish shifting towards warmer water temperatures also existed in streams with a limited range of available temperatures.

Temperature ranged from 25 - 36°C in the James River. The coolest temperatures were found in pool habitats, whereas, the warmest temperatures occurred in non-vegetated edge habitats (Table 5). Young of year selected (use was greater than availability) temperatures from 28-30 °C whereas older age classes shifted to cooler temperatures (25 - 28 °C for age-2^+ fish) (Figure 3).

At the time of sampling, temperatures in Indian Creek ranged from 18 - 30 °C with local upwelling resulting in the coolest temperatures being found in side-channel habitats (Table 5). Young of year selected the warmest temperatures available as did age-1 fish, with a slightly broader range (Figure 4). Age-2^+ smallmouth bass exhibited bimodal selection in a cooler temperature range at temperatures ≤ 22 °C and 26 - 28 °C.

Greasy Creek had a much more narrow range of temperatures available (28 - 31°C) when compared to the other sampled streams with the broadest range available in pool habitats (Table 5). Age classes gradually shifted their selected temperatures from the warmest available (YOY) to the coolest available (age-2^+) (Figure 5).

Big Sugar Creek had temperatures ranging from 22 - 29°C with the entire range occurring in pool habitats (Table 5). Mean stream temperatures were lower in this stream than the other stream sampled but selection trends were similar. Young-of-year smallmouth bass selected the warmest temperatures available (26 - >28°C), with a gradual shift toward cooler temperatures with older age classes (Figure 6).

Length-frequency distributions of young-of-year smallmouth bass

A two-sample Kolmogrov-Smirnov test revealed the length-frequency (TL) distribution of YOY occurring in stream segments classified by HSF versus those classified by LSF were statistically different ($D = 0.26$, $P = 0.0003$). The distribution of TL was skewed to the right in stream segments classified by LSF (mean TL = 53 mm) whereas, the distribution was skewed to the left in stream segments classified by HSF (mean TL = 47 mm) (Figure 7). Quantile estimates for TL in each subgroup were: Q1 (25%) = 35 mm, Q2 (median) = 57 mm, and Q3 (75%) = 65 mm for the LSF group and Q1 = 33 mm, Q2 = 45 mm, and Q3 = 60 mm for the HSF group.

Discussion

Flow stability associated with spring-fed streams likely results in increased reproductive success and YOY survival of smallmouth bass. Temperature was the only variable I found to be significantly different at the time of sampling, but I cannot account for temperature or discharge during the reproductive period. The timing of streamflow fluctuations is associated with reproductive success or failure in field-based studies (Lukas and Orth 1995) and modeling applications (Peterson and Kwak 1999). Graham and Orth (1986) found mean daily temperature explained the most variation in Virginia and West Virginia stream conditions (i.e., flow or temperature related conditions) associated with spawning conditions (prior to spawning, during spawning, and when no spawning occurred); however, the authors also acknowledged that spawning was interrupted by flooding during the study period and resumed when stream flow was receding. Changes in temperature and discharge are often correlated, but it seems plausible that temperature is more influential to spawning success when flows are stable and discharge appears to overrides temperature effects during periods of high flows.

Growth and survival of YOY are considered bottlenecks to population recruitment. Strong positive correlations between temperature during the first growing season and recruitment of smallmouth bass led many researchers to conclude that first year growth affects overwinter survival and this survival is important to year-class strength (*see* Shuter et al. 1980 and references therein). I agree that increasing YOY survival leads to stronger year classes. This study shows higher densities of YOY which presumably will lead to a strong year class.

If environmental conditions (e.g., discharge) have been relatively consistent between years, there may be other implications for higher densities of YOY, but not of adult fish. Research has shown an increase in smallmouth bass densities in stream segments containing less percent pool when compared to other sampled reaches (Dauwalter et al. 2007) (*see* Chapter 3 herein) and a negative relation between density and percent pool area (Sowa and Rabeni 1995). Pool habitats are the most likely to be used by age-2^{+} fish, but runs were also used quite often by adult fish. For the exception of two outliers (Crane Creek and Wet Glaize), there was a general linear increase in adult densities with an increase in percent run habitat. I did not identify fish age classes at a resolution fine enough to demonstrate this statistically, but it was apparent while sampling that the average adult fish occupying run habitats belonged to a younger age class (likely ages 2 and age 3) than those using pools. Probst et al. (1984) found mean depth was positively related to smallmouth bass size (between 100 and 300 mm total length) in the Jack’s Fork River, Missouri. The importance of run habitats may be key to fully understanding smallmouth bass recruitment, perhaps based on density-dependent processes. I believe additional research focusing on the importance of run habitats to the abundance of riverine smallmouth bass is necessary to fully understand the patterns and relations observed between run habitats and increased fish densities.

The effects of habitat selection on fish growth occur via several mechanisms including effective foraging and energetic efficiency. Foraging is most effective in habitats where food is abundant and temperature favors efficient consumption. Field and lab-based studies indicate the majority of YOY smallmouth bass uses habitats dominated by cobble substrates and feeding rates are higher while predation risk is lower in these habitats (Olsen et al. 2003). The streams I sampled had predominately cobble substrates so it appears there are no obstacles to effective foraging, although the abundance of YOY prey in these stream systems is unknown. Mean stream segment temperature in HSF streams was lower than streams classified as LSF; however, at the microhabitat scale, the warmer temperatures available were selected by YOY regardless of spring-flow classification. This indicates appropriate temperatures were available for YOY growth regardless of spring-flow influence, in a variety of CUs. Relations between growth rate and temperature are unknown at this latitude. However, field studies on northern lake populations indicate a linear relation between daily growth rate and temperature up to 27° C, but lab studies showed this relation also depended on diet (Shuter et al. 1980). Shuter and Post (1990) report the optimum temperature for YOY growth at 29° C and bioenergetics modeling indicates growth will decline rapidly at higher temperatures (Hewett and Johnson 1992). Spring flow had no relation to CU habitat use (interactive effect) by any of the age classes I examined indicating mean temperature or discharge during the sampling period did not influence CU habitat use by any age class. However, obvious selection of microhabitats based on temperature indicates temperature was influencing the distribution of these fish at a microhabitat scale.

The presence of different habitat elements and specific activities (i.e., feeding) interactively determine whether or not specific temperatures in streams are selected by fish. For example, physical cover is often considered a major habitat element affecting habitat use by adult smallmouth bass in lotic systems (Probst et al. 1984; Sechnick et al. 1986; Todd and Rabeni 1989). Bevelhimer (1996) supported the importance of cover by adult smallmouth bass through field and laboratory studies with several caveats. Laboratory experiments demonstrated, in the absence of cover, smallmouth bass preferred the coolest available temperatures. The coolest temperatures were also selected by satiated fish when there was an abundance of food available in warmer areas. Todd and Rabeni (1989) found adult smallmouth bass movement to be highly correlated with water temperature with most movements occurring during warmer seasonal periods with diel peaks in activity near sunrise and after sunset; however, most of these movements occurred within the same pool. I did not investigate the importance of cover in this study, but I did demonstrate that age-2^{+} smallmouth bass generally select cooler available water temperatures. Temperature selection in two streams (i.e., Indian Creek and Big Sugar Creek) exhibited patterns indicating an interactive effect with some other abiotic or biotic components. The bimodal selection in Indian Creek was associated with pool and side-channel habitats. Use of pools was not surprising since this was the most used CU regardless of spring-flow category. However, side-channel habitats were not a highly used CU but may have been used due to cooler temperatures or the presence of cover.

Whitledge et al (2002) identified the optimal growth temperature of adult smallmouth bass as 22° C, which corresponds to the temperatures found in this side-channel habitat. Temperature selection in Big Sugar Creek occurred at temperatures lower than in all other streams (≤ 24° C) but the cooler temperatures also occurred in pool habitats. This apparent correlation between pool habitats and cooler water temperatures makes it difficult to ascertain the relative importance of each habitat element. Regardless, if growth rates are diminished when temperatures are > 27° C for extended periods of time (Whitledge et al 2006), using habitats that offer the coolest temperatures (e.g., Greasy Creek) available will still result in reduced growth and possibly fecundity.

Differences in the distributions of YOY total lengths between stream types makes YOY appear to grow faster in streams with limited spring-flow influence. This may be due to several factors. First, spawning may occur earlier in warmer streams which I would assume would be represented by those stream segments with limited amounts of spring-flow influence (especially early in the spring when spawning occurs). Sabo and Orth (1995) found YOY smallmouth bass in a Virginia stream grew faster when hatched later (in warmer water temperatures) than those that hatched earlier in the year (in cooler water temperatures); however, by the end of the summer growing season, there were no differences in the length-distributions of each cohort. Size structure of age-0 smallmouth bass was more strongly correlated with daily growth rate than hatch date in South Dakota glacial lakes (Phelps et al. 2008). These results suggest hatch date may be less important in determining overall total length during the growing season. Another plausible explanation is that density-dependent factors may allow YOY to achieve longer lengths in streams with lower densities. Fish populations may be regulated by density-dependent factors, not limited to, but including the juvenile phase of the life cycle. Regardless, the implication is that larger young-of-year fish at the end of the growing season have a greater chance of surviving the first winter.

The influence of groundwater on smallmouth bass appears to be primarily related to first-summer survival of YOY and the availability of appropriate temperature microhabitats for adult smallmouth bass growth. As temperatures continue to increase due to land-use activities and global warming, spring-fed streams will likely become more important to the conservation of smallmouth bass in the southern portion of their range. Riparian management (including an intact corridor along the length of a river) to reduce summer water temperatures may help prevent adult fish from being subjected to extended periods of temperatures above which diminished growth and perhaps, fecundity may occur. Reducing channel morphological changes that result in the widening, shallowing, and ultimately homogenization of stream habitats would also alleviate temperature increases (less very shallow habitat subject to solar warming) and provide appropriate habitat for different life stages of riverine smallmouth bass.

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TABLE 1.- Description of land conversion streams sampled in southwest Missouri. The channel units sampled (% contribution) in each stream segment were: 1 = pool, 2 = run, 3 = riffle, 4 = vegetated edge, 5 = non-vegetated edge, and 6 = side channel (frontwaters and backwaters)

Stream	Mean discharge (m^3/s)	Length (m)	Area (m^2)	Mean width (m)	Channel unit (%)						Mean pool depth (cm)	Max pool depth (cm)	Dominant substrate types
					1	2	3	4	5	6			
Streams with spring flow > 1 standard deviation below the mean spring-flow value													
Big Sugar	0.04	340	2241	6	44	43	9	0	4	0	59	145	cobble & gravel
Greasy	0.09	692	9322	11	92	4	3	0	1	0	33	94	gravel
Little Niangua	0.13	528	5716	8	52	25	10	1	5	7	74	237	cobble & pebble
Little	0.56	710	7958	14	52	32	6	1	5	4	97	250	boulder

Sugar													& cobble
Pomme de Terre	0.25	1102	25185	21	92	2	2	0.5	1	2.5	42	79	boulder & cobble
Wet Glaize	0.55	589	7156	12	40	49	8	1	1	1	74	176	gravel
Whetstone	0.19	436	5255	10	84	12	2	0	2	0	57	130	cobble
Streams with spring flow > 1 standard deviation above the mean spring-flow value													
Crane	0.47	458	6993	10	39	50	6	0	5	0	66	142	pebble & gravel
Finley	0.29	853	12793	15	62	28	8	0	1	1	54	96	cobble
Flat	0.51	648	10461	14	50	36	10	1	3	0	56	101	cobble
Indian	0.63	777	8835	12	31	44	18	1	1	5	125	360	cobble
James	0.06	877	10591	13	91	0	1	1	2	5	57	130	bedrock & cobble
Niangua	0.31	563	7845	10	69	14	7	2	5	3	53	120	cobble

TABLE 2.- Generalized linear model results for young-of-year smallmouth bass. Asterisks identify significant logit values (P < 0.10) indicating an unequal probability of presence versus absence in a particular spring-flow category, CUs (NVE = non-vegetated edge; VE = vegetated edge; SC = side channel) and individual interactions. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

			Channel Unit				
Spring flow	Pool	Run	Riffle	NVE	VE	SC	
	*1.95	*1.19	*-1.79	1.09	0.51	-0.22	0.46
High	(7.02)	(3.29)	(0.17)	(2.97)	(1.66)	(0.80)	(1.58)
	*2.40	*-0.61	*-2.40	0.00	*-1.18	-0.69	-0.41
Low	(11.02)	(0.54)	(0.09)	N/A	(0.31)	(0.50)	(0.66)
	*2.17	0.29	*-2.09	0.55	-0.33	-0.46	
	(8.76)	(1.33)	(0.12)	(1.73)	(0.71)	(0.63)	

TABLE 3.- Generalized linear model results for age-1 smallmouth bass. Asterisks identify significant logit values (P < 0.10) indicating an unequal probability of presence versus absence in a particular spring-flow category, CUs (SC = side channel) and individual interactions. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

	Channel Unit			
Spring flow	Pool	Run	SC	
	*1.95	*0.85	-0.69	*0.07
High	(7.02)	(2.34)	(0.50)	(1.07)
	*1.61	-0.12	-1.61	-0.04
Low	(5.00)	(0.89)	(0.20)	(0.96)
	*1.78	0.36	*-1.15	
	(5.93)	(1.43)	(0.32)	

TABLE 4.- Generalized linear model results for age-2^{+} smallmouth bass. Asterisks identify significant logit values ($P < 0.10$) indicating an unequal probability of presence versus absence in a particular spring-flow category, CUs (SC = side channel) and individual interactions. Negative values indicate fish were more likely to be absent than present (< 50% probability of occurrence) and positive values indicate fish were more likely to be present than absent (> 50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses

	Channel Unit			
Spring flow	Pool	Run	SC	
	*2.71	*0.69	-1.25	0.72
High	(15.03)	(2.00)	(0.29)	(2.03)
	*2.40	0.12	-1.61	0.30
Low	(11.02)	(1.13)	(0.20)	(1.34)
	*2.55	0.41	*-1.43	
	(12.81)	(1.50)	(0.24)	

TABLE 5.- Descriptive statistics for the distribution of temperature in channel units of streams used in temperature selection analyses. Channel units (CU) are: 1 = pool, 2 = run, 3 = riffle, 4 = vegetated edge, 5 = non-vegetated edge and 6 = side channel

Stream	CU	Mean	Minimum	Maximum
James River	1	27.8	25	30
	4	29.8	29	31
	5	30.1	28	36
	6	28.2	27	30
Indian Creek	1	28.4	24	30
	2	28.8	24	30
	3	28.8	27	30
	4	25.7	24	27
	5	29.3	29	30
	6	26.3	18	29
Greasy Creek	1	29.4	28	31
	2	29.5	29	30
	3	29.5	28	30
	5	30.2	30	31
Big Sugar	1	25.1	22	29
	2	24.5	23	29
	3	24.3	23	27

FIGURE 1.- Mean temperature (°C), turbidity (nephelometric turbidity units [NTU]) and discharge (m^3/s) (+/- 90 % confidence intervals) of streams in respective spring-flow categories. Asterisks indicate significant differences between means in each spring-flow category

FIGURE 2.- Mean density (number/m^2) of smallmouth bass (+/- 90 % confidence intervals) in stream segments with high spring-flow influence and stream segments with low spring-flow influence by age class. Asterisks indicate significant differences between means in each spring-flow category for each age class

FIGURE 3.- Percent frequency of use and availability histograms for temperature (°C) where selection (use is greater than availability) occurred for riverine smallmouth bass in the James River, by age class

FIGURE 4.- Percent frequency of use and availability histograms for temperature (°C) where selection (use is greater than availability) occurred for riverine smallmouth bass in Indian Creek, by age class

FIGURE 5.- Percent frequency of use and availability histograms for temperature (°C) where selection (use is greater than availability) occurred for riverine smallmouth bass in Greasy Creek, by age class

FIGURE 6.- Percent frequency of use and availability histograms for temperature (°C) where selection (use is greater than availability) occurred for riverine smallmouth bass in Big Sugar Creek, by age class

FIGURE 7.- Percent frequency of young-of-year smallmouth bass length distributions (total length) from stream segments with low spring-flow influence and stream segments with high spring-flow influence

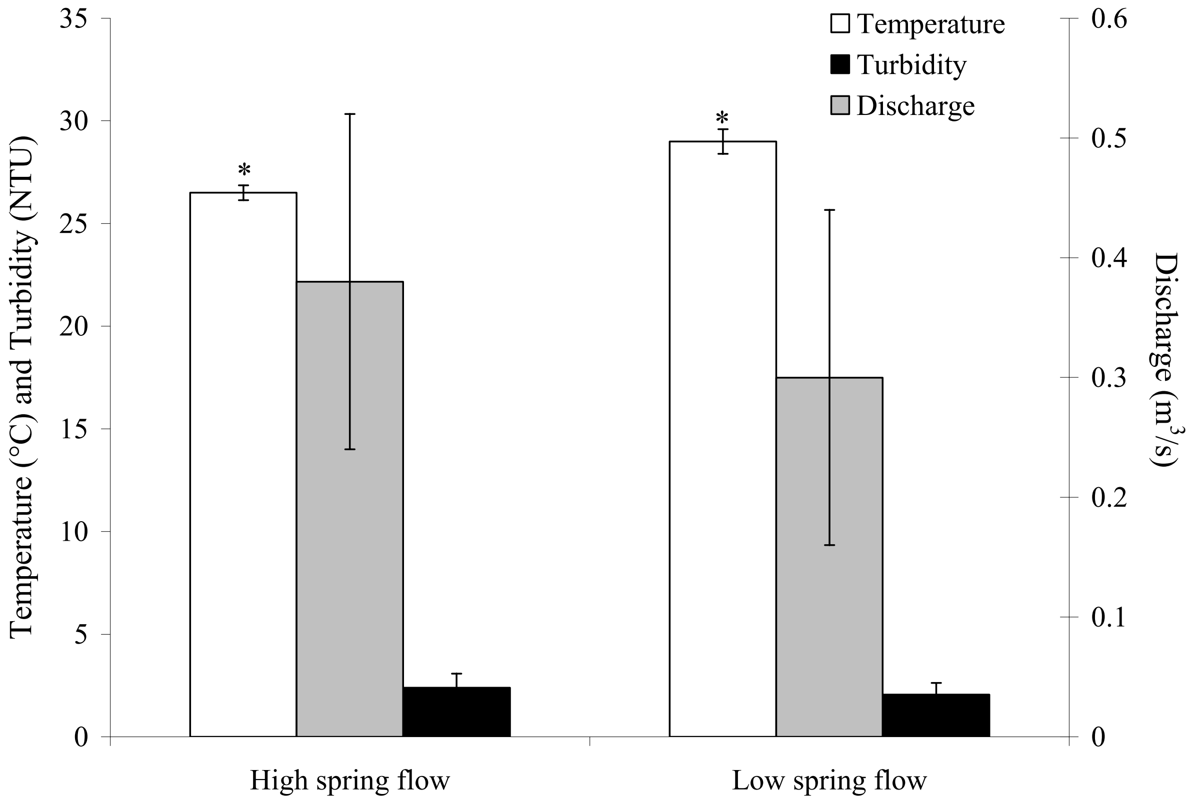

35
30
25
20
15
10
5
0
Temperature (°C) and Turbidity (NTU)
0.6
0.5
0.4
0.3
0.2
0.1
0
Discharge (m3/s)
Temperature
Turbidity
Discharge
*
*
High spring flow
Low spring flow

FIGURE 1.-

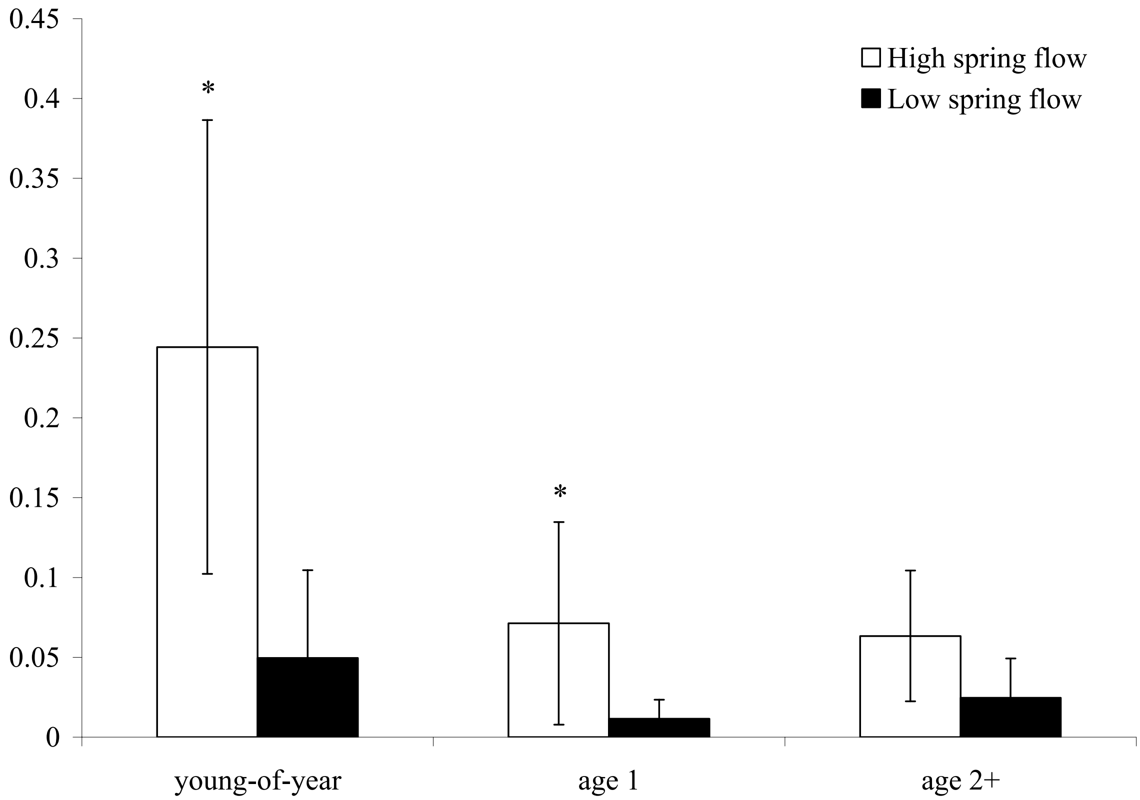
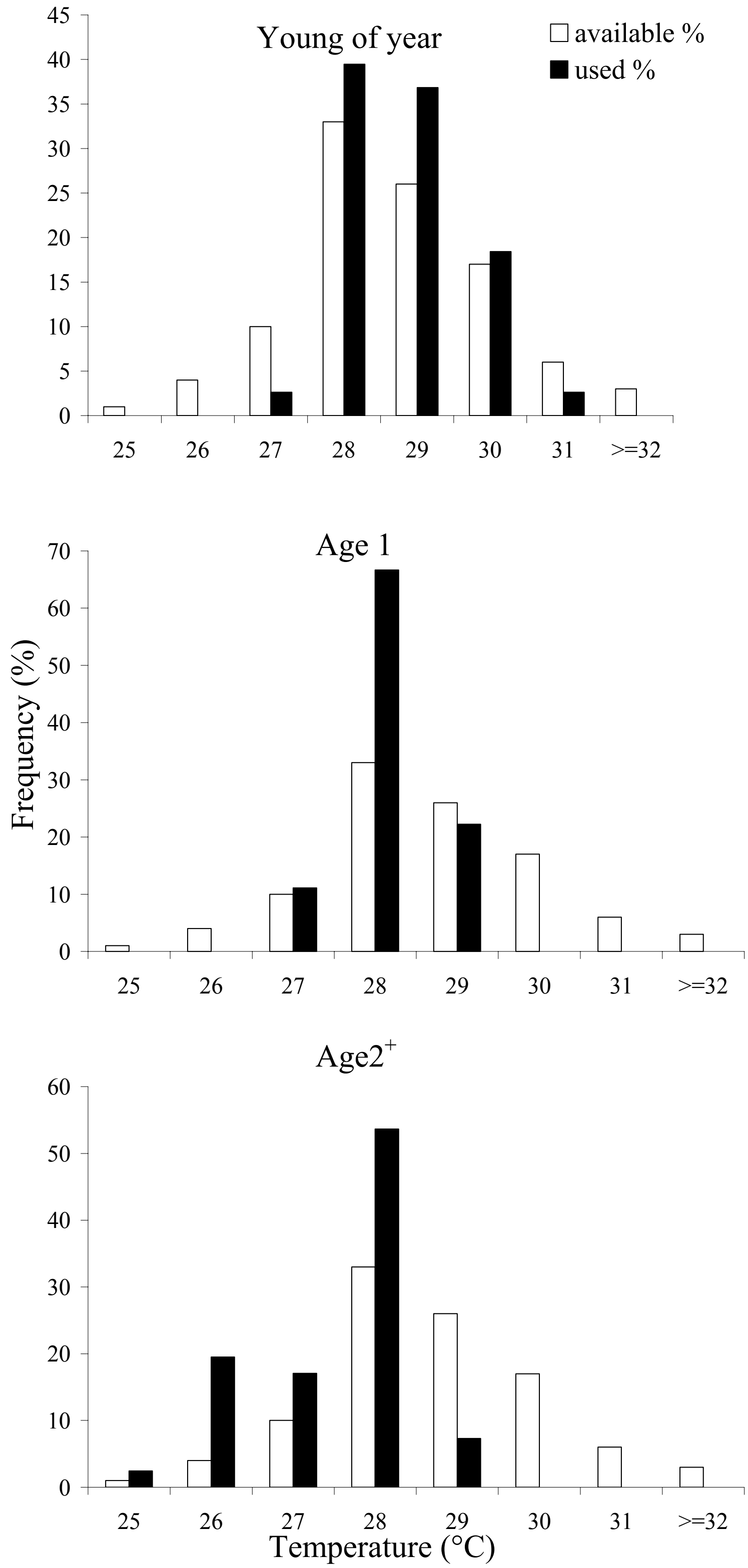

0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
High spring flow
Low spring flow
*
*
young-of-year
age 1
age 2+

FIGURE 2.-



Young of year
available %
used %
45
40
35
30
25
20
15
10
5
0
25
26
27
28
29
30
31
>=32
Age 1
Frequency (%)
70
60
50
40
30
20
10
0
25
26
27
28
29
30
31
>=32
Age2+
60
50
40
30
20
10
0
25
26
27
28
29
30
31
>=32
Temperature (°C)

FIGURE 3.-

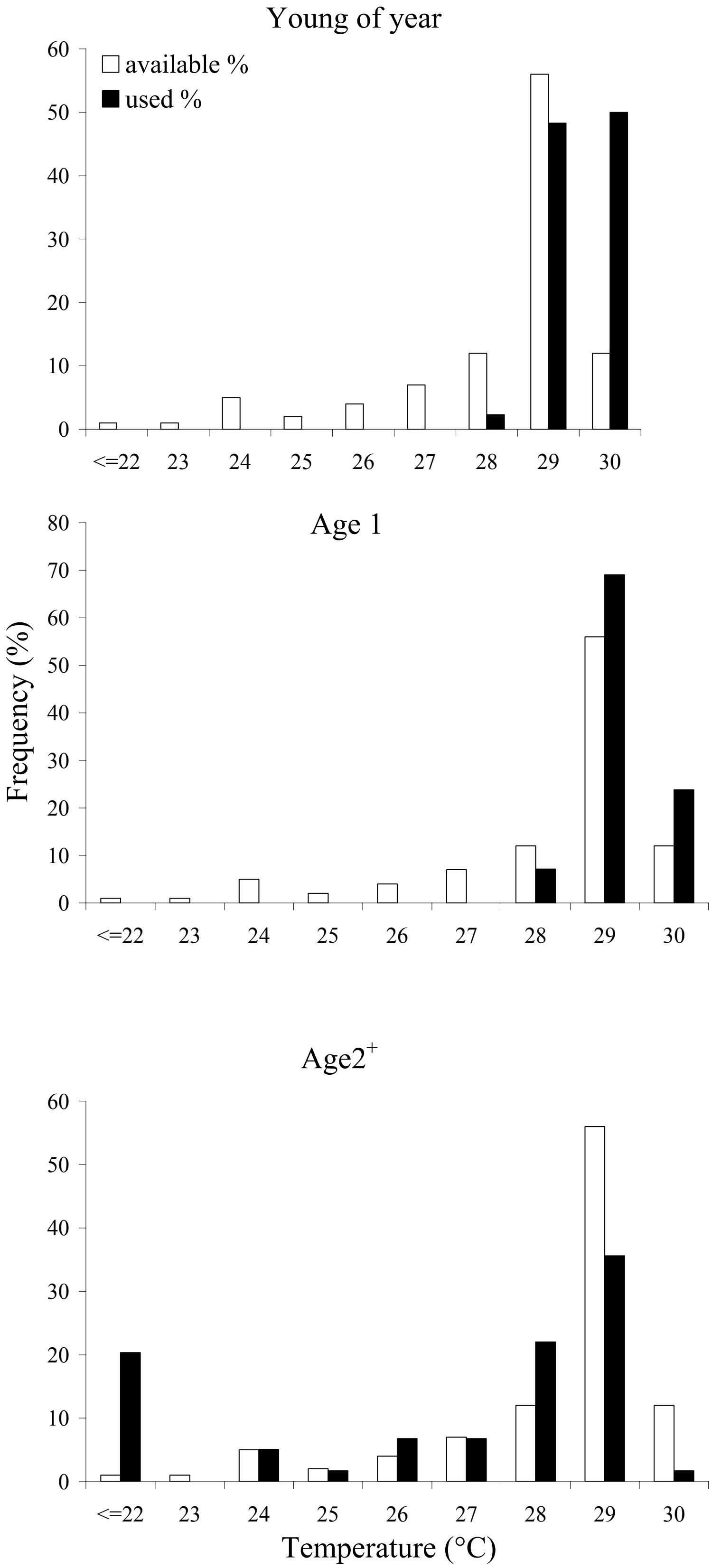

Young of year
available %
used %
60
50
40
30
20
10
0
<=22
23
24
25
26
27
28
29
30
Age 1
Frequency (%)
80
70
60
50
40
30
20
10
0
<=22
23
24
25
26
27
28
29
30
Age2+
60
50
40
30
20
10
0
<=22
23
24
25
26
27
28
29
30
Temperature (°C)

FIGURE 4.-

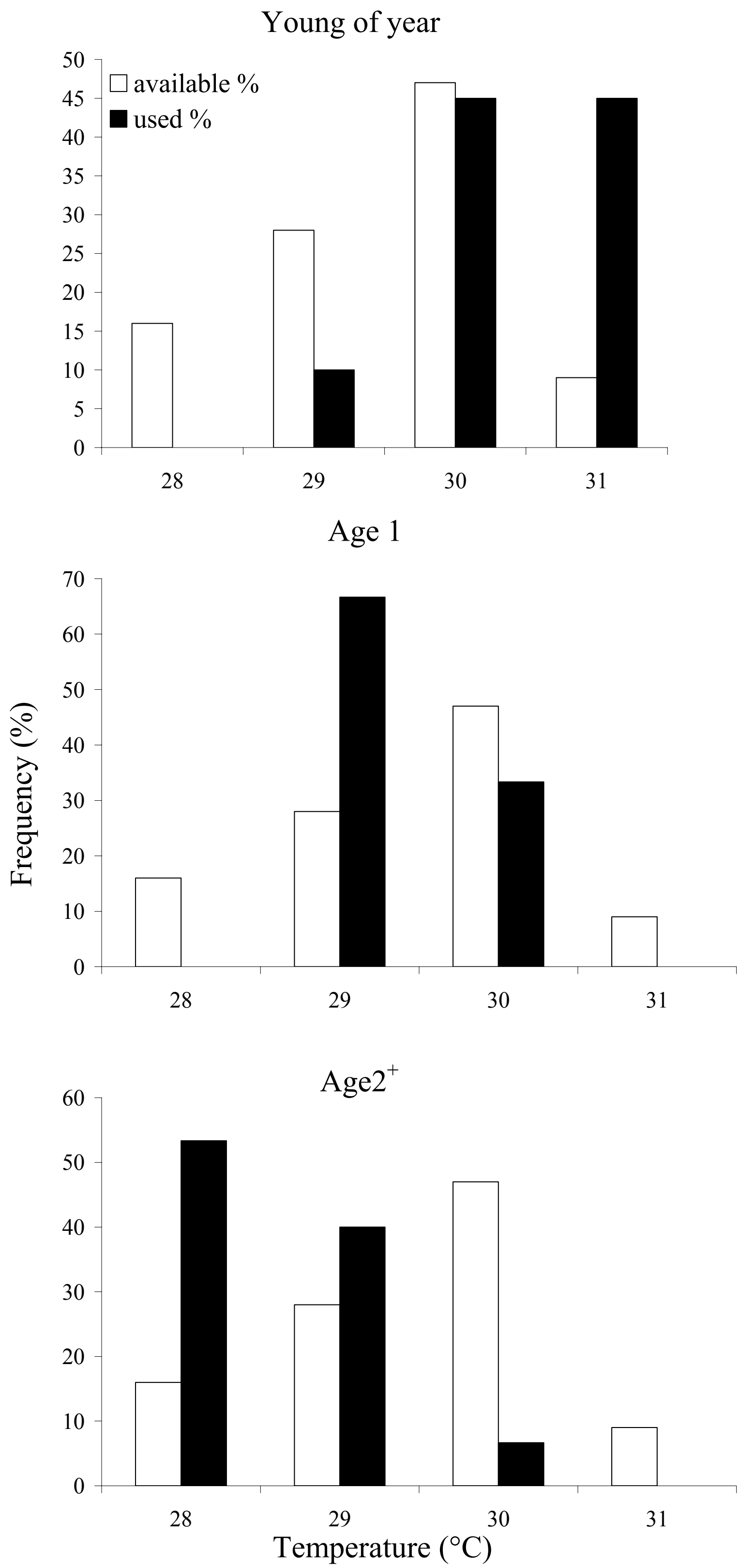

Young of year
50
45
40
35
30
25
20
15
10
5
0
available %
used %
28
29
30
31
Age 1
70
60
50
40
30
20
10
0
Frequency (%)
28
29
30
31
Age2+
60
50
40
30
20
10
0
28
29
30
31
Temperature (°C)

FIGURE 5.-

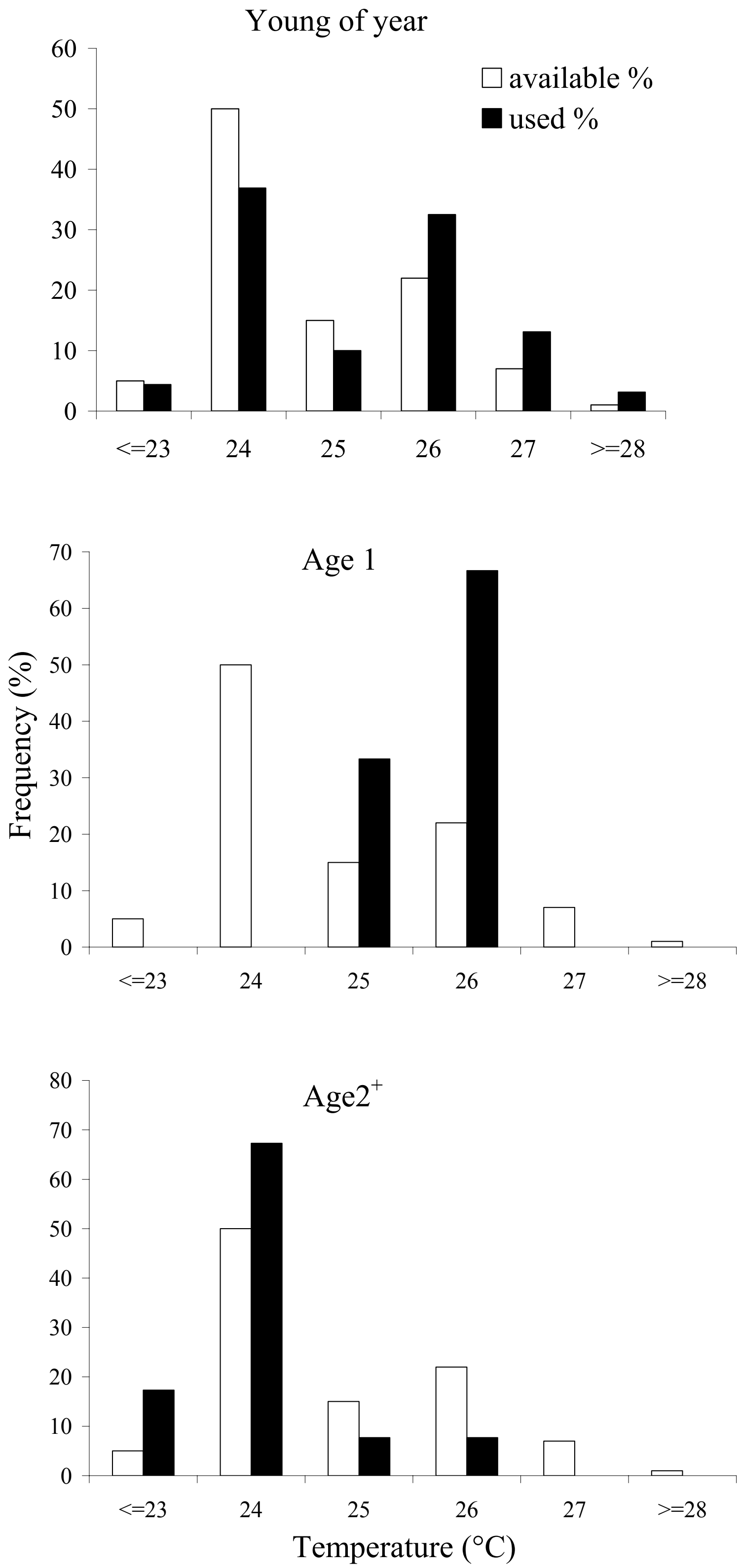

Young of year
available %
used %
Age 1
Age2+
Frequency (%)
Temperature (°C)
<=23
24
25
26
27
>=28

FIGURE 6.-

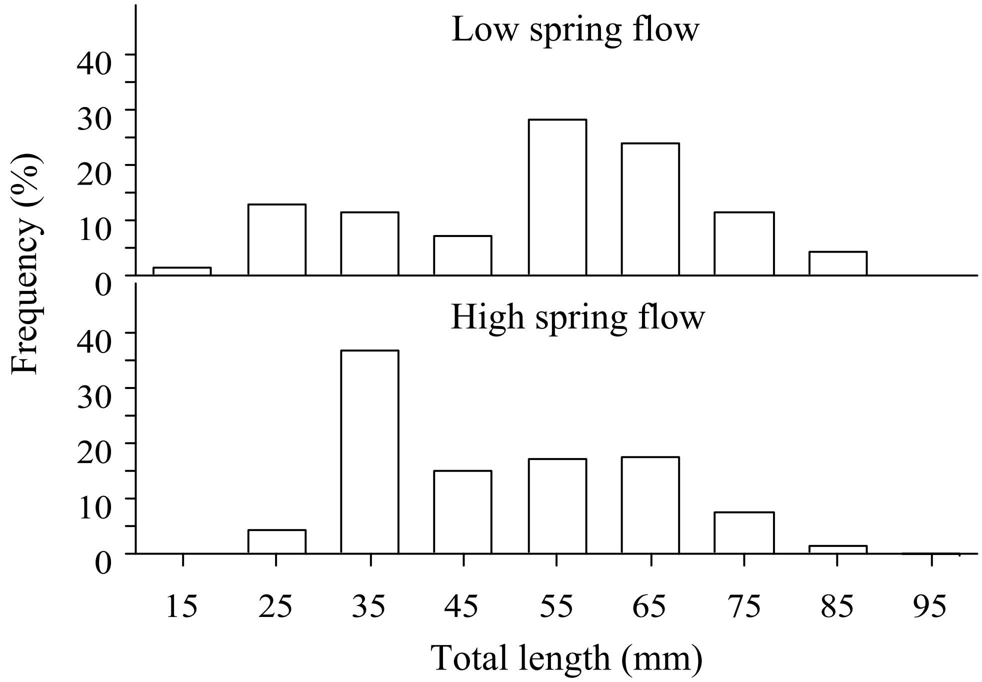

Low spring flow
High spring flow
Frequency (%)
40
30
20
10
0
40
30
20
10
0
15
25
35
45
55
65
75
85
95
Total length (mm)

FIGURE 7.-

Chapter 5

Patterns of young of year smallmouth bass *Micropterus dolomieu* microhabitat use in multiple stream segments under land-use constraints

Abstract.- This study examines how-young-of-year smallmouth bass *Micropterus dolomieu* use microhabitats under a variety of stream conditions. My objective was to discriminate between microhabitat use and availability of water depth, focal velocity and substrate composition by young-of-year smallmouth bass during summer in eight individual stream segments, and then under different land-use constraints by grouping stream segments into those classified by pasture land use and those classified by forested land use. Stepwise discriminant function analyses were used to determine a subset of variables that best revealed differences among used and available microhabitats. Velocity was significant in analyses in 88% of the stream segments whereas, depth was only significant in the smallest stream and the majority (75%) of stream segments classified by pasture land use. Mean velocities used by young of year were lower than available and mean depth was greater than mean availability in all cases. There was a lot of variation in significant substrate variables between stream segments, likely due to particular availabilities within stream segments and correlations between substrate classes and hydraulic variables. Grouping data by land-use constraints revealed significant patterns of discrimination among classes: velocity was the most significant variable regardless of land-use classification; depth was only significant in stream segments classified by pasture land use; and significant substrate variables varied by land use. Error rates associated with classifications were generally high (> 30%), regardless of

analyses (individual stream segments or grouped by land use). These results indicate young-of-year smallmouth bass are generally opportunistic with respect to microhabitat use. Velocity was the most important variable associated with microhabitat use (using microhabitats with low velocities), whereas, depth was only important in streams highly impacted by pasture land use, and likely subsequent morphological changes (e.g., widening and shallowing). Substrate use appears to depend on availability within individual streams or associations with hydraulic parameters (i.e., correlation with velocity).

Smallmouth bass *Micropterus dolomieu* are a valuable ecological and recreational component of many streams. Because smallmouth bass are an important sport fish and a top-level predator, they have been extensively studied. Scientists have generated a plethora of data regarding habitat use by adult smallmouth bass, but also by younger life stages that are important to recruitment of adults and subsequent year class strengths.

Microhabitats (i.e., combinations of depths, velocities and substrates at fish locations) important to young-of year (YOY) smallmouth bass vary among studies (*see* Pert et al 2002 for a review). Undoubtedly, some of the disparate results are due to habitat and food availability (Pert et al. 2002), the definitions of different habitat types, differences of size classes of YOY at the time of the studies (Orth and Newcomb 2002; Fore et al. 2007), and the biotic composition of the streams (i.e., the presence of predators, density-dependent considerations; Sabo et al. 1996). Smallmouth bass have been considered habitat specialists (Bain et al. 1988; Aadland 1993), habitat generalists (Sabo and Orth 1994; Pert et al 2002), and opportunistic with respect to habitat use (*see* Chapter 3). Regardless of the particular reasons for these disparate reports, it is clear that YOY use a variety of habitats.

Habitat data collected from multiple spatial scales are often important in decisions surrounding habitat improvements for fishes. Factors affecting particular population responses to habitat "improvements" may be influenced by multiple spatial scales (Frissell et al 1986; Rabeni and Sowa 1996) but microhabitats are often considered necessary to decisions regarding appropriate habitat-improvement measures. The importance of spatial scale is generally well recognized; however, studies addressing habitat use at finer spatial scales are often not placed within the context of important landscape constraints.

Resource managers often manage lotic fishes under a variety of landscape characteristics, many of which have been altered. Understanding constraints imposed by landscape factors allows managers to focus on local habitat conditions and the relative importance of these conditions to the growth and survival of populations. The natural conditions of soil permeability, represented by hydrologic soil group D, and the percentage of rocky soils within the watershed, significantly influence the potential success of riverine smallmouth bass in Missouri (Brewer et al. 2007). In this study, I kept these significant landscape features relatively constant while documenting YOY microhabitat use in eight stream segments. These stream segments were divided on the basis of land use (forested versus pasture land use) to identify the potential influence land use has on microhabitat use. My objectives were to determine which microhabitats were used by YOY smallmouth bass by differentiating between used and available microhabitats and to determine how stream segments located in watersheds classified by forest or pasture land use influences YOY use of microhabitats.

Study Area

Sampling was conducted on eight streams (Table 1) located in the east-central and southwestern portions of the Ozark Highland biogeographic region of Missouri (Nigh and Schroeder 2002). The Ozark Highland region is restricted to southern Missouri and is characterized by extensive geologic erosion, carbonate bedrock, and karst features.

Stream segments in east-central Missouri were located in the Current River Hills Subsection. This subsection is dominated by secondary growth forest with limited development and a significant portion of public lands under control of the Mark Twain National Forest, the National Park Service, and the Missouri Department of Conservation. Stream segments in southwest Missouri were located in the Springfield Plains Subsection and the Central Plateau Subsection. These subsections are subject to extensive human activities, primarily due to native grasses, savannas, and woodlands having been converted largely to pasture agriculture for cattle (Nigh and Schroeder 2002). Remaining woodland areas are primarily restricted to the most dissected parts of these sections. Stream segments in all of these subsections (Current River Hills, Springfield Plains, and the Central Plateau) have relatively low suspended sediment loads, except during periods of high runoff.

Methods

*Study design and site selection***.-** Eight stream segments were selected using criteria that held natural-occurring watershed conditions reasonably constant while altering land use criteria. Geographic information system (GIS) was used to select an initial pool of stream segments. Criteria pertaining to natural variation in habitat conditions expected to influence smallmouth bass densities were kept relatively constant (*see* Brewer et al. 2007 for complete description); hydrologic soil group D was < 7% in all watersheds and rocky soils were > 50%. Stream segments classified by pasture land use were only included in our initial pool of sample sites if there was < 30% of forested land in the watershed.

Stream segments classified as forested land use contained a minimum of 85% forest in their respective watersheds.

Fish sampling.- Multiple methods of sampling were used to balance my ability to detect young-of-year fish in shallow versus deeper-water habitats: a combination of snorkeling and above-water visual observation. The choice of method used depended on water depth and surface agitation (i.e. wind conditions) and used the same methods as described in Chapter 4. Briefly, underwater observation (snorkeling) was the primary sampling method and was used when depths were > 0.5-m and above water observation was used in depths were < 0.5 m if surface conditions did not impede observation.

Fish sampling was conducted in July - September 2005 and 2006. Stream segments classified by forested land use were sampled in 2005 specifically for this study whereas segments classified by pasture land use were sampled in 2006 in conjunction with another study. Forested stream segments were delineated into channel units using the classification system described in Chapters 3 and 4 (e.g., riffles, runs, pools, side channels, etc). Replicates of three of each channel unit were identified (if available within 1600 linear meters) and 30-m^2 of each channel unit was randomly sampled by selecting a random number as a starting point within the available length of that channel unit and determining a 30-m^2 area that would be accommodated by that particular channel unit providing the greatest differences in habitat available. Stream segments classified by pasture land use were sampled in conjunction with the study reported in Chapter 3 so a minimum of 40 times the channel width was sampled regardless of channel units present. Sampling protocols were the same regardless of method used to delineate the sample area. When snorkeling was used, two snorkelers began at the downstream end of the area and moved upstream at a rate of approximately 5 m^2 per 1 min to the end of the sample area (either marked discretely with a flag or using natural features). Each snorkeler limited their observations to half of the area sampled and covered their half by swimming in a zig-zag pattern. Snorkelers reduced the possibility of double counting individual fish at the center of the area sampled by pointing out any fish counted in this area to the other observer. The same approach was used for above-water visual observations by walking slowly through the sample area in a zig-zag pattern and verbally identifying fish counted with the other observer. Exception to this approach occurred only when sampling edgewater habitats. In non-vegetated edge habitats, above-water observations were made by one observer on the bank and another streamside. In shallow vegetated-edge habitats, observers on each side would slowly look through the stands of vegetation (usually water willow *Justicia americana*) working from the downstream to upstream end of the CU; if water depth permitted ($\geq$ 0.25 m), the streamside observer would snorkel slowly along the outside band of the water willow. Observers placed a lead-weighted fluorescent flag on the substrate at the location where any YOY smallmouth bass was observed and then used a sweeping motion (if snorkeling) to encourage the fish to move downstream.

Microhabitat availablity.- Each stream segment was mapped prior to sampling so the area to be sampled could be determined and flags could be placed as boundaries where necessary. Transects, perpendicular to stream flow, were established in each CU sampled at 10-m intervals to determine the availability of depth (cm), bottom velocity (m/s), and substrate composition. This was done throughout the entire CU even if only a subsample was actually sampled for fish so I could determine if my subsample was representative of the microhabitats available to the fish in the entire CU.

Microhabitat use.- Microhabitat variables were measured following sampling at the flagged locations. Water depth (cm) was measured at depths < 1 m using a wading rod and with a copper pipe marked in 1-cm increments at depths > 1 m. Focal velocity (m/s) was measured approximately 2-cm above the substrate (to ensure the cups on the current meter rotated properly) using a Gurley Pygmy current meter (Model 625). Substrate composition was estimated visually over a 1-m^2 area surrounding the flagged location by assigning percentages using a modified Wentworth scale as: silt (< 0.06 mm), sand (< 0.06 - 2 mm), gravel (> 2 - 16 mm), pebble (>16 - 64 mm), cobble (> 64 - 256 mm), boulder (> 256 - 4000), and bedrock (> 4000). The same person estimated substrate composition in each microhabitat so any potential bias would remain constant throughout the study.

Analyses.- The Shapiro-Wilks test indicated microhabitat availability data were not normally distributed ($P < 0.05$) so I used a Kruskal Wallis test to assess whether available mean microhabitats sampled in 2005 were statistically different ($P < 0.10$) than the microhabitats available in the entire channel unit. Each microhabitat variable (e.g., depth, velocity, boulder, etc) was assessed independently to determine if the area sampled was representative of the entire channel unit area.

Discriminant function analyses were used to classify observations into groups based on quantitative microhabitat variables. I used stepwise selection (proc genmod: SAS 2000) to determine a subset of microhabitat variables that best revealed differences among classes (i.e., used microhabitats versus available microhabitats) ($\alpha \leq 0.10$). The performance of discriminant function analyses was evaluated by estimating error rates (the probability of misclassification). First, separate analyses were completed for individual streams (n = 8 stream segments) and then for individual land-use categories where streams were combined in each category (n = 4 stream segments per category) and then analyzed under the broader umbrella of land use. Mean microhabitat use (for each variable) and availability was also provided for individual stream segments to provide insight on the relation between fish and individual variables because disriminant function analysis does not designate a specific relation (positive or negative) between variables.

Pearson's product-moment correlations procedure was used to identify highly correlated relations between variables significant in the discriminant function analysis for each stream. I limited the results to variables included in the discriminant analyses because of the high number of possible combinations that exist with eight different streams and nine variables per stream. There is no strict cutoff used to define highly correlated variables; however, Graham (2003) indicated $r \geq 0.28$ could bias multiple regression results. I identified high correlations between significant variables in the discriminant function analyses using a cutoff of $r > 0.30$.

Results

The Kruskal Wallis test indicated there were minimal occurrences ($\leq$ 8% of all cases for each stream segment) when significant differences ($P \leq 0.10$) occurred between mean microhabitats available in my sub-samples versus the microhabitats that would have been available had I sampled the entire channel unit in each stream segment classified by forested land use. I accepted this level of error and proceeded with analyses because a level of error this small is unlikely to bias the results to any appreciable degree.

Classifying microhabitat use in individual stream segments

Microhabitat variables significant in these analyses varied considerably among stream segments (Table 2). Velocity was the hydraulic variable most often (88% of the stream segments) significant in discriminating between used and available microhabitats. Mean velocity used was lower than the mean availability in all stream segments (Table 3). Depth was only significant in classifying used from available microhabitats in the smallest stream (i.e., Blair Creek) classified by forested land use. Alternatively, depth was significant in 75% of the analyses on individual streams classified by pasture land use. Mean depth used by young-of-year fish was deeper than available in all stream segments (Table 3). Sand, gravel, and boulder substrates were significant in discriminating used and available points in stream segments classified by forested land use whereas bedrock, gravel, and sand were most often significant in stream segments classified by pasture land use. Likewise, there was a lot of variation in mean percentages of different substrate classes used (Table 3).

Error rates associated with classifying between used and available microhabitats were generally quite high. Correctly classifying used versus available points occurred 61-95% of the time, depending on stream segment (Table 2). The average misclassification rate was 30%. Errors of omission (predicting fish to be absent when they were actually present) and commission (predicting fish to be present when they were actually absent) were approximately equally distributed among stream segments. Omission and commission errors were equal in Blair Creek (36%). Four stream segments (upper and lower Jack's Fork, Indian Creek and Finley Creek) had higher errors of commission (61%, 21%, 47% and 40% respectively) whereas three stream segments (Sinking Creek, James River and Greasy Creek) had higher errors of omission (21%, 60% and 40% respectively).

Many of the microhabitat variables were correlated to some degree. However, most correlations were not considered severe with $r < 0.30$. Highly correlated variables ($r \geq 0.30$) that were included in discriminant analyses results were: sand and velocity (-) in Sinking, Indian, Greasy and Finley Creeks; velocity and depth (-) in Blair and Greasy Creeks; and bedrock and velocity (-) in the James River.

Classifying microhabitat use under land use constraints

Stream segments grouped by land-use classification revealed patterns in microhabitat use under particular land use constraints. The most significant variable discriminating used from available microhabitats was velocity, regardless of classification as pasture or forested land use (Table 4). Depth was only a significant variable in stream segments classified by pasture land use. Substrates variables used to discriminate used and available points differed depending on land-use constraint. The percentages of boulder and sand were significant in stream segments classified by forested land use whereas percentages of pebble and cobble were significant in stream segments classified by pasture land use.

Error rates associated with classifying between used and available microhabitats after grouping stream segments by land use were expectedly high. The average misclassification rate was 38% (Table 4). Omission errors were higher than commission errors in stream segments classified by forested or pasture land use (40% and 44% respectively).

Discussion

This study identifies the microhabitat conditions used by YOY smallmouth bass in eight stream segments individually and then grouped on the basis of dominant land use within each respective watershed. It differs from most microhabitat studies on smallmouth bass because I looked at habitat use under a variety of available habitat conditions (i.e., eight streams) whereas most studies occur on one stream (e.g., Livingstone and Rabeni 1991; Sabo and Orth 1994; Fore et al. 2007), and I placed stream segments within a relatively constant coarse resolution (i.e., landscape scale) framework which to my knowledge has not been done in any other study on YOY smallmouth bass.

Velocity was the variable that was repeatedly significant among stream segments and the most important variable in the combined analysis addressing land use. Velocity can exert a substantial influence on first year growth and survival of smallmouth bass (Shuter et al. 1980). Velocity is not responsible for controlling metabolic processes directly; however, indirectly, velocity may influence feeding activities and swimming performance (Simonson and Swenson 1990). Velocity is also an important contributor to overwinter survival because growth rate is maximized over a relatively narrow range of velocities (6-13 cm/s) (Simonson and Swenson 1990). Increasing the amount of time spent in habitats with optimal growth velocity should result in increased growth and subsequent survival. Regardless, the choice to occupy one habitat over another is often dependent on more than abiotic conditions alone.

Biotic conditions in a stream segment or specific habitat within a stream may influence the microhabitat used by YOY smallmouth bass. A study of habitat use and prey selection on the Jack's Fork River, Missouri showed the abundance of prey items was greatest in habitats "preferred" by YOY (Livingstone and Rabeni 1991). These authors also indicated the importance of shallow-water (e.g., waterwillow *Justicia americana*) habitats. The discrepancy in depths used by YOY in this study and Livingstone and Rabeni (1991) is likely due to the timing of studies (I sampled in July whereas Livingstone and Rabeni (1991) sampled beginning in June) therefore size of YOY and perhaps sampling gear used (primarily seining versus under-water observation). Other studies have found YOY to use deeper habitats as they increase in size during their first summer (Probst et al. 1984; Rankin 1986). Prey and potential predators may also influence particular substrates used by YOY fish. Livingstone and

Rabeni (1991) indicate the "apparent growth" of YOY was higher in waterwillow habitats with fine substrates, rubble, or open-water habitats potentially because of the availability of small fish and the ability of YOY to capture fish in these habitats. Higher densities of YOY may also affect their spatial distribution by creating antagonistic interactions (Sabo et al. 1996). Alternatively, the presence of predators may influence use of particular microhabitats, especially for larger YOY that use deeper-water habitats shared by adults of the same species and other piscivores (e.g., largemouth bass, spotted bass, etc). Other studies have reported YOY use of gravel-pebble habitats (Fore et al. 2007), gravel or larger substrates (Rankin 1986), cobble (Newcomb et al. 1995), and rubble habitats (Livingstone and Rabeni 1991). It is possible that finer substrates are used when predators are limited and prey fish are abundant or in the absence of other available choices (i.e., limited availability of other substrates). Olsen et al. (2003) supports a portion of this hypothesis with results indicating YOY smallmouth bass feeding rates were higher and predation risk lower in cobble habitats.

Substrate variables are often correlated with hydrologic variables and the availability of substrate classes can vary greatly among streams. I found high correlations between velocity and several substrate variables, especially sand. In this instance, it is likely that sand is not necessarily the habitat feature of interest; rather, it may simply correspond to areas of lower current velocity (where sand may be deposited due to a decrease in velocity below some threshold value). I can find no instance where YOY smallmouth bass have been found to use sand substrates. The importance of this variable in distinguishing between used and available points appears to be correlative. Alternatively, some substrate classes (e.g., bedrock) were only available in stream segments in watersheds classified by a particular land use. Bedrock was only available and therefore, only used, in stream segments classified by pasture land use. The appearance of bedrock substrates is thus limited to these stream types.

The importance of depth to YOY smallmouth bass varied depending on stream size and land-use classification. Depth was only significant in distinguishing between used and available points in the smallest streams sampled (e.g., Blair Creek and Greasy Creek) and streams classified as a group by pasture land use. Piscivores are generally not abundant in smaller stream reaches because they lack deeper-water habitats (Schlosser 1987). Young of year appear to do well in smaller streams with fewer competing piscivores; however, as they increase in size they may seek out deeper-water habitats that are limited in stream segments of this size. Fore et al. (2007) found YOY in an Oklahoma stream selected shallower depths in the absent of any appreciable velocity whereas deeper-water habitats were selected as velocity increased. Others have reported use of both shallow habitats (Bain et al. 1988; Livingstone and Rabeni 1991; Sabo and Orth 1994; Dewaulter et al. 2007), run habitats (Leonard and Orth 1988), and deeper-water habitats (Walters and Wilson 1996). None of these studies considered the influence of the surrounding landscape. The importance of deeper water in distinguishing used microhabitats could be related to changes in channel morphology associated particular land uses. Channel morphological changes such as widening, shallowing, and ultimately homogenization of stream habitats may increase the importance of the remaining available deeper-water habitats, especially as YOY increase in size and stream temperatures warm during summer. The optimum temperature for YOY growth is 29° C (Shuter and Post 1990) with a rapid decline in growth at higher temperatures (Hewett and Johnson 1992). In Chapter 4, I reported results indicating YOY generally use the warmest temperatures available at a microhabitat scale. However, when stream temperatures were ≥ 32°C, these habitats were not used indicating this temperature may be near their upper threshold in field-based studies.

Factors influencing the distribution of fish at the microhabitat scale are rarely due to a single variable or set of variables. It is difficult to identify why a fish resides in a particular location. At the coarsest scale, we can identify factors relative to biogeography and then filter to the finest scales (e.g., channel unit and microhabitat). However, the relation between coarse-scale influential features and fine-sale features often changes depending on the natural conditions in the watershed and particular land-use attributes that may be present, thereby limiting the transferability of many habitat-based studies. Only when we identify meaningful patterns observed in several stream segments and relate those patterns to coarse-scale factors can we begin to understand the importance fine-scaled environmental features may have on the distribution of fish.

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TABLE 1.- Description of stream segments sampled for this study. The first four stream segments were classified by forested land use and the last four stream segments listed were classified by pasture land use

Stream	Mean discharge (m^3/s)	Mean width (m)	Mean pool depth (cm)	Dominant substrate type(s)
Blair Creek	0.13	10	74	cobble & pebble
Jack's Fork (upper)	0.67	17	72	cobble & boulder
Jack's Fork (lower)	1.34	12	101	boulder & cobble
Sinking Creek	1.08	14	85	boulder & cobble
Finley Creek	0.29	15	54	cobble
Greasy Creek	0.09	11	33	gravel
Indian Creek	0.63	12	125	cobble
James River	0.06	13	57	bedrock & cobble

TABLE 2.- Variables significant in discriminant function analyses for each stream segment located in watersheds classified by forest or pasture land use ($\alpha \leq 0.10$). The error rate indicates error associated with classifying the microhabitat used versus an available microhabitat

Land use	Stream	Variables	F value	Pr > F	Error rate
Forest	Blair Creek	velocity	54.02	<0.0001	0.37
		depth	36.61	<0.0001	
		sand	9.99	0.002	
		gravel	8.51	0.004	
	Sinking Creek	sand	33.45	<0.0001	0.05
		boulder	7.36	0.007	
		velocity	4.09	0.04	
	Jack's Fork (lower)	bolder	9.87	0.002	0.24
		velocity	6.5	0.01	
	Jack's Fork (upper)	velocity	6.96	0.0008	0.35
Pasture	James River	bedrock	21.94	<0.0001	0.35

	depth	7.52	<0.0001	
Indian Creek	velocity	10.93	0.001	0.39
	gravel	10.93	0.001	
	sand	3.31	0.07	
Greasy Creek	sand	15.65	0.0001	0.38
	velocity	3.71	0.05	
	depth	3.35	0.07	
Finley Creek	depth	28.93	< 0.0001	0.30
	sand	16.08	< 0.0001	
	silt	3.51	0.06	
	velocity	3.23	0.07	
	bedrock	3.65	0.06	

TABLE 3.- Mean of microhabitat variables used and, in parentheses, mean available for each stream segment. The first four stream segments were classified by forested land use and the last four stream segments listed are classified by pasture land use

Stream	Depth (cm)	Velocity (m/s)	Silt (%)	Sand (%)	Gravel (%)	Pebble (%)	Cobble (%)	Boulder (%)	Bedrock (%)
Blair Creek	38 (12)	0.05 (0.43)	1 (1)	2 (1)	28 (17)	28 (17)	20 (32)	21 (32)	0 (0)
Jack's Fork (upper)	42 (35)	0.03 (0.16)	1 (2)	17 (9)	21 (19)	17 (20)	19 (28)	25 (17)	0 (0)
Jack's Fork (lower)	44 (40)	0.02 (0.15)	1 (1)	4 (4)	15 (13)	18 (23)	33 (45)	28 (11)	0 (0)
Sinking Creek	48 (45)	0.02 (0.21)	1 (1)	25 (6)	31 (23)	17 (26)	7 (31)	19 (10)	0 (0)
Finley Creek	57 (33)	0.08 (0.17)	1 (3)	6 (2)	28 (21)	17 (19)	36 (41)	9 (7)	1 (7)
Greasy Creek	26 (23)	0.009 (0.07)	11 (8)	16 (4)	22 (22)	23 (28)	18 (24)	10 (14)	0 (0)
Indian Creek	64 (51)	0.09 (0.21)	3 (1)	3 (5)	17 (11)	16 (19)	40 (46)	10 (6)	10 (12)
James River	43 (35)	0.002 (0.006)	1 (1)	9 (9)	14 (17)	11 (17)	21 (36)	3 (2)	40 (15)

TABLE 4.- Variables significant in discriminant function analyses for stream segments combined to represent watersheds classified by forest or pasture land use ($\alpha \leq 0.10$). The error rate indicates error associated with classifying the microhabitat used versus an available microhabitat

Land use	Variables	F value	Pr>F	Error rate
Forest	velocity	42.98	< 0.0001	0.33
	boulder	9.53	0.002	
	sand	5.12	0.02	
Pasture	velocity	32.66	< 0.0001	0.42
	depth	13.09	0.0003	
	pebble	5.54	0.02	
	cobble	3.78	0.05	

VITA

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