RELATIONSHIPS AMONG GEOMORPHOLOGY, HABITAT, AND FISHES IN EASTERN OKLAHOMA STREAMS: IMPLICATIONS FOR STREAM RESTORATION

By

DANIEL CARL DAUWALTER

Bachelor of Arts
Gustavus Adolphus College
St. Peter, Minnesota
1999

Master of Science
University of Arkansas at Pine Bluff
Pine Bluff, Arkansas
2002

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Oklahoma State University in partial fulfillment of
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Dissertation Approved:

William L. Fisher

Dissertation Advisor

Richard A. Marston

Anthony A. Echelle

Joseph R. Bidwell

A. Gordon Emslie

Dean of the Graduate College

PREFACE

All chapters of this dissertation were written as manuscripts that will be submitted to peer-reviewed journals. Therefore, each chapter follows the style and guidelines of the respective journal to which it will be submitted: Chapter 1, *Ecology of Freshwater Fish*; Chapter 2, *Canadian Journal of Fisheries and Aquatic Sciences*; Chapter 3, *Transactions of the American Fisheries Society*; and Chapter 4, *Transactions of the American Fisheries Society*. Chapter 5, which is a summary chapter and will not be submitted in its current form, is formatted to *North American Journal of Fisheries Management*. Subjects in sentences are written in active voice to recognize contributions of coauthors of manuscripts (W.L. Fisher, D.K. Splinter, and R.A. Marston) in this dissertation; for example, *we* is used in place of *I*.

ACKNOWLEDGMENTS

Many people assisted me in my pursuit of a Ph.D. degree through the Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Zoology at Oklahoma State University. William (Bill) L. Fisher has been an exceptional advisor. He gave me many important suggestions regarding this research, including data management, conceptual ideas, and analytical approaches. Sometimes it took me a while to realize their importance, but I think I have tried to use many of them somehow. Despite those suggestions, Bill gave me complete freedom to do with this research whatever I wanted from the start. He ensured that there was enough money to complete each research component, and he helped me get even more money from the Environmental Institute at OSU. Bill was simply an outstanding advisor throughout.

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Personnel in the Oklahoma Cooperative Fish and Wildlife Research Unit, overseen by Dr. David M. Leslie, Jr., made the logistical aspects of conducting research very easy. They were: Judy Gray, Sheryl Lyon, Helen Murray, and Dionne Craig.

Dale K. Splinter was my partner in crime (or the other graduate student) throughout this matter. Dale questioned just about every decision I tried to make in the field, including every channel-unit classification and bankfull-stage identification – of course I reciprocated. Despite these arguments, we had a hell of a time in a little less than four years. We talked to more 'interesting' landowners in eastern Oklahoma than I think both of us realized existed; we also talked to many very nice and courteous landowners too. We survived adverse weather conditions that made tree branches almost crush tents (and Bryce Marston) on several occasions, and counted more cottonmouths *Agkistrodon piscivorous* than we ever care to see again. We also did numerous cannon balls, abused (and broke) many rope swings constructed by local river rats, and did some cliff jumping. Most importantly, as a result of this project I think that Dale has risen out of the C horizon, above the O, and into the real world of stuff that occurs above the soil and in flowing waters (I am only slightly kidding). More importantly, Dale is now a lifelong friend.

Several people survived some hellaceous field seasons during this research. Valerie Horncastle suffered through the first summer field season, 2003, and listened to countless hours of Dale and I argue about channel unit classifications, bankfull identification, split channels, organization skills, how to read a map, where to turn, and countless other things. She also survived many days over 100°C. By the second summer, 2004, Kyle Winters, Raymond Ary, and Bryce Marston experienced smoother waters, as Dale and I did more working rather than fighting. All that work and some personal hygiene issues required Dale to call mandatory bath nights on occasion. Mark Murray, Bryce Marston, and James Morel experienced the best of conditions during the third summer in 2005, even though most of it was spent in cottonmouth country, i.e., the Ouachita Mountains. Kyle Winters, Brian Collins, and Jeff Fore also helped with this research, specifically with seasonal stream sampling. Winter sampling was very cold in December 2003, and was made even colder by leaky waders. Many other research associates and graduate and undergraduate students helped with field work at some point: Dustin Amey, Jeff Batchelder, Kevin Belt, Evan Comer, Lyndi Custard, Donny Driskell, Bullit Farris, Jason Freund, Christopher Hargis, Mike Herzeburger, Chas Jones, Alicia Krystaniak, Lucas Negus, Seth Rambo, Sabrina Rust, Jason Schaffler and Nick Utrup. Even Bill made it into the field, and made some of those mentioned above and myself push him around on an electrofishing boat a few times.

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Lastly, I thank my parents, Mary and Thomas Sexton, and Stacey Kathleen Davis. I'm not sure my parents still completely understand why I have been in school so long. Regardless, they understand that I'm doing something that I truly enjoy, and that has let me work in streams, play with fishes, and live in several places around the central United States: mom, maybe someday I'll end up a little closer to home. And Stacey………

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INTRODUCTION

Stream restoration is a multidisciplinary practice aimed at reestablishing the structure and function of disturbed stream ecosystems. Current instream restoration practices emphasize fluvial geomorphic processes and channel form when planning instream habitat projects. More recently, principles of landscape ecology, including spatial scale and habitat juxtaposition, complementation, and supplementation, have been applied to aquatic systems and are now considered imperative to the conservation of fish populations. However, fluvial geomorphology and landscape ecology principles typically are not both considered when stream restoration projects are planned and implemented.

The objectives of this dissertation were to: 1) relate geomorphology and stream habitat to fish species composition and smallmouth bass abundance at several spatial scales in eastern Oklahoma streams, 2) determine spatial and temporal changes in stream habitat and population characteristics of smallmouth bass in two eastern Oklahoma streams, 3) evaluate the applicability of a landscape model developed for stream fishes to those streams, and 4) reveal how both geomorphology and landscape ecology can be important and need to be considered when conducting stream restoration projects. These objectives are addressed within five dissertation chapters.

Chapter 1 addresses a portion of Objective 1 by using a survey of streams to reveal the importance of longitudinal and local geomorphic factors in explaining fish species composition in eastern Oklahoma. The importance of geomorphology is discussed relative to biogeography, ecoregions, and stream habitat: factors previously associated with regional fish assemblages. Finally, findings are discussed in the context of the River Continuum Concept, Process Domains Concept, and hierarchical landscape filters.

Chapter 2 focuses on smallmouth bass *Micropterus dolomieu* to fully meet Objective 1. Relations among geomorphology, stream habitat, and smallmouth bass density were evaluated at several spatial scales using data from a stream survey. Results were discussed in the context of spatial scale, geomorphic processes, and stream restoration.

Chapter 3 addresses Objectives 2 and 3 and presents research that investigates spatial and temporal variability in stream habitat and smallmouth bass population characteristics in two streams representative of northeastern and southeastern Oklahoma. Complementation and supplementation of habitats needed by smallmouth bass to meet life history requirements are discussed.

Chapter 4 details the nesting behavior of smallmouth bass. Spawning chronology, selection of nest sites by spawning males, and determinants of nest success are determined. Results are used to support habitat complementation patterns discussed in Chapter 3 and to meet Objective 3.

Chapter 5 synthesizes results from the first four chapters and discusses their importance relative to current stream restoration principles to address Objective 4.

Stream morphology data collected for Chapters 1 and 2 suggest that eastern Oklahoma streams are sensitive to changes in streamflow and sediment dynamics, but they are capable of recovering naturally. Eastern Oklahoma streams are also good candidates for many fish habitat improvement structures according to some restoration guidelines. However, results from previous chapters suggested that, in addition to geomorphology, the spatial structure of habitats also needs to be considered when developing expectations for how fish populations and communities might respond to stream restoration activities.

CHAPTER 1

LONGITUDINAL AND LOCAL GEOMORPHIC EFFECTS ON FISH SPECIES COMPOSITION IN EASTERN OKLAHOMA STREAMS

Abstract

Stream fish assemblages are structured by biogeographical, physical and biological factors acting on different spatial scales. Our objectives were to determine how physical factors, geomorphology and stream habitat, influenced fish species composition (presence-absence) in eastern Oklahoma streams relative to ecoregion and biogeographic effects previously reported. We sampled fish assemblages and surveyed habitat and geomorphology at 107 stream sites in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma. We used partial canonical correspondence analyses (pCCAs) to determine the geomorphic and habitat variables that best explained variability in fish species composition, and used variance partitioning to compare the amount of variation in species composition attributable to geomorphology and stream habitat, ecoregions, and biogeography. Geomorphic variables representing stream size were most important in explaining variability in fish species composition in both northeastern and southeastern Oklahoma streams. Local channel morphology and substrate characteristics were secondarily important. Variables typically considered important as fish habitat (woody debris, aquatic vegetation, etc.) explained little variation in fish species composition. Variance partitioning demonstrated that geomorphic variables explained twice as much variation in fish species composition, per variable, than did ecoregions in northeastern streams, and four times as much variation than did drainage basins in southeastern streams. Our results supported the hierarchical filter theory as applied to stream fishes, and are discussed relative to the River Continuum Concept and Process Domains Concept.

Introduction

Stream fish communities are structured by three sequential factors: biogeography, physical habitat, and biological interactions. Poff (1997) unified these factors in a framework describing how functional species traits allow species in the regional species pool (resulting from biogeography) to pass through hierarchically nested habitat filters that determine which species are present at a given locality. Biotic interactions act as additional filters on local community composition.

The longitudinal profile of a stream has long provided a spatial context for stream ecology theory (Shelford 1911). Sheldon (1968) reported that species richness increased downstream in a New York stream system as a result of species additions to headwater assemblages. Horwitz (1978) found that streamflow variability changed predictably from upstream to downstream. He suggested that a decrease in streamflow variability downstream allowed additional fish species to join the species pool that consisted of those already present upstream (sensu Sheldon 1968). The rate of species additions reflected the temporal constancy of specific rivers. Subsequently developed stream ecology theories, such as the River Continuum Concept, emphasized longitudinally varying processes (e.g., heterotrophy versus autotrophy, energy processing and transport, physical and biological stability and diversity) and how longitudinal changes influenced fish community composition (Vannote et al. 1980). However, the predictions of the concept sometimes proved untenable when applied to regions other than those they were developed for (Minshall et al. 1985) and in river systems with anthropogenic interruptions (e.g., dams) of the continuum itself (Ward & Stanford 1983).

The influence of longitudinal processes on local habitat conditions and fish community composition varies among streams and rivers. A recent theory, the Process Domains Concept (Montgomery 1999), suggests that spatial and temporal variability in geomorphic processes (e.g., hydrology, sediment transport, woody debris recruitment) often creates homogenous zones within the river continuum, and that those zones may contrast expectations from the River Continuum Concept. The spatial structure of these zones can strongly influence stream ecosystem structure and function and how ecosystems respond to disturbance. Patchy, local (i.e., reach scale) geomorphic processes, such as reach slope and bed mobility, influenced stream disturbance regimes and fish assemblage structure more than longitudinal processes in a Piedmont river drainage in the southeastern United States (Walters et al. 2003b). However, the dominance of local processes may have reflected the spatial scale of the study (Wiens 1989). Studies focusing on a small range of stream sizes from a single river basin may show little variation in longitudinal process such that local processes dominate (Sheldon 1968; Walters et al. 2003b), whereas longitudinal processes may be more evident in studies with a larger spatial extent (Horwitz 1978).

Eastern Oklahoma contains parts of the Ozark Highlands, Boston Mountains, Arkansas River Valley, Ouachita Mountains, and South Central Plains ecoregions (Omernik 1987; Woods et al. 2005). Streams in these regions in Arkansas have relatively distinct water quality, stream habitat, and fish species composition (Rohm et al. 1987; Matthews et al. 1992). Biogeography related to the Arkansas and Red River drainages explained much variability in fish species composition in Arkansas highland streams (Matthews & Robison 1988), as did longitudinal effects related to basin size (Matthews

& Robison 1998). Historical biogeographical and ecoregional patterns in fish species composition also exist for these same regions in eastern Oklahoma (Howell 2001). However, Tejan (2004) suggested that only the Ouachita Mountains ecoregion contained predictable fish species composition, whereas no strong patterns were evident in other eastern Oklahoma ecoregions. Tejan found that underlying geology, precipitation, land use, and longitudinal variables explained fish species composition, irrespective of ecoregions. Despite the noted occurrence of longitudinal trends in fish species composition over large regions in eastern Oklahoma, less is known about how local geomorphology, such as channel morphology and bedrock outcrops, influences stream habitat and disrupts longitudinal patterns in fish species composition.

We determined how longitudinal and local geomorphology and stream habitat affected fish species composition relative to ecoregions and biogeography in eastern Oklahoma streams. Understanding the effects of geomorphology and stream habitat is imperative given that much stream ecology theory and stream restoration principles have a geomorphic basis. Moreover, determining the magnitude of geomorphic effects relative to previously reported ecoregion differences and biogeographic effects will further reveal mechanisms influencing fish species composition in eastern Oklahoma.

Methods

Stream survey

We used a geographic information system (GIS) to randomly select 175 stream sites for an inventory of fluvial geomorphology, habitat, and fishes in eastern Oklahoma streams in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions

(Omernik 1987). Sites were allocated among the three ecoregions approximately in proportion to their areas in Oklahoma and equally distributed among stream orders 1 to 4 within each ecoregion. Forty sites were selected in the Boston Mountains and Ozark Highlands ecoregions, and 95 were selected in the Ouachita Mountains ecoregion in Oklahoma.

Watershed and reach geomorphology, along with instream habitat, were measured at each stream site. We derived geomorphic variables at the watershed scale by using a GIS. Drainage area and elongation ratios were measured for each site (Morisawa 1968). ArcGIS 9.1 software (ESRI, Redlands, California) and the National Elevation Dataset (USGS 1999) were used to delineate watersheds upstream of each site.

From May 2003 to August 2005 we measured geomorphic variables at the reach scale at each stream site. A global positioning system (GPS) receiver was used to navigate to each randomly selected stream site. Stream reaches were defined as 20 times the mean channel width upstream from each site (Rosgen 1994). We classified channel units (e.g., riffles and pools) in each reach using the scheme of Hawkins et al. (1993). Transects perpendicular to the channel were surveyed across two riffles and two pools when available, with a maximum of two transects in a single channel unit. Two to four transects were surveyed per reach. Bankfull channel width:depth ratios were calculated; bankfull channel depths were measured at 20 equally-spaced locations along transects (Arend & Bain 1999). We calculated entrenchment ratio as the ratio of width of floodprone area to bankfull channel width (Rosgen 1994). Median particle sizes (D_{50}) were calculated by collecting 100 particles along each transect and measuring the intermediate axis of each (Bain 1999). Slopes of individual channel units were measured and cumulatively represented reach slope. Sinuosity was measured as thalweg length:valley length. Width:depth ratios and median particle sizes for each reach were calculated from transect data as weighted averages based on the proportion of each reach length that comprised riffles and pools.

Instream habitat variables were estimated or measured in each channel unit of each reach. Channel units were mapped with GPS, and dimensions were measured in a GIS (Dauwalter et al. 2006). Thalweg depths were measured systematically. We estimated substrate distributions using a modified Wentworth scale (Wolman 1954; Bain 1999). We visually estimated, and enumerated when logistically feasible, rootwads and large woody debris (10+ cm diameter, 4+ m in length) in each channel unit. Percent coverage of aquatic vegetation was also estimated. Data from each channel unit were combined for reach estimates.

Fish species composition was estimated using snorkeling and electrofishing (Reynolds 1996; Dolloff et al. 1996). Most reaches were snorkeled by 1 to 3 persons depending on stream size and water clarity. Snorkelers swam in a zig-zag pattern in an upstream direction. Fish species observed were noted on a diving cuff. The senior author had previous experience identifying fish species in each region (Dauwalter et al. 2003; Dauwalter & Jackson 2004). We wrote descriptions of unidentifiable species on a diving cuff and later identified them, if possible, by using field guides and knowledge of species distributions (Miller & Robison 2004); some fish individuals could not be identified and were omitted. Five groups of species could not be identified to species while snorkeling, and were placed into groups (but are hereafter referred to as species): redhorses *Moxostoma spp.*, spotted bass *Micropterus punctulatus* (Rafinesque) and largemouth *M. salmoides* (Lacepede) (both recorded as *M. salmoides*), lampreys *Ichthyomyzon spp.*, buffalo fishes *Ictiobus spp.*, and *Lythrurus spp*. Seventeen streams were too turbid to snorkel (visibility <1 m), and were electrofished with a Smith Root, Inc. model 15-D backpack electrofisher, or a Smith-Root 2.5 GPP model electrofisher mounted in a 3 m john boat with a portable anode or a 4.3 m john boat with a ring anode with 6 stainless steel droppers. Electrofishing power density was standardized at 1,000 μS / cm^3. When electrofishing, unidentifiable fish species were preserved in 10% formalin and later identified in the laboratory.

Fish species associations with geomorphology and stream habitat

Using CANOCO for Windows software version 4.5 (Biometris-Plant Research International, Wageningen, The Netherlands), we performed partial canonical correspondence analysis (pCCA) to determine which geomorphic and stream habitat variables were associated with fish species composition in northeastern (Boston Mountains and Ozark Highlands) and southeastern Oklahoma streams (Ouachita Mountains). Canonical correspondence analysis is a direct gradient analysis that uses weighted averaging resulting in a unimodal species model whereby variations in species composition can be explained by environmental variables (ter Braak 1986). Using pCCA, variation attributed to certain environmental variables can be factored out to focus on the specific variables of interest. We used forward stepwise selection procedures to select geomorphic and habitat variables for each pCCA, with the exception that basin area was always included as a surrogate for stream size. All remaining variables were entered given $P \leq 0.05$ from a Monte Carlo permutation test with 9999 permutations

(Lepš & Šmilauer 2003). Selection of environmental variables for northeastern streams was done in a pCCA with data from both ecoregions and with ecoregions as covariables. Variable selection for Ouachita Mountains streams was done in a pCCA in which drainages were used as covariables. Separate analyses were warranted for northeastern (Boston Mountains and Ozark Highlands) and southeastern (Ouachita Mountains) streams because of distinct landscape features associated with each region (Fisher et al. 2004), and fish species composition was not predictable in northeastern Oklahoma ecoregions but was in the Ouachita Mountains (Howell 2001; Tejan 2004). We used biplot scaling conducted on inter-species differences and downweighted rare species in all pCCAs.

We ran additional analyses for variance partitioning (Økland 2003) after initial pCCAs were run for each region to select geomorphic and stream habitat variables explaining the most variation in fish species composition. In the northeast we ran additional analyses to partition variance associated with ecoregions (Boston Mountains and Ozark Highlands), selected geomorphic and stream habitat variables, and shared variance. In the southeast, we ran additional analyses to estimate variance associated with drainages (Arkansas and Red Rivers), selected geomorphic and stream habitat variables, and variance shared.

Results

Stream survey

We surveyed fluvial geomorphic features, stream habitat, and stream fishes at 107 of the 175 selected stream sites in the Boston Mountains, Ouachita Mountains, and Ozark

Highlands ecoregions. Seventeen stream sites were inaccessible or access was denied by landowners. Four streams had primary channel disturbances (e.g., gravel mining, concrete channels) and were not sampled, and no definable channel was found at three sites. Nineteen streams were dry. Trained personnel were not available to snorkel and identify fish species at 20 sites, and no fish were observed at four. This resulted in presence-absence data of fish species at 107 stream sites (Fig. 1.1).

Streams among ecoregions differed mostly in substrate and some channel morphology characteristics (Table 1.1). Two main stream types were observed among the 107 sites where species presence-absence data were collected (Rosgen 1994). Ninety-one sites were classified as Rosgen type C streams, characterized as low gradient, meandering with point bars, riffle-pool structure, and alluvial channels with broad, well-defined floodplains. Thirteen streams were type E streams, having a low gradient, meandering with riffles and pools, low width:depth ratios and little sediment deposition. Three remaining sites were type B streams, being moderately entrenched dominated by riffles with moderate gradient and stable banks.

We observed 61 fish species total during stream surveys (Appendix 1.1). Fifty-eight species were observed in 43 stream sites in the Boston Mountains and Ozark Highlands ecoregions combined. On average, 10.0 fish species were observed in Boston Mountains streams, and richness ranged from 3 to 20. In the Ozark Highlands, the number of species observed averaged 12.0, and ranged from 1 to 26. In the Ouachita Mountains, 58 species were observed at 64 sites; an average of 7.7 species per site were observed, ranging from 1 to 18.

Fish species associations with geomorphology and stream habitat

Longitudinal and local geomorphology explained most of the variation in fish species composition in eastern Oklahoma streams. In the northeastern streams, reach slope ($P = 0.001$), width:depth ratio ($P = 0.002$), and D_{50} ($P = 0.024$) were entered during forward stepwise procedures. These variables explained most of the variation in fish species composition in addition to the known effects of basin area (stream size). D_{50} ($P < 0.001$), slope ($P = 0.005$), and percent silt-clay ($P = 0.021$) were entered during the forward stepwise selection of variables in analysis of Ouachita Mountains streams, in addition to basin area.

In all streams, variation was primarily explained by longitudinal trends in species composition, but local channel morphology and substrate characteristics explained additional variation. Axis 1 from the pCCA in northeastern streams accounted for 54.0% of the observed species-environment variance (Table 1.2), and represented a notable longitudinal gradient whereby there was nearly a direct relationship between basin area and reach slope. Southern redbelly dace are found in clear, spring-fed headwater streams (Robison & Buchanan 1988) that represented one end of the longitudinal gradient, with rock bass, redhorses, logperch, and the banded darter representing larger stream species (Fig. 1.2). Axis 2 represented a substrate-size gradient, again with southern redbelly dace at one end of the gradient and multiple species at the other. Larger variation in substrate size in the Boston Mountains appears to be influencing this gradient (Fig. 1.2). The ubiquitous green sunfish fell at the center of axes 1 and 2.

There also were longitudinal and substrate gradients in the Ouachita Mountains. Axis 1, accounting for 40.8% of the variance in species-environment data (Table 1.2), incorporated both stream size and substrate effects. Smallmouth bass and leopard darter were associated with large streams with large substrates and western mosquitofish and yellow bullheads were associated with smaller streams with finer substrates. Brook silversides, spotted gar, and some other notable larger stream species were associated with larger basins (Fig. 1.3). Substrate size was also an important environmental gradient with D_{50} and percent silt-clay negatively correlated, but uncorrelated with basin area. Again, green sunfish fell at the center of axes 1 and 2.

Variance partitioning showed that longitudinal and local geomorphic factors explained more variance in fish species composition than ecoregions or biogeography (Table 1.3). In northeastern streams, longitudinal and local geomorphic factors explained about twice the amount of variation, per variable, than did other factors associated with ecoregions, with little shared variance. In the southeast, geomorphic factors explained almost four times more variation per variable than did the Arkansas and Red River drainages that have endemic species: a small amount of variation could not be distinguished between geomorphology and drainages.

Discussion

Longitudinal and local geomorphology best explained the variance in fish species composition in streams of the Boston Mountains, Ozark Highlands, and Ouachita Mountains ecoregions in eastern Oklahoma. Longitudinal changes in fish species richness and composition have been documented by others in these regions. In these regions in Arkansas, species richness increased with stream size (Matthews & Robison 1998). In eastern Oklahoma streams downstream link (a measure of stream size) was important in explaining variation in fish species composition, with southern redbelly dace in small streams and gars in larger streams (Tejan 2004).

Longitudinal and local geomorphology each influenced fish species composition, but some selected variables were not unique to either spatial scale. Reach slope was almost directly but negatively correlated with basin area in northeastern Oklahoma streams. Reach slope had a weak, negative relationship with basin area in the Ouachita Mountains, suggesting at least some local, reach-scale influence on stream gradient; for example, some reaches of small streams were in the mountains, and others were in floodplains of larger streams and rivers. For that reason, we could not treat reach slope solely as a longitudinal variable. This precluded partitioning variance between longitudinal and local effects. Negative correlation between reach slope and basin area is concordant with expected concave longitudinal profiles of streams (Knighton 1998), but differs from findings for a Piedmont drainage where basin area was weakly correlated with reach slopes (Walters et al. 2003b). Substrate size (D_{50}) was relatively independent of basin area in our study and reflected spatial variability in sediment dynamics within the stream-size continuum. Western mosquitofish were indicative of small streams with fine sediments in southeastern streams, whereas darters and minnows inhabited small streams with larger substrates. Width:depth ratio was also important in explaining variation in northeastern streams and was slightly and positively correlated with basin area. Larger width:depth ratios typically indicate more alluvial, less stable stream channels (Rosgen 1994). Width:depth ratios were negatively related to both large woody debris and rootwad density (Chapter 2), which is peculiar considering rock bass were associated with larger width:depth ratios but they prefer instream cover (boulders, woody debris; Miller & Robison 2004).

Ecoregion and historical biogeographic effects on species composition were smaller than longitudinal and local geomorphic effects. Previously reported differences among ecoregions may have reflected differences in local channel morphology that influenced species composition within ecoregions (Rohm et al. 1987; Matthews & Robison 1988; Tejan 2004), especially between northeastern and southeastern streams (that we did not directly compare). Channel morphology was expected to differ between ecoregions and is why we analyzed northeastern and southeastern streams separately; some variables also change longitudinally, and at different rates among ecoregions (e.g., channel width:depth ratio; D. K. Splinter, Oklahoma State University, unpublished data). McCormick et al. (2000) ascertained that anthropogenic effects and site-specific differences were primary reasons that stream fish assemblages in the Mid-Atlantic Highlands did not coincide with the large-scale geographic classifications of ecoregions and catchments. The ecoregion effects observed in the Boston Mountains and Ozark Highlands probably reflected underlying geology, climate, land-use, and soils (Omernik 1987; Fisher et al. 2004). However, a small part of the observed variation in fish species composition was indistinguishable between geomorphology and ecoregions, and reflected differences in geomorphology among ecoregions (D. K. Splinter, Oklahoma State University, unpublished data; Chapter 2). Some researchers have noted the influence of endemic species on ordination analyses conducted in these regions (Matthews & Robison 1988; Howell 2001). We observed small effects of biogeography, that is, species endemic to Arkansas River and Red River basins in the Ouachita Mountains. This result may have been a sampling artifact, since most endemic species in the region have low population sizes that may have led to some species being falsely classified as absent during snorkeling surveys.

Surprisingly, variables typically considered instream habitat (woody debris, aquatic vegetation, etc.) were not selected during stepwise procedures, and consequently explained little or no variation in fish species composition in eastern Oklahoma streams. Stream habitat has been considered a dominant factor in structuring fish communities (Gorman & Karr 1978), and the lack of explanatory power of habitat variables likely reflected our use of presence-absence data instead of abundance. Our analyses suggested that certain watershed (longitudinal) and reach (local geomorphology) scale variables impart selective forces on fish species within the region. However, other studies from these regions have suggested that stream habitat (Bart 1989; Taylor 2000; Peterson & Rabeni 2001; Wilkinson & Edds 2001) and biotic interactions (Harvey 1991; Taylor 1996) are important in structuring fish assemblages. Consequently, our results, when considered in the context of these other studies, support the hierarchical landscape filter framework proposed by Poff (1997). Our data suggest that selected species within the regional species pools have traits allowing them to pass through nested hierarchical habitat filters at the basin and reach scale to join the species pool within a reach, and their abundances (that we did not measure) are then primarily affected by local habitat variables and biotic interactions.

Both longitudinal and local geomorphic factors affected fish species composition and suggest that both the River Continuum and Process Domains Concepts apply to eastern Oklahoma streams. Longitudinal variable(s) explained most of the variation in fish species composition (i.e., they were most correlated with axis 1 of pCCAs) for both northeastern and southeastern streams. This suggests that longitudinal processes related to the River Continuum Concept (Vannote et al. 1980) were the primary factors in structuring fish species composition. Channel geometry and substrate size within reaches were conditions that influenced fish species presence on a local scale and were relatively independent of stream size. This suggests that spatial variability in geomorphic processes exists in the longitudinal continuum of these streams and that the Process Domains Concept (Montgomery 1999) applies secondarily.

The spatial and temporal distribution of natural or anthropogenic disturbances within channel networks can impart specific impacts on local geomorphic processes that lead to habitat patches that disrupt the longitudinal processes of rivers. Floods, fires, and debris flows are spatially and temporally explicit natural disturbances that affect local geomorphic processes, especially at tributary junctions (Benda et al. 2004). We did not document specific anthropogenic disturbances that might have resulted in changes in channel morphology or substrates, but land use changes alter hydrology and sediment regimes that can change channel form and sediment inputs (Marston et al. 2003; Walters et al. 2003a). Pastureland dominates the landscape in northeastern Oklahoma (Balkenbush & Fisher 2001; Fisher et al. 2004), but a legacy of previous logging activity may still be impacting geomorphic processes in certain watersheds (Rabeni & Jacobson 1993; Harding et al. 1998). Silviculture activity has and continues to dominate the landscape in the Ouachita Mountains in southeastern Oklahoma (Rutherford et al. 1992; Balkenbush & Fisher 2001). Gravel mining and removal of riparian vegetation, which occurs in the Ozark Highlands and Boston Mountains ecoregions, can cause local bank instability and result in wider, less sinuous channels having higher slopes (Rosgen 1994). Such changes in channel morphology adversely affect stream habitat and sensitive fish species (Brown et al. 1998). Understanding variability in hydrology, geomorphology, and disturbance history (e.g., landslides, floods, land use) is important in understanding processes affecting fish habitat (Montgomery & Bolton 2003), and this is why geomorphic evaluations are at the forefront of stream restoration practices (Rosgen 1996; FISRWG 1998; Wissmar & Bisson 2003).

We found that fish species composition in eastern Oklahoma streams varied longitudinally and with variation in local geomorphology. Consequently, longitudinal and local geomorphic processes are likely primary and secondary determinants of those fish species that are found locally within a stream reach. We also found stream habitat variables to be relatively unimportant in explaining fish species composition. However, there is overwhelming evidence that stream habitat structures fish communities. Thus, stream habitat likely plays at least a role in determining the relative abundances of fish species after geomorphic processes determine the local species pool. Accordingly, changes in geomorphic processes should lead to predictable changes in stream habitat and fish species composition. As a result, application of watershed or local restoration principles that restore geomorphic processes should produce specific responses from the fish community given individual species are available for recolonization. However, quantifying exactly how each species will respond to geomorphic change remains unknown, and should be the focus of future research in eastern Oklahoma and similar streams.

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Table 1.1. Summary (mean ± 1 SD) of geomorphology and habitat from streams in the Boston Mountains (n = 23), Ouachita Mountains (n = 64), Ozark Highlands (n = 20), Oklahoma.

	Boston Mountains		Ouachita Mountains		Ozark Highlands	
Variable	Mean	SD	Mean	SD	Mean	SD
Basin area (km^2)	127.9	167.84	70.0	91.41	184.4	235.78
D_{50} (mm)	37.6	19.02	78.3	69.25	27.4	7.45
Elongation ratio	0.57	0.094	0.52	0.135	0.50	0.109
Large woody debris density (#/m^2)	0.003	0.0084	0.003	0.0046	0.003	0.0028
Mean thalweg depth (m)	0.30	0.148	0.39	0.213	0.42	0.182
% Bedrock	20.9	25.53	11.2	16.69	8.7	17.92
% Pool	61.5	25.89	87.9	16.85	65.2	24.73
% Silt-Clay	4.2	7.60	7.5	10.50	4.9	5.91
% Vegetation	1.3	2.16	7.9	10.79	3.9	4.93
Rootwad density (#/m^2)	0.004	0.0084	0.006	0.0100	0.008	0.0127
Sinuosity	1.13	0.130	1.19	0.280	1.17	0.215
Slope	0.007	0.0064	0.006	0.0065	0.005	0.0042
Width:depth ratio	23.5	7.93	17.2	6.41	25.3	11.94

Table 1.2. Cumulative percent variance of species data and species-environment data explained by axes from pCCAs of fish species (presence-absence) and geomorphic and stream habitat variables from 107 northeastern and southeastern Oklahoma streams.

Region / Variance component	Axis 1	Axis 2	Axis 3	Axis 4
Northeast				
species data	11.3	15.7	18.7	20.9
species-environment data	54.0	74.9	89.5	100.0
Southeast				
species data	6.2	11.6	13.7	15.3
species-environment data	40.8	75.9	89.6	100.0

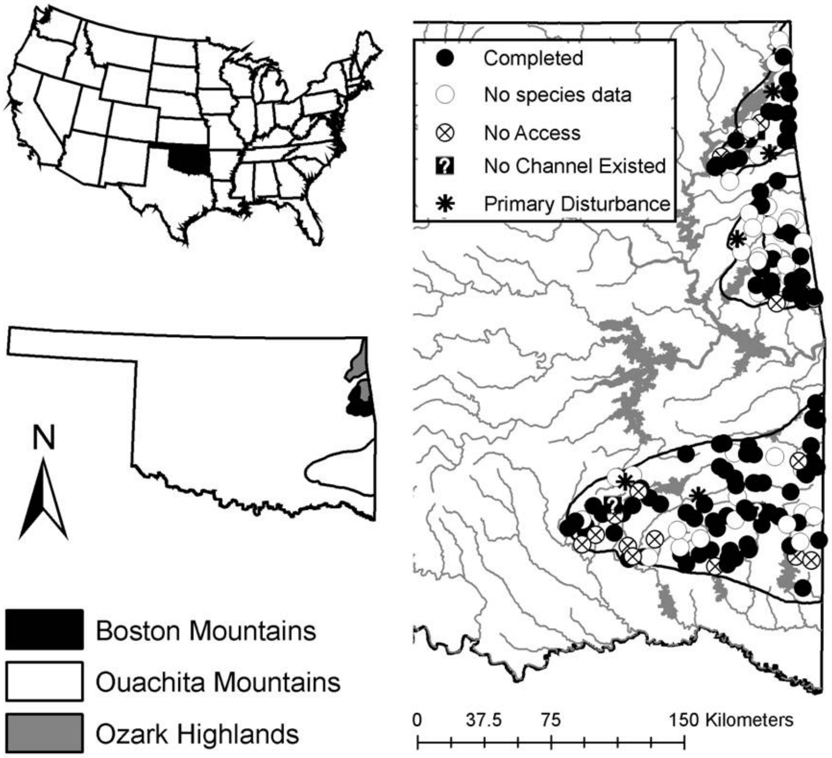
Table 1.3. Variance in fish species composition (presence-absence) attributable to ecoregions, geomorphic variables, or variance shared in northeastern streams in the Boston Mountains and Ozark Highlands ecoregions, and variance attributable to drainages, geomorphic variables, or that shared in southeastern streams in the Ouachita Mountains ecoregion, Oklahoma.

Region / Factor	Number of variables	∑ canonical eigenvalues	% of variance	Mean % per variable
Northeast				
Ecoregions	2	0.078	20.6	10.3
Geomorphology	4	0.292	77.0	19.3
Ecoregions∩Geomorph	6	0.009	2.4	0.4
Sum		0.379		
Southeast				
Drainages	2	0.040	11.6	5.8
Geomorphology	4	0.288	83.7	20.9
Drainages∩Geomorph	6	0.016	4.7	0.8
Sum		0.344		

Fig. 1.1. Locations of 175 randomly selected stream sites used for an inventory of fluvial geomorphology, stream habitat, and stream fishes in eastern Oklahoma, of which completed species lists were collected at 107.

Fig. 1.2. pCCA biplots of fish species (A) and samples (B) and basin area, reach slope, channel width:depth ratio, and median particle size (D_{50}) summarizing differences in fish species composition along longitudinal and local geomorphic gradients in Boston Mountains (▲) and Ozark Highlands (□) streams. Species having weights greater than 5% are displayed. Species codes represent the first two letters of genus and first six of species.

Fig. 1.3. pCCA biplots of fish species and basin area, reach slope, median particle size (D_{50}), and percent silt-clay summarizing differences in fish species composition along longitudinal and local geomorphic gradients in Ouachita Mountains streams. Species having weights greater than 5% are displayed. Species codes represent the first two letters of genus and first six of species.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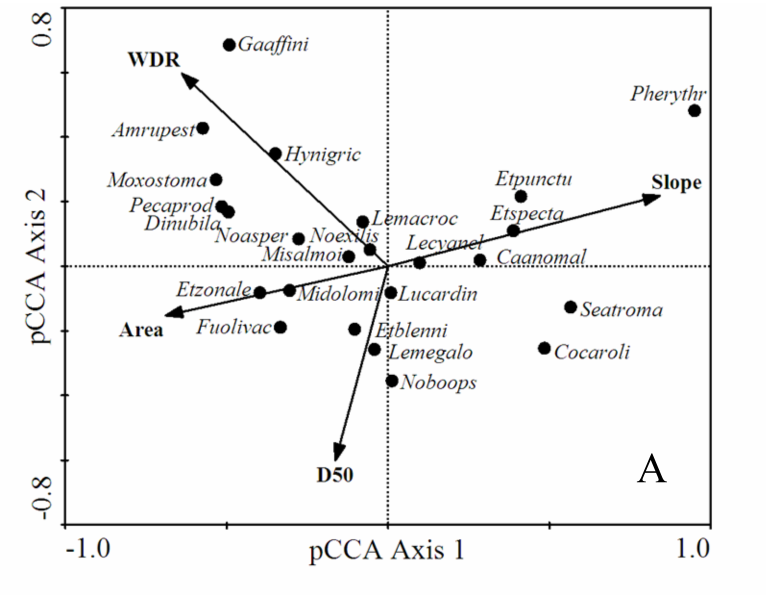
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Hynigric
Moxostoma
Pecaprod
Dinubila
Noasper
Noexilis
Lemacroc
Misalmoi
Lecyanel
Caanomal
Etpunctu
Etspecta
Pherythr
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Etblenni
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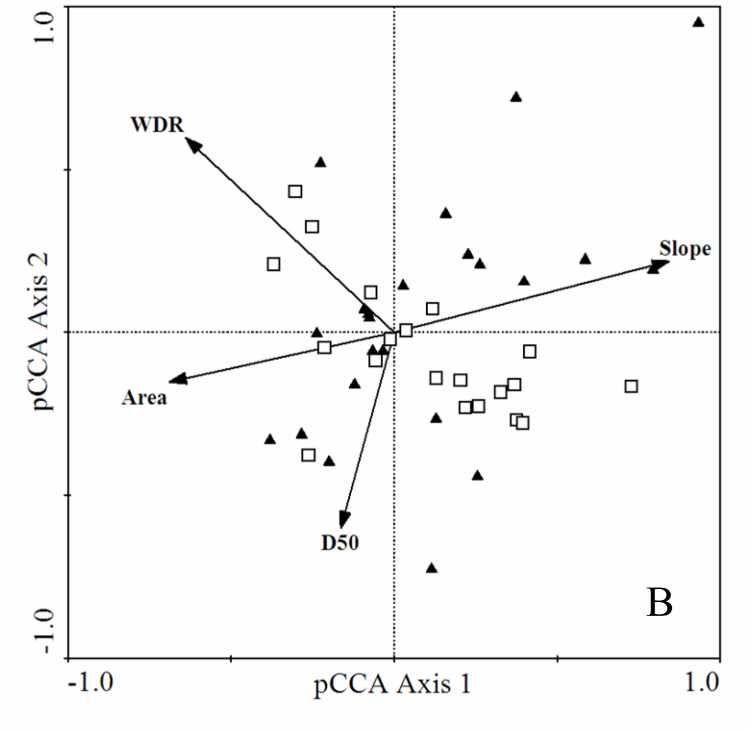
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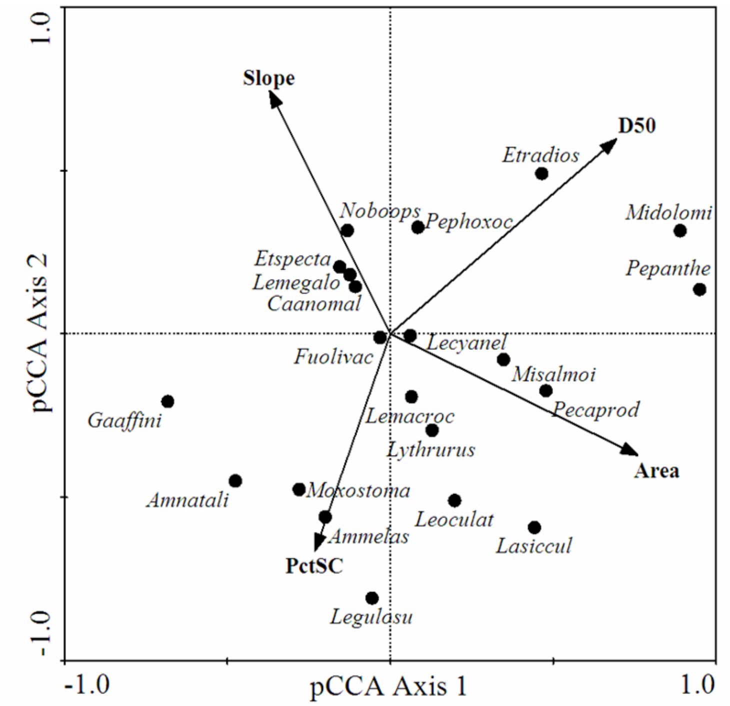
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Midolomi
Etspecta
Lemegalo
Caanomal
Pepanthe
Fuolivac
Lecyanel
Misalmoi
Pecaprod
Gaaffini
Lemacroc
Lythrurus
Amnatali
Moxostoma
Leoculat
Ammelas
Lasiccul
Legulosu

Appendix 1.1. Fish species by Boston Mountains (BM), Ouachita Mountains (OM), and Ozark Highlands (OH) ecoregions observed during snorkeling surveys of eastern Oklahoma streams. Nomenclature adopted from Miller and Robison (2004).

Family / Species	Common Name	BM	OM	OH
Petromyzontidae				
Ichthyomyzon spp.	lampreys		x	x
Lepisosteidae				
Lepisosteus oculatus Winchell	spotted gar	x	x	x
Lepisosteus osseus (Linnaeus)	longnose gar		x	x
Clupeidae				
Dorosoma cepedianum (Lesueur)	gizzard shad		x	x
Cyprinidae				
Campostoma anomalum (Rafinesque)	central stoneroller	x	x	x
Cyprinella lutrensis (Baird and Girard)	red shiner		x	
Cyprinella whipplei Girard	steelcolor shiner	x	x	x
Cyprinus carpio Linnaeus	common carp		x	x
Dionda nubila (Forbes)	Ozark minnow	x		x
Luxilus cardinalis (Mayden)	cardinal shiner	x		x
Lythrurus spp.	lythrurus shiners		x	
Nocomis asper Lachner and Jenkins	redspot chub	x		x
Notropis boops Gilbert	bigeye shiner	x	x	x
Phoxinus erythrogaster (Rafinesque)	southern redbelly dace	x		x
Pimephales notatus (Rafinesque)	bluntnose minnow	x		x
Semotilus atromaculatus (Mitchell)	creek chub	x		x
Catostomidae				
Catostomus commersoni (Lacépède)	white sucker	x	x	x
Ictiobus spp.	buffalos			x
Hypentelium nigricans (Lesueur)	northern hogsucker	x		x
Minytrema melanops (Rafinesque)	spotted sucker			x
Moxostoma spp.	redhorses	x	x	x
Ictaluridae				
Ameiurus melas (Rafinesque)	black bullhead	x	x	
Ameiurus natalis (Lesueur)	yellow bullhead	x	x	x
Ictalurus punctatus (Rafinesque)	channel catfish			x
Noturus exilis Nelson	slender madtom	x	x	x
Noturus nocturnus Jordan and Gilbert	freckled madtom		x	
Pylodictis olivaris Rafinesque	flathead catfish		x	
Esocidae				
Esox americanus Gmelin	redfin pickerel		x	
Salmonidae				
Oncorhynchus mykiss (Walbaum)	rainbow trout			x
Aphredoderidae				
Aphredoderus sayanus (Gilliams)	pirate perch		x	
Fundulidae				
Fundulus catenatus (Storer)	northern studfish			x
Fundulus olivaceus (Storer)	blackspotted topminnow	x	x	x
Poeciliidae				
Gambusia affinis (Baird and Girard)	western mosquitofish	x	x	x
Atherinopsidae				
Labidesthes sicculus (Cope)	brook silverside	x	x	

Cottidae				
Cottus carolinae (Gill)	banded sculpin	x		x
Centrarchidae				
Ambloplites rupestris (Rafinesque)	rock bass	x		x
Lepomis cyanellus Rafinesque	green sunfish	x	x	x
Lepomis gulosus (Cuvier)	warmouth		x	
Lepomis humilis (Girard)	orangespotted sunfish		x	
Lepomis macrochirus Rafinesque	bluegill	x	x	x
Lepomis megalotis (Rafinesque)	longear sunfish	x	x	x
Lepomis microlophus (Gunther)	redear sunfish	x	x	x
Micropterus dolomieu Lacepede	smallmouth bass	x	x	x
Micropterus salmoides[1] (Lacepede)	largemouth bass	x	x	x
Pomoxis annularis Rafinesque	white crappie	x	x	x
Pomoxis nigromaculatus (Lesueur)	black crappie			x
Percidae				
Etheostoma blennioides Rafinesque	greenside darter	x	x	x
Etheostoma flabellare Rafinesque	fantail darter	x	x	
Etheostoma punctulatum (Agassiz)	stippled darter	x		x
Etheostoma radiosum (Hubbs and Black)	orangebelly darter		x	
Etheostoma spectabile (Agassiz)	orangethroat darter	x	x	x
Etheostoma whipplei (Girard)	redfin darter		x	
Etheostoma zonale (Cope)	banded darter	x		x
Percina caprodes (Rafinesque)	logperch	x	x	x
Percina copelandi (Jordan)	channel darter		x	
Percina maculata (Girard)	blackside darter		x	
Percina pantherina (Moore and Reeves)	leopard darter		x	
Percina phoxocephala (Nelson)	slenderhead darter		x	
Sciaenidae				
Aplodinotus grunniens (Rafinesque)	freshwater drum			x

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[1] included spotted bass *Micropterus punctulatus*

CHAPTER 2

GEOMORPHOLOGY AND STREAM HABITAT RELATIONSHIPS WITH SMALLMOUTH BASS ABUNDANCE AT MULTIPLE SPATIAL SCALES IN EASTERN OKLAHOMA

Abstract

Fluvial geomorphic processes play a major role in structuring habitats that are important to stream fishes. We determined relationships between densities of smallmouth bass (*Micropterus dolomieu*) and ecoregions, basin and reach geomorphology, and stream habitat in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions of eastern Oklahoma. One hundred seventy-five stream sites were randomly selected; sites were allocated in proportion to ecoregion areas and equally distributed among stream orders 1 to 4. Geomorphology was measured at the basin and reach scales at 128 stream sites, and stream habitat and smallmouth bass abundance was measured in 1788 channel units. Some sites were inaccessible, dry, or had a primary disturbance (e.g., gravel mining) and were not sampled. Variation in geomorphology and stream habitat at the basin and reach scales was related to stream size, channel morphology, and substrate size. Channel morphology differed among ecoregions in the largest streams. Channel units were typically riffles, runs, mid-channel pools, and backwaters. Habitat characteristics varied widely among channel unit types and ecoregions. Densities of age-0 and age-1+ smallmouth bass were approximately an order of magnitude greater in the Boston Mountains and Ozark Highlands than in the Ouachita Mountains. Regression tree analysis explained less variation in age-0 (10-fold cross-validated relative error = 0.844) than age-1+ (relative error = 0.637) smallmouth bass densities, and showed that stream size and channel-unit size were primary determinants of density. However, stream morphology and channel-unit habitat were important in explaining additional variation in densities somewhat independent of ecoregion. Understanding of geomorphic and stream habitat influences on smallmouth bass abundance at multiple, nested spatial scales is

imperative for the management, conservation and restoration of smallmouth bass populations.

Introduction

Fluvial geomorphology governs fluvial hydraulics and the physical habitat in streams required by fishes (Yang 1971; Beschta and Platts 1986; Newson and Newson 2000). Longitudinal processes reflecting basin characteristics, especially stream size, have been shown to influence stream processes and biota (Vannote et al. 1980), but spatial variability in geomorphic processes, controls, and disturbances within and among basins and regions can affect local geomorphology and stream habitat within the longitudinal continuum (Montgomery 1999; Benda et al. 2004).

Geomorphology affects stream biota at different organismal and organizational levels. It has been shown to determine the distribution of stream habitat, ultimately influencing macroinvertebrate community function and production in Appalachian streams (Huryn and Wallace 1987). Geomorphology also influences the location of bull trout (*Salvelinus confluentus*) redds (Baxter and Hauer 2000), influences essential sport-fish habitat (Rabeni and Jacobson 1993), and structures stream fish assemblages (Walters et al. 2003; Rhoads et al. 2003). Although geomorphic processes acting on specific spatial scales have been implicated in affecting stream habitat and biota, connecting geomorphology to physical habitat and biota in streams often requires incorporation of processes at multiple spatial scales (Frissell et al. 1986; Newson and Newson 2000; Frothingham et al. 2002).

Many stream habitat enhancement and restoration principles are geomorphically based. Rosgen (1994; 1996) developed a stream classification system to determine, in part, the potential for enhancement of fish habitat and river restoration. He suggested that installation of instream structures intended as fish habitat may result in detrimental channel adjustments and create disequilibrium stream conditions, and that only streams exhibiting certain morphologic and sediment characteristics should be candidates for habitat improvement structures. Rosgen also suggested that restoration principles should incorporate the natural stable tendencies of a river that result from the interaction of morphological variables. Champoux et al. (2003) found that long-term success of instream structures was related to different glacial deposits (moraine versus outwash plain), and argued that reach geomorphology needed to be considered during restoration planning to ensure long-term effectiveness of habitat improvement structures and management actions.

Eastern Oklahoma has several distinct regions. These ecoregions have characteristic climate, landform, land use, vegetation, and soils (Omernik 1987; Woods et al. 2005). There are also regional differences in fish assemblages and sport-fish populations (Stark and Zale 1991; Balkenbush and Fisher 2001; Howell 2001; Tejan 2004); similarities among stream habitat and fish assemblages have been shown for the same ecoregions in Arkansas (Rohm et al. 1987). Although seven ecoregions have been delineated in eastern Oklahoma, Fisher et al. (2004) used ecoregion characteristics to identify three fishery management regions: northeast, east-central, and southeast. They showed that these management regions had distinct patterns of species richness and population abundance, and the regions were developed to enhance the future management of stream fisheries.

Although regional differences have been identified, it is unknown whether observed patterns in these fisheries are reflective of regional scale characteristics or basin and local scale geomorphic processes that may or may not be associated with those regions. Our goal was to determine how longitudinal and local geomorphic processes influenced smallmouth bass (*Micropterus dolomieu*) abundance in streams of the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma. These ecoregions harbor most of the native distribution of smallmouth bass in Oklahoma. Relations among geomorphology, habitat, and smallmouth bass abundance will help guide conservation, management, and enhancement of stream habitats formed by geomorphic processes and used by smallmouth bass.

Study area

Relations between fluvial geomorphology and stream habitat, and smallmouth bass were determined for small streams to mid-sized rivers in the Boston Mountains, Ouachita Mountains, and Ozark Highlands level III ecoregions in eastern Oklahoma (Omernik 1987). The Boston Mountains ecoregion is a dissected mountainous plateau composed of flat-lying shale and sandstone lithology and oak-hickory forest. Annual rainfall is 112 to 130 cm and land is used is mostly for logging and recreation (Woods et al. 2005). The Ouachita Mountains consist of folded, Paleozoic sandstone, shale, and chert. Oak-hickory-shortleaf pine forests in this region receive from 109 to 145 cm of annual rainfall. Common land uses are: logging, pastureland, hayfields, farming, and recreation (Rutherford et al. 1992; Woods et al. 2005). The Ozark Highlands are dominated by flat-lying cherty limestone, but shale, limestone, and dolomite are present in valley bottoms. Annual precipitation is 104 to 124 cm, and land use is primarily logging, recreation, and cattle and poultry farming, including pastureland and hayfields (Rabeni and Jacobson 1993; Woods et al. 2005).

Methods

Stream survey

A geographic information system (GIS) was used as an aid in the random selection of 175 stream sites for an inventory of fluvial geomorphology, stream habitat, and smallmouth bass populations in the study area. To select stream sites, a stream network was generated in a GIS using a 30 m digital elevation model (DEM) from the National Elevation Dataset (USGS 1999). The network was then created by identifying all cells in the DEM with a watershed size ≥ 1.35 km^2, and defining them as a stream. Stream orders (Strahler 1957) were assigned to each stream segment in the network. One-hundred seventy-five sample sites were randomly selected on regional streams; they were allocated to the three ecoregions approximately in proportion to ecoregion area, and they were equally distributed among stream orders 1 to 4 in each ecoregion to ensure that larger streams were represented. Forty sites each were selected in the Boston Mountains and Ozark Highlands ecoregions, and 95 were selected in the Ouachita Mountains ecoregion within Oklahoma. The GIS layer of sample sites was uploaded into a global positioning (GPS) receiver that was used to navigate to each site. Streams were sampled from mid-May to mid-August, 2003 to 2005, during low streamflow conditions.

Watershed and reach geomorphology and habitat

Watershed scale geomorphic variables for each site were derived using a GIS. The aforementioned DEM was used to delineate drainage basins, and GIS was then used to measure basin areas and lengths. Elongation ratio was measured as the diameter of a circle with the same area as the basin divided by basin length (Morisawa 1968).

We measured fluvial geomorphic variables at each stream site. The stream reach at each site was defined as 20 times the mean channel width (i.e., bankfull width) upstream of each sample point; bankfull stage was identified by using visual and physical indicators (Rosgen 1996). Channel units in each reach were classified using the scheme of Hawkins et al. (1993). Transects perpendicular to the channel were surveyed across two riffles and two pools when available, with a maximum of two transects in a single channel unit; two to four transects were surveyed per reach. Entrenchment ratio, width:depth ratio, and median particle size (i.e., D_{50}) were calculated for each transect. Entrenchment ratio was calculated as the ratio of floodprone width to bankfull channel width. Floodprone elevation was equal to twice the maximum channel depth, and floodprone width was estimated as the valley floor width at the floodprone elevation. Maximum floodprone width was measured if it was less than 2.2 times the channel width at each transect, otherwise it was recorded as 2.2. Width:depth ratio was calculated as the ratio of bankfull channel width to mean bankfull channel depth. Channel depths were measured at 20 equally-spaced locations along transects. Median particle size of surficial substrates was calculated by collecting 100 particles along each transect and measuring the intermediate axis of each; bedrock was excluded from analysis. Water surface slope of each reach was measured. Sinuosity was measured as the ratio of stream length to straight-line distance as measured on maps of the stream reach created with a GPS (see below). Width:depth ratio and median particle size for the reach were calculated from transect data as weighted averages based on the proportion of each reach length that comprised riffles and pools (Zar 1999). Reach entrenchment ratios were calculated as the median of transect values.

Channel-unit habitat

Stream habitat was measured in each channel unit within each reach using methods conducive to a large-scale stream survey. Channel units were mapped with a GPS, and lengths and areas of channel units were measured in a GIS (Dauwalter et al. 2006). Thalweg depths were measured multiple times per channel unit at equally spaced intervals; more measurements were made in longer and more heterogeneous channel units. A modified Wentworth scale was used to visually estimate substrate distributions within each channel unit (Bain 1999). We estimated, and enumerated when logistically feasible, boulders, rootwads, and large woody debris (10+ cm diameter, 4+ m in length) in each channel unit. Percent undercut bank and percent vegetative coverage were also estimated. Water velocity was coded by channel unit type as: falls = 4, riffle = 3, run = 2, all other types = 1. Habitat variables for each channel unit were combined for reach habitat estimates.

Smallmouth bass abundance

Smallmouth bass abundance was estimated by snorkeling or electrofishing individual channel units within reaches (Dolloff et al. 1996; Reynolds et al. 1996). When snorkeling, 1 to 3 person snorkel teams moved upstream in a zig-zag pattern and counted and estimated sizes of smallmouth bass individuals. One electrofishing pass was made using a backpack, barge, or boat electrofisher when water clarity prohibited effective snorkeling (i.e., < 1 m). Water clarity was measured as the maximum distance at which a snorkeler could see a 100 mm model of a smallmouth bass. Electrofishing power density was standardized at approximately 1000 $\mu S \cdot cm^{-3}$ (Reynolds 1996; Miranda and Dolan 2003); however, settings on the backpack electrofisher prohibited obtaining 1000 $\mu S \cdot cm^{-3}$ exactly. Counted individuals were placed into <100 and ≥100 mm size categories. Individuals <100 mm represent age-0 individuals and those ≥100 mm are age-1+ (Balkenbush and Fisher 2001); ages will be referred to hereafter. Snorkeling counts of smallmouth bass were adjusted using a model comparing snorkeling counts to abundance estimates, and electrofishing counts were adjusted using a 1-pass capture probability model (Appendix 2.A).

Data analysis

We used a principle components analysis (PCA) to determine relationships among variables at the basin and reach scales and to eliminate redundant covariables. The PCA was conducted on the correlation matrix, and eigenvalues greater than those predicted under the broken stick model were considered meaningful (Jackson 1993; McGarigal et al. 2000). The predicted eigenvalue (b) for the k^{th} component under the broken stick model was calculated as: $b_k = \sum_{i=k}^{p} \frac{1}{i}$, where p was the number of variables. Pearson correlations were used to examine relationships among channel unit variables; the limited number of variables precluded use of PCA at the channel unit spatial scale. Analyses were run using SAS Version 9.1 software (SAS Institute Inc., Cary, North Carolina).

We used regression tree analysis (RTA) to determine the influence of ecoregions, geomorphology, and stream habitat at the reach and channel unit spatial scales on the density of smallmouth bass. RTA is a flexible and robust nonparametric method used to assess complex relationships between explanatory variables and a response variable that may be non-linear with high order interactions. It explains variation in the response variable by splitting the dataset into homogenous groups using specific values of the categorical or continuous explanatory variables. Groups include observations that have common values of explanatory and response variables. Regression trees are displayed graphically for ease of interpretation (Breiman et al. 1984; De'ath and Fabricius 2000). RTA has been used in other ecological studies of complex relationships between explanatory and response variables when common linear modeling approaches have failed (Rejwan et al. 1999; De'ath and Fabricius 2000).

We conducted RTA for data collected at the ecoregion, basin and reach, and channel-unit scales in one analysis for each age group. Explanatory variables included in RTA were dependent on results of PCA and correlation analyses to limit variable redundancy. Smallmouth bass densities (no.$\cdot$ha^{-1}) were transformed ($\log_e[X + 0.01]$) to reduce the effects of zero densities on variances. Each RTA was performed with CART version 5.0 software (Steinberg and Colla 1995). We used sums of squares about the group means as the measure to maximize homogeneity within groups; sums of absolute deviations about the median is more robust, but can be ineffective when many zeros are present (De'ath and Fabricius 2000). The final tree selected was the one with the smallest relative error (similar to the coefficient of nondetermination, $1 - r^2$) based on 10-fold cross-validation (Breiman et al. 1984; De'ath and Fabricius 2000).

Results

Stream survey

We surveyed channel geomorphology, stream habitat, and smallmouth bass abundance at 128 of 175 selected stream sites. Seventeen stream sites were either inaccessible or access was denied by landowners. Direct channel alteration by humans (e.g., gravel mining) was observed at five stream sites, and these sites were not sampled. Twenty-two streams were dry. Two sites were not snorkeled, and habitat measurements were incomplete at another. Complete information on geomorphology, stream habitat, and smallmouth bass abundance was collected at 128 stream sites (Figure 2.1); electrofishing was conducted at 17 sites in the Ouachita Mountains. Among all sites, 1788 channel units were sampled.

Watershed and reach geomorphology and habitat

Geomorphology and stream habitat were more similar at the basin and reach scales in the Boston Mountains and Ozark Highlands than in the Ouachita Mountains (Table 2.1). Ouachita Mountains streams had smaller basin sizes on average, likely because most small streams in the other ecoregions were dry and excluded from analyses. These streams generally had higher reach slopes and particle sizes and more vegetation, silt-clay substrate, and pool area. They were also typically deeper, had less wood, and lower width:depth ratios than streams in the other regions. Stream reaches in the Boston

Mountains were typically shallower and had more bedrock. Ozark Highland streams were generally deeper with more wood, wider channels, smaller particle sizes, and less bedrock on average when compared to streams in the other two regions. Variability in geomorphology and stream habitat was often greater in the Ouachita Mountains, the largest ecoregion.

At the basin and reach scales, PCA revealed two informative principle components according to the broken stick criterion; however, the third principle component also appeared important (Table 2.2). Axis 1 reflected stream size, with high loadings for basin area, reach slope, and mean thalweg depth. Axis 2 reflected channel morphology. Width:depth ratio loaded most heavily on axis 2, but percent silt-clay also had a high loading followed by percent pool and percent bedrock. Axis 3 represented a particle size axis, dominated by D_{50} and followed by percent pool and sinuosity. PCA biplots showed that channel morphology (axis 2) in the largest streams differed between the Ozark Highlands and Ouachita Mountains ecoregions (axis 1; far right of Figure 2.2).

Channel-unit habitat

We observed 11 channel unit types in all. Riffles, runs, and mid-channel pools were the most abundant types in each ecoregion. Habitat characteristics were highly variable among channel unit types and ecoregions (Table 2.3). No variables among the 1788 channel units were highly correlated (Table 2.4). Velocity and mean thalweg depth had the highest Pearson correlation at $r = -0.398$.

Smallmouth bass abundance

Smallmouth bass densities varied widely, but were typically higher in the Boston Mountains and Ozark Highlands. No smallmouth bass were collected in stream reaches that were electrofished. Density estimates of age-0 smallmouth bass in channel units ranged from 0·ha^{-1}in all ecoregions to 1,492·ha^{-1} in the Boston Mountains, 770·ha^{-1} in the Ouachita Mountains, and 629·ha^{-1} in the Ozark Highlands. Densities of age-1+ smallmouth bass ranged from 0·ha^{-1} in all ecoregions, to 2,010·ha^{-1} in the Boston Mountains, 381·ha^{-1} in the Ouachita Mountains, and 1,217·ha^{-1} in the Ozark Highlands. Densities were consistently high in runs and pools, although some riffles, abandoned channels, and backwaters also had high densities (Table 2.5).

Stream size, channel unit depth, and reach geomorphology variables explained variation in densities of age-0 smallmouth bass. Seven basin-reach and seven channel-unit scale variables were included in RTAs. Although reach slope was correlated with basin area, we retained both because of variability observed in the Ouachita Mountains ecoregion. Rootwad and large woody debris densities were combined (added) to form a wood density variable. Elongation ratio was not included because of the lack of direct biological influence on fish abundance. The regression tree with the minimum cross-validated relative error, 0.825, had 17 nodes, 9 that were terminal. Densities were higher in deeper channel units in larger streams, and were dependent on reach morphology (Figure 2.3).

Several basin-reach and channel-unit variables explained most of the variation in densities of age-1+ smallmouth bass. Variables included in the RTA were the same as those for age-0 smallmouth bass. The regression tree with the minimum cross-validated relative error, 0.627, had 24 splitting nodes and 25 terminal nodes. Shallow channel units, regardless of stream size had the lowest densities, followed by deeper channel units in small streams. However, high densities were also observed in some channel units of small streams having unique reach and channel unit characteristics. Densities in deeper channel units of small and large streams were higher, but dependent on reach geomorphology and channel unit habitat specific to stream size (Figure 2.4).

Discussion

Our survey of 128 randomly selected stream reaches revealed that geomorphic and habitat characteristics of streams at different spatial scales were differentially related to densities of age-0 and age-1+ smallmouth bass. Densities of age-0 and age-1+ smallmouth bass were primarily explained by measures of stream and channel-unit size. Although basin area was used as the surrogate measure of stream size, water-surface slope and mean thalweg depth in the reach were negatively and positively related, respectively, to basin area. Stream size likely influenced suitable nesting habitat and fry production by smallmouth bass. Orth and Newcomb (2002) suggested that stochastic streamflows and poor reproductive habitat limit smallmouth bass reproduction in small streams; streamflow variability and unpredictability is typically greater in small streams (Poff and Ward 1989). Some populations have individuals that migrate into tributaries in spring to spawn, but they return to larger rivers after spawning (Lyons and Kanehl 2002). In addition, many small streams in the Ozark Highlands region become intermittent or dry. Smallmouth bass densities did not decrease in the largest streams we sampled. This reflected our sampling design. Had we sampled larger streams (e.g., > fourth order), we likely would have observed decreased densities or absence of smallmouth bass, as shown by Tejan (2004) and suggested by Stark and Zale (1991). Rabeni and Jacobson (1993) suggested that smallmouth bass densities decrease with increased valley width due to finer bedload materials and less stream contact with valley walls resulting in a lower number of bluff pools that are important smallmouth bass habitats. Thus, intermediate-sized streams and rivers in eastern Oklahoma likely provide the streamflow and habitat conditions most suitable for smallmouth bass populations.

Water depth has previously been shown to be important for determining smallmouth bass abundance. Shallow channel units typically had zero or low densities regardless of stream size. Smallmouth bass typically do not use depths less than about 0.25 m regardless of size (Todd and Rabeni 1989; Orth and Newcomb 2002). Avoidance of shallow water may be a behavioral adaptation to circumvent predation by terrestrial vertebrates. As noted above, small streams are likely reproduction limited, so even deep channel units in small streams will have few if any smallmouth bass. Regression tree analyses showed that deeper channel units in larger streams had higher densities; however, microhabitat studies have shown that the deepest areas of channel units are used less (Orth and Newcomb 2002). This may reflect the proximity of cover to stream banks away from deep areas near the thalweg, but smallmouth bass may still select channel units with deeper areas that can be used as escape cover.

Beyond the observed stream and channel unit-size effects, reach morphology explained some additional variation in smallmouth bass densities. We found that stream reaches with intermediate to high width:depth ratios (26-31) had channel units that supported the highest fish densities. Width:depth ratio typically reflects channel stability and percent silt-clay in the channel perimeter and banks (both negatively related), and is positively related to discharge and sediment loads; sinuosity also reflects silt-clay content of banks and typically varies inversely with width:depth ratio (Knighton 1998). In the Ozark Highlands, accelerated erosion due to logging and overgrazing has likely increased runoff and bedload dynamics, resulting in wider, gravel-dominated channels (Rabeni and Jacobson 1993). This may have affected historical smallmouth bass production, as gravel is required spawning substrates for smallmouth bass (Pflieger 1966), and may be why age-0 densities were higher in reaches with high width:depth ratios. Increased channel widths also result in less canopy cover per stream width and increased production of stream invertebrates beneficial to fishes, such as juvenile smallmouth bass (Livingstone and Rabeni 1991), as long as the increased sediment load is primarily gravel and not fines (Waters 1995).

Other studies in Ozark streams have suggested that channel instability and widening are detrimental to smallmouth bass. In northern Arkansas, gravel mining led to wider channels and larger pools, and resulted in decreased abundances of smallmouth bass (Brown et al. 1998). We did not sample streams with extreme width:depth ratios resulting from anthropogenic activities, because we did not sample physically disturbed stream sites, such as those with signs of gravel extraction. This may explain why we observed increases in density with higher width:depth ratios. Sowa and Rabeni (1995) found maximum summer water-temperature to be negatively related to smallmouth bass densities but positively related to largemouth bass densities (*M. salmoides*) in Missouri streams. They suggested that thermal inputs from reduced canopy cover and wider channels increased water temperatures. We did not measure water temperatures, but they are typically cooler and less variable in Boston Mountains and Ozark Highlands streams (Robel 1996; Balkenbush and Fisher 2001) and likely increase with stream size (Allan 1995). Warmer temperatures (above 22°C) limit the growth scope of age-1+ smallmouth bass and lead to a potential competitive advantage for largemouth bass (Zweifel et al. 1999; Whitledge et al. 2002). This may be why smallmouth bass mortality is higher (Balkenbush and Fisher 2001) and densities lower in Ouachita Mountains streams compared to northeastern streams. Thus, the relation between smallmouth bass density and width:depth ratio is expected to be unimodal whereby intermediate width:depth ratios support the highest densities of smallmouth bass, but confirmation of this relationship in eastern Oklahoma is needed.

We also found that reaches with more riffle-pool structure (less percent pool overall) in larger streams had higher smallmouth bass densities. This is interesting because smallmouth bass densities are higher in deep pool habitats. However, Sowa and Rabeni (1995) reported that smallmouth bass densities were higher in Missouri streams that had a smaller reach area represented as pool habitat. They suggested that low velocity habitats, such as pools, have more fine substrates that would be detrimental to food resources (crayfish) preferred by smallmouth bass. Crayfish production has been reported to be higher in riffles than pools in larger streams (Roell and Orth 1992). Consequently, as riffle:pool ratios decrease, such as in southeastern Oklahoma streams, there is less crayfish production in riffles per unit of pool habitat, leading to reduced prey availability to smallmouth bass. Although riffle:pool structure is influenced by geomorphic processes, anthropogenic activities (e.g., gravel mining) can also lower riffle:pool ratios and negatively impact smallmouth bass populations (Brown et al. 1998).

Spatial variability in geomorphic processes and disturbances in the landscape produces reaches that are morphologically homogenous and appear as patches (sensu Townsend 1989) in the longitudinal continuum of streams (Montgomery 1999). Some researchers have argued that this often occurs at tributary junctions (Poole 2002; Benda et al. 2004). We did not attempt to document abrupt changes and subsequent spatial variability in geomorphic process or disturbance. But, because stream morphology influences smallmouth bass populations and is often similar throughout a reach, the degree to which this patch phenomena exists and what exactly causes it in eastern Oklahoma streams needs further study.

Except for water depth, channel-unit variables were not related to age-0 densities of smallmouth bass. Sabo and Orth (1994) found that, although age-0 smallmouth bass transitioned to using shallower, higher velocity areas as they grew through the summer, their use of microhabitats also became more generalized. Pert et al. (2002) suggested that age-0 smallmouth bass may be habitat generalists among stream systems, but specialists within a stream. This is because they can adapt to a range of stream environments but use specific resources that are most beneficial to them within a system. Swimming ability of age-0 individuals may also prohibit them from moving into desired channel units, especially between pools separated by riffles. Consequently, densities of age-0 smallmouth bass in channel units may reflect the quality of spawning habitat (Cleary 1956), number of successful nests and nest production (Reynolds and O'Bara 1991; Lukas and Orth 1995), and/or survival dynamics of fry and juveniles through their first summer (Knotek and Orth 1998). Selection of specific channel units with certain habitat characteristics may be less important, especially in reaches with high width:depth ratios dominated by gravel substrates.

Channel-unit characteristics were related to age-1+ smallmouth bass densities, but these relations changed depending on stream size and reach morphology. The presence of bedrock in shallow channel units led to increased densities, likely because local bed scour along bedrock outcroppings resulted in small, deep areas in otherwise shallow channel units. Deeper channel-units in larger streams with high wood densities had low densities of fish: wood may have been too dense for smallmouth bass to use effectively. We also observed no density relations with boulders. At the reach scale, smallmouth bass abundance was not related to wood or boulder densities in a study of 23 reaches (250-500m) on 19 Missouri streams (Sowa and Rabeni 1995). McClendon and Rabeni (1987) found that boulder abundance, but not wood abundance, was positively related to smallmouth bass biomass and density at the channel unit scale in Jacks Fork River, Missouri; however, smallmouth bass size structure (i.e., proportional stock density) increased with wood abundance. Rabeni and Jacobson (1993) suggested that boulders were important and were often associated with bluff pool habitats. In our study, channel units with lower wood densities and a fraction of silt-clay substrate also had low densities. Fine sediments represent unsuitable habitat for the benthic macroinvertebrates and crayfishes consumed by smallmouth bass in these streams (Waters 1995; Pflieger 1996; Fenner et al. 2004). Smallmouth bass were less abundant or absent in stream reaches with more fines in Wisconsin (Lyons 1991). In some instances, we observed that channel units with vegetation also had lower densities. Use of vegetation can be detrimental to age-0 smallmouth bass when compared to other habitats (Olson et al.

2003), but abundance of vegetation was unrelated to abundance of adult smallmouth bass in Missouri streams (McClendon and Rabeni 1987).

Microhabitat studies have shown that smallmouth bass are associated with woody debris (Probst et al. 1984; Todd and Rabeni 1989; Lobb and Orth 1991) and boulders (Probst et al. 1984; Rankin 1986; Todd and Rabeni 1989), but these associations are often weak or absent at the channel-unit and reach spatial scales. Relations between fish and cover density are likely complicated because multiple individuals may use a single cover structure (Probst et al. 1984; Todd and Rabeni 1989), or cover may only determine the distribution of individuals within a channel unit or reach and not influence production and population dynamics. Production and population dynamics are more likely to be affected by larger scale phenomena such as geomorphology and/or regional factors that may or may not be independent of geomorphology (e.g., water temperature, land use; Rabeni and Sowa 1996).

Interestingly, ecoregion did not have a direct influence on smallmouth bass density in regression tree analyses. Others have reported higher smallmouth bass densities in northeastern (Boston Mountains and Ozark Highlands) than southeastern (Ouachita Mountains) Oklahoma streams (Stark and Zale 1991; Balkenbush and Fisher 2001). We also found densities in northeastern streams to be higher. However, the regional differences were more related to variation in reach morphology in larger streams with high densities than they were to ecoregions. Reach morphology of large streams was different between ecoregions, and reflects differences in lithology, sediment regimes, land use, and hydrology among ecoregions (Woods et al. 2005). It also incorporates differences in watershed and local processes that vary within ecoregions. Consequently, reach morphology is more closely linked to stream habitats used by smallmouth bass than are ecoregions.

The need to understand how physical characteristics of streams influence stream fishes at multiple spatial scales is not a new concept (Frissell et al. 1986; Wiens 2002), but essential for effective stream restoration. We observed strong stream-size effects, but geomorphic influences on smallmouth bass were complex and different between small and large streams. Rabeni and Sowa (1996) stressed the importance of realizing the nestedness of spatial scales and understanding how factors acting on different spatial scales are important to the conservation of stream fishes. Geomorphic processes are naturally hierarchical, and understanding spatial variability associated with those processes is important to understanding how they structure fish habitat in streams (Montgomery 1999). Most often, large-scale processes influence stream morphology and function at smaller spatial scales but local impacts do not always influence large-scale processes. There are exceptions, as upstream and downstream channel adjustments may occur from a localized disturbance. Consequently, many stream restoration and habitat enhancement projects have a geomorphic basis that includes different spatial scales (Rosgen 1996; FISRWG 1998; Montgomery and Bolton 2003). Thus, understanding how smallmouth bass populations respond to geomorphic processes is essential in realizing how certain conservation and management practices aimed at changing geomorphology may influence fishing for popular sport fish (Fisher et al. 2002) and affect indicator species (Hlass et al. 1998) in these upland regions of the central United States.

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Table 2.1. Geomorphology and habitat from stream basins and reaches in the Boston Mountains (n = 29), Ouachita Mountains (n = 78), and Ozark Highlands (n = 21) ecoregions in eastern Oklahoma.

Variable		Boston Mountains	Ouachita Mountains	Ozark Highlands
Basin area (km^2)	Mean	116.1	61.5	182.0
	Min.	1.3	1.2	4.8
	Max	587.5	393.5	951.3
D_{50} (mm)	Mean	35.4	79.6	27.6
	Min.	2.7	1.5	16.8
	Max	83.5	309.0	51.5
Elongation ratio	Mean	0.57	0.53	0.49
	Min.	0.43	0.22	0.32
	Max	0.82	0.84	0.67
Large woody debris (no.·m^{-2})	Mean	0.0034	0.0030	0.0030
	Min.	0.0000	0.0000	0.0000
	Max	0.0405	0.0235	0.0113
Mean thalweg depth (m)	Mean	0.30	0.37	0.43
	Min.	0.11	0.10	0.22
	Max	0.72	1.89	0.83
%Bedrock	Mean	16.9	10.5	8.4
	Min.	0.0	0.0	0.0
	Max	88.5	67.7	68.8
%Pool	Mean	63.8	86.2	62.9
	Min.	11.6	23.2	34.6
	Max	98.9	100.0	100.0
%Silt-Clay	Mean	4.2	7.5	5.2
	Min.	0.0	0.0	0.0
	Max	30.2	45.0	24.9
%Vegetation	Mean	2.0	8.2	3.8
	Min.	0.0	0.0	0.0
	Max	17.6	61.1	17.4
Rootwads (no.·m^{-2})	Mean	0.0033	0.0055	0.0072
	Min.	0.0000	0.0000	0.0000
	Max	0.0595	0.0235	0.0593
Sinuosity	Mean	1.14	1.16	1.18
	Min.	1.00	1.00	1.00
	Max	1.51	3.04	1.80
Slope	Mean	0.0069	0.0075	0.0045
	Min.	0.0008	0.0000	0.0005
	Max	0.0274	0.0315	0.0194
Width:depth ratio	Mean	23.1	16.9	27.5
	Min.	11.4	6.9	6.6
	Max	44.0	36.7	54.7
Wood (no.·m^{-2})	Mean	0.0067	0.0085	0.0102
	Min.	0.0000	0.0000	0.0000
	Max	0.1000	0.1192	0.0593

Table 2.2. Statistics and eigenvalues for eigenvectors from a PCA of geomorphic and stream habitat variables from 128 stream reaches in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma.

	PC 1	PC 2	PC 3
Summary statistics			
Observed eigenvalue	2.448	1.785	1.345
Broken stick eigenvalue	1.000	1.500	1.833
% of variance explained	20.4	14.9	11.2
Variables			
Basin area (km^2)	0.402	0.332	0.055
D_{50} (mm)	-0.027	0.166	0.621
Elongation ratio	-0.255	0.018	0.273
Mean thalweg depth (m)	0.458	0.097	0.324
%Bedrock	-0.086	0.353	-0.141
%Pool	0.253	-0.349	0.427
%Silt-Clay	0.219	-0.447	-0.144
%Vegetation	0.138	-0.113	0.009
Sinuosity	0.154	-0.277	-0.377
Slope	-0.544	0.020	0.115
Width:depth ratio	0.107	0.528	-0.208
Wood ($no.\cdot m^{-2}$)	-0.306	-0.195	0.100

Table 2.3. Habitat characteristics of common channel units types in streams of the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma. All variables were included in regression tree analyses.

Ecoregion / Variable		Riffle	Run	Mid-Channel Pool	Lateral Pool	Back-water
Boston Mountains	n	191	183	160	16	31
Mean Depth (m)	Mean	0.156	0.307	0.329	0.526	0.304
	Min.	0.03	0.07	0.05	0.07	0.07
	Max.	0.55	1.08	1.67	1.04	0.72
%Bedrock	Mean	19.4	23.9	20.3	4.4	4.2
	Min.	0	0	0	0	0
	Max.	100	100	95	20	70
%Boulder	Mean	7.7	5.0	5.9	5.4	2.4
	Min.	0	0	0	0	0
	Max.	75	80	60	15	15
%Silt-Clay	Mean	0.4	1.3	2.9	12.3	10.1
	Min.	0	0	0	0	0
	Max.	10	20	80	85	50
%Vegetation	Mean	2.6	1.5	1.4	1.8	3.9
	Min.	0	0	0	0	0
	Max.	80	70	35	10	60
Velocity (coded)	Mean	3	2	1	1	1
	Min.	3	2	1	1	1
	Max.	3	2	1	1	1
Wood (no.·m^{-2})	Mean	0.00875	0.01000	0.11812	0.08463	0.02307
	Min.	0.0000	0.0000	0.0000	0.0000	0.0000
	Max.	0.5882	0.6250	12.0482	0.9091	0.1427
Ouachita Mountains	n	259	164	356	8	9
Mean Depth (m)	Mean	0.123	0.265	0.375	0.610	0.403
	Min.	0.01	0.03	0.03	0.18	0.06
	Max.	0.83	0.76	1.63	1.89	1.15
%Bedrock	Mean	10.0	9.0	12.9	6.3	8.8
	Min.	0	0	0	0	0
	Max.	100	95	95	50	50
%Boulder	Mean	16.4	18.0	13.2	10.9	4.0
	Min.	0	0	0	0	0
	Max.	80	90	80	55	20
%Silt-Clay	Mean	1.0	1.5	5.0	9.6	8.9
	Min.	0	0	0	1	0
	Max.	45	90	70	25	40
%Vegetation	Mean	13.2	5.4	8.7	3.8	6.9
	Min.	0	0	0	0	0
	Max.	99	70	95	10	30
Velocity (coded)	Mean	3	2	1	1	1
	Min.	3	2	1	1	1
	Max.	3	2	1	1	1
Wood (no.·m^{-2})	Mean	0.01460	0.05080	0.01415	0.00415	0.00422
	Min.	0.0000	0.0000	0.0000	0.0000	0.0000

	Max.	0.3682	3.8760	0.6667	0.0139	0.0180
Ozark Highlands	n	105	113	92	10	46
Mean Depth (m)	Mean	0.254	0.475	0.518	0.636	0.382
	Min.	0.04	0.12	0.13	0.15	0.10
	Max.	0.71	1.42	1.97	1.17	1.09
%Bedrock	Mean	8.6	9.6	6.8	6.0	1.8
	Min.	0	0	0	0	0
	Max.	100	90	95	10	35
%Boulder	Mean	0.8	1.5	1.3	3.7	1.0
	Min.	0	0	0	0	0
	Max.	15	30	18	20	25
%Silt-Clay	Mean	2.5	3.5	6.0	2.6	30.3
	Min.	0	0	0	0	0
	Max.	85	80	70	10	100
%Vegetation	Mean	5.1	3.0	3.5	2.4	12.7
	Min.	0	0	0	0	0
	Max.	90	80	80	15	95
Velocity (coded)	Mean	3	2	1	1	1
	Min.	3	2	1	1	1
	Max.	3	2	1	1	1
Wood (no.·m^{-2})	Mean	0.00764	0.01829	0.01490	0.00288	0.02148
	Min.	0.0000	0.0000	0.0000	0.0000	0.0000
	Max.	0.2648	0.4348	0.2302	0.0113	0.2412

Table 2.4. Pearson correlations (*r*) between habitat variables of 1788 channel units in 128 stream reaches in the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma.

Variable	%Vegetation	%Bedrock	%Boulder	%Silt-Clay	Velocity	Wood
Mean Depth	-0.053	-0.033	-0.005	0.146	-0.398	-0.046
% Vegetation		-0.096	0.045	0.060	0.047	-0.025
% Bedrock			-0.144	-0.135	-0.001	-0.018
% Boulder				-0.155	0.068	0.003
% Silt-Clay					-0.223	0.008
Velocity						-0.039

Table 2.5. Smallmouth bass densities (no.·ha^{-1}) per age group per channel unit type in streams of the Boston Mountains, Ouachita Mountains, and Ozark Highlands ecoregions in eastern Oklahoma.

		Age-0		Age-1+	
Ecoregion / Type	n	Mean	Range	Mean	Range
Boston Mountains					
Abandoned Channel	4	144.0	0-576	0.0	0-0
Backwater	31	36.7	0-635	23.7	598
Debris Pool	2	0.0	0-0	0.0	0-0
Eddy Pool	2	0.0	0-0	330.0	0-660
Fall	3	0.0	0-0	0.0	0-0
Lateral Pool	16	22.3	0-96	78.9	0-385
Mid-Channel Pool	160	15.0	0-328	54.0	0-2010
Plunge Pool	3	0.0	0-0	0.0	0-0
Riffle	191	2.8	0-272	0.4	0-50
Run	183	28.3	0-1492	79	0-1154
Sheet	5	0.0	0-0	0.0	0-0
Ouachita Mountains					
Abandoned Channel	1	0.0	0-0	0.0	0-0
Backwater	9	0.0	0-0	0.0	0-0
Eddy Pool	3	0.0	0-0	0.0	0-0
Fall	4	0.0	0-0	0.0	0-0
Lateral Pool	8	0.0	0-0	0.0	0-0
Mid-Channel Pool	356	2.7	0-232	2.4	0-156
Riffle	259	1.5	0-173	1.1	0-293
Run	164	15.9	0-770	8.7	0-381
Ozark Highlands					
Abandoned Channel	1	0.0	0-0	0.0	0-0
Backwater	46	34.7	0-629	24.3	0-510
Debris Pool	1	0.0	0-0	0.0	0-0
Eddy Pool	11	72	0-344	189.1	0-833
Fall	2	0.0	0-0	18.8	0-38
Lateral Pool	10	26.7	0-153	112.7	0-360
Mid-Channel Pool	92	7.3	0-69	87.3	0-1061
Plunge Pool	1	0.0	0-0	0.0	0-0
Riffle	105	7.6	0-574	8.2	0-574
Run	113	16.2	0-406	66.4	0-1217
Sheet	2	0.0	0-0	0.0	0-0

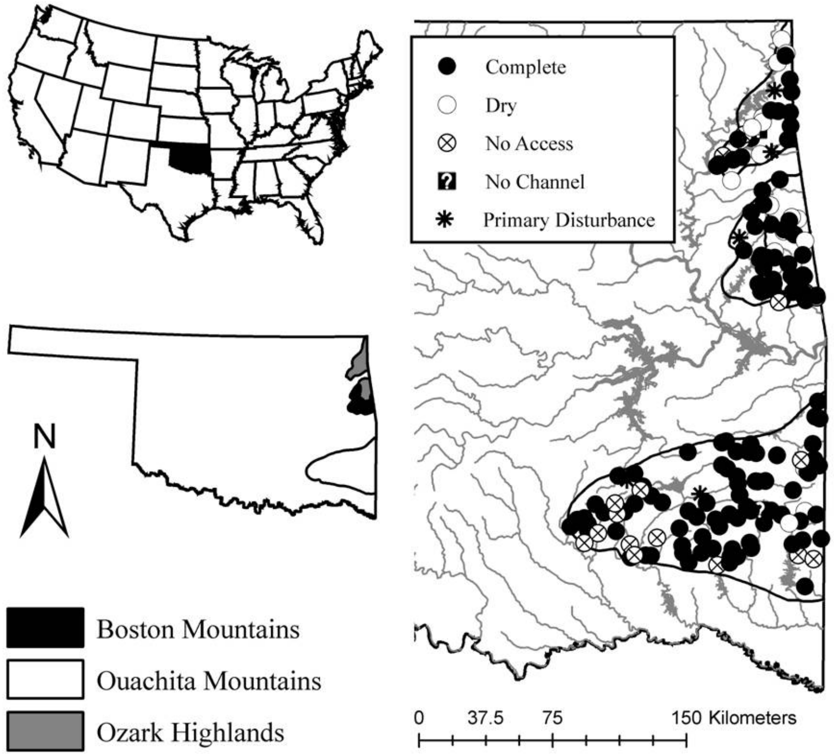
Figure 2.1. Sites selected (175) and sampled (128) for an inventory of fluvial geomorphology, stream habitat, and smallmouth bass in eastern Oklahoma streams.

Figure 2.2. PCA biplots of geomorphology and habitat of 128 stream reaches in three eastern Oklahoma ecoregions. Axis 1 represented stream size, where slope (-0.544), mean thalweg depth (0.458), and basin area (0.402) had the highest axis loadings. Axis 2 represented channel stability; width:depth ratio (0.528), percent silt-clay (-0.447), and percent bedrock (0.353) had high axis loadings. D_{50} (0.621), percent pool (0.427), and sinuosity (-0.377) had high axis loadings for axis 3.

Figure 2.3. Regression tree analysis of effects of ecoregion, basin and reach geomorphology and habitat, and channel unit habitat on age-0 smallmouth bass densities (no.$\cdot$ha^{-1}) in 1788 channel units from 128 stream reaches in three eastern Oklahoma ecoregions. Mean densities per node are given, with sample sizes in parentheses. Observations with variable values less than or equal to node value split to the left, and values greater than split right. Terminal nodes are oval. 10-fold cross-validated relative error was 0.825.

Figure 2.4. Regression tree analysis of effects of ecoregion, basin and reach geomorphology and habitat, and channel unit habitat on age-1+ smallmouth bass densities (no.$\cdot$ha^{-1}) in 1788 channel units from 128 stream reaches in three eastern Oklahoma ecoregions. Mean densities per node are given, with sample sizes in parentheses. Observations with variable values less than or equal to node value split to

the left, and values greater than split right. Terminal nodes are oval. 10-fold cross-validated relative error was 0.627. Broad descriptions of channel units related to primary splits are given.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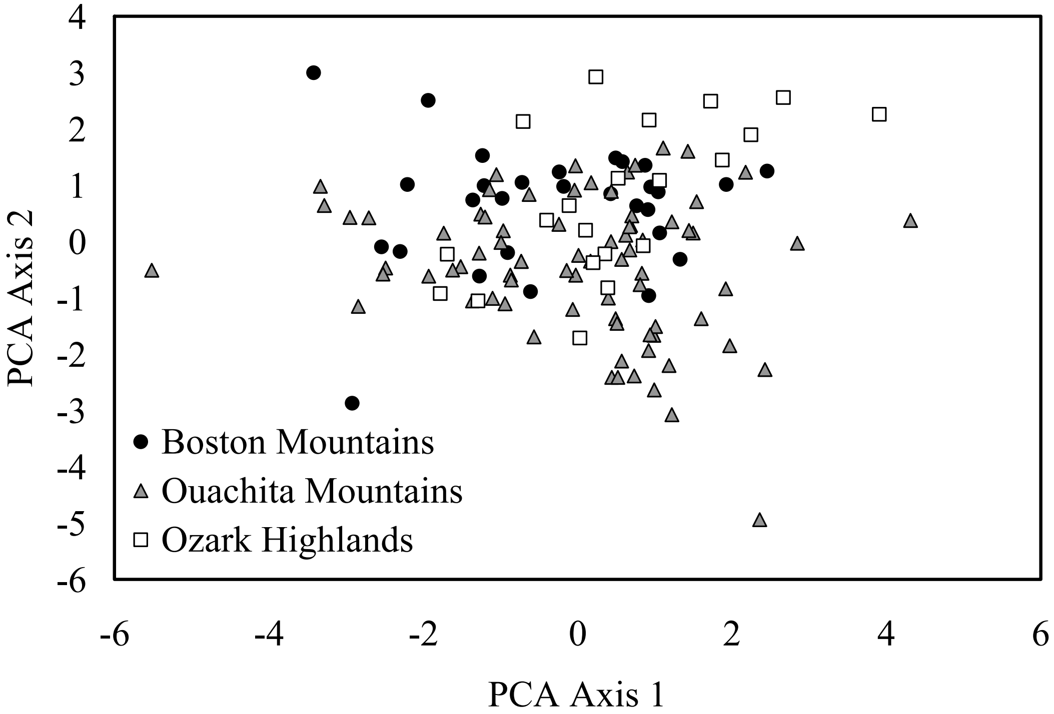
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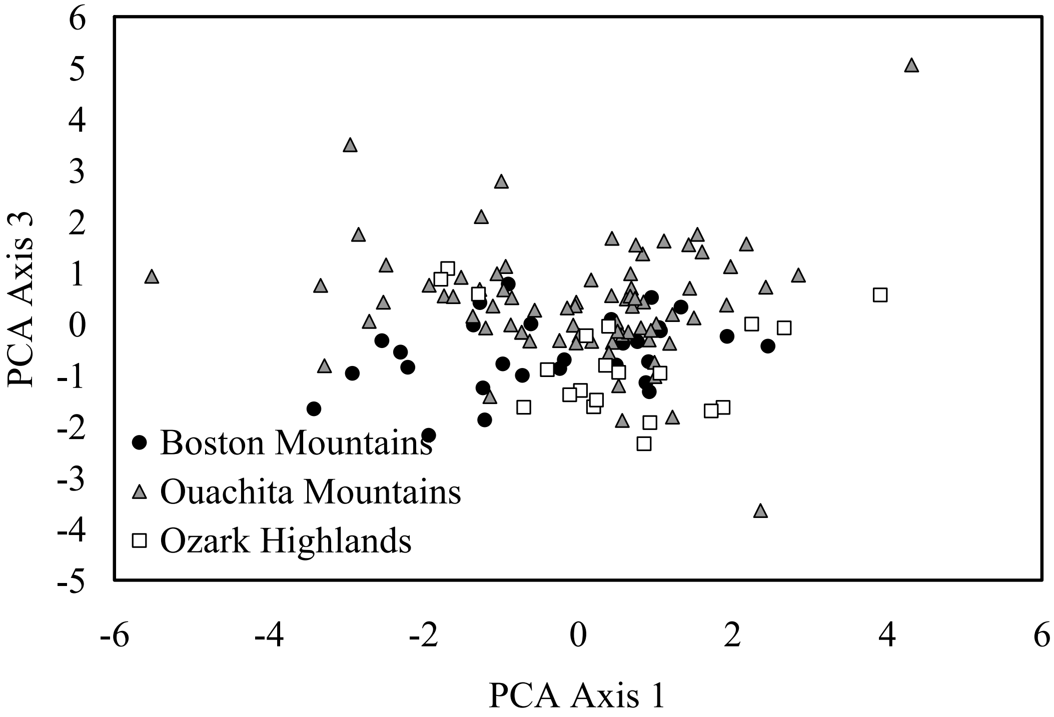
□ Ozark Highlands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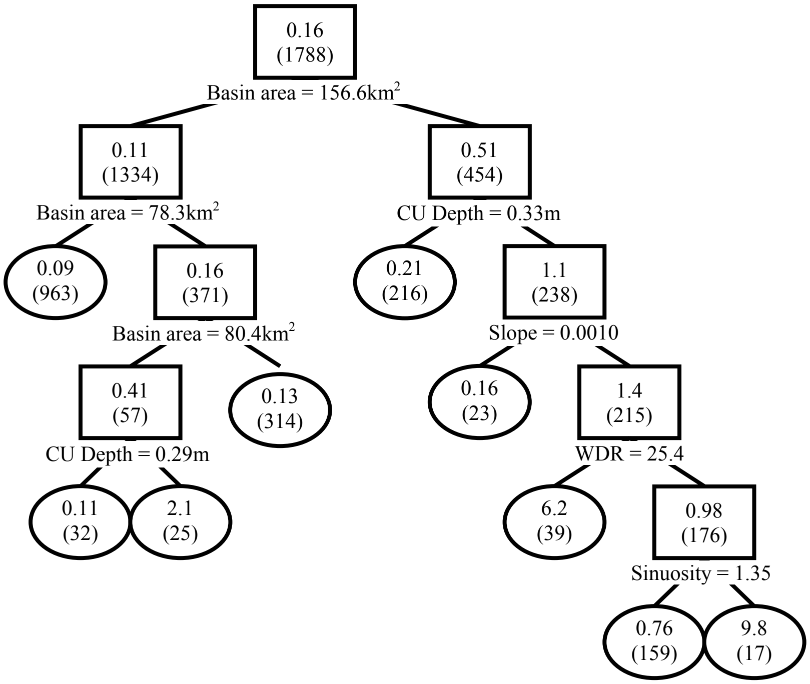
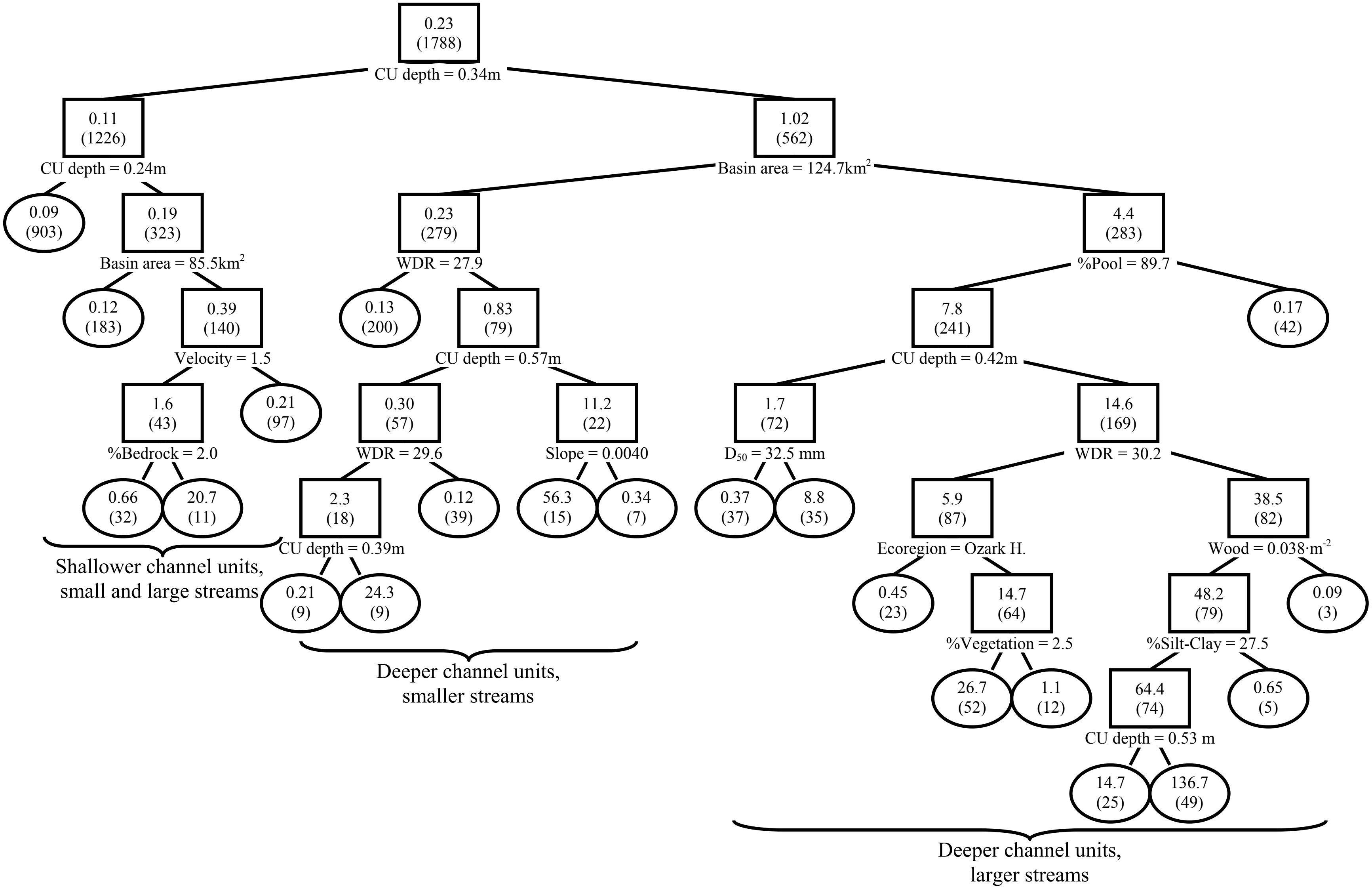
PCA Axis 1
● Boston Mountains
▲ Ouachita Mountains
□ Ozark Highlands


0.16
(1788)
Basin area = 156.6km²
0.11
(1334)
0.51
(454)
Basin area = 78.3km²
CU Depth = 0.33m
0.09
(963)
0.16
(371)
0.21
(216)
1.1
(238)
Basin area = 80.4km²
Slope = 0.0010
0.41
(57)
0.13
(314)
0.16
(23)
1.4
(215)
CU Depth = 0.29m
WDR = 25.4
0.11
(32)
2.1
(25)
6.2
(39)
0.98
(176)
Sinuosity = 1.35
0.76
(159)
9.8
(17)


0.23 (1788)
CU depth = 0.34m
0.11 (1226)
1.02 (562)
CU depth = 0.24m
Basin area = 124.7km²
0.09 (903)
0.19 (323)
0.23 (279)
4.4 (283)
Basin area = 85.5km²
WDR = 27.9
%Pool = 89.7
0.12 (183)
0.39 (140)
0.13 (200)
0.83 (79)
7.8 (241)
0.17 (42)
Velocity = 1.5
CU depth = 0.57m
CU depth = 0.42m
1.6 (43)
0.21 (97)
0.30 (57)
11.2 (22)
1.7 (72)
14.6 (169)
%Bedrock = 2.0
WDR = 29.6
Slope = 0.0040
D50 = 32.5 mm
WDR = 30.2
0.66 (32)
20.7 (11)
2.3 (18)
0.12 (39)
56.3 (15)
0.34 (7)
0.37 (37)
8.8 (35)
5.9 (87)
38.5 (82)
CU depth = 0.39m
Ecoregion = Ozark H.
Wood = 0.038·m⁻²
Shallower channel units, small and large streams
0.21 (9)
24.3 (9)
0.45 (23)
14.7 (64)
48.2 (79)
0.09 (3)
%Vegetation = 2.5
%Silt-Clay = 27.5
Deeper channel units, smaller streams
26.7 (52)
1.1 (12)
64.4 (74)
0.65 (5)
CU depth = 0.53 m
14.7 (25)
136.7 (49)
Deeper channel units, larger streams

Appendix 2.A. Snorkeling and electrofishing methods for estimating smallmouth bass abundance.

Snorkeling model

Methods

We developed a linear model to adjust snorkeling counts of smallmouth bass to obtain abundance estimates. The model was developed by using data whereby 21 channel units were snorkeled, and smallmouth bass < and ≥100mm were counted. The same channel units were then electrofished, and an electrofishing abundance estimate was made by adjusting the number in individuals collected by the 3-pass predicted capture probability (see below). Channel-unit habitat was also measured and estimated (see Methods). Multiple linear regression and forward selection of fish size and habitat variables (variable entry, $P \leq 0.15$) was used to predict: snorkeling counts:electrofishing abundance estimates. We could not use logistic regression because snorkeling counts were sometimes greater than abundance estimates. In addition to fish size, the habitat variables evaluated for their effect on snorkeling counts were: water clarity (m); mean thalweg depth (m); wood density ($\text{no.}\cdot\text{m}^{-2}$); and channel-unit width (m). Statistical Analysis Systems software, version 9.1 (SAS Institute Inc., Cary, North Carolina) was used to fit a model of 42 observations (21 channel units · 2 size classes). Studentized deleted residuals were plotted against explanatory variables to assess heteroscedasticity.

Results

Forward selection included no fish size or habitat variable in the model. Thus, we fit a direct proportion model (no intercept) to predict abundance estimates from snorkel counts. The final model was:

(1) $\hat{N} = 1.3529(\text{snorkeling count})$

Model fit was: $r^2 = 0.617$. Residual plots revealed homogeneity of error variance. Results demonstrated that snorkelers adjusted their searches, as intended, to account for habitat complexity within channel units, and were equally effective at observing small and large fishes.

Electrofishing model

Methods

Mark-recapture data were used to develop a 1- and 3-pass capture probability model to estimate smallmouth bass abundance in channel units. In 24 channel units in two eastern Oklahoma streams, smallmouth bass were collected, marked, and returned. Habitat variables measured were: mean thalweg depth (m), %bedrock, %silt-clay, wood density (no.·m^{-2}). After a recovery period, three electrofishing passes were made to recapture individuals. Capture probability for 1 and 3 electrofishing passes was estimated using multiple logistic regression and Statistical Analysis Systems software, version 9.1 (SAS Institute Inc., Cary, North Carolina) with fish size (< and ≥100 mm), electrofishing power (µS·cm^{-3}), and all habitat variables as potential explanatory variables:

(2) $\hat{p} = [1 + \exp(-\hat{\beta}_0 - \hat{\beta}_1 x_i ....)]^{-1}$

All combinations of explanatory variables, including fish size×depth, depth×%bedrock and depth×%silt-clay interactions, were evaluated using model selection and averaging methods. Abundance estimates were obtained by correcting number of individuals collected by model averaged, predicted capture probability, $\hat{N} = C \cdot \hat{p}^{-1}$.

Results

All habitat variables, except mean thalweg depth×%silt-clay interaction, were included in at least one candidate model (Table 2.A.1). Fish size and mean thalweg depth, and their interaction, had the largest effect on capture probabilities (Table 2.A.2). Precision of abundance estimates from the 1-pass model, when compared to known abundances using linear regression, were lower ($r^2 = 0.769$) than precision for the 3-pass model ($r^2 = 0.881$), but both models produced unbiased abundance estimates ($b_i = 1$, $P \geq 0.462$).

Table 2.A.1. $QAIC_c$ differences (Δ_i) and recalculated Akaike weights (w_i) for the best 1- and 3-pass smallmouth bass capture probability models. Best models were those with original w_i within 10% of the w_i for the best model. Names of variables are shortened.

Model	Δ_i	w_i
1 Pass		
Size+Depth+Size×Depth	0.000	0.138
Size+Depth+Size×Depth+%Bedrock	0.716	0.097
Size+Depth+%Bedrock	1.064	0.081
Size+Depth	1.087	0.080
Size+Depth+Size×Depth+Wood	1.469	0.066
Size+Depth+Size×Depth+%SiltClay+%Bedrock	2.031	0.050
Size+Depth+%SiltClay+%Bedrock	2.088	0.049
Size+Depth+Size×Depth+%SiltClay	2.405	0.042
Size+Depth+Size×Depth+Power	2.409	0.041
Size+Depth+Wood	2.514	0.039
Size+Depth+Size×Depth+%Bedrock+Wood	2.560	0.038
Size+Depth+%Bedrock+Wood	2.866	0.033
Size+Depth+Size×Depth+%Bedrock+Depth×%Bedrock	3.164	0.028
Size+Depth+Size×Depth+Power+%Bedrock	3.169	0.028
Size+Depth+%Bedrock+Depth×%Bedrock	3.312	0.026
Size+Depth+%SiltClay	3.342	0.026
Size+Power+Depth	3.384	0.025
Size+Power+Depth+%Bedrock	3.434	0.025
Size+Depth+Size×Depth+Power+Wood	3.887	0.020
Size+Depth+Size×Depth+%SiltClay+Wood	3.985	0.019
Size+Depth+%SiltClay+%Bedrock+Wood	4.286	0.016
Size+Depth+Size×Depth+%SiltClay+%Bedrock+Wood	4.295	0.016
Size+Depth+%Bedrock+Depth×%Bedrock+%SiltClay	4.570	0.014
3 Pass		
Size+Depth+Size×Depth	0.000	0.227
Size+Depth+Size×Depth+%Bedrock	1.997	0.084
Size+Depth	2.133	0.078
Size	2.160	0.077
Size+Depth+Size×Depth+Power	2.399	0.068
Size+Depth+Size×Depth+%SiltClay	2.411	0.068
Size+Depth+Size×Depth+Wood	2.415	0.068
Size+Depth+%Bedrock	3.546	0.039
Size+Depth+Size×Depth+%SiltClay+%Bedrock	3.977	0.031
Size+Depth+Size×Depth+%Bedrock+Depth×%Bedrock	4.058	0.030
Size+%Bedrock	4.204	0.028
Size+Wood	4.300	0.026
Size+Power	4.309	0.026
Size+%SiltClay	4.326	0.026
Size+Power+Depth	4.345	0.026
Size+Depth+%SiltClay	4.412	0.025
Size+Depth+Wood	4.432	0.025
Size+Depth+Size×Depth+%Bedrock+Wood	4.531	0.024
Size+Depth+Size×Depth+Power+%Bedrock	4.534	0.024

Table 2.A.2. Model averaged parameter estimates (b_i ± 2 SE) estimates for parameters in 1- and 3-pass capture probability models for smallmouth bass when electrofishing channel units in two eastern Oklahoma streams.

	1 pass	3 pass
Parameter	b_i	b_i
Intercept	-0.624 (1.284)	-0.488 (1.144)
Size	1.710 (1.832)	1.758 (2.130)
Electrofishing Power Density ($\mu S \cdot cm^{-3}$)	-0.001 (0.043)	0.002 (0.045)
Mean Thalweg Depth (m)	-1.424 (2.460)	0.166 (1.787)
%Bedrock	0.010 (0.029)	0.003 (0.013)
%Silt-Clay	-0.010 (0.051)	-0.002 (0.019)
Rootwad-Large Woody Debris Density ($no. \cdot m^{-2}$)	-9.413 (40.652)	0.284 (12.643)
Size × Depth	-1.421 (3.169)	-1.610 (3.199)
Depth × %Bedrock	-0.001 (0.010)	-0.001 (0.006)
Depth × %Silt-Clay		
Models averaged	23	19

CHAPTER 3

SMALLMOUTH BASS POPULATIONS AND STREAM HABITAT IN EASTERN OKLAHOMA: SPATIOTEMPORAL PATTERNS AND HABITAT COMPLEMENTATION AND SUPPLEMENTATION

Abstract

Spatial and temporal dynamics of stream habitat and fish populations are important considerations for the conservation and management of stream fishes. We determined differences in stream habitat and smallmouth bass *Micropterus dolomieu* demographics among stream orders 3 – 5 in two regional streams in eastern Oklahoma from 2003 to 2005. Water temperature, streamflow, and habitat differed between streams and longitudinally within streams. Recruitment variability of smallmouth bass was highest in upstream reaches of both streams, and higher in Glover River than Baron Fork Creek in reaches with the highest smallmouth bass densities. Survival was higher in Baron Fork Creek than Glover River and was typically lowest from summer to fall in both streams. Relative growth in length of smallmouth bass was not different between streams or ages, but was highest from summer to fall. Relative weights were higher in Baron Fork Creek than Glover River in upstream reaches, and decreased linearly as stream order increased in Baron Fork Creek but not in Glover River. Relative weights were lowest in spring and highest in summer in both streams. Movement among channel units was highest from fall to winter, and there was evidence that older individuals moved more. Habitat complementation was evident whereby smallmouth bass used different channel units for spawning versus winter thermal refugia. However, food and cover were apparently substitutable or ubiquitous and supplemented in different habitats because they did not strongly affect distributions of individuals in summer and fall. Integrating spatiotemporal patterns in stream habitat and population demographics with knowledge of habitat complementation and supplementation is important for conservation and management of habitat and fishes in stream resources that provide important angling opportunities.

Introduction

A critical element in the conservation and management of a fish population is to understand factors affecting population demographics. Stream habitat and its constituent components reflect a myriad of physical and biological processes acting on hierarchically nested spatial and temporal scales (Frissell et al. 1986). Habitat is often regarded as a major factor affecting stream fish populations and structuring fish assemblages (Gorman and Karr 1978). Habitats are defined according to whether their components (abiotic and biotic) are consumed directly by fishes and their supply is affected by fish density (Hayes et al. 1996). The consumable and dynamic properties of habitat components determine the relationship between habitat and fish population dynamics.

Although specific habitats can affect fish population dynamics, it is important to understand the spatial and temporal distribution of all habitats needed by fishes to complete life processes. Many fish species use different habitats to reproduce, feed and grow, and seek refuge from harsh environmental conditions (Figure 3.1; Schlosser 1991; Schlosser 1995). An area of a stream system that contains all needed habitats has been defined as a functional habitat unit (Kocik and Ferreri 1998). Schlosser (1995) suggested that habitat complementation (different habitats with non-substitutable resources), habitat supplementation (different habitats with substitutable resources), source-sink interactions (spatial variation in juvenile production), and neighborhood effects (spatial structure and connectivity of habitats) influence fish population dynamics. Movement of fishes into and out of habitats (turnover) has been used as a measure of habitat quality (Bélanger and Rodríguez 2002) and has energetic and predation costs. Thus, high levels of habitat supplementation (versus complementation) and smaller functional habitat units would result in population dynamics leading to large local population sizes, and more functional habitat units in a system would result in higher abundances of a fish species within a stream system. Kocik and Ferreri (1998) demonstrated how incorporating the spatial structure (interspersion and juxtaposition) of functional habitat units (including spawning and rearing habitat) increased the predicted production of juveniles and decreased extirpation probabilities of Atlantic salmon *Salmo salar* in the Narraguagas River, Maine. Fausch et al. (2002) suggested that information critical to conservation of stream fish populations is needed at intermediate spatial scales (10 – 10,000 m), because such scales likely encompass the size of functional habitat units of most fish species. They also recommended that information be collected continuously throughout the river network in order to document specific critical habitats or disturbances that might be missed under probabilistic sampling designs.

The smallmouth bass *Micropterus dolomieu* is both a popular sport fish and an indicator of habitat conditions. The species has been introduced into waters outside of its native range for angling opportunities (the Mississippi and Great Lakes drainages; MacCrimmon and Robbins 1975) and is now found throughout most of North America and in many parts of the World in both lakes and streams (Jackson 2002). The smallmouth bass generally inhabits clear, coolwater streams with notable current and gravel substrates (Coble 1975). Microhabitat studies show that suitability of microhabitats (e.g., water velocity and depth, cover) change with life stage, and may differ among streams (Groshens and Orth 1993; Orth and Newcomb 2002). At larger spatial scales, variability in abundance of smallmouth bass exists within and among streams. Smallmouth bass abundance is typically unimodal along the longitudinal gradient of a stream: abundances are lower in headwater streams (Coble 1975; Lyons 1991) and in larger downstream reaches where smallmouth bass are replaced by largemouth bass *M. salmoides* (Rabeni and Jacobson 1993a; Sowa and Rabeni 1995), often in response to different geomorphic processes and land use practices that have population level effects (Rabeni and Sowa 1996). Regional differences in smallmouth bass population characteristics likely reflect landscape features (Stark and Zale 1991). Studies conducted at different spatial scales (sensu Frissell et al. 1986) have all elucidated important information about stream habitat associations with smallmouth bass populations (Rabeni and Sowa 1996).

Smallmouth bass, in addition to the other black basses (spotted *M. punctulatus* and largemouth bass), are generally preferred by stream anglers in eastern Oklahoma (Fisher et al. 2002). Smallmouth bass demographics apparently differ between regions in eastern Oklahoma (Stark and Zale 1991; Balkenbush and Fisher 2001), but longitudinal and seasonal changes in abundance have not been related to population dynamics (Pezold et al. 1997; Walsh 2003; Walsh and Winkelman 2004a). Additionally, these spatial and temporal changes have not been evaluated in a stream habitat context. Our objectives were: 1) to determine how stream habitat and smallmouth bass population demographics vary spatially and temporally between and within two regional streams in eastern Oklahoma, and 2) evaluate habitat complementation and supplementation patterns within these streams. Understanding spatial and temporal variation in stream habitat and how population characteristics are related to that habitat will advance understanding of stream processes influencing smallmouth bass populations. This understanding is needed to guide conservation and management strategies aimed at protecting and enhancing stream habitats that influence demographic rates of smallmouth bass that influence population size.

Methods

Study streams

We sampled smallmouth bass populations and surveyed stream habitat in three reaches each on Baron Fork Creek and Glover River (Figure 3.2). Baron Fork Creek originates in northwest Arkansas and flows west-southwest through the Boston Mountains and Ozark Highlands ecoregions to its confluence with the Illinois River at Lake Tenkiller, Oklahoma. The Boston Mountains ecoregion is a dissected mountainous plateau composed of flat-lying shale and sandstone lithology and oak-hickory forest. Annual rainfall is 112 to 130 cm and land use is mostly logging and recreation (Woods et al. 2005). The Ozark Highlands are dominated by flat-lying cherty limestone, but shale, limestone, and dolomite are present in valley bottoms. Annual precipitation is 104 to 124 cm, and land use is primarily logging, recreation, and cattle and poultry farming, including pastureland and hayfields (Rabeni and Jacobson 1993a; Woods et al. 2005). Baron Fork Creek has hard water (60-99 mg/l $CaCO^3$; Balkenbush and Fisher 2001). Mean annual streamflow upstream for Baron Fork Creek at Dutch Mills, Arkansas (United States Geological Survey [USGS] gauge 07196900; period of record, 1958 to 2005) was 1.3 m^3/s (CV = 540), and 9.3 m^3/s (CV = 560) downstream at Eldon, Oklahoma (USGS gauge 07197000; 1948 to 2004). The Glover River flows south, mainly through the Ouachita Mountains, to its confluence with the Little River, Oklahoma. The Ouachita Mountains consist of folded, Paleozoic sandstone, shale, and chert lithology. Oak-hickory-shortleaf pine forests in this region receive from 109 to 145 cm of annual rainfall. Common land uses are logging, pastureland, hayfields, farming, and recreation (Rutherford et al. 1992; Woods et al. 2005). Glover River has turbid, soft water (12-38 mg/l CaCO3; Balkenbush and Fisher 2001). Mean annual streamflow for the lower Glover River near Glover, Oklahoma was 14.1 m^3/s (CV = 540) (USGS gauge 07337900; 1961 to 2004). Small floods, defined as a streamflow pulse that has a recurrence interval of 2 years, have durations (median days ± [75th - 25th]/50th percentiles; Indicators of Hydrologic Alteration software, Version 7, The Nature Conservancy) that indicate the lower Glover River is flashier (26 d ± 0.93) than both upper (30 d ± 1.28) and lower (32 d ± 0.84) Baron Fork Creek.

Sampling

Water temperature and streamflow were measured or estimated for each reach. Water temperatures were recorded every 1 to 2 hr at each reach using StowAway® Tidbit® temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) in Baron Fork Creek, and Solinst Levelloggers® (Solinst Canada Ltd., Georgetown, Ontario) in Glover River. Streamflow for each reach was prorated using USGS gauging station data. Estimates were made by relating measured discharge (Gallagher and Stevenson 1999) at each reach on multiple dates to USGS gauge data. A proportional model was then used to adjust gauge data to obtain reach estimates. Gauge 07196900 at Dutch Mills, Arkansas was used to estimate streamflow at the 3rd and 4th order reaches on Baron Fork Creek, and gauge 07197000 at Eldon was used to prorate streamflow at the 5th order reach. Gauge 07337900 near Glover, Oklahoma was used to estimate streamflow at all three Glover River reaches. Streamflow was only estimated from 15 July 2003 to 15 July 2004 because only provisional data were available after 30 September 2004.

Study sites on Baron Fork Creek and Glover River were located on 3rd, 4th, and 5th order stream reaches. We sampled 3rd and 4th order reaches once each season, and the 5th order sites during summer and fall; streamflows prohibited sampling at the 5th order sites during winter and spring. We conducted spring sampling in late March, summer sampling from late July to early August, fall sampling in mid-October, and winter sampling from mid-December to mid-January from July 2003 to August 2005.

During each sampling period, channel units were identified and classified within a defined reach 20+ times the mean channel width. All channel units were classified using the scheme of Hawkins et al. (1993), and they were mapped with a global positioning system (GPS) and measured in a GIS (Dauwalter et al. 2006). Mapping with a GPS and GIS allowed quantification of channel unit areas and relative positions. Thalweg depths were measured multiple times per channel unit; more measurements were made in longer channel units. A modified Wentworth scale was used to visually estimate substrate distributions of silt (<0.059 mm), sand (0.06-1.00 mm), gravel (2-15 mm), pebble (16-63 mm), cobble (64-256 mm), boulders (>256 mm), and bedrock (Bain 1999) within each channel unit. We estimated, and enumerated when logistically feasible, boulders, rootwads, and large woody debris (10+ cm diameter, 4+ m in length) in each channel unit.

We collected fish within each channel unit (except riffles) by using multi-pass backpack, barge, or boat electrofishing. Each channel unit was block netted (≤ 6.35 mm mesh), except in Glover River reaches in winter and spring when elevated streamflows and large surficial substrates prohibited effective block netting. Two electrofishing passes were conducted, and if one or more smallmouth bass were collected in the first two passes a third pass was made. Smallmouth bass collected during electrofishing were measured (TL) and weighed. Scales were taken posterior to the pectoral fin from individuals >90 mm TL for age analysis (individuals could not be sacrificed for otoliths), and individuals were tagged with a Floy t-bar anchor tag adjacent to the dorsal fin. A subsample of individuals was double tagged to estimate tag retention. Individuals were then returned to the channel unit from which they were captured after a recovery period. Crayfish were collected from a subset of channel units at 4th order sites with a 1-m^2 quadrat sampler (DiStefano et al. 2003) as an index of prey abundance (Probst et al. 1984). Voucher specimens were preserved on site and identified in the laboratory (Pflieger 1996). One to nine quadrat samples were collected per channel unit.

Smallmouth bass scales collected for age analysis were pressed onto acetate microscope slides, and aged by two readers. A third reader was used when ages differed between the first two readers. Individuals <90 mm were assumed to be age-0 (Balkenbush and Fisher 2001). Hatch dates were assigned between spring and summer samples in correspondence with the late-spring spawning season.

Statistical analyses

Unless otherwise noted, analyses were done in SAS Version 9.1 software (PROC MIXED and GENMOD; SAS Institute, Inc., Cary, North Carolina). Type I error rate was set at $\alpha = 0.05$. A Kenward-Roger degrees of freedom adjustment was used if variances were unequal, sometimes resulting in fractional degrees of freedom (Kenward and Roger 1997). Linear contrasts were used to assess differences between streams, seasons, and ages when applicable, and polynomial contrasts were used to evaluate trends with stream order (Kuehl 2000).

Recruitment variability

We used residuals from a weighted catch-curve analysis to estimate smallmouth bass recruitment variability for each reach (Maceina 1997). A weighted catch-curve analysis regresses $\log_e$(number individuals collected) against age, and uses $\log_e$(number individuals collected) as the weight. Higher coefficients of determination (r^2) from regressions for each reach indicated lower recruitment variability. Data from July and October 2003 samples were pooled and used for analysis of Baron Fork Creek reaches, and August and October 2004 samples were pooled and used for the Glover River.

Seasonal survival and recapture rates

We evaluated apparent survival and recapture rates of smallmouth bass by age class and season for each reach and season. All individuals that died from sampling were excluded from analyses. We modeled apparent survival and recapture rates by using an open population, time-independent model (Williams et al. 2002), and used model selection to evaluate a set of candidate models. Apparent survival is actual survival multiplied by permanent immigration (not estimated); hereafter, we refer to apparent survival as survival. A model including seasonal and age (1, 2, and 3+) effects in both survival and recapture rates was used as the global model. Fit of the global model was evaluated by comparing observed model deviance to a distribution of bootstrapped deviance estimates from 500 simulations (Burnham and Anderson 2002). Other models evaluated were subsets of the global model that included combinations of: 1) age and season or season effects only on survival, and 2) age and season, age only, and season only effects on recapture rates or constant recapture rates. Models were compared using Akaike's Information Criterion corrected for small sample bias (AIC_c, or $QAIC_c$ when overdispersion was evident), and model averaging was conducted using Akaike weights (Burnham and Anderson 2002). Survival estimates were adjusted for three-month tag retention rates (Arnason and Mills 1981). All analyses were done using Program MARK (White and Burnham 1999).

Relative growth rates

Relative daily growth rates in length and weight (% initial body length or weight per day) were measured using individuals recaptured in successive seasons (Busacker et al. 1990). Fixed effects of stream, season, and age (at the end of the season) on relative growth were determined by using a mixed model with year as a random effect. The only interaction tested was age×season.

Condition

We determined the effects of stream, stream order, and season on condition of smallmouth bass. Condition was determined using relative weights of individuals ≥160 mm (Kolander et al. 1993). Differences in condition were determined using a mixed model whereby stream, stream order, and season were treated as fixed effects and year was treated as a random variable. A stream×stream order interaction was included in the model.

Within reach movements

We evaluated seasonal within reach movements of smallmouth bass by determining how many individuals moved from one channel unit to another between successive seasons. A descriptive multiple logistic regression model was developed to determine the effects of season, age, reach and year on movement probability. Season was modeled as a dummy variable, with winter as the baseline. Adequacy of model fit was determined using a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000).

Densities and size structure in channel units

We determined how abundance of age-0 and age-1+ smallmouth bass, and mean size of age-1+ individuals, differed among channel units between streams, stream order, and seasons, and how they were related to habitat within channel units. Relations were determined using regression tree analysis (RTA), a non-parametric analysis that explains complex, nonlinear, and interacting relationships between multiple explanatory variables and a response variable. Observations are split into homogenous groups using categorical or continuous explanatory variables. Thus, each group of observations has common values of explanatory and response variables. The analysis is displayed as a dendrogram whereby each branch reflects the value of an explanatory variable that results in the lowest variance in the response variable between groups (Breiman et al. 1984; De'ath and Fabricius 2000).

We conducted RTAs using each channel unit as an observation, and with age-0 smallmouth bass densities, age-1+ densities, and mean length (mm) of age-1+ smallmouth bass as response variables. Explanatory variables included in RTA were dependent on results of correlation analyses to limit variable redundancy. Smallmouth bass densities (no./ha) were estimated using a 3-pass capture probability model (Appendix 3.A.) and were transformed ($\log_e[X + 0.01]$) to stabilize variances resulting from zero densities. Mean length (mm) of age-1+ individuals were not transformed, and only channel units having age-1+ smallmouth bass were analyzed. Each RTA was performed using CART, version 5.0 software (Steinberg and Colla 1995). We used sums of squares about group means to maximize homogeneity within groups (De'ath and Fabricius 2000). The final tree selected was the one having the smallest relative error (similar to the coefficient of nondetermination, $1 - r^2$), as determined from 10-fold cross-validation (Breiman et al. 1984; De'ath and Fabricius 2000).

We used Spearman rank correlation to relate smallmouth bass abundance to crayfish densities. Crayfish are important foods for smallmouth bass in these streams (Probst et al. 1984; Ebert and Filipek 1991). We evaluated crayfish separately from channel-unit habitat variables because we only estimated crayfish densities in 4th order streams.

Results

Stream habitat differed between Baron Fork Creek and Glover River and changed longitudinally in each stream. Baron Fork Creek had smaller substrates; less pool habitat and wood; lower gradient; and smaller channel width per basin area than did the Glover

River. In both streams, mean thalweg depths, width:depth ratios, and sinuosity increased with stream size. Slope was higher in upstream reaches, as were substrate sizes. The 5th order Glover River reach was somewhat anomalous, as it had larger substrates and higher reach gradient than the 4th order reach (Table 3.1).

Water temperatures were typically more stable in Baron Fork Creek than in Glover River (Figure 3.3). Temperature loggers were lost during floods from all Baron Fork Creek reaches at some time during the study and, in addition to one logger malfunction, resulted in discontinuous temperature records. Temperatures were typically lower in Baron Fork Creek than Glover River during summer, but were similar in winter. Temperatures were also generally colder from summer to winter in upstream reaches and cooler from winter to summer in downstream reaches, suggesting that upstream areas with less water volume responded faster to changes in air temperature. Temperatures also varied most in the upstream reaches in Baron Fork Creek.

Streamflows were more variable upstream compared to downstream in Baron Fork Creek, but less variable overall in Glover River; however, Glover River flood peaks indicated flashier streamflows (Figure 3.4). Mean annual streamflows (CV) for 3rd, 4th, and 5th order reaches were 0.06 (534), 0.23 (534), and 9.27 (354) m^3/s, respectively, in Baron Fork Creek, and 0.81 (198), 2.95 (198), and 9.15 (198), respectively, in Glover River. Longitudinal changes in streamflow variation in Glover River could not be assessed because all reach estimates were derived from the same USGS gauge.

More individuals were collected during electrofishing from Baron Fork Creek than Glover River. Including recaptures, we collected 1227 individuals from the 4th order reach of Baron Fork Creek but only 5 from the 4th order reach of Glover River. Forty-seven smallmouth bass were collected from the 3rd order Glover River reach. The oldest individual was age-6, and several age-5 individuals were collected from the 4th and 5th order reaches of Baron Fork Creek. Mean length at age was similar between streams (Table 3.2). Of all individuals double-tagged and recaptured during the next season (approximately 3 months), 10 of 11 individuals retained both tags (91%).

Recruitment variability

Recruitment variability differed between streams and among upstream and downstream reaches. Low numbers of individuals prohibited analysis of 4th and 5th order Glover River reaches. Age-0 individuals were underrepresented and were omitted from catch-curve analyses, as were a few age-5 and older individuals and recaptures. Recruitment was most variable in 3rd order reaches in Baron Fork Creek ($r^2 = 0.20$) and Glover River ($r^2 = 0.58$) when compared to 4th ($r^2 = 0.95$) and 5th ($r^2 = 0.92$) order Baron Fork Creek reaches.

Seasonal survival and recapture rates

Survival and recapture rates were primarily dependent on season, with age-specific survival being evident in one reach. Although temporary emigration was suspected, permanent emigration was assumed to be low since many smallmouth bass show affinity to ‘home pools’ (Lyons and Kanehl 2002), and electrofishing beyond reach boundaries resulted in few tagged individuals. Low numbers of individuals and recapture rates limited survival analyses to the 4th and 5th order Baron Fork Creek reaches, and the 3rd order Glover River reach. Bootstrapped deviances for each reach suggested that overdispersion (estimated as: $\hat{c}$ = observed model deviance / mean bootstrapped deviance) was evident in both Baron Fork models (4th order, $P = 0.022$, $\hat{c} = 1.208$; 5th order, $P < 0.001$, $\hat{c} = 2.277$), but not in the Glover River ($P = 0.746$). The model with seasonal effects on survival and recapture rates was best supported in 5th order Baron Fork Creek reach and 3rd order Glover River reach, with the 4th order Baron Fork Creek reach also showing evidence for age-specific survival (Table 3.3). Survival was generally lowest from summer to fall, and recapture rates were typically highest in fall (Table 3.4). Survival was often higher in Baron Fork Creek reaches than Glover River, but not for all ages or seasons.

Relative growth rates

There were differences in smallmouth bass relative daily growth in length among seasons, but not among ages or between Baron Fork Creek and Glover River. There were no observed differences in daily growth in length between streams ($F_{1,\,158} = 0.00$; $P = 0.953$), among ages ($F_{2,\,158} = 1.13$; $P = 0.324$), and no season×age interaction ($F_{6,\,157} = 0.54$; $P = 0.774$). There was a significant difference in relative daily growth among seasons ($F_{3,\,44.4} = 4.60$; $P = 0.007$). Linear contrasts showed that growth in length was lowest from winter to spring and highest from summer to fall (Figure 3.5). There was no difference in daily growth in weight between streams ($F_{1,\,157} = 0.01$; $P = 0.939$), among seasons ($F_{3,\,93.2} = 0.11$; $P = 0.953$), among ages ($F_{2,\,158} = 0.13$; $P = 0.880$), and no season×age interaction ($F_{6,\,156} = 0.22$; $P = 0.972$). Stream×age and stream×season interactions were not tested due to missing treatment combinations. Effects of stream order were not tested due to a lack of recaptures in some reaches.

Condition

Relative weights differed between Baron Fork Creek and Glover River in some reaches and changed seasonally. There was a stream×stream order interaction ($F_{2,\,1226}$ = 9.68; $P < 0.001$) and an effect of season ($F_{3,\,1210}$ = 11.04; $P < 0.001$). Linear contrasts demonstrated that relative weights were higher in Baron Fork Creek than Glover River only in 3rd order reaches ($F_{1,\,1227}$ = 138.27; $P < 0.001$), but not 4th ($F_{1,\,1225}$ = 1.04; P = 0.307) and 5th order reaches ($F_{1,\,1226}$ = 3.15; P = 0.076). Polynomial contrasts showed that relative weights also decreased linearly ($F_{1,\,1226}$ = 70.97; $P < 0.001$) but not quadratically ($F_{1,\,1226}$ = 2.81; P = 0.094) with stream order in Baron Fork Creek. There was no trend in Glover River reaches (linear; $F_{1,\,1226}$ = 1.25; P = 0.263). Relative weights were lower in spring when compared to other seasons (Figure 3.6).

Within reach movements

Movement of individuals among channel units between successive seasons was common, and movement changed among seasons. Limited numbers of recaptures or lack of winter and spring samples in lower reaches restricted this analysis to the 4th order Baron Fork Creek and 3rd order Glover River reaches. In the 4th order Baron Fork Creek reach, 39% of individuals were recaptured in channel units other that those where they were collected the previous season. In the 3rd order Glover River, 33% moved to other channel units. The descriptive model suggested movement was highest from fall to winter, and spring to summer, and that there was some evidence of more movement among older individuals (Table 3.5). Model fit was good (Hosmer-Lemeshow test; χ^2 = 4.252, df = 6, P = 0.643).

We conducted a post hoc movement analysis of smallmouth bass in the 4th order Baron Fork Creek reach to examine winter movement into and out of a backwater and adjacent run (2003-04) or pool (2004-05) with unique water temperatures resulting from groundwater influx (see below). Of those individuals collected in the backwater-run in winter 2003-04 or backwater-pool in 2004-05, 24 of 31 and 3 of 5 individuals, respectively, were collected in other channel units in the summer or fall. Of individuals collected in the backwater-run or backwater-pool channel units in summer or fall prior to each winter, 0 of 10 and 0 of 2 individuals recaptured in winter were collected outside of those habitats. Thus, there was strong evidence of movement into, but not out of, those habitats in winter of both years.

Densities and size structure in channel units

Stream habitat and densities of smallmouth bass in channel units changed over time. This was especially true of the 4th order reach of Baron Fork Creek. Repeated seasonal sampling showed the dynamic nature of stream habitat within the reach, especially in response to seasonal streamflows. Densities of smallmouth bass within the reach decreased from summer through spring, but also varied among years (Figure 3.7). Patterns of abundance suggested that individuals remaining in the reach concentrated in specific backwater and adjacent run habitat in winter-spring 2003-04. Groundwater influx was observed along the north edge of the backwater that was located along a bedrock bluff. Water temperatures in this backwater habitat were warmer than those in the main channel during winter, cooler during summer, and they fluctuated less (Figure 3.8, 3.9). A late-spring, near-record flood in 2004 created a mid-channel pool adjacent to this backwater.

Smallmouth bass densities were related to reach and channel-unit characteristics, but these relationships differed among age groups. Age-0 densities ranged from 0 to 11101 / ha, and were highest on average in the 4th order Baron Fork Creek reach. No channel-unit habitat variables were highly correlated ($r_{max} = 0.304$) and all were included in RTA analysis: percent bedrock, percent boulder, percent silt-clay, percent vegetation, wood density (rootwads + large woody debris / ha), water velocity (coded), and mean thalweg depth (m). Water velocity was coded by channel-unit type; runs were coded 2, and all other types as 1. Backwaters were given the same velocity code as pools because low water velocities were observed in some parts of pools and in some backwaters due to subsurface flow and groundwater influx; riffles were not sampled. Channel-unit habitat was variable within and among types, as were smallmouth bass densities (Table 3.6). Regression tree analysis on age-0 smallmouth bass densities had 4 splitting nodes and 5 terminal nodes. Relative error was 0.797. Densities were only weakly explained by streams, reaches, and seasons (Figure 3.10).

Densities of age-1+ smallmouth bass ranged from 0 to 3684 / ha. Stream, reach, and channel-unit habitat explained more variation in age-1+ densities than in age-0 densities. The RTA had 8 split and 9 terminal nodes. Relative error was 0.724. Mean thalweg depth was an important determinant of densities, but densities were higher in Baron Fork Creek than in Glover River and higher in Baron Fork Creek in summer and fall than in winter and spring (Figure 3.11).

Little variation in mean size of age-1+ smallmouth bass was explained by stream, reach, and channel unit habitat. RTA showed 6 split and 7 terminal nodes, but had a relative error of 0.856. Larger fish were found in deeper channel units in larger stream reaches, but also in shallower channel units that had some, but not much boulder cover (Figure 3.12).

Smallmouth bass distributions were not strongly related to those of crayfish. Ringed crayfish *Orconectes neglectus* and Neosho pygmy crayfish *O. macrus* were numerically dominant in Baron Fork Creek, and summed channel-unit densities averaged 6.4 / m^2 (n = 208; SD = 9.5). There was a weak but significant positive correlation between crayfish density and both age-0 (n = 188; $r_s = 0.322$; $P < 0.001$) and age-1 (n = 188; $r_s = 0.338$; $P < 0.001$) smallmouth bass density (no. / ha) in channel units of Baron Fork Creek. We did not analyze data from Glover River because only five smallmouth bass were collected from the 4th order reach.

Discussion

We observed strong spatial and temporal patterns in stream habitat and smallmouth bass population characteristics in Baron Fork Creek and Glover River, eastern Oklahoma. Patterns were evident despite the fact that some population parameters could not be estimated due to low numbers of individuals and recaptures in some reaches. Data from a Baron Fork Creek reach also suggested strong patterns of habitat complementation and supplementation within the stream landscape.

Spatial variation

We observed spatial variation in stream habitat and smallmouth bass population characteristics in Baron Fork Creek and Glover River. Baron Fork Creek and Glover River differed in stream habitat, streamflow regime, and water temperatures reflecting regional differences in underlying geology, topography, climate, and land use (Omernik 1987; Woods et al. 2005). In reaches with the highest smallmouth bass densities, recruitment variability was higher in Glover River than Baron Fork Creek, probably because Glover River had less gravel substrate and cover for spawning and flashier streamflows. Although growth was not different among streams, condition of individuals was lower in Glover River than Baron Fork Creek. In addition, water temperatures were high and smallmouth bass survival was low in late summer-early fall in Glover River. At temperatures greater than 22°C, as observed in the lower Glover River in summer, maximum consumption rates and growth scope decrease for smallmouth bass in Ozark streams (Zweifel et al. 1999; Whitledge et al. 2002), especially when temperatures fluctuate (Diana 1995; Whitledge et al. 2002). Thus, variable recruitment in combination with high summer water temperatures appear to be negatively affecting condition and survival of smallmouth bass in Glover River, possibly explaining why smallmouth bass densities were markedly lower in Glover River than in Baron Fork Creek.

Differences in smallmouth bass populations in northeastern and southeastern Oklahoma streams have been noted previously. Balkenbush and Fisher (2001) reported that Glover River smallmouth bass had lower abundances, poor recruitment, and higher mortality rates compared to those in Baron Fork Creek. A previous study also suggested that lower recruitment in southeastern than in northeastern Oklahoma streams, possibly reflected a combination of streamflow, habitat, and temperature differences (Stark and Zale 1991).

Longitudinal variation in stream habitat and smallmouth bass populations was also observed. Within each stream, abundances were lowest in the upstream reach of Baron Fork Creek, but highest in the upstream reach of Glover River. Both upstream reaches exhibited high recruitment variability, compared with more stable recruitment in 4th and 5th order Baron Fork Creek reaches. Larger substrates, more bedrock, less cover and flashier streamflows in upper Baron Fork Creek resulted in variable recruitment similar to that observed in the upper Glover River. High discharge events result in nest failures and low recruitment to age-1+ (Lukas and Orth 1995; Swenson et al. 2002; Smith et al. 2005). Small, upstream reaches have less spawning gravel adjacent to cover that provides nesting refugia during flashy and unpredictable spring streamflows common in smaller temperate streams (Poff and Ward 1989). These characteristics offset behavioral responses used by nesting smallmouth bass (e.g., use of velocity shelters, renesting, protracted spawning season) to circumvent streamflow disturbances during spawning (Orth and Newcomb 2002). These behavioral responses likely increase reproductive success in larger streams with more cover, gravel, and velocity shelters.

Despite harsh reproductive conditions, upstream reaches sometimes provided quality summer habitat. Most age-1+ individuals collected in the 3rd order Baron Fork Creek reach were collected only in July 2003, suggesting the presence of a temporary, transient group of individuals. However, individuals in that reach were in better condition than those in all other reaches. This suggests that in light of harsh reproductive and streamflow conditions in spring, if individuals spawn successfully, or otherwise populate these reaches, they will experience good physical and biological conditions in summer, possibly from reduced intraspecific competition for consumable resources (e.g., prey). In contrast, these benefits were not observed upstream in Glover River. Temporary resource abundance in habitats typically considered unsuitable has been suggested to lead to temporarily high densities of animal populations. However, individuals subsequently redistribute themselves when normal low-suitability conditions return, leading to high turnover rates of individuals within those habitats (Winker et al. 1995).

Temporal variation

Smallmouth bass population dynamics differed seasonally. Not surprisingly, growth in length was variable but lowest from fall to spring when water temperatures were lowest. However, growth in weight showed no seasonal differences, which may reflect variability in growth and conversion of energy stores to reproductive tissues from fall to spring when growth has otherwise ceased. Interestingly, condition of smallmouth bass was lowest during spring sampling periods approximately 1 to 1.5 months prior to spawning. Poor condition probably reflected empty stomachs and depleted energy reserves despite some gonad development prior to spawning. Brown and Murphy (2004) found that relative weights of largemouth bass were low before and just after early-spring spawning, but then increased rapidly beyond prespawn values in response to increased prey availability and subsequent feeding.

Seasonal changes in survival were also apparent. Survival was typically lowest from summer to fall, especially in Glover River. Low survival from summer to fall may reflect bioenergetic costs resulting from high late-summer water temperatures as discussed above. It may also reflect density dependent mortality resulting from shrinking of stream habitats or harvest by anglers. Water levels are typically lowest in late summer-early fall and results in less habitat area and volume, particularly in Baron Fork Creek. Habitat shrinking concentrates individuals in certain habitats and may increase intraspecific competition, especially in upstream reaches that can become intermittent; however, relative weights were highest in summer reflecting good health and full stomachs. Paragamian and Wiley (1987) reported that growth of age-1 smallmouth bass was lowest during low streamflows and highest during intermediate streamflows in the Maquoketa River, Iowa. They suggested that low streamflows reduced cover for smallmouth bass and limited macroinvertebrate production, resulting in increased intraspecific competition for prey resources. Harvest by anglers may also result in higher summer-fall mortality. Martin (1995) reported that fishing mortality was 6 to 15% for smallmouth bass (≥180 mm) in lower Baron Fork Creek, and harvest was highest from May through August but was at least twice as high in August than in any other month. In lower Glover River, fishing mortality was 2 to 11%, but was highest in April. We do not know the extent of fishing pressure and harvest of smallmouth bass in the upper Glover River. However, if harvest was the sole reason for low late-summer survival, mortality would have been higher among older individuals. Even if harvest was absent, fish experience physiological stress from being caught by anglers, which may result in delayed mortality when they are released. Interestingly, survival was lowest for age-1 individuals from spring to summer in the 4th order Baron Fork Creek reach. Energy reserves are most depleted just after the spawning period (Mackereth et al. 1999;

Brown and Murphy 2004), even for age-1 individuals that do not spawn because of size-dependent condition and mortality (Shuter and Post 1990). Some age-1 individuals may not have enough reserves to survive to mid-spring when water temperatures warm and feeding resumes. Also, age-1 individuals may not have the ability to migrate to habitats that offer physiological advantages for increased survival throughout the winter-spring seasons (see below).

Relations with channel-unit habitat

Habitat characteristics of channel units were related to age-1+ smallmouth bass densities but not age-0 densities. Age-0 densities were related to stream, stream order, and season; densities were highest in the 4th order reach of Baron Fork Creek. However, densities of age-0 smallmouth bass were not related to channel-unit habitat and reflected generalized habitat use (Sabo and Orth 1994), the inability or unwillingness to move across riffles to other channel units (Simonson and Swenson 1990), or density of spawners and fry survival within channel units. Thalweg depths of channel units were most important in explaining densities of age-1+ smallmouth bass in all reaches, but bedrock substrate and woody cover also were related to densities. Densities were highest in deeper channel units. Smallmouth bass are typically more abundant in deeper pools (Peterson and Rabeni 2001; Walsh and Winkelman 2004b), even though they generally use areas of intermediate depths within those habitats (Todd and Rabeni 1989; Orth and Newcomb 2002). Bedrock was only related to age-1+ densities in Baron Fork Creek in spring and winter, reflecting use of a backwater and adjacent habitats in the 4th order reach during those seasons. Age-1+ densities in summer and fall were higher in channel units with less wood. Although smallmouth bass typically associate with woody cover (Todd and Rabeni 1989), densities of smallmouth bass and wood can vary independently at the channel unit or reach scales (McClendon and Rabeni 1987; Sowa and Rabeni 1995).

Mean size of age-1+ smallmouth bass varied among stream reaches and channel-unit habitat. Larger individuals used deeper channel units, although shallow channel units with some boulders sometimes had larger fish. In Missouri streams, size structure of smallmouth bass was positively related to woody and vegetative cover (McClendon and Rabeni 1987).

Habitat complementation and supplementation

Changes in the spatial distribution of abundance and movement in the 4th order reach of Baron Fork Creek suggested among-season habitat complementation and supplementation by smallmouth bass in the stream landscape. Winter densities were generally low, with highest densities in backwater-run (2003-04) or backwater-pool (2004-05) habitats. Smallmouth bass moved into but not out of these habitats in winter. Temperature data suggested that groundwater inflow into the backwater resulted in a thermal refuge during winter. Electrofishing the run adjacent to the backwater during the first winter indicated that individuals were using crevasses in fractured bedrock that likely had some groundwater influx. Smallmouth bass move to protective cover when water temperatures drop to 10°C, and they become torpid at 4.5°C (Coble 1975). Use of this winter thermal refuge was complementary to spawning habitat in late-spring because high amounts of silt and sand substrates made the backwater unsuitable for reproduction (Chapter 4).

Thermal refugia in channel units and stream reaches have been reported for other streams (Sedell et al. 1990). In Missouri, smallmouth bass used a spring-fed tributary most in winter and least during warmer seasons. In winter, temperatures were warmer and more stable in the tributary than in the adjoining stream, and the tributary potentially afforded positive physiological benefits in terms of feeding and reproductive success (Peterson and Rabeni 1996).

Habitats formed by streambed scour along bedrock outcrops, similar to the backwater noted above, have been reported to be important to smallmouth bass. Rabeni and Jacobson (1993a) suggested that bluff pools in Ozark streams are important habitats for smallmouth bass, especially in winter. These habitats likely have high rates of groundwater influx. If bluff pools possess unique thermal properties, they may also provide bioenergetic benefits. These benefits would be important, because most bluff pools would also have suitable spawning habitat given that they are not backwaters with silt-sand substrates. Bluff pools, which result from scour along bedrock faces, also may be the only permanent habitats in temporally variable Ozark streams (Rabeni and Jacobson 1993b). Thus, fish would not have to use complementary habitats for spawning and winter refugia.

In contrast, smallmouth bass flexibility in use of cover and food resources in summer and fall suggested habitat supplementation. We did not observe a strong association between smallmouth bass and crayfish densities. Smallmouth bass in these streams also consume fish (Probst et al. 1984; D. C. Dauwalter, unpublished data), and streams in the Ozarks support high secondary production and crayfish abundances (Brown and Matthews 1995). Thus, distribution of food is probably not determining distributions of smallmouth bass abundance. Furthermore, we did not observe strong associations of smallmouth bass with habitat variables except for water depth. Smallmouth bass associate with a variety of cover types (Todd and Rabeni 1989), and can likely substitute one cover type for another, including water depth as a refuge. Thus, substitutable cover and food resources are both available in most large habitats (i.e., large pools) and, consequently, are also in close proximity. Moreover, the close proximity of spawning habitat and winter thermal refugia (i.e., small scale of functional habitat unit), in addition to food and cover, may be why smallmouth bass densities in the 4th order reach of Baron Fork Creek were high. Because bluff pools are a single habitat and potentially meet the spawning, feeding and cover, and thermal refugia requirements of smallmouth bass, they likely are a complete functional habitat unit in themselves and support large population sizes that play an important role in the metapopulation dynamics of smallmouth bass in Ozark streams. Furthermore, the presence of bluff pools throughout middle and lower Baron Fork Creek (D. Dauwalter, personal observation) may be one reason why smallmouth bass densities are high relative to those in the Glover River (Kocik and Ferreri 1998). Continuous stream surveys would identify the abundance and spatial position of such habitats within the stream network (Fausch et al. 2002).

Conclusions

Smallmouth bass populations are affected by spatially and temporally dynamic processes. Comparisons between regional streams and their longitudinal profile revealed spatial differences in stream habitat and smallmouth bass population characteristics. Seasonal sampling showed temporally dynamic thermal regimes and habitat creation, loss, and size fluctuations. These habitat and population dynamics were facilitated by studying longer (up to 1,000 m) stream reaches than those traditionally sampled (200 m; Fausch et al. 2002). Moreover, we documented the importance of habitat complementation, supplementation, and refugia in Baron Fork Creek; however, their importance in environmentally harsh streams like Glover River, which have low population densities and different demographics, is unknown and was difficult to assess because of the low number of individuals available for study. The effects of stream habitat on fishes are complex, and, thus, it is important to consider both spatial and temporal aspects of habitat when considering their effects on fish populations. Taking such a comprehensive approach will help guide stream habitat and fish population management efforts in streams with fish species that are sensitive to environmental disturbance and also provide important recreational fishing opportunities for anglers (Fisher et al. 1998; Fisher et al. 2002).

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Table 3.1. Geomorphic and habitat characteristics of 3rd, 4th, and 5th order study reaches on Baron Fork Creek and Glover River, eastern Oklahoma in summer 2003.

	Baron Fork Creek			Glover River		
Variable	3rd order	4th order	5th order	3rd order	4th order	5th order
Basin area (km^2)	46	156	831	52	194	485
Channel width (m)	15.9	25.9	39.7	17.9	29.5	55.1
Reach length (m)	670	1030	1000	450	570	870
D_{50} (mm)	55	28	20	166	70	148
Entrenchment ratio	1.5	>2.2	>2.2	>2.2	>2.2	>2.2
%Pool	66.2	70.3	61.6	68.6	83.2	91.7
Sinuosity	1.05	1.5	2.0	1.06	1.3	1.3
Slope	0.0032	0.0022	0.0020	0.0091	0.0029	0.0040
Width:depth ratio	22.0	22.4	32.2	20.3	21.8	35.1
Mean thalweg depth (m)	0.160	0.420	0.661	0.272	0.274	0.558
%Bedrock	38	13	0	15	16	44
%Boulder	1	<1	2	12	6	7
%Silt-clay	22	8	2	1	15	2
%Vegetation	2	3	2	<1	1	17
Wood (no. / m^2)	0.0007	0.0091	0.0106	0.0008	0.0039	0.0002

Table 3.2. Mean (± 1 SD; number collected) length (mm) at age of smallmouth bass by stream reach and season from 3rd, 4th, and 5th order reaches on Baron Fork Creek and Glover River, 2003-05.

		Age					
Stream / order	Season	0	1	2	3	4	5
Baron Fork Creek							
3rd order	Summer	74.3 (15.0; 8)	157.4 (12.0; 8)	190.9 (21.3; 8)	242.0 (18.8; 11)	303.8 (15.2; 4)	[a]
	Fall	110.6 (11.9; 8)	[a]	[a]	263.0 (--; 1)	282.0 (--; 1)	[a]
	Winter	100.3 (12.8; 10)	[a]	[a]	[a]	[a]	[a]
	Spring	110.2 (8.1; 5)	[a]	[a]	[a]	[a]	[a]
4th order	Summer	54.4 (10.0; 976)	132.2 (15.4; 246)	188.6 (19.4; 143)	237.3 (24.6; 83)	291.1 (33.4; 18)	306.5 (7.8; 2)
	Fall	82.0 (23.4; 126)	150.9 (16.7; 145)	202.0 (23.8; 119)	250.9 (24.6; 64)	278.1 (23.0; 11)	[a]
	Winter	80.2 (18.7; 102)	146.7 (16.2; 73)	201.2 (20.6; 26)	248.6 (29.0; 8)	319.5 (29.0; 2)	[a]
	Spring	92.7 (20.7; 38)	155.0 (20.7; 45)	214.1 (23.5; 42)	271.5 (13.9; 8)	310.0 (42.4; 2)	[a]
5th order	Summer[b]	64.1 (13.9; 178)	136.4 (22.4; 69)	198.1 (21.3; 63)	239.7 (20.6; 38)	307.1 (29.3; 21)	364.0 (46.7; 4)
	Fall	98.3 (33.1; 28)	163.7 (14.9; 81)	210.4 (24.3; 77)	245.5 (22.3; 51)	313.3 (22.2; 35)	378.1 (38.3; 7)
Glover River							
3rd order	Summer	83.5 (7.8; 2)	144.7 (9.6; 3)	188.5 (24.7; 2)	239.3 (13.4; 3)	269.0 (--; 1)	[a]
	Fall	[a]	185.0 (60.7; 3)	169.0 (--; 1)	268.5 (30.4; 2)	349.0 (--; 1)	[a]
	Winter	[a]	145.0 (8.8; 5)	210.8 (7.9; 5)	271.0 (--; 1)	279.0 (--; 1)	[a]
	Spring	103.0 (7.9; 3)	143.1 (19.7; 10)	205.3 (12.5; 4)	278.0 (--; 1)	[a]	[a]
4th order	Summer	67.7 (3.8; 3)	163.0 (--; 1)	[a]	[a]	[a]	[a]
	Fall	[a]	[a]	[a]	248 (--; 1)	[a]	[a]
	Winter	120.5 (2.1; 2)	[a]	[a]	[a]	[a]	[a]
	Spring	104.0 (--; 1)	[a]	[a]	[a]	[a]	[a]
5th order	Summer	78.4 (10.4; 27)	[a]	169.0 (35.7; 3)	[a]	305.0 (--; 1)	[a]
	Fall	114.0 (12.7; 2)	[a]	[a]	218.0 (--; 1)	[a]	[a]

[a] No individuals were collected

[b] One age-6 individual was collected, 355 mm

Table 3.3. Number of parameters (k), AIC_c or QAIC_c, and Akaike weights (w_i) for candidate models evaluated in modeling survival (Φ_i: survival×immigration) and recapture rates (p_i) of smallmouth bass in Baron Fork Creek and Glover River, eastern Oklahoma. Model subscripts indicate season (s) and age (a) effects.

Reach / Model	k	$[\text{Q}]\text{AIC}_c$	$\Delta[\text{Q}]\text{AIC}_c$	w_i
Baron Fork Creek, 4th order				
$\Phi_{a\cdot s}p_{s}$	16	1363.02	0.00	0.920
$\Phi_{a\cdot s}p_{a\cdot s}$	24	1369.39	6.37	0.038
$\Phi_{s}p_{a\cdot s}$	16	1370.17	7.15	0.028
$\Phi_{s}p_{s}$	8	1371.17	8.15	0.016
$\Phi_{a\cdot s}p_{.}$	13	1394.63	31.61	0.000
$\Phi_{a\cdot s}p_{a}$	15	1398.67	35.65	0.000
$\Phi_{s}p_{.}$	5	1409.80	46.78	0.000
$\Phi_{s}p_{a}$	7	1411.92	48.90	0.000
Baron Fork Creek, 5th order				
$\Phi_{s}p_{s}$	4	230.51	0.00	0.810
$\Phi_{a\cdot s}p_{s}$	8	235.22	4.71	0.077
$\Phi_{s}p_{.}$	3	236.11	5.61	0.049
$\Phi_{s}p_{a\cdot s}$	8	237.35	6.84	0.026
$\Phi_{s}p_{a}$	5	237.82	7.31	0.021
$\Phi_{a\cdot s}p_{.}$	7	238.75	8.24	0.013
$\Phi_{a\cdot s}p_{a\cdot s}$	12	242.31	11.81	0.002
$\Phi_{a\cdot s}p_{a}$	9	242.65	12.14	0.002
Glover River, 3rd order				
$\Phi_{s}p_{s}$	8	75.40	0.00	0.717
$\Phi_{s}p_{.}$	5	77.62	2.21	0.237
$\Phi_{s}p_{a}$	7	80.91	5.51	0.046
$\Phi_{a\cdot s}p_{s}$	15	95.32	19.92	0.000
$\Phi_{a\cdot s}p_{.}$	13	95.78	20.38	0.000
$\Phi_{a\cdot s}p_{a}$	14	100.72	25.32	0.000
$\Phi_{s}p_{a\cdot s}$	16	103.84	28.44	0.000
$\Phi_{a\cdot s}p_{a\cdot s}$	18	112.89	37.49	0.000

Table 3.4. Model averaged seasonal survival (Φ_i: survival× immigration) and recapture rates by age group (± unconditional SE) for smallmouth bass in Baron Fork Creek and Glover River, eastern Oklahoma. All rates were adjusted for tag retention rates of 0.91.

	Survival			Recapture[a]		
Reach / Season	Age 1	Age 2	Age 3+	Age 1	Age 2	Age 3+
Baron Fork Creek, 4th order						
Spring to summer	0.21(0.16)	0.51(0.14)	0.96(0.22)	0.27(0.09)	0.23(0.05)	0.23(0.05)
Summer to fall	0.53(0.09)	0.51(0.08)	0.44(0.10)	0.64(0.08)	0.63(0.08)	0.65(0.09)
Fall to winter	0.74(0.16)	0.73(0.12)	0.42(0.11)	0.17(0.04)	0.17(0.04)	0.16(0.04)
Winter to spring	0.79(0.20)	1.00(0.00)	1.00(0.00)	0.21(0.04)	0.22(0.04)	0.21(0.04)
Baron Fork Creek, 5th order						
Summer to fall	0.42(0.16)	0.44(0.16)	0.45(0.17)	0.65(0.23)	0.66(0.22)	0.60(0.22)
Fall to Summer	0.58(0.21)	0.58(0.21)	0.56(0.21)	0.18(0.08)	0.16(0.09)	0.19(0.09)
Glover River, 3rd order						
Spring to summer	1.05(0.14)	1.05(0.14)	1.05(0.14)	0.46(0.17)	0.45(0.17)	0.44(0.17)
Summer to fall	0.26(0.16)	0.26(0.16)	0.26(0.16)	0.94(0.24)	0.94(0.25)	0.92(0.26)
Fall to winter	0.66(0.52)	0.66(0.52)	0.66(0.57)	0.15(0.23)	0.15(0.23)	0.13(0.21)
Winter to spring	0.53(0.24)	0.53(0.24)	0.53(0.24)	0.94(0.24)	0.94(0.25)	0.92(0.26)

[a] recapture rates pertain to the last season of interval

Table 3.5. Covariables, parameter estimates (b_i), and *P*-values from a multiple logistic regression model used to determine the effects of season, reach, and year (of study) on probability of movement between channel units in a 4th order Baron Fork Creek and 3rd order Glover River reach, eastern Oklahoma. Seasonal movement from fall to winter was used as the baseline.

Variable	b_i (±1 SE)	*P*
Intercept	-0.235 (1.063)	[a]
Spring to summer	-1.438 (0.807)	0.075
Summer to fall	-1.508 (0.435)	<0.001
Fall to winter	baseline	
Winter to spring	-1.628 (0.534)	0.002
Age	0.363 (0.203)	0.074
Reach	0.002 (0.792)	0.998
Year	0.384 (0.433)	0.375

[a] not statistically tested

Table 3.6. Mean (range) channel unit and smallmouth bass characteristics in Baron Fork Creek and Glover River, eastern Oklahoma.

		Baron Fork Creek			Glover River		
Type	Variable	3rd order	4th order	5th order	3rd order	4th order	5th order
Run	Mean thalweg depth (m)	0.23 (0.08-0.48)	0.54 (0.09-1.24)	0.72 (0.10-1.51)	0.33 (0.11-0.68)	0.37 (0.14-0.80)	0.45 (0.22-0.91)
	%Bedrock	47.6 (0-99)	6.6 (0-90)	0.0 (0-0)	38.3 (0-95)	4.3 (0-50)	28.4 (0-90)
	%Boulder	3.4 (0-35)	<0.1 (0-1)	<0.1 (0-1)	19.9 (0-95)	4.3 (0-35)	23.9 (0-75)
	%Silt-clay	0.9 (0-10)	1.0 (0-15)	0.9 (0-20)	<0.1 (0-1)	2.4 (0-40)	0.6 (0-10)
	%Vegetation	0.7 (0-30)	<0.1 (0-1)	1.2 (0-20)	0.1 (0-3)	243.4 (0-1982)	7.4 (0-70)
	Wood (no. / ha)	0.0 (0-0)	174.5 (0-4288)	125.3 (0-860)	5.4 (0-183)	243.4 (0-1382)	10.4 (0-374)
	Age-0 (no. / ha)	1.7 (0-134)	418.3 (0-11101)	37.5 (0-348)	0.0 (0-0)	0.86 (0-51)	21.8 (0-356)
	Age-1+ (no. / ha)	0.0 (0-0)	158.2 (0-3684)	162.5 (0-1938)	23.3 (0-1511)	0.0 (0-0)	0.0 (0-0)
	Mean size age-1+ (mm)		164.7 (128-226)	205.0 (138-302)	238.7 (206-280)		
Pool	Mean thalweg depth (m)	0.25 (0.09-0.59)	0.52 (0.02-1.35)	0.82 (0.17-1.63)	0.45 (0.05-1.31)	0.42 (0.04-0.89)	0.93 (0.11-1.39)
	%Bedrock	38.4 (0-95)	7.8 (0-92)	0.0 (0-0)	41.4 (0-100)	4.4 (0-40)	48.9 (0-90)
	%Boulder	2.8 (0-45)	0.5 (0-5)	0.1 (0-5)	18.2 (0-80)	4.5 (0-20)	17.9 (1-50)
	%Silt-clay	4.5 (0-40)	2.8 (0-27)	3.5 (0-30)	0.1 (0-5)	6.2 (0-90)	0.56 (0-5)
	%Vegetation	1.3 (0-30)	0.9 (0-50)	1.8 (0-10)	0.1 (0-3)	3.9 (0-35)	9.4 (0-40)
	Wood (no. / ha)	8.3 (0-259)	357.8 (0-14909)	205.8 (0-2555)	3.0 (0-85)	156.6 (0-1845)	0.4 (0-6)
	Age-0 (no. / ha)	7.3 (0-173)	504.9 (0-5833)	61.5 (0-636)	1.8 (0-54)	1.3 (0-78)	6.6 (0-43)
	Age-1+ (no. / ha)	5.5 (0-328)	190.9 (0-2149)	191.8 (0-2701)	14.8 (0-139)	0.1 (0-4)	3.7 (0-92)
	Mean size age-1+ (mm)	233.3 (212-272)	180.1 (114-252)	204.9 (136-258)	184.2 (142-278)	206.0 (164-248)	210.5 (130-306)
Backwater	Mean thalweg depth (m)	0.22 (0.15-0.30)	0.72 (0.12-1.49)	0.61 (0.31-1.31)	[a]	0.50 (0.22-0.80)	[a]
	%Bedrock	7.0 (0-23)	6.8 (0-90)	0.0 (0-0)		7.2 (0-60)	
	%Boulder	2.0 (0-7)	<1.0 (0-1)	0.0 (0-0)		6.0 (0-25)	
	%Silt-clay	1.3 (0-5)	31.5 (0-100)	26.6 (0-90)		11.8 (0-60)	
	%Vegetation	0.0 (0-0)	9.3 (0-50)	17.0 (0-90)		1.3 (0-10)	
	Wood (no. / ha)	0.0 (0-0)	487.3 (0-4823)	533.7 (0-2535)		75.6 (0-153)	
	Age-0 (no. / ha)	0.0 (0-0)	290.2 (0-5553)	89.4 (0-574)		0.0 (0-0)	
	Age-1+ (no. / ha)	0.0 (0-0)	114.3 (0-919)	30.9 (0-235)		0.0 (0-0)	
	Mean size age-1+ (mm)		203.2 (134-300)	295.0 (152-282)			

[a] No channel units sampled.

Figure 3.1. Conceptual model of fish life cycles emphasizing habitat use and movement (adapted from Schlosser 1991; 1995).

Figure 3.2. Study reaches on Baron Fork Creek and Glover River, eastern Oklahoma. Reaches on 3rd, 4th, and 5th order stream segments were selected on each stream, and sampled seasonally from July 2003 to August 2005.

Figure 3.3. Mean (± 1 SD) monthly water temperatures in 3rd (black), 4th (gray), and 5th (dashed) order reaches of Baron Fork Creek (A) and Glover River (B), eastern Oklahoma from July 2003 to July 2005.

Figure 3.4. Mean daily streamflow at 3rd, 4th, and 5th order reaches of Baron Fork Creek (A) and Glover River (B), eastern Oklahoma from July 2003 to July 2004. Provisional data from USGS gauging stations after September 2004 were excluded.

Figure 3.5. Mean relative growth rate (± SE) in length of smallmouth bass by season in Baron Fork Creek and Glover River, eastern Oklahoma. Different letters indicate significant differences among seasons.

Figure 3.6. Mean relative weights (± SE) of smallmouth bass by stream and stream order (top), and by season (bottom) in Baron Fork Creek and Glover River, eastern Oklahoma. Asterisk indicates differences in relative weights between streams at a stream order. Linear contrasts suggested a linear decrease in relative weight with stream order in Baron

Fork Creek ($F_{1,\,1227} = 68.74$; $P < 0.001$); no quadratic trend was evident ($F_{1,\,1226} = 2.16$; $P = 0.142$). No trend was observed for the Glover River (linear: $F_{1,\,1226} = 1.21$; $P = 0.272$). Seasons where relative weights differed are indicated by different letters.

Figure 3.7. Densities of age-1+ smallmouth bass in Baron Fork Creek, eastern Oklahoma from July 2003 to July 2005. Non-contiguous channel units indicate dry stream segments during low flow periods.

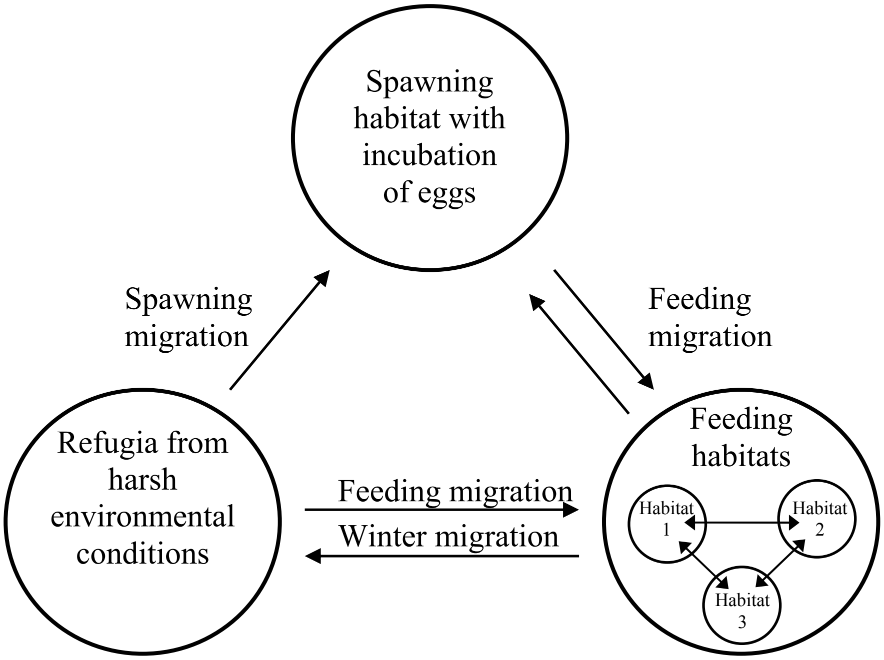
Figure 3.8. Location of temperature loggers upstream, downstream, at the outlet, and in a backwater in a 4th order reach of Baron Fork Creek, eastern Oklahoma.

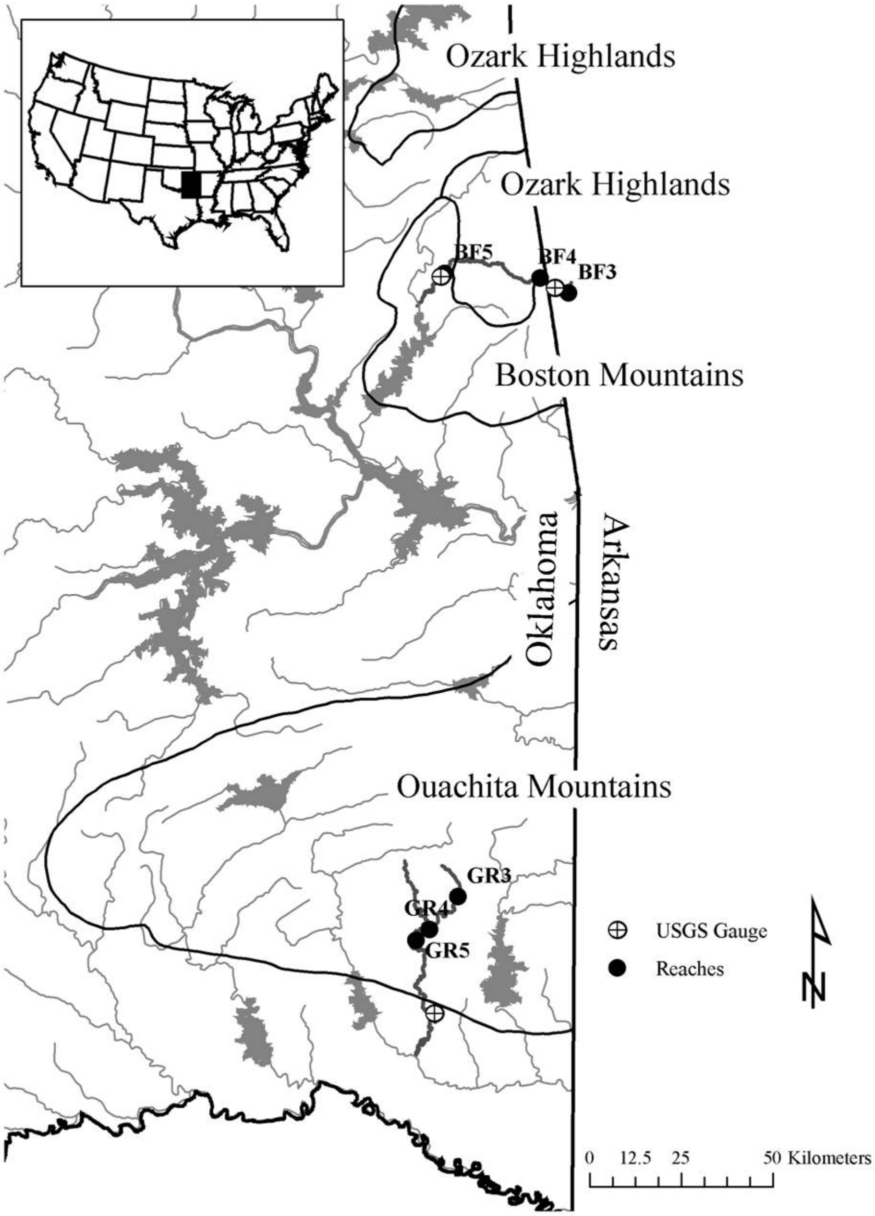
Figure 3.9. Winter and summer temperatures upstream, downstream, at the outlet, and at the back of a backwater habitat in the 4th order reach of Baron Fork Creek, eastern Oklahoma. Temperature loggers that malfunctioned or that were lost to floods resulted in non-continuous temperature records for some locations.

Figure 3.10. Regression tree analysis of effects stream, stream order, season, and channel unit habitat on age-0 smallmouth bass densities (no / ha) in 849 channel units from three reaches each in Baron Fork Creek and Glover River, eastern Oklahoma. Mean densities per node are given, with sample sizes in parentheses. Observations with variable values less than or equal to node value split to the left, and values greater than split right. Terminal nodes are oval. 10-fold cross-validated relative error was 0.797.

Figure 3.11. Regression tree analysis of effects stream, stream order, season, and channel unit habitat on age-1+ smallmouth bass densities (no / ha) in 849 channel units from three reaches each in Baron Fork Creek and Glover River, eastern Oklahoma. Mean densities per node are given, with sample sizes in parentheses. Observations with variable values less than or equal to node value split to the left, and values greater than split right. Terminal nodes are oval. 10-fold cross-validated relative error was 0.724.

Figure 3.12. Regression tree analysis of effects stream, stream order, season, and channel unit habitat on size of age-1+ smallmouth bass in 156 channel units from three reaches each in Baron Fork Creek and Glover River, eastern Oklahoma. Mean lengths (mm) per node are given, with sample sizes in parentheses. Observations with variable values less than or equal to node value split to the left, and values greater than split right. Terminal nodes are oval. 10-fold cross-validated relative error was 0.856.


Spawning habitat with incubation of eggs
Spawning migration
Feeding migration
Feeding habitats
Habitat 1
Habitat 2
Habitat 3
Refugia from harsh environmental conditions
Feeding migration
Winter migration


Ozark Highlands
Ozark Highlands
BF5
BF4
BF3
Boston Mountains
Oklahoma
Arkansas
Ouachita Mountains
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GR5
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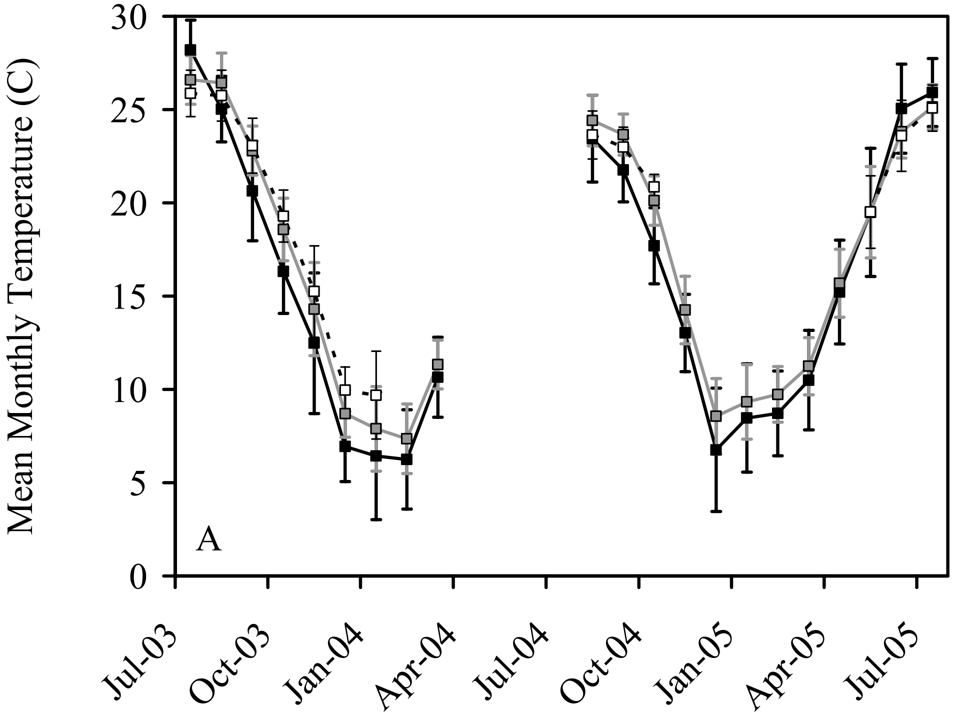
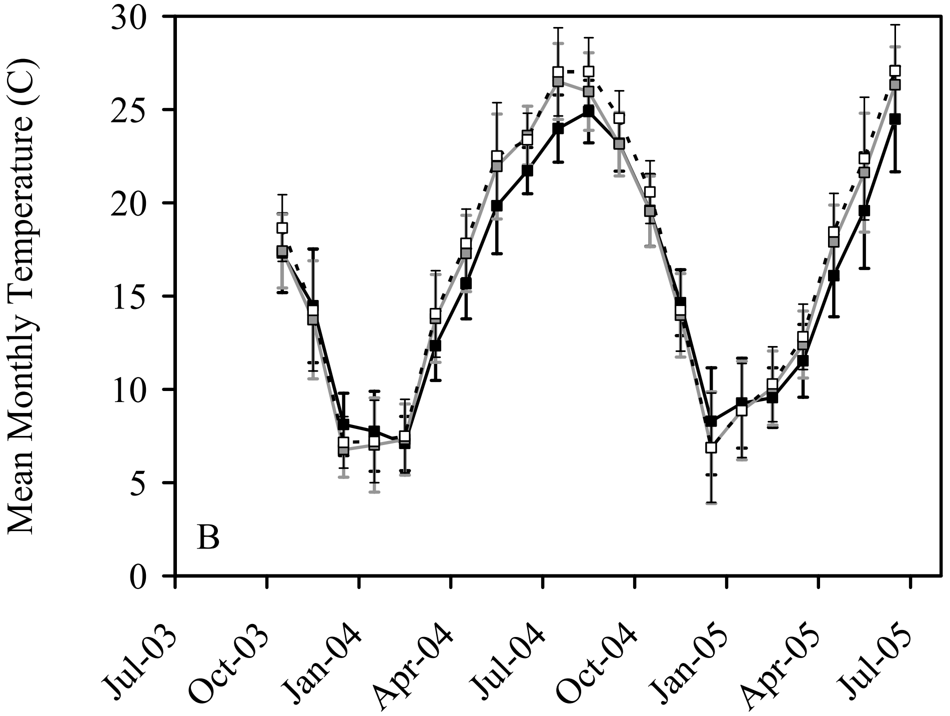
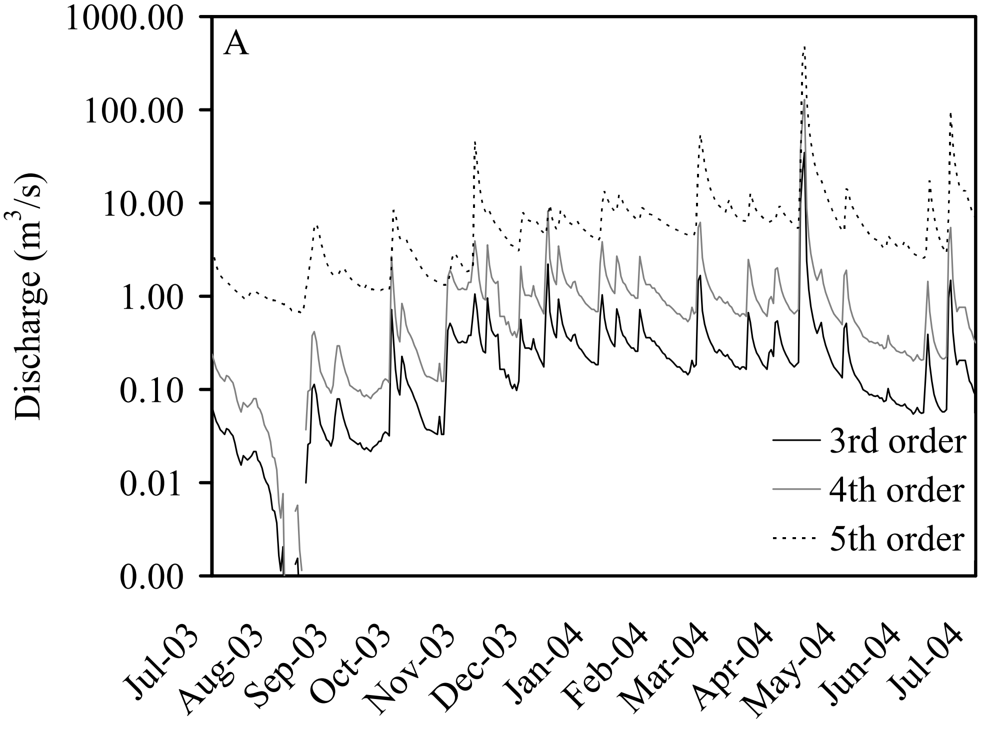
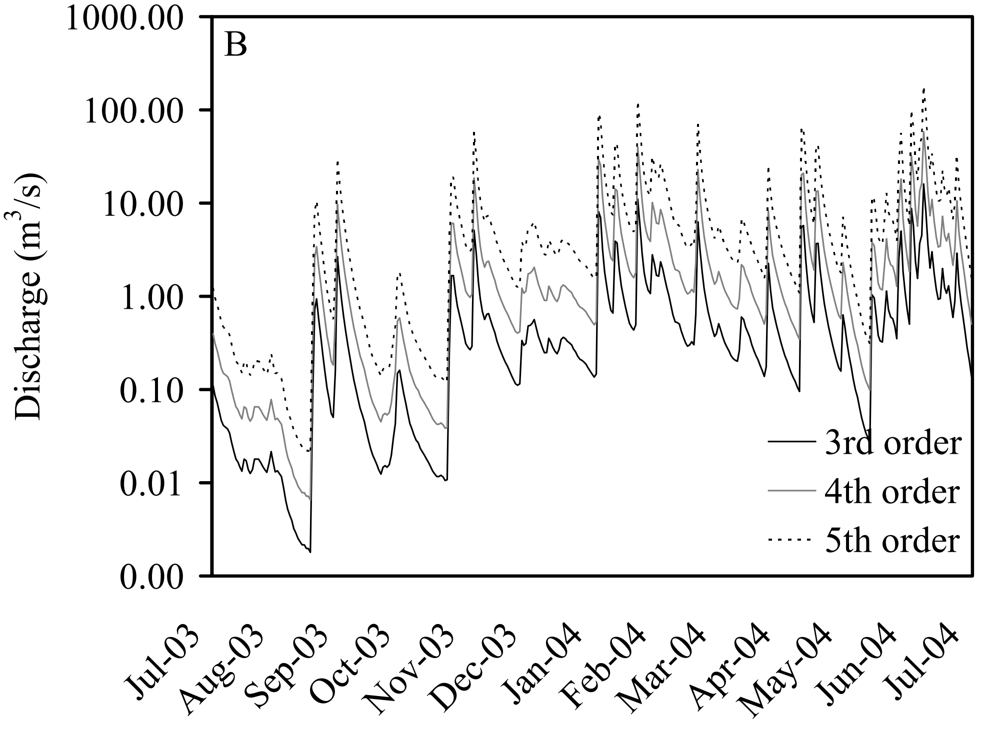


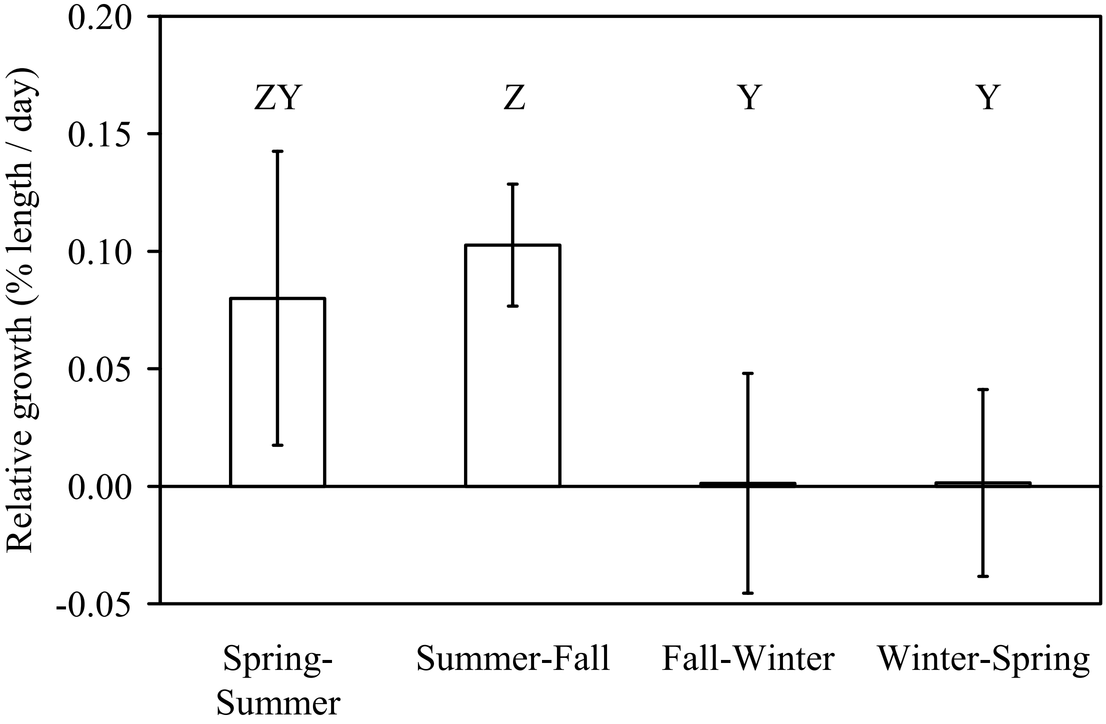
Mean Monthly Temperature (C)
30
25
20
15
10
5
0
A
Jul-03
Oct-03
Jan-04
Apr-04
Jul-04
Oct-04
Jan-05
Apr-05
Jul-05

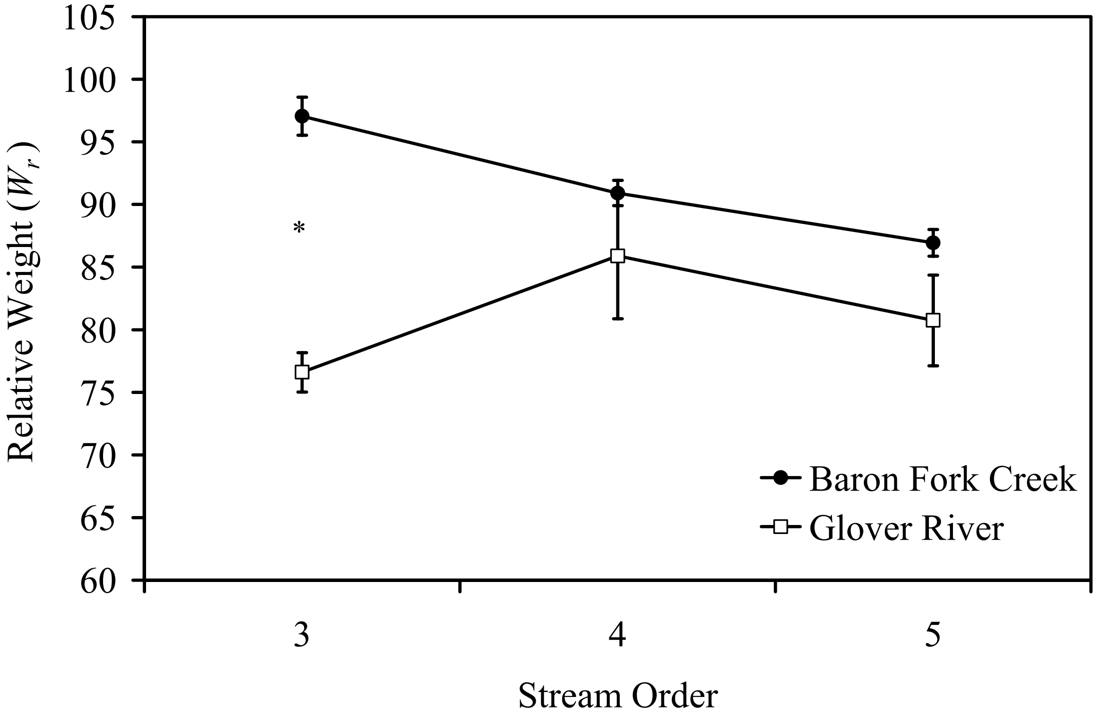


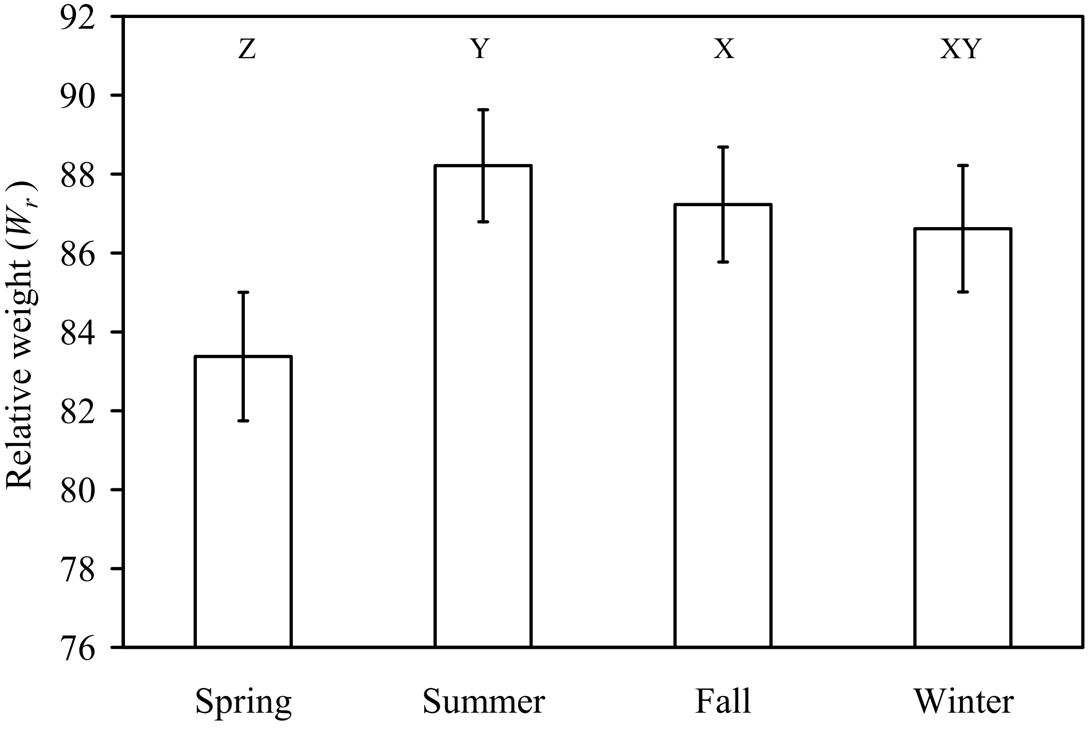
Mean Monthly Temperature (C)
30
25
20
15
10
5
0
B
Jul-03
Oct-03
Jan-04
Apr-04
Jul-04
Oct-04
Jan-05
Apr-05
Jul-05

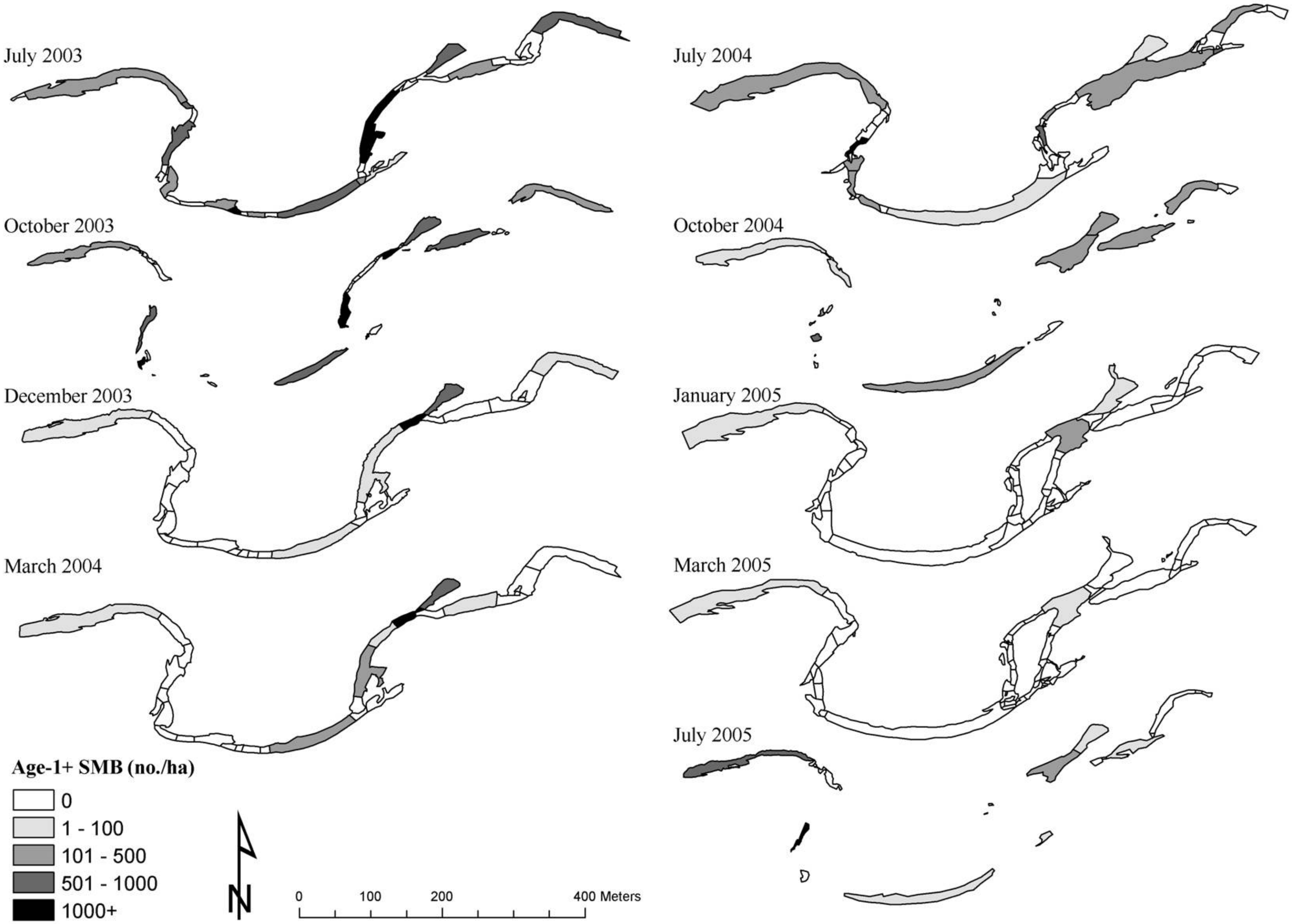

A
Discharge (m³/s)
1000.00
100.00
10.00
1.00
0.10
0.01
0.00
Jul-03
Aug-03
Sep-03
Oct-03
Nov-03
Dec-03
Jan-04
Feb-04
Mar-04
Apr-04
May-04
Jun-04
Jul-04
3rd order
4th order
5th order

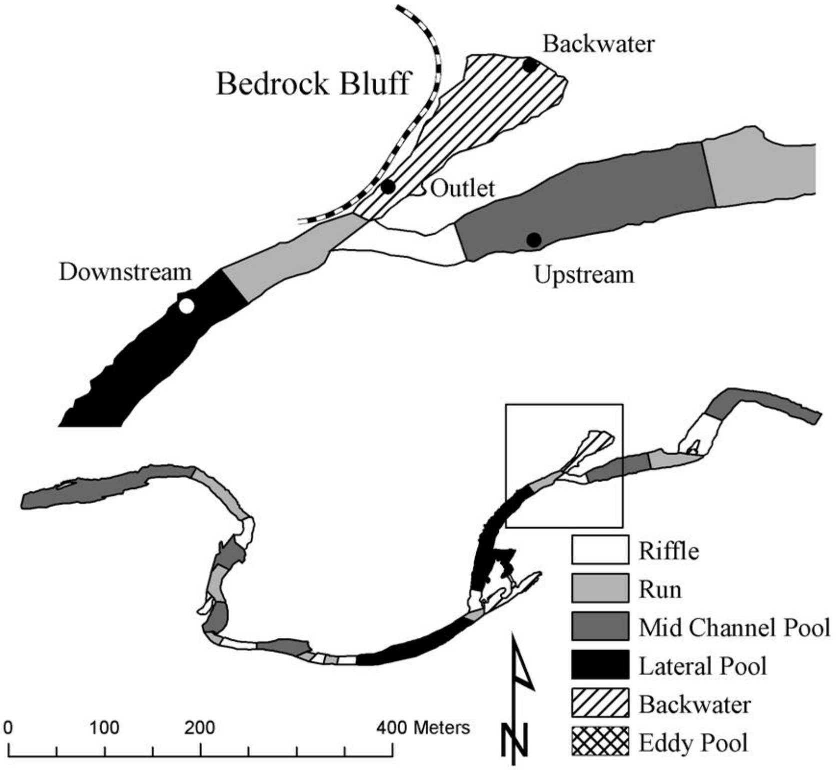

B
Discharge (m³/s)
1000.00
100.00
10.00
1.00
0.10
0.01
0.00
Jul-03
Aug-03
Sep-03
Oct-03
Nov-03
Dec-03
Jan-04
Feb-04
Mar-04
Apr-04
May-04
Jun-04
Jul-04
3rd order
4th order
5th order

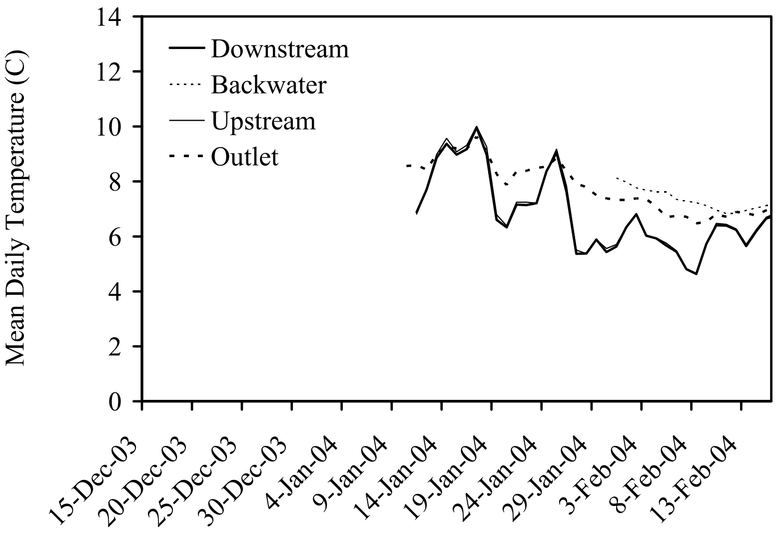

0.20
0.15
0.10
0.05
0.00
-0.05
Relative growth (% length / day)
ZY
Z
Y
Y
Spring-Summer
Summer-Fall
Fall-Winter
Winter-Spring


Relative Weight (W_r)
105
100
95
90
85
80
75
70
65
60
*
Baron Fork Creek
Glover River
3
4
5
Stream Order


Relative weight (W_r)
92
90
88
86
84
82
80
78
76
Z
Y
X
XY
Spring
Summer
Fall
Winter


July 2003
October 2003
December 2003
March 2004
July 2004
October 2004
January 2005
March 2005
July 2005
Age-1+ SMB (no./ha)
0
1 - 100
101 - 500
501 - 1000
1000+
N
0
100
200
400 Meters


Backwater
Bedrock Bluff
Outlet
Downstream
Upstream
Riffle
Run
Mid Channel Pool
Lateral Pool
Backwater
Eddy Pool
0
100
200
400 Meters
N


Mean Daily Temperature (C)
0
2
4
6
8
10
12
14
Downstream
Backwater
Upstream
Outlet
15-Dec-03
20-Dec-03
25-Dec-03
30-Dec-03
4-Jan-04
9-Jan-04
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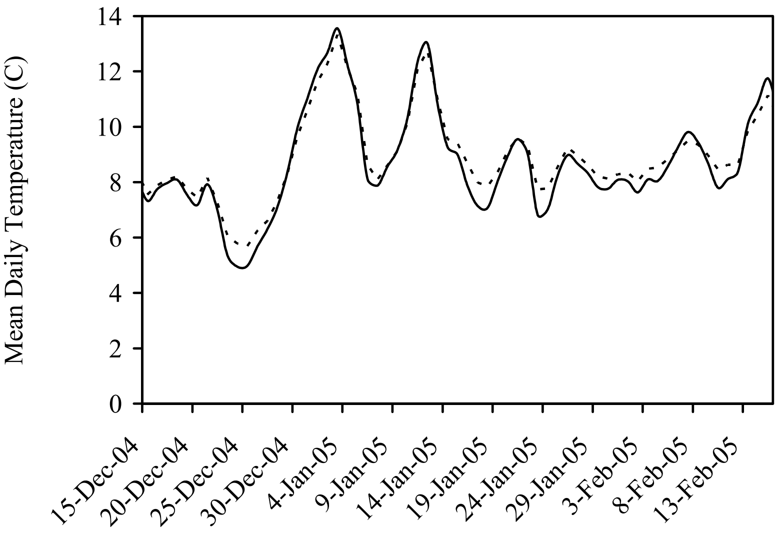
19-Jan-04
24-Jan-04
29-Jan-04
3-Feb-04
8-Feb-04
13-Feb-04


Mean Daily Temperature (C)
0
2
4
6
8
10
12
14
15-Dec-04
20-Dec-04
25-Dec-04
30-Dec-04
4-Jan-05
9-Jan-05
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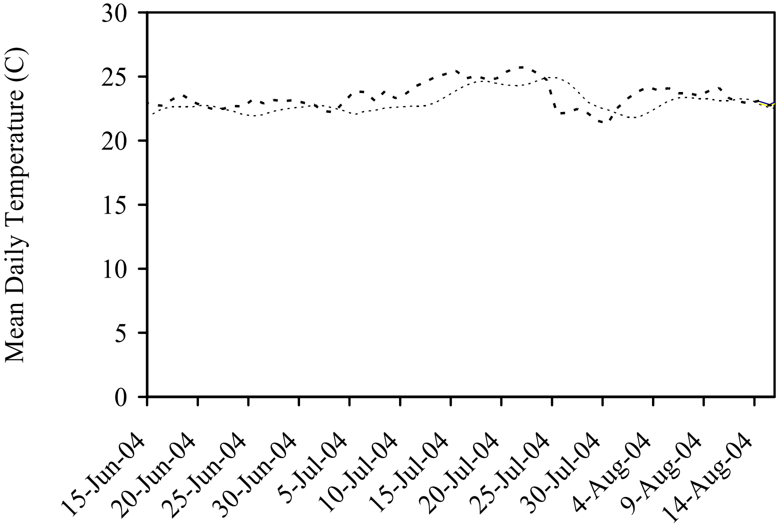
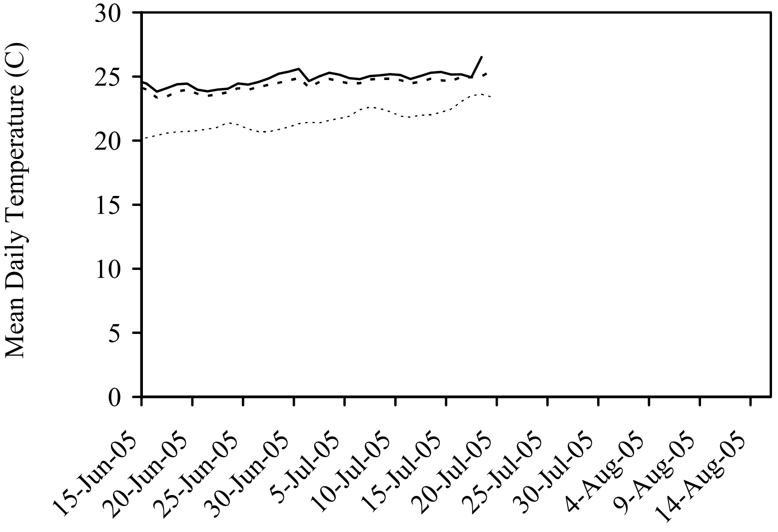
29-Jan-05
3-Feb-05
8-Feb-05
13-Feb-05


Mean Daily Temperature (C)
0
5
10
15
20
25
30
15-Jun-04
20-Jun-04
25-Jun-04
30-Jun-04
5-Jul-04
10-Jul-04
15-Jul-04
20-Jul-04
25-Jul-04
30-Jul-04
4-Aug-04
9-Aug-04
14-Aug-04


Mean Daily Temperature (C)
0
5
10
15
20
25
30
15-Jun-05
20-Jun-05
25-Jun-05
30-Jun-05
5-Jul-05
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15-Jul-05
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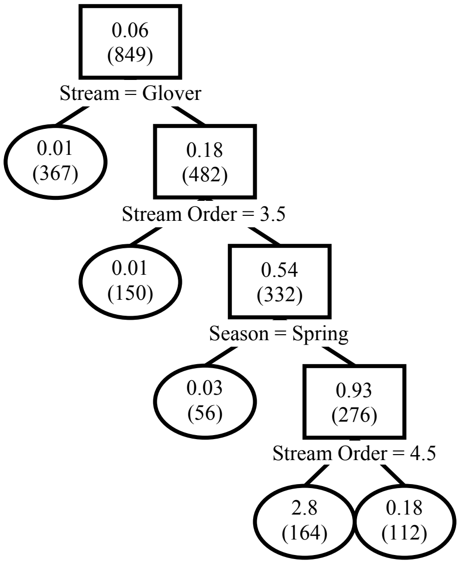
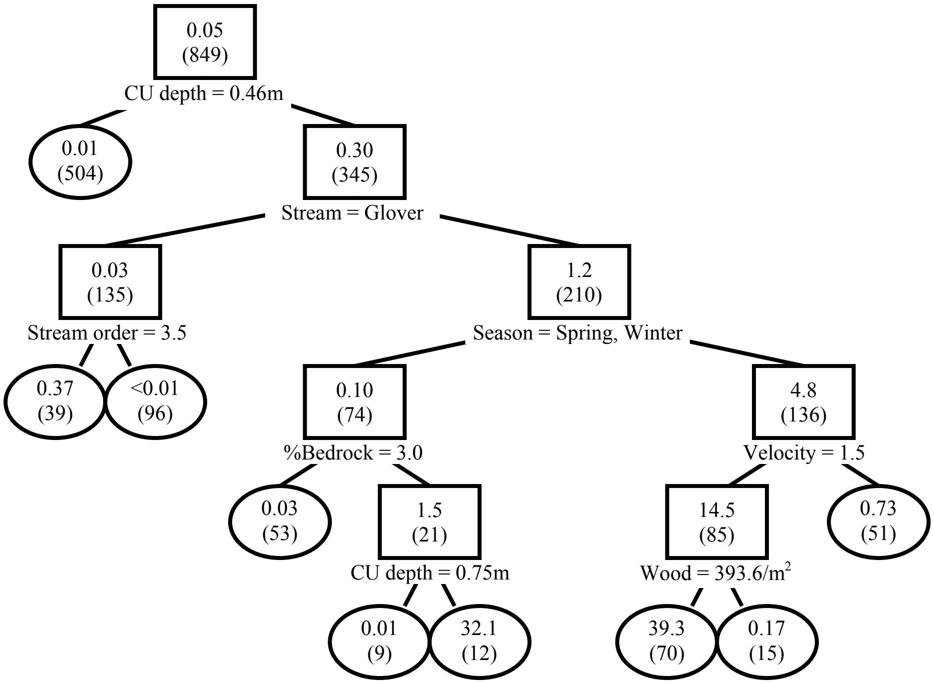
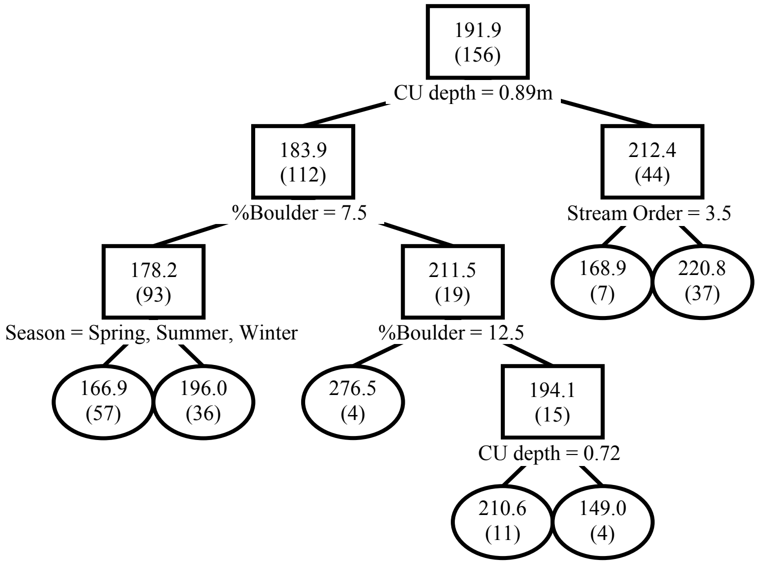
4-Aug-05
9-Aug-05
14-Aug-05


0.06
(849)
Stream = Glover
0.01
(367)
0.18
(482)
Stream Order = 3.5
0.01
(150)
0.54
(332)
Season = Spring
0.03
(56)
0.93
(276)
Stream Order = 4.5
2.8
(164)
0.18
(112)


0.05
(849)
CU depth = 0.46m
0.01
(504)
0.30
(345)
Stream = Glover
0.03
(135)
Stream order = 3.5
0.37
(39)
<0.01
(96)
1.2
(210)
Season = Spring, Winter
0.10
(74)
%Bedrock = 3.0
0.03
(53)
1.5
(21)
CU depth = 0.75m
0.01
(9)
32.1
(12)
4.8
(136)
Velocity = 1.5
14.5
(85)
Wood = 393.6/m2
39.3
(70)
0.17
(15)
0.73
(51)


191.9
(156)
CU depth = 0.89m
183.9
(112)
212.4
(44)
%Boulder = 7.5
Stream Order = 3.5
178.2
(93)
211.5
(19)
168.9
(7)
220.8
(37)
Season = Spring, Summer, Winter
%Boulder = 12.5
166.9
(57)
196.0
(36)
276.5
(4)
194.1
(15)
CU depth = 0.72
210.6
(11)
149.0
(4)

Appendix 3.A. Snorkeling and electrofishing methods for estimating smallmouth bass abundance.

Methods

Mark-recapture data were used to develop a 3-pass capture probability model to estimate smallmouth bass abundance in channel units. In 24 channel units in two eastern Oklahoma streams, smallmouth bass were collected, marked, and returned. Habitat variables measured were: mean thalweg depth (m), %bedrock, %silt-clay, wood density (no./m^2). After a recovery period, three electrofishing passes were made to recapture individuals. Capture probability was estimated using multiple logistic regression using SAS software, version 9.1 (SAS Institute Inc., Cary, North Carolina) with fish size (< and ≥100 mm), electrofishing power (μS/cm^3), and all habitat variables as potential explanatory variables: $\hat{p} = [1 + \exp(-\hat{\beta}_0 - \hat{\beta}_1 x_i ....)]^{-1}$

All combinations of explanatory variables, including fish size×depth, depth×%bedrock and depth×%silt-clay interactions, were evaluated using model selection and averaging methods. Abundance estimates were obtained by correcting number of individuals collected (*C*) by model averaged, predicted capture probability, $\hat{N} = C / \hat{p}$.

Results

All habitat variables, except mean thalweg depth×%silt-clay interaction, were included in at least one candidate model (Table 3.A.1). Fish size and mean thalweg depth, and their interaction, had the largest effect on capture probabilities (Table 3.A.2). Abundance estimates from the 3-pass model, when compared to known abundances using linear regression, were precise (r^2 = 0.881) and unbiased (b_i = 1, P = 0.462).

Table 3.A.1. QAIC$_c$ differences (Δ_i) and recalculated Akaike weights (w_i) for the best 3-pass smallmouth bass capture probability models. Best models were those with original w_i within 10% of the w_i for the best model. Names of variables are shortened.

Model	Δ_i	w_i
Size+Depth+Size×Depth	0.000	0.227
Size+Depth+Size×Depth+%Bedrock	1.997	0.084
Size+Depth	2.133	0.078
Size	2.160	0.077
Size+Depth+Size×Depth+Power	2.399	0.068
Size+Depth+Size×Depth+%SiltClay	2.411	0.068
Size+Depth+Size×Depth+Wood	2.415	0.068
Size+Depth+%Bedrock	3.546	0.039
Size+Depth+Size×Depth+%SiltClay+%Bedrock	3.977	0.031
Size+Depth+Size×Depth+%Bedrock+Depth×%Bedrock	4.058	0.030
Size+%Bedrock	4.204	0.028
Size+Wood	4.300	0.026
Size+Power	4.309	0.026
Size+%SiltClay	4.326	0.026
Size+Power+Depth	4.345	0.026
Size+Depth+%SiltClay	4.412	0.025
Size+Depth+Wood	4.432	0.025
Size+Depth+Size×Depth+%Bedrock+Wood	4.531	0.024
Size+Depth+Size×Depth+Power+%Bedrock	4.534	0.024

Table 3.A.2. Model averaged parameter estimates (b_i ± 2 SE) estimates for parameters in a 3-pass capture probability model for smallmouth bass when electrofishing channel units in two eastern Oklahoma streams.

Parameter	b_i
Intercept	-0.488 (1.144)
Size	1.758 (2.130)
Electrofishing Power Density (µS/cm^3)	0.002 (0.045)
Mean Thalweg Depth (m)	0.166 (1.787)
%Bedrock	0.003 (0.013)
%Silt-Clay	-0.002 (0.019)
Rootwad-Large Woody Debris Density (no./m^2)	0.284 (12.643)
Size × Depth	-1.610 (3.199)
Depth × %Bedrock	-0.001 (0.006)
Models averaged	19

CHAPTER 4

NESTING CHRONOLOGY, NEST SITE SELECTION, AND NEST SUCCESS OF SMALLMOUTH BASS DURING BENIGN STREAMFLOW CONDITIONS

Abstract

We documented the nesting chronology, nest site selection, and nest success of smallmouth bass *Micropterus dolomieu* in an upstream (4th order) and downstream (5th order) reach of Baron Fork Creek, Oklahoma. Males started nesting in mid-April when water temperatures increased to 16.9°C upstream, and in late-April when temperatures increased to 16.2°C downstream. Streamflows were low (77% upstream to 82% downstream of mean April streamflow, and 12 and 18% of mean June streamflow; 47 and 55 years of record), and decreased throughout the spawning period. Larger males nested first upstream, as has been observed in other populations, but not downstream. Upstream, 62 of 153 nests developed to swim-up stage. Downstream, 31 of 73 nests developed to swim-up. Nesting densities upstream (147 / km) and downstream (100 / km) were both higher than any densities previously reported. Males selected nest sites with intermediate water depths, low water velocity, and near cover, behavior that is typical of smallmouth bass. Documented nest failures resulted from human disturbance, angling, and longear sunfish predation. Logistic exposure models showed that water velocity at the nest was negatively related and length of the guarding male was positively related to nest success upstream. Male length and number of degree days were both positively related to nest success downstream. Our results, and those of other studies, suggest that biological factors account for most nest failures during benign (stable, low flow) streamflow conditions, whereas nest failures attributed to substrate mobility or nest abandonment dominate when harsh streamflow conditions (spring floods) coincide with the spawning season.

Introduction

The spawning behaviors of smallmouth bass *Micropterus dolomieu* in streams are well documented. Spawning begins in April or May when water temperature rise to ~15°C (Wrenn 1984; Graham and Orth 1986). Male smallmouth bass build circular depressions for nests in areas with gravel or larger substrates and adjacent to cover, with the extent of cover use changing among years (Pflieger 1966; Reynolds and O'Bara 1991). After nest construction, hours to weeks may pass before a male coaxes a female to deposit eggs in the nest (Pflieger 1966). Males will guard the nest until nest failure or fry swim up off the nest and disperse about two weeks after egg deposition.

The ability of a male smallmouth bass to raise a successful brood in streams is dependent on both physical and biological factors. Proximity of the nest to cover, streamflow, water temperature, and male size determine nest success, with larger males being more successful (Reynolds and O'Bara 1991; Lukas and Orth 1995). Larger males typically spawn earlier than smaller males (Ridgway et al. 1991; Lukas and Orth 1995), but they may lose broods during flood events early in the spawning period (Lukas and Orth 1995). Other biological factors such as nest predation or fungus development also affect nest success (Reynolds and O'Bara 1991; Lukas and Orth 1995).

Oklahoma has two genetically divergent, peripheral populations of native smallmouth bass, the Neosho smallmouth bass in the Ozark Highlands and Boston Mountains ecoregions (Omernik 1987) in the northeast and the Ouachita smallmouth bass in the Ouachita Mountains of the southeast (MacCrimmon and Robbins 1975; Stark and Echelle 1998). Coincidentally, smallmouth bass in eastern Oklahoma show demographic differences from other populations in the native range of the species; they have higher mortality rates and are generally shorter lived (Balkenbush and Fisher 2001). Whether these demographic differences are genetically or habitat related is unknown. Regardless, studies on nesting habits of smallmouth bass in eastern Oklahoma are lacking, and it is unknown whether the nesting habits typically observed in smallmouth bass transfer to these peripheral and divergent populations.

Our goal was to document the spawning of smallmouth bass in Baron Fork Creek, Oklahoma. Specifically, we documented the chronology of Neosho smallmouth bass spawning, evaluated microhabitats selected by nesting males, and assessed physical and biological factors influencing nest success.

Study sites

Our study occurred in two reaches of Baron Fork Creek, Oklahoma (Figure 4.1). Baron Fork Creek originates in northwest Arkansas and flows west-southwest through the Ozark Highlands and Boston Mountains ecoregions (Omernik 1987; Woods et al. 2005) and into the Illinois River system at Lake Tenkiller in northeast Oklahoma. The drainage area of Baron Fork Creek is 936 km^2 and consists mostly of forest and pastureland (Balkenbush and Fisher 2001). The upstream reach, hereafter referred to as Baron, is located in Adair County near the Arkansas state line, 35°54’53.64”N, 94°32’23.76”W. The reach was 1038.8 m in length, with a slope of 0.22%. Substrates consisted mostly of pebbles (D_{50} = 28.2 mm). The downstream reach, Eldon, is in Cherokee County, 35°56’5.10”N, 94°49’46.17”W. The reach length was 728.2 m, and had a slope of 0.20%. Substrates were dominated by pebbles (D_{50} = 20.0 mm). Both reaches were characterized as low gradient, meandering with point bars, riffle-pool morphology, and alluvial with wide floodplains (Rosgen 1994).

Methods

Nesting chronology

We started monitoring each reach for spawning activity in April 2005. Sites were visited weekly until spawning activity was observed from the streambank. Each reach was surveyed completely after spawning activity was detected, usually every 2-5 days by one or two snorkelers. New nests were marked on their downstream side with a rock containing a unique number, and an identically numbered flag was placed on the streambank perpendicular to each nest to facilitate relocation. The total length of the guarding male was estimated by underwater observation; snorkelers were trained on 100 and 300 mm models of bass. A subset of males was angled from the nest and measured for total length. A relation between estimated and actual lengths (Actual Length = 43.18+Estimated Length×0.896; $r^2 = 0.803$) was used to correct for estimated length bias when an actual length was not available.

To document size trends in spawning chronology we evaluated the relation between the $\log_{10}$ number of degree days (sum of mean daily temperature >10°C) and $\log_{10}$ male total length using linear regression (Lukas and Orth 1995). Only the first nesting attempts of males that knowingly renested were analyzed. Age frequencies of spawning males were estimated using an age-length key (DeVries and Frie 1996) with 2.5 cm length groups developed using aged individuals sampled in spring and summer 2003 to 2005 from both study reaches.

Nest site selection

Microhabitat characteristics associated with each nest were measured to estimate habitat selection by nesting males. Characteristics measured were: mean velocity (m/s; 0.6 of water depth); velocity at the nest (0.04 m above substrate); water depth (m); nest and surrounding dominant substrate, classified visually using the modified Wentworth scale (Bain 1999) and coded using rank of size (bedrock = 0, silt/clay = 1, sand = 2, gravel = 3, pebble = 4, cobble = 5, boulder = 6); and number of submerged cover structures within 1 and 2 m of the nest. Large woody debris (≥ 4 m in length and 10 cm in diameter), rootwads, boulders, aquatic vegetation, and undercut banks were considered cover.

We compared habitat use by nesting smallmouth bass males versus available habitat to determine selected microhabitat characteristics. Habitat availability was measured (same variables as above) at randomly selected points within the reach. Approximately midway through the spawning period, each reach was mapped at the channel unit spatial scale (Hawkins et al. 1993) using a Trimble GeoXT global positioning system (GPS) receiver (Dauwalter et al. 2006). Reach maps were downloaded into a geographic information system and 300 random points were selected within reach boundaries. Existing microhabitat data from the Baron reach suggested that a sample size of 300 was needed to estimate water depth and velocity means with ≤20% precision (D. C. Dauwalter, unpublished data). Each data layer of random points was uploaded into a GPS receiver that was used to navigate to within 0.5 m of each random point.

We assessed microhabitat selection by nesting smallmouth bass by using a resource selection function (Manly et al. 1993). The resource selection function equated to a multiple logistic regression (Hosmer and Lemeshow 2000) because our data were spatially continuous. Multiple logistic regression (PROC GENMOD; SAS Institute, Inc., Version 9, Cary, NC) was used to predict whether a sample was from a nest location or random point by using microhabitat variables. The model used microhabitat variables to predict relative probabilities of use by nesting smallmouth bass; only relative probabilities could be determined because both use and availability data were point samples, and we could not determine the exact proportion of available habitat that was used (Manly et al. 1993).

All microhabitat variables were evaluated for use in the resource selection functions for each reach. Pearson correlations were used to identify correlations ($r > 0.50$) among variables. If needed, one variable from a correlated set was retained in the global models. Retained microhabitat variables were used to model resource selection using an information-theoretic framework (Burnham and Anderson 2002). Quadratic terms for water depth and substrate, and a depth × velocity interaction were also included in the global models. Lack-of-fit of the global models was assessed using a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000). All combinations of variables included in the global models, including an intercept only model, were evaluated, with the condition that quadratic and interaction terms were only considered in combination with their constituent variables. Akaike's Information Criterion corrected for small sample bias (AIC_c) was used to quantify parsimony in each model, and Akaike weights (w_i) were computed. Model averaging was conducted only with models having an original w_i

within 10% of the best model. The recalculated w_i for the best subset of models was used to average parameter estimates from each model; parameters not included in a specific model were given a value of zero for that model during averaging (Burnham and Anderson 2002).

Nest success

Each nest was revisited 1 to 7 times to document nest development, success, or failure. Stage of nest development was recorded during each revisit as: eggs, yolk sac, black fry, or swim up. Nests were considered successful when 100% of fry had swum up from the nest. Nests containing zero eggs or fry were considered failures.

We evaluated effects of physical and biological variables on nest success. Variables evaluated included water depth (m), mean water velocity (m/s), water velocity at the nest (m/s), abundance of submerged cover within 1 and 2 m (defined as above), distance to shore (m), degree days (defined as above), mean daily temperature during incubation (°C), mean discharge during incubation (m^3/s), and length of guarding male (mm). Water temperature was recorded at one location in the middle-third of each reach with StowAway® Tidbit® temperature loggers (Onset Computer Corporation, Bourne, Massachusetts). Streamflow data were obtained from United States Geological Survey (USGS) stream gauges. Data from gauge 07196900 at Dutch Mills, Arkansas were used for the Baron reach (~7.5 km upstream of reach), and gauge 07197000 at Eldon, Oklahoma was used for the Eldon reach (~1.5 km downstream from reach). Streamflow data used were classified as provisional by the USGS.

A logistic exposure model was used to evaluate effects of physical and biological characteristics on nest success. The logistic exposure model extends the typical multiple logistic regression model to allow for variable exposure periods (time between nest revisits) in the link function,

$$\log_e\left(\frac{\theta^{\frac{1}{t}}}{1-\theta^{\frac{1}{t}}}\right)=\beta_0+\beta_1 x_1+\ldots+\beta_i x_i$$

where θ is probability of a nest surviving an exposure period, t = the length of the exposure period, and β = slope coefficients for predictor variables, x (Shaffer 2004). Variable exposure periods that are not accounted for can bias survival estimates. Assumptions of the model are that nest success is independent of other nests, and that daily survival probabilities are homogenous within and among nests. As in multiple logistic regression, multiple independent variables (physical and biological variables in this case) can be included in the predictor function.

Information-theory methods again were used to model nest success. One predictor variable out of a correlated set ($r > 0.50$) was retained in the global models. Global models were assessed using a Hosmer-Lemshow test (Hosmer and Lemeshow 2000). All combinations of variables in the global model were evaluated using $\mathrm{AIC_c}$, including an intercept-only model, and model selection and averaging proceeded as described in the previous section (Burnham and Anderson 2002).

Results

Nesting chronology

The 2005 nesting period of smallmouth bass in Baron Fork Creek began in mid-April and lasted through most of June (Figure 4.2). Streamflows were low, and decreased throughout the spawning period. In April, streamflows were 77 and 82% of mean monthly streamflows upstream (47 years of record) and downstream (55 years), respectively. In June, they were 12% upstream and 18% downstream of mean monthly streamflows. Spawning started earlier and lasted just as long in the Baron reach when compared to the downstream reach at Eldon. Smallmouth bass nests were first observed on 17 April at Baron when water temperatures reached 16.9°C. We found four recently dispersed schools of fry at Eldon during our first extensive snorkeling survey after noting nest activity on 10 May, and back-calculated dates of egg deposition to 27 April when water temperatures were 16.2°C. Spawning ceased prior to 18 June at Baron, but we observed one new nest at Eldon on 18 June during our last survey but did not document its development. In all, 153 (147 / km) nests attempts were observed at Baron, 3 were second attempts in the same nest. Seventy-three (100 / km) nest attempts were observed at Eldon, and 5 were second attempts. We were unable to uniquely identify all individuals to document all renesting attempts, especially those in different nests.

A size trend in spawning chronology of males was detected for only one of the two Baron Fork Creek reaches. In the Baron reach, there was a negative but weak relation; $\log_{10}$ male total length = $2.925 - 0.174 \cdot \log_{10}$ degree days ($n = 127$, $r^2 = 0.211$, $P < 0.001$). The null hypothesis of no relation between degree days and male length in the Eldon reach was not rejected ($n = 65$, $r^2 = 0.027$, $P = 0.191$). Spawning males were mostly represented by age 2, 3, and 4 individuals in the Baron reach, and age 3 and 4 individuals in the Eldon reach (Table 4.1).

Nest site selection

Nests were typically constructed in pool and backwater habitats (Figures 4.3, 4.4) of low velocity in areas at least 0.24 m in depth (maximum = 1.8 m). Nests located adjacent to cover typically were associated with woody structure and boulders (Figure 4.5). They were built in areas surrounded by most substrate size classes (Table 4.2), but 97.3% of all nests had pebble substrates, which was the predominant substrate type in both reaches.

Resource selection functions suggested that smallmouth bass selected nesting sites in specific microhabitats. In the Baron reach, habitat at 153 nests was compared to habitat at 294 random points. Six of the 300 random points fell outside of stream margins during GPS navigation and were omitted. Habitat at 73 nests was compared to habitat at 297 random points in the Eldon reach. Each nesting attempt was treated as an observation because we were unable to uniquely identify each individual to document renesting in new nests. Mean velocity was correlated with nest/bottom velocity (Baron, $r = 0.897$; Eldon, $r = 0.885$), and was excluded from the global model. Amount of cover within 2 m was correlated with the amount in 1 m (Baron, $r = 0.877$; Eldon, $r = 0.862$) and also was excluded. The global models for the Baron ($\chi^2 = 12.38$, df = 8, $P = 0.135$) and Eldon ($\chi^2 = 2.49$, df = 0.962, $P > 0.999$) reaches did not show lack of fit. Thirty-one candidate models were considered for each reach. The global model had the highest Akaike weight in both reaches, and three other models had weights within 10% of the best (Appendix 4.1). Model averaging of parameters was completed using only the four best models. Model-averaged parameter estimates for both reaches showed that only depth, depth quadratic term, and amount of cover within 1 m had parameter estimates with unconditional (on a specific model) 95% confidence intervals (b_i ± 2 SE) that excluded zero (Table 4.3). Model-averaged relative probabilities of use showed that smallmouth bass selected nest areas with intermediate water depths and near areas with cover in both reaches (Figure 4.6). They were not selective for substrate sizes.

Nest success

Of the nesting attempts observed, 62 of 153 developed to swim up in the Baron reach, and 31 of 73 did so in the Eldon reach. We observed fungus development on most nests, presumably water mold *Saprolegnia parasitica* or related species (Knotek and Orth 1998), and nests located in shallow water and reaching an advanced stage typically had high algal growth as well. The range of fungus coverage on eggs prior to egg hatch was 0 to 100% for each site, and averaged 54.3% at Baron and 26.7% at Eldon. Estimated time to swim-up was 8 to 19 days, and was less later in the spawning period. No floods occurred during the spawning period, and most documented nest failures resulted from longear sunfish *Lepomis megalotis* predation. On several occasions we observed nest depredation by a school of longear sunfish. In these instances, the guarding male smallmouth bass could not defend the nest, and sometimes he did not attempt to do so. Depredated nests usually contained clean gravel, as all eggs, fungus, and algae (if present) were consumed, and were easily classified as failed. Three nests in the Baron reach were physically disturbed: human footprints were observed at two nest locations and motor vehicle tracks at another. Two nests in the Eldon reach were lost to human disturbance. An angler caught and harvested the male from one nest, and another was physically disturbed.

Logistic exposure models indicated that only a few of the studied variables affect nest success. Nesting attempts already at swim up stage (Eldon, $n = 6$) or disturbed by humans (see above) were excluded from logistic exposure models. In the Baron reach, 149 nests were analyzed and 62 were successful. In the Eldon reach, 65 nests were analyzed and 25 were successful (Table 4.4). The amount of cover within 2 m of a nest was correlated with the amount within 1 m (Baron, $r = 0.877$; Eldon, $r = 0.801$), and mean daily temperature was correlated with number of degree days (Baron, $r = 0.936$; Eldon, $r = 0.935$). We did not include nest substrate in the global models because almost all nest substrates were pebble. Variables included in the global model for each reach were water depth, water velocity at the nest, amount of submerged cover within 1 m, distance to shore, male length, and number of degree days. Male length was only estimated for 128 nests at Baron and 63 at Eldon because some males were spooked from the nest during snorkeling surveys or by observers on the streambank. Consequently, those males were never observed on the nest prior to failure. This reduced sample size for models containing male length as an independent variable. Global models for the Baron reach ($\chi^2 = 2.86$, df = 8, $P = 0.943$) and the Eldon reach ($\chi^2 = 0.008$, df = 8, $P > 0.999$) did not show lack of fit. Sixty-four candidate models were considered overall. Fourteen models had Akaike weights within 10% of the best model for Baron nests, and 16 models were within 10% in the Eldon reach (Appendix 4.2). Six variables plus the intercept were included in at least one of the best models for the Baron reach. However, only water velocity at the nest and male length had model-averaged parameter estimates with unconditional 95% confidence intervals that excluded zero. All six variables were included in at least one of the best models for the Eldon reach also, but only the intercept, degree days, and male length had approximate 95% confidence intervals that excluded zero (Table 4.5).

Discussion

Although nesting densities during the 2005 smallmouth-bass spawning season in Baron Fork Creek were higher than those previously reported, nesting chronology and microhabitat selection of nest sites in Baron Fork Creek was typical for smallmouth bass, with slight differences between upstream and downstream reaches. Streamflow conditions were benign throughout the spawning period, and no nests were lost to streamflow disturbances as is often found when spring floods coincide with the spawning season. Most nest failures apparently resulted from nest depredation.

In Baron Fork Creek, spawning was initiated in mid- to late-April when water temperatures reached 16.2-16.9°C. In Little Saline Creek, Missouri smallmouth bass spawned from 26 April to 31 May when water temperatures were greater than 15.5°C (Pflieger 1966). Over a 10-year period in Courtois Creek, Missouri they began spawning with an abrupt rise in water temperature when daily minimum and maximum were 12.8 and 18.3°C (Pflieger 1975). Studies in Tennessee and Virginia streams reported similar findings (Reynolds and O'Bara 1991; Lukas and Orth 1995). Graham and Orth (1986) built a discriminate function model for five stream sites in the New River drainage, Virginia and West Virginia that suggested mean and maximum daily water temperature, streamflow, and daily accumulation of degree days >15°C were most important in identifying days when smallmouth bass had spawned. Spawning activity had mostly ended when we stopped surveying at the end of June. However, on 13 July 2004 we observed a school of fry in the Baron reach, suggesting sporadic summertime spawning.

We found 100 to 147 nests per stream kilometer in Baron Fork Creek. To our knowledge, the highest density reported in the literature was 75.3 / km in the Green River, Tennessee (Table 4.6). It has been suggested that high nesting densities reflect concentrations of individuals in limited areas of suitable spawning habitat, such as in Iowa streams where many stream kilometers had been channelized and affected by sedimentation (Cleary 1956; Pflieger 1975). Although we did not model habitat suitability in each reach, spawning habitat did not appear limited. Baron Fork Creek is a gravel-dominated stream, and most areas with low water velocities would be suitable nest sites. Even when fine substrates existed, they were often only shallow deposits. An exception was in some large backwaters. Many nests in the Baron reach were constructed in a sandy area underlain by gravel and pebble substrates, and males were able to fan out the finer sediments to expose larger buried substrates. High nesting densities likely reflected high densities of smallmouth bass, as 100 / ha have been reported in Baron Fork Creek (Balkenbush and Fisher 2001).

Despite high spawning densities, only one of the two reaches showed evidence, albeit weak, of larger males spawning earlier in the season. High mortality and a subsequent lack of age 5+ individuals may have weakened or masked potential trends. Or, populations in Baron Fork Creek just do not strongly exhibit this tendency. Regardless, this is contrary to observations for both stream and lake populations

(Ridgway et al. 1991; Lukas and Orth 1995) that has lead earlier investigators to infer earlier spawning in larger males is advantageous because it allows them to renest after nest failures.

Nesting microhabitats of smallmouth bass differed between the upstream and downstream reach of Baron Fork Creek. Males selected areas intermediate in depth in both reaches, but selected shallower depths in Baron than in Eldon. However, nests were constructed and successfully defended in some of the deepest parts of the deeper Eldon reach when there was nearby cover and negligible water velocities. In both reaches, probabilities of use decreased with increased water velocity. Males selected areas with more cover, but relative use differed between reaches with intermediate amounts of cover. Substrate generally was not important in nest-site selection because, as noted above, fine sediments were shallow enough to be fanned out during nest construction. However, in one backwater in the Baron reach nesting was confined to margins because deeper areas had thick layers of silts and clays.

Male smallmouth bass in Baron Fork Creek chose nesting sites with characteristics similar to those found in other studies. Smallmouth bass nested mainly in pools, near shore and cover, and on gravel substrates in Missouri streams (Pflieger 1966; Pflieger 1975). Similar nest locations were reported in Tennessee streams, although complex cover was used more in a year with high streamflow (Reynolds and O'Bara 1991). In addition to using low water velocity areas near shore and cover with gravel substrates, males building nests in the North Anna River, Virginia built nests in areas sheltered from streamflow during elevated flow levels (Lukas and Orth 1995). Nests built in shelters from high water velocity are less likely to be affected by future flood events. Upstream cover can provide velocity shelters, but velocity shelters would also occur on inner bank regions of lateral scour pools because of higher velocities on outer banks (Knighton 1998). In an Ohio stream, most smallmouth bass nests occurred along the outer bank of a scour pool (Winemiller and Taylor 1982). We observed that many males constructed nests on inner bank regions of point bars devoid of cover in the Baron reach, but not in the Eldon reach. A better understanding regarding use of inner bank areas devoid of cover is needed, especially regarding how the selection of those areas translates into nest success.

Nest success in Baron Fork Creek was within the range reported from other studies, but we did not observe nest failure due to flood events because there were no such events and streamflow was lower than average and decreased steadily in Baron Fork Creek during the spawning season. Thirty-three of 40 nests were successful in Little Saline Creek, Missouri (Pflieger 1966). In Tennessee streams, 35 to 73% of nests developed to fry dispersal. Nest success was dependent on male size, distance to upstream cover, day of spawning, and nest velocity, but differed between years. Nests were less successful during years with elevated streamflows during spawning (Reynolds and O'Bara 1991). Successful smallmouth bass nests were found within 1 to 2 m of nearshore cover in the Huron River, Michigan (Bovee et al. 1994). In the North Anna River, Virginia 45 of 105 nests were successful, and 42 of 81 males raised successful broods. Nests success was influenced by streamflow, temperature, and distance to shore. Male size was not important, probably because of elevated discharge events early in the spawning period and resultant nest failures for early-spawning, larger males (Lukas and Orth 1995).

We found that male size, water velocity at the nest, and time during the spawning period were important determinants of nest success during a year with low streamflows. The importance of male size reflected the ability of larger males to defend the nest because we found little evidence of earlier spawning by larger males. We also observed negative effects of water velocity at the nest on nest success, even though velocity was only slightly different between successful and unsuccessful nests. The impact of degree days on nest success in the downstream reach may include the effects of renesting fish that failed in earlier nest attempts.

Nest failures resulted from human disturbance (angling, vehicular traffic, etc.) or predation by longear sunfish. One other failure may have resulted from localized bank collapse, but the collapse might have occurred after nest abandonment. Depredated nests typically contained clean, disturbed substrates. Abandoned but undepredated nests would still contain egg or fry remnants, which were never observed. Longear sunfish and bluegill *L. macrochirus* were reported predators of smallmouth bass fry in Little Saline Creek, Missouri (Pflieger 1966), and longear sunfish were suggested to be the dominant predator of eggs and fry in Courtois Creek (Pflieger 1975). Sunfish and shiners *Notropis spp.* were suggested predators of smallmouth bass nests in Tennessee streams (Reynolds and O'Bara 1991). Lukas and Orth (1995) suggested that only 3% of nests were lost to fish predators in North Anna River, Virginia where most nest failures were attributed to high streamflows. Knotek and Orth (1998) reported that 14 of 20 nest failures were attributed to predation, most likely by American eels *Anguilla anguilla*.

Nest predation has not been well-studied in streams. In lakes, male smallmouth bass increase nest guarding activity in the presence of abundant nest predators, resulting in declines in weight and energy reserves (Steinhart et al. 2005). In streams, Pflieger (1975) suggested that contrasting reports on the intensity of nest guarding by male smallmouth bass might be related to nest predator abundance, in particular the presence of longear sunfish. Consequently, nest success during low or intermediate streamflows may be related to predator abundance or proximity to quality predator habitat. Longear sunfish in Ozark streams are more abundant in deeper pools (Walsh and Winkelman 2004), particularly those with higher densities of woody cover (Peterson and Rabeni 2001). Although smallmouth bass nest mostly in pools, often in close proximity to woody cover, we found no effect of proximity to cover during benign streamflow conditions that prevailed during our study.

Avoidance of predators might explain why smallmouth bass tend use cover less during low streamflows. The positive effects of cover exist primarily during high streamsflows (Reynolds and O'Bara 1991), otherwise cover is just an attractor for nest predators. Understanding how smallmouth bass nests and predator abundance and habitat are positioned in the stream landscape, both within and among large areas of suitable habitat (e.g., pools), should further elucidate factors affecting nest success during periods of low streamflow.

Several studies have reported that flood events during the spawning period adversely affected nest success. Nest failure during high streamflow events has been attributed to nest predation or nest abandonment due to high water velocities, high water turbidity, or substrate mobilization (Winemiller and Taylor 1982; Reynolds and O'Bara 1991; Lukas and Orth 1995; Knotek and Orth 1998). Discharge decreased throughout the study period on Baron Fork Creek, and no nests were lost to high streamflows.

There is an apparent continuum of physical and biological factors influencing nest success of smallmouth bass in streams, which coincides with a continuum of benign to harsh streamflow conditions during the spawning period. We found no nest failures attributable to streamflow, despite previous reports that streamflow can account for a large percentage of nest failures (Lukas and Orth 1995). Theoretically, very large flood events extending through the spawning period could result in large amounts of sediment transport, or at least nest abandonment, and account for 100% of nest failures. In contrast, in Baron Fork Creek in 2005, when streamflows are generally low throughout the spawning period, biological factors such as predation were predominant causes of nest failure. This suggests that physical forces primarily affect nest success during harsh streamflow conditions, and that biological factors are most influential when streamflow conditions are benign (Figure 4.7). Similar models have been proposed to explain stream community structure. Peckarsky (1983) advanced an idea developed for marine invertebrate communities (Menge and Sutherland 1987) and suggested that abiotic forces affect stream macroinvertebrate communities primarily during harsh environmental conditions (e.g., diel and seasonal fluctuation, and predictability of environment, including streamflows), but that predation is the predominant factor under benign environmental conditions; competition was dominant during intermediate conditions. Extreme streamflows (i.e., benign or harsh) result in nest failures due to either biological or physical factors, but it is unknown whether physical or biological factors are additive or compensatory during intermediate streamflow conditions. Researchers studying Virginia rivers found smallmouth bass recruitment to be highest during intermediate streamflows (Smith et al. 2005), possibly suggesting that some level of intermediate streamflow may not disturb nests but may dampen the effects of predation, resulting in high levels of nest success, fry production and subsequent recruitment.

In summary, nesting chronology and microhabitat selection by smallmouth bass in Baron Fork Creek was typical for that reported for smallmouth bass in streams elsewhere, with two exceptions. We observed very high nest densities, and there was little tendency for earlier nesting by larger males. High mortality resulting in low numbers of older individuals (age 5+) may have masked any size trend in spawning chronology. A higher density of nests was observed in the upstream reach, compared to downstream, but densities in both reaches were higher than previously reported. Selection of nest sites was typical for smallmouth bass, with some change between the upstream and downstream reaches, and likely reflected longitudinal changes in available stream habitat. Nest success and factors influencing it were also similar between upstream and downstream reaches. Information about the position of predator habitat and predator abundance in relation to nests should strengthen our understanding of how biological factors such as predation affect nest success when streamflows are low throughout the spawning period. More interestingly, there is a contrast in physical and biological factors resulting in nest failures during high and low streamflows, but more understanding is needed regarding what percentage of nest failures are attributed to physical factors (streamflow) and biological factors (predation) during intermediate streamflows, and if such factors are additive or compensatory.

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Table 4.1. Age-frequency distribution of spawning male smallmouth bass in an upstream (Baron) and downstream reach (Eldon) of Baron Fork Creek, Oklahoma in 2005. Spawning males within a 2.5 cm length group were randomly assigned an age in proportion to the age distribution of a length class in an age-length key developed for Baron Fork Creek, Oklahoma.

	Baron		Eldon	
Age	Number	%	Number	%
1	0	0.0	0	0.0
2	21	15.9	5	7.6
3	80	60.6	22	33.3
4	28	21.2	33	50.0
5	2	1.5	6	9.1
6	1	0.8	0	0.0
Total	132		66	

Table 4.2. Summary of nest habitat and habitat availability in an upstream (Baron) and downstream reach (Eldon) of Baron Fork Creek, Oklahoma in 2005.

Reach / Variable	Nest / Avail	N	Mean	SD	Range
Baron					
Depth (m)[1,2,3]	Nest	153	0.57	0.178	0.24-1.19
	Availability	294	0.36	0.337	0.01-1.46
Mean water velocity (m/s)	Nest	153	0.04	0.027	0.00-0.14
	Availability	294	0.13	0.157	0.00-1.10
Velocity at stream bottom or nest (m/s)[1,3]	Nest	153	0.02	0.014	0.00-0.07
	Availability	294	0.08	0.121	0.00-0.70
Surrounding dominant substrate (coded)[1,2,4]	Nest	153	2.6	1.47	0-4
	Availability	294	3.4	1.24	0-5
Amount of cover within 1 m[1]	Nest	153	0.4	0.93	0-6
	Availability	294	0.1	0.37	0-3
Amount of cover within 2 m	Nest	153	0.8	1.59	0-8
	Availability	294	0.2	0.53	0-4
Eldon					
Depth (m)[1,2,3]	Nest	73	0.97	0.297	0.41-1.80
	Availability	297	0.50	0.426	0.01-2.00
Mean water velocity (m/s)	Nest	73	0.06	0.060	0.00-0.26
	Availability	297	0.33	0.332	0.00-1.52
Velocity at stream bottom or nest (m/s)[1,3]	Nest	73	0.02	0.026	0.00-0.15
	Availability	297	0.18	0.188	0.00-0.84
Surrounding dominant substrate (coded)[1,2,4]	Nest	73	2.7	1.42	1-4
	Availability	297	3.5	1.01	1-5
Amount of cover within 1 m[1]	Nest	73	1.7	1.41	0-6
	Availability	297	0.3	0.76	0-7
Amount of cover within 2 m	Nest	73	2.8	2.02	0-7
	Availability	297	0.6	1.16	0-7

[1] Variables used in resource selection function.

[2] Quadratic term included in resource selection function.

[3] Depth × Velocity interaction included in resource selection function.

[4] See Methods for substrate codes.

Table 4.3. Model averaged parameter estimates (b_i ± 2 SE) for resource selection function of microhabitats at smallmouth bass nests in an upstream (Baron) and downstream (Eldon) reach of Baron Fork Creek, Oklahoma in 2005.

	Baron		Eldon	
Variable	b_i	2 SE	b_i	2 SE
Intercept	-4.857	1.925	-6.815	3.481
Bottom velocity (m/s)	-36.648	28.641	-24.151	31.635
Cover within 1 m	0.966	0.622	0.952	0.447
Depth (m)	21.338	5.782	15.270	6.069
Depth×bottom velocity	-8.546	44.144	-7.918	30.389
Depth^2	-18.1548	4.916	-6.991	2.967
Substrate (coded)	0.708	1.226	-0.503	1.967
Substrate^2	-0.171	0.260	0.087	0.371
Models averaged	4		4	

Table 4.4. Summary of nest variables used in logistic exposure models of nest success in an upstream (Baron) and downstream (Eldon) reach of Baron Fork Creek, Oklahoma in 2005. Nests already at swim-up stage when found and nests disturbed by humans were excluded.

Reach / Variable	Success / Fail	N	Mean	SD	Range
Baron					
Depth (m)	Success	62	0.59	0.193	0.24-1.19
	Fail	87	0.55	0.169	0.28-1.04
Mean velocity (m/s)	Success	62	0.03	0.025	0.00-0.10
	Fail	87	0.04	0.029	0.00-0.14
Velocity at nest (m/s)	Success	62	0.01	0.013	0.00-0.06
	Fail	87	0.02	0.014	0.00-0.07
Amount of cover within 1 m	Success	62	0.5	0.94	0.0-4.0
	Fail	87	0.3	0.96	0.0-6.0
Amount of cover within 2 m	Success	62	1.1	1.58	0.0-7.0
	Fail	87	0.7	1.62	0.0-8.0
Distance to shore (m)	Success	62	2.12	1.223	0.50-7.30
	Fail	87	2.24	1.354	0.30-7.16
Length of male (mm)	Success	59	266.0	29.60	204-368
	Fail	69	255.9	21.63	214-318
Degree days (sum of mean	Success	62	913.7	224.6	602.3-1321.0
daily temperatures >10°C)	Fail	87	888.0	246.52	602.3-1555.3
Mean incubation temp. (°C)	Success	62	19.3	1.91	16.4-21.7
	Fail	87	18.4	2.23	15.8-24.0
Eldon					
Depth (m)	Success	25	1.04	0.310	0.62-1.80
	Fail	40	0.98	0.285	0.41-1.56
Mean velocity (m/s)	Success	24	0.05	0.055	0.00-0.26
	Fail	40	0.07	0.065	0.00-0.26
Velocity at nest (m/s)	Success	25	0.02	0.022	0.00-0.09
	Fail	40	0.03	0.029	0.00-0.15
Amount of cover within 1 m	Success	25	1.88	1.590	0.00-6.00
	Fail	40	1.65	1.350	0.00-6.00
Amount of cover within 2 m	Success	25	2.96	2.245	0.00-7.00
	Fail	40	2.65	1.861	0.00-6.00
Distance to shore (m)	Success	25	3.35	3.148	0.50-11.89
	Fail	40	3.05	3.029	0.20-10.89
Length of male (mm)	Success	25	297.8	36.03	237-366
	Fail	38	281.4	32.77	240-353
Degree days	Success	25	791.5	178.87	514.4-1153.3
daily temperatures >10°C)	Fail	40	615.2	115.51	467.1-983.4
Mean incubation temp. (°C)	Success	25	20.8	1.16	18.9-23.5
	Fail	40	19.2	1.17	16.9-21.6

Table 4.5. Model averaged parameter estimates (b_i ± 2 SE) for logistic exposure models of smallmouth bass nest success in an upstream (Baron) and downstream (Eldon) reach of Baron Fork Creek, Oklahoma in 2005.

	Baron		Eldon	
Variable	b_i	2 SE	b_i	2 SE
Intercept	-0.749	3.001	-6.937	4.284
Depth (m)	0.278	1.057	0.287	0.999
Velocity at nest (m/s)	-22.227	18.118	-3.423	11.270
Cover within 1 m	-0.002	0.080	0.138	0.165
Distance to shore (m)	-0.039	0.142	0.046	0.134
Fish length (mm)	0.014	0.012	0.012	0.011
Degree days	0.000	0.000	0.008	0.004
Models averaged	14		16	

Table 4.6. Smallmouth bass nest densities (number receiving eggs per stream kilometer) reported from streams and rivers in the United States. Only densities reported from nearly complete surveys throughout the spawning period were included.

Stream / River	No. / km	Reference
Baron Fork Creek, OK	100.2-147.3	Present study
Cacapon River, WV	9.9	(Surber 1939)
Courtois Creek, MO	3.1-7.7	(Pflieger 1975)
Green River, TN	35.0-75.3	(Reynolds and O'Bara 1991)
Indian Creek, OH	14.0-16.0	(Winemiller and Taylor 1982)
Indian Creek, TN	40.0	(Reynolds and O'Bara 1991)
Little Saline Creek, MO	25.5	(Pflieger 1966)
North Anna River, VA	21.9	(Lukas and Orth 1995)
North Anna River, VA	50.9	(Knotek and Orth 1998)
North Fork Shenandoah River, VA	1.0	(Surber 1939)
Shenandoah River, VA	4.3	(Surber 1939)
South Branch Potomac R., WV	3.1	(Surber 1939)

Figure 4.1. Locations of upstream (Baron) and downstream (Eldon) reaches of Baron Fork Creek, Oklahoma whereby nesting behavior, nest site selection, and nest success of smallmouth bass were evaluated in 2005.

Figure 4.2. Number of active smallmouth bass nests observed during snorkeling surveys in relation to mean daily temperature and discharge in an upstream (Baron, A) and downstream (Eldon, B) reach of Baron Fork Creek, Oklahoma in 2005. Asterisk indicates nests receiving eggs prior to first snorkeling survey (10 May) and determined from back-calculated dates of nest development.

Figure 4.3. Channel units and nest locations in an upstream (Baron) reach of Baron Fork Creek, Oklahoma in 2005. 10 nests locations are missing because of errors in GPS data.

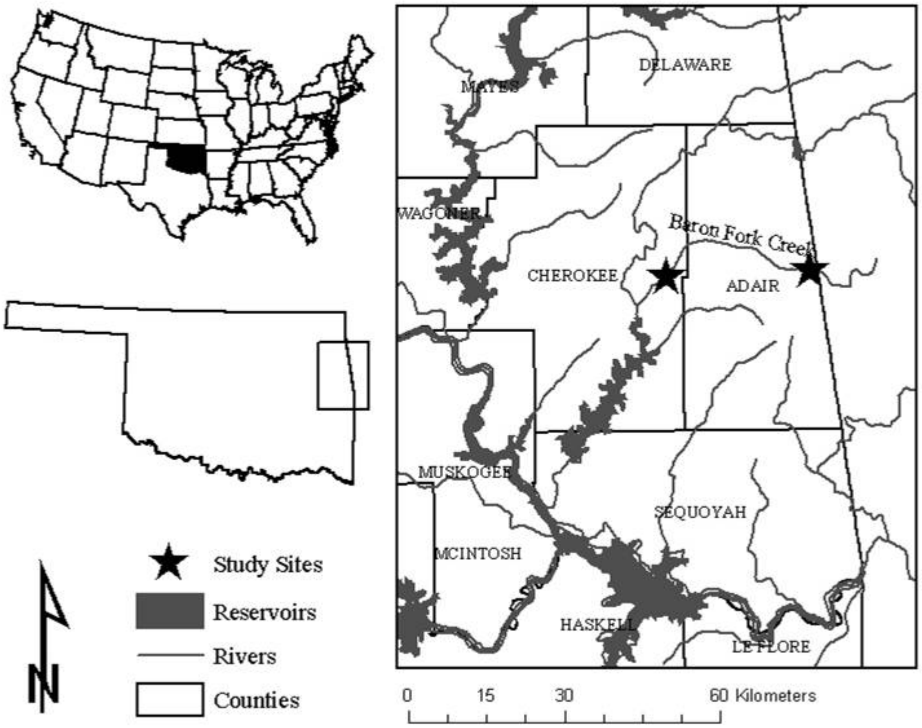
Figure 4.4. Channel units and nest locations in a downstream (Eldon) reach of Baron Fork Creek, Oklahoma in 2005.

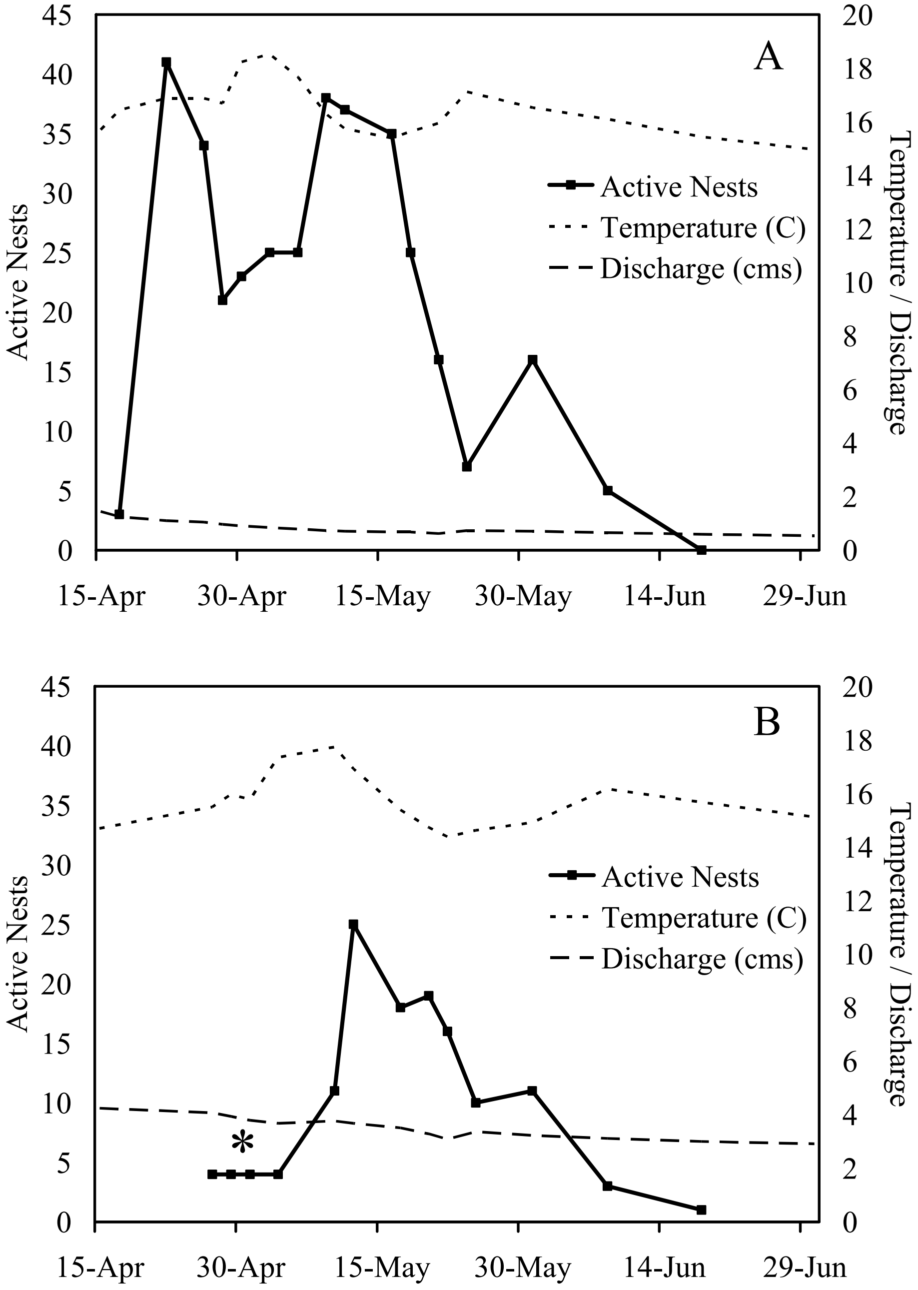
Figure 4.5. Number of submerged cover types (within 1 m) used by individual nesting male smallmouth bass, and total amount of cover used by all nesting males for an upstream (Baron, A) and downstream (Eldon, B) reach in Baron Fork Creek, Oklahoma in 2005.

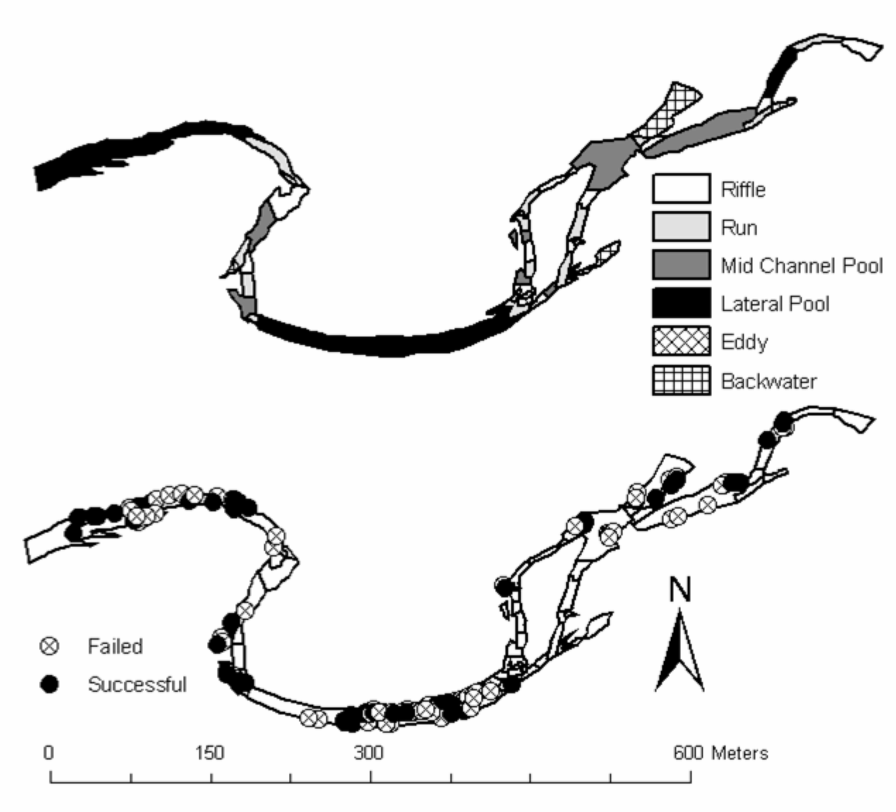
Figure 4.6. Model averaged relative probabilities of use for water depths at different water velocities at upstream (Baron, A) and downstream (Eldon, B) reaches in Baron

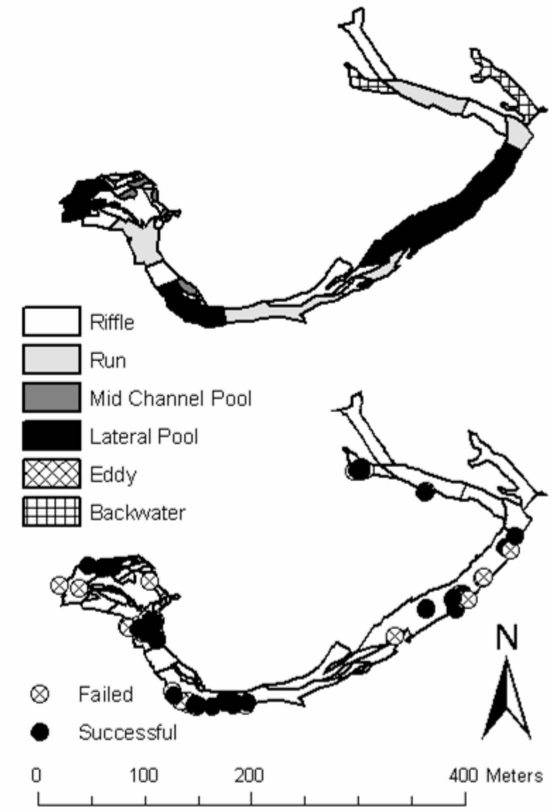
Fork Creek, Oklahoma in 2005, and relative probabilities of use for cover at both reaches (C). All variables were held at their mean values except the variable(s) of interest.

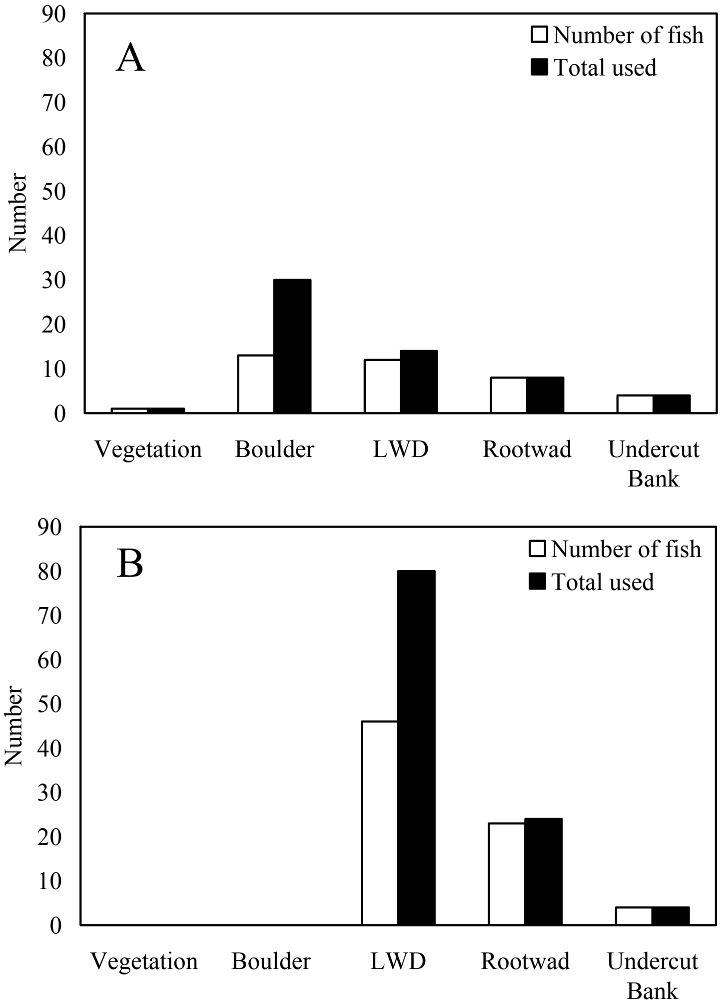
Figure 4.7. Conceptual model of percent of physically (solid line) or biologically (hashed line) related nest failures during harsh versus benign streamflow conditions. Current understanding is lacking regarding the form of physical (streamflows) versus biological (predation) factors at intermediate streamflows, and whether they are additive or compensatory.

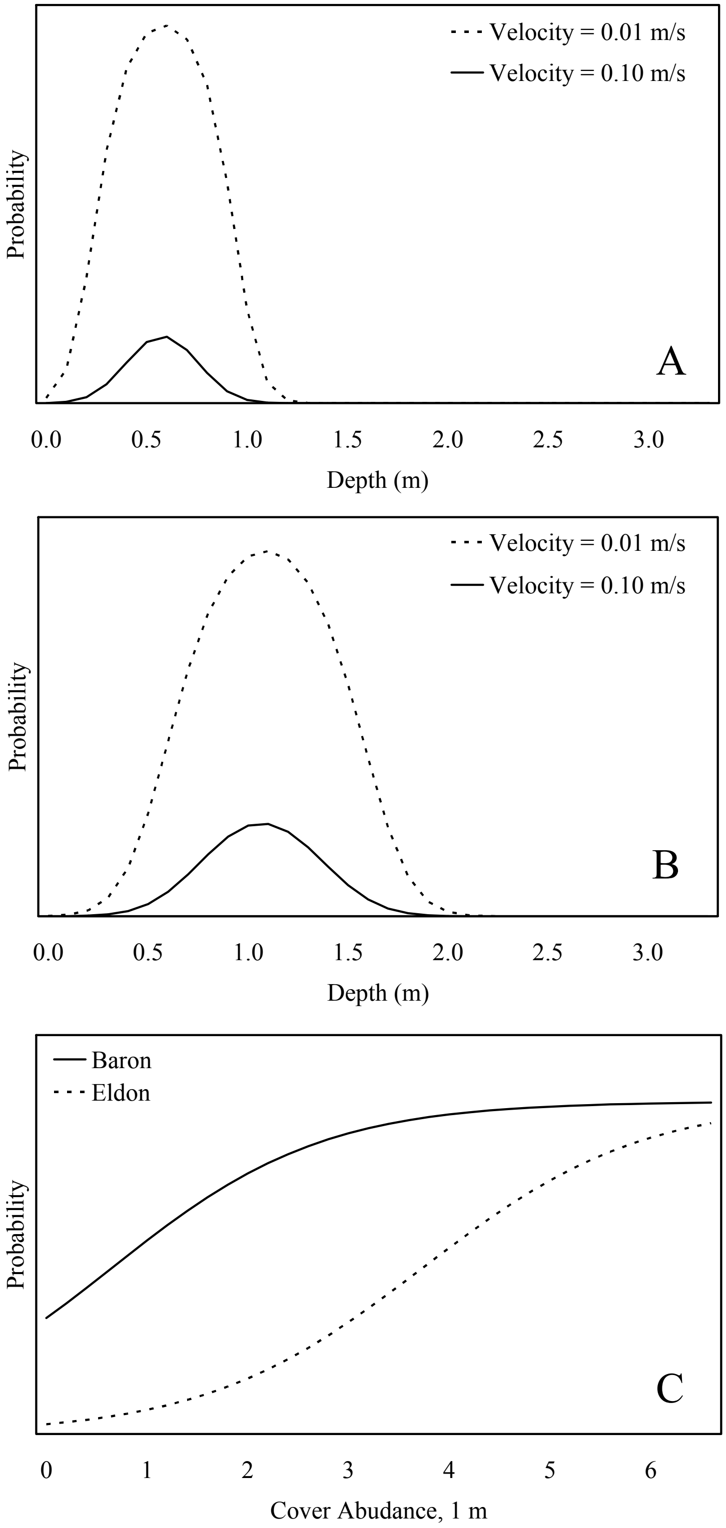

MAYES
DELAWARE
WAGONER
Baron Fork Creek
CHEROKEE
ADAIR
MUSKOGEE
SEQUOYAH
MCINTOSH
HASKELL
LE FLORE
Study Sites
Reservoirs
Rivers
Counties
N
0
15
30
60 Kilometers

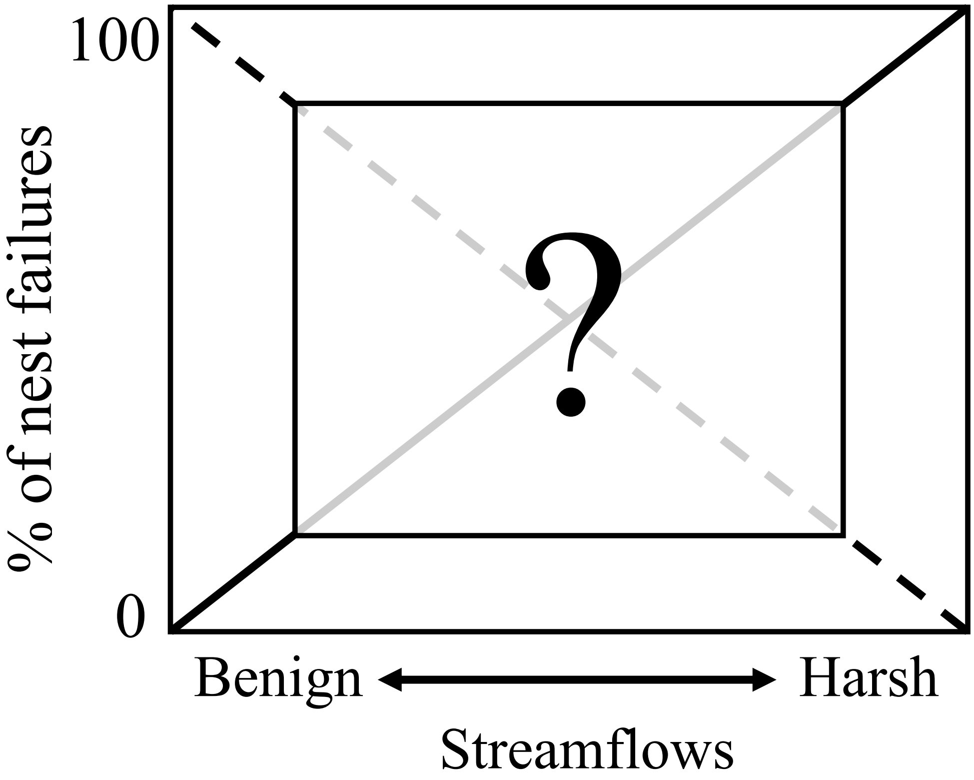

A
Active Nests
Temperature / Discharge
Active Nests
Temperature (C)
Discharge (cms)
0
5
10
15
20
25
30
35
40
45
0
2
4
6
8
10
12
14
16
18
20
15-Apr
30-Apr
15-May
30-May
14-Jun
29-Jun
B
*
Active Nests
Temperature / Discharge
Active Nests
Temperature (C)
Discharge (cms)
0
5
10
15
20
25
30
35
40
45
0
2
4
6
8
10
12
14
16
18
20
15-Apr
30-Apr
15-May
30-May
14-Jun
29-Jun


Riffle
Run
Mid Channel Pool
Lateral Pool
Eddy
Backwater
N
Failed
Successful
0
150
300
600 Meters


Riffle
Run
Mid Channel Pool
Lateral Pool
Eddy
Backwater
Failed
Successful
N
0
100
200
400 Meters


A
Number of fish
Total used
Number
90
80
70
60
50
40
30
20
10
0
Vegetation
Boulder
LWD
Rootwad
Undercut Bank
B
Number of fish
Total used
Number
90
80
70
60
50
40
30
20
10
0
Vegetation
Boulder
LWD
Rootwad
Undercut Bank


Velocity = 0.01 m/s
Velocity = 0.10 m/s
Probability
A
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Depth (m)
Velocity = 0.01 m/s
Velocity = 0.10 m/s
Probability
B
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Depth (m)
Baron
Eldon
Probability
C
0
1
2
3
4
5
6
Cover Abudance, 1 m


100
0
% of nest failures
?
Benign
Harsh
Streamflows

Appendix 4.1. Linear predictor functions of resource selection function models for nesting smallmouth bass males in Baron Fork Creek, Oklahoma having Akaike weights (w_i) within 10% of the best model. See methods for variable definitions.

Reach / Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i
Baron			
Depth+Velocity+Depth×Velocity+Depth^2+Substrate+$\mathrm{Substrate}^2$+Cover	314.98	0.00	0.468
Depth+Velocity+Depth^2+Substrate+$\mathrm{Substrate}^2$+Cover	315.20	0.23	0.418
Depth+Velocity+Depth×Velocity+Depth^2+Cover	319.04	4.06	0.061
Depth+Velocity+Depth^2+Cover	319.32	4.34	0.053
Eldon			
Depth+Velocity+Depth×Velocity+Depth^2+Substrate+$\mathrm{Substrate}^2$+Cover	149.70	0.00	0.337
Depth+Velocity+Depth^2+Substrate+$\mathrm{Substrate}^2$+Cover	150.22	0.52	0.260
Depth+Velocity+Depth×Velocity+Depth^2+Cover	150.51	0.81	0.224
Depth+Velocity+Depth^2+Cover	150.96	1.26	0.179

Appendix 4.2. Linear predictor functions for logistic exposure models of smallmouth bass nest success in Baron Fork Creek, Oklahoma having Akaike weights (w_i) within 10% of the best model. See methods for variable definitions.

Reach / Model	AIC_c	ΔAIC_c	w_i
Baron			
Velocity+Length	317.14	0.00	0.222
Velocity+DistanceToShore+Length	318.37	1.23	0.120
Depth+Velocity+Length	318.49	1.35	0.113
Velocity+Length+DegreeDays	319.07	1.93	0.085
Depth+Velocity+DistanceToShore+Length	319.08	1.93	0.084
Velocity+Cover+Length	319.15	2.00	0.082
Velocity+DistanceToShore+Length+DegreeDays	320.32	3.18	0.045
Velocity+Cover+DistanceToShore+Length	320.37	3.23	0.044
Depth+Velocity+Cover+Length	320.44	3.30	0.043
Depth+Velocity+Length+DegreeDays	320.50	3.36	0.041
Depth+Velocity+Cover+DistanceToShore+Length	320.93	3.79	0.033
Velocity+Cover+Length+DegreeDays	321.09	3.94	0.031
Depth+Velocity+DistanceToShore+Length+DegreeDays	321.10	3.96	0.031
Length	321.52	4.38	0.025
Eldon			
Cover+Length+DegreeDays	128.45	0.00	0.117
DistanceToShore+Length+DegreeDays	128.61	0.16	0.108
Velocity+Cover+Length+DegreeDays	128.80	0.35	0.098
Cover+DistanceToShore+Length+DegreeDays	129.00	0.55	0.089
Depth+Cover+Length+DegreeDays	129.26	0.81	0.078
Depth+Velocity+Cover+Length+DegreeDays	129.74	1.29	0.061
Depth+DistanceToShore+Length+DegreeDays	129.77	1.33	0.060
Velocity+Cover+DistanceToShore+Length+DegreeDays	129.91	1.46	0.056
Velocity+DistanceToShore+Length+DegreeDays	129.96	1.51	0.055
Length+DegreeDays	130.21	1.76	0.049
Depth+Length+DegreeDays	130.25	1.80	0.048
Depth+Cover+DistanceToShore+Length+DegreeDays	130.27	1.82	0.047
Velocity+Length+DegreeDays	130.77	2.32	0.037
Depth+Velocity+Length+DegreeDays	130.88	2.43	0.035
Depth+Velocity+DistanceToShore+Length+DegreeDays	131.06	2.61	0.032
Depth+Velocity+Cover+DistanceToShore+Length+DegreeDays	131.19	2.74	0.030

CHAPTER 5

RELATIONSHIPS AMONG GEOMORPHOLOGY, HABITAT, AND FISHES IN EASTERN OKLAHOMA STREAMS: THEIR IMPORTANCE TO STREAM RESTORATION

Abstract

Fluvial geomorphic processes at multiple spatial scales control instream habitat used by fishes. In eastern Oklahoma, fish species composition is affected by longitudinal and local geomorphic processes, and smallmouth bass *Micropterus dolomieu* abundance is influenced by geomorphology and stream habitat at different spatial scales. In addition, smallmouth bass use different habitats, including thermally unique habitats, within the stream landscape to meet different life history requirements. Channel form reflects watershed and local geomorphic processes, and it is often used in stream classification systems. Streams in eastern Oklahoma are sensitive to disturbance, but they can recover naturally; therefore, many streams are good candidates for habitat improvement structures. However, use of stream classification systems for restoration projects has been criticized because some projects using these systems have failed. Classification systems are a good starting point for initial understanding of geomorphic processes influencing a river, but watershed assessment and historical evaluation of river conditions also yield important information and should be used as well. Although channel restoration projects can be successful, response of fish populations and communities depends on the full suite of habitats needed to meet life history requirements. Presence of or distance to all needed habitats plays a role in the ability of a fish population to respond to stream restoration activities. Consequently, geomorphic and biological factors must both be considered when developing expectations for projects with a goal of restoring stream or river habitat.

Introduction

Rivers route water and sediment downstream, and the routing processes are distributed throughout a hierarchy of nested spatial and temporal scales (Frissell et al. 1986). At large spatial scales, regional variation in geology, topography, climate, and land use affect hydrologic and sediment regimes. Zones of erosion, transport, and deposition are associated with the longitudinal profiles of streams (Knighton 1998), and water and sediment movement through a stream reach interact with channel and bank materials (including vegetation) to determine channel form (Leopold et al. 1964). Streamflow and sediment regimes and channel form play a large role in riffle/pool development and structure within a reach. The degree of spatial variability in natural (e.g., debris flows, bedrock controls) and anthropogenic (e.g., land use) disturbances within a watershed determine whether changes in channel form occur gradually or abruptly from upstream to downstream (Montgomery 1999); however, some change in sediment, streamflow, or water chemistry is expected at tributary junctions (Poole 2002; Benda et al. 2004). These geomorphic processes are complex and interacting, and result in channel features used as habitat by fishes at different spatial scales (Frissell et al. 1986; Rabeni and Jacobson 1993b; Walters et al. 2003).

Eastern Oklahoma streams

Channel morphology

Channel form is often used as a proxy for trends in channel process and response (Simon and Castro 2003). As a result, channel form has been incorporated into a variety of stream classifications systems, some of which are used in stream channel restoration projects (Arend 1999; Kondolf et al. 2003). Arguably the most widely applied stream classification system was developed by Rosgen (1994; 1996).

A survey of 155 streams, including those that were intermittent, in the Boston Mountains, Ouachita Mountains, and Ozark Highlands (Omernik 1987) in eastern Oklahoma revealed three Rosgen stream types, with additional subclasses (Table 5.1). Smaller streams were more confined by valley slopes and dominated by riffles, and they had moderate gradients and stable channel form (Rosgen Type B). However, most streams were typically low gradient, meandering, riffle/pool, alluvial streams (Type C). Gravel bed streams predominated, but there was more variability in sizes of surficial substrates in the southeastern Ouachita Mountain streams (C3 [cobble] and C4 [gravel]) when compared to northeastern streams (largely C4). Some streams were low gradient, meandering, with riffle/pool structure and stable channel form (Type E).

Geomorphology, stream habitat, and fishes

Several factors determine the fish species residing in a stream reach (Poff 1997). Historical biogeography is important in explaining the distribution of some stream fishes in upland regions in eastern Oklahoma (Chapter 1; Howell 2001). However, fluvial geomorphic processes were also found to be important determinants of species composition, among those evaluated, in eastern Oklahoma streams (Chapter 1). Concomitant changes in physical, chemical, and biological processes with increasing stream size were important in dictating habitat conditions and the fish species within the regional species pool that were observed within a stream reach. However, spatial variability in sediment regimes and channel cross-section form was also important in determining fish species composition.

Smallmouth bass *Micropterus dolomieu* populations are largely influenced by longitudinal processes in eastern Oklahoma streams, in addition to other factors (Chapters 2 and 3). In headwater streams, smallmouth bass populations are recruitment limited due to streamflow dynamics and spawning habitat limitations and, therefore, are largely absent. They are also limited in downstream reaches, likely in response to increased water temperatures, turbidity, and fine substrates (Rabeni and Jacobson 1993a; Sowa and Rabeni 1995). Longitudinal changes in population dynamics, however, differ between northeastern and southeastern Oklahoma streams. In reaches with large numbers of individuals, densities were higher in deepwater habitats. Channel morphology is also related to smallmouth bass populations beyond the effects of stream and habitat size; abundances are higher in larger streams with less pool area, higher channel width:depth ratios, and gravel substrates. Habitat within channel units (vegetation, wood, bedrock) was also related to abundance, but relations were dependent on stream size and channel morphology.

Smallmouth bass also used different habitats within the stream landscape to meet different life cycle requirements (Chapters 3 and 4). Food and cover availability did not strongly influence the distribution of individuals within a reach, perhaps because they were abundant and not limiting resources. Different complementary habitats, however, were used for spawning and winter refugia. Smallmouth bass that remained in a reach of Baron Fork Creek in winter moved into a backwater and adjacent habitats that had observable groundwater influx resulting in warmer water temperatures during cold winter days. These thermal characteristics were unique in summer as well, but apparently were not important enough to be used by smallmouth bass in summer. High levels of water exchange and mixing between subsurface flow, surface flow, and groundwater apparently kept water temperatures low enough in the main channel during summer so thermal refugia were not needed. In contrast, the backwater used in winter was largely unsuitable for spawning in spring due to a thick layer of sand-silt substrates, although a few nests were observed along the margins where some gravel was present (Chapter 4).

Use of the stream landscape by smallmouth bass was only documented in Baron Fork Creek in northeastern Oklahoma, and it is unknown to what degree different habitats are used by smallmouth bass in southeastern Ouachita Mountain streams. Given that Ouachita Mountains streams are more runoff dominated and have higher water temperatures in summer than northeastern streams (Chapter 3), summer refugia may be important to smallmouth bass populations because of the detrimental effects that water temperatures greater than 22°C have on the growth scope of smallmouth bass (Zweifel et al. 1999; Whitledge et al. 2002). Interestingly, Big Eagle Creek near Octavia, LeFlore County, Oklahoma, had consistently high channel-unit densities of smallmouth bass during stream surveys in the Ouachita Mountains; it had the 4th through 10th highest densities of smallmouth bass (greater than 100 mm) of all channel units sampled in the Ouachita Mountains. It was also the only southeastern stream where a smallmouth bass nest and individuals over 300 mm were observed while snorkeling. Big Eagle Creek was the only stream sampled in the southeast that had a large cold-water spring adjacent to a bedrock outcrop. Channel units with high densities of smallmouth bass were located above and below the spring. Thus, if the spring mitigated high summer water temperatures (water temperature was not measured), enhanced smallmouth bass production and survival in this area resulted in individuals dispersing to other areas within the reach. A better understanding is needed regarding potential summer and winter thermal refugia in southeastern Oklahoma streams.

Stream channel and habitat restoration

Streams in eastern Oklahoma, particularly in the northeast, are sensitive to disturbances but have a natural ability to recover. According to Rosgen's classification system (1994; Table 3), most stream reaches we sampled in eastern Oklahoma are sensitive to increased streamflow magnitude and sediment loads. However, Rosgen also suggests that they have a 'good' recovery potential given that factors causing stream instability are resolved. Moreover, several instream structures suggested to improve fish habitat are applicable to streams in eastern Oklahoma (Table 5.2). Following channel recovery, fish species composition might also respond, because the presence or absence of fish species is affected by channel form and sediment regimes in addition to longitudinal processes. However, smallmouth bass were only found in large type C streams, but show substantial variation within this stream type (Figure 5.1).

Although most stream types observed in eastern Oklahoma are good candidates for stream habitat improvement structures, caution must be exercised when using guidelines presented by classification schemes for such structures. Instream restoration projects will not be successful without fully considering geomorphic processes during restoration planning (Frissell and Nawa 1992; Kondolf et al. 2001); however, some successful instream structures have been reported even when watershed disturbances were not resolved (House 1996). Some researchers have questioned stream classification systems designed for stream restoration and habitat improvement because they are not linked to current channel equilibrium conditions, do not always consider larger scale processes such as climate and hydrology, and facilitate a shortcut from a true geomorphologic analysis of a river system (Miller and Ritter 1996; Doyle et al. 1999). Stream classifications may be a starting point for stream restoration planning, but other information is needed. A tiered or hierarchical approach that evaluates different spatial and temporal scales is most informative, including watershed assessments and sediment budgets (Kondolf 2000; Roni et al. 2002) and review of historical information (Rosgen 1996; Kondolf et al. 2003). Although a true geomorphologic analysis should include a study of river system history to understand its past behavior, classification schemes that describe the existing channel form, which reflects historical processes to some degree, can facilitate communication among managers (Simon and Castro 2003; Kondolf et al. 2003). Kondolf et al. (2003) provided three reasons why classification of stream channels is useful for stream restoration: to survey existing conditions and set restoration priorities, to envision the end state resulting from restoration activities, and to offer insight into restoration measures likely to be successful.

Although channel restoration or fish habitat improvement structures may be successful from a geomorphic standpoint, additional factors dictate whether stream fishes will respond to activity[1]. For example, smallmouth bass were found only in certain Rosgen stream types, but densities varied widely within those types. So even if channel form is restored, smallmouth bass abundances may not respond predictably because of other important factors (stream size, habitat size, wood, vegetation; Chapter 2). In

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[1] Biological response may not be a priority goal of a channel restoration project.

addition, if a functional habitat unit, defined as the suite of habitats needed by a fish to complete its life cycle, is incomplete, a population might not respond to the channel or habitat modification. Moreover, the distance between required habitats will determine the degree of response, because distance to complementary habitats affects population dynamics and size (Schlosser 1995; Kocik and Ferreri 1998). Proximity of restoration projects to habitats (e.g., bluff pools, backwaters, and springs) offering a thermal refuge during winter or summer may partially dictate the type and magnitude of response by smallmouth bass populations to instream habitat projects. Bluff pools are important habitats for smallmouth bass, and valley walls that form bluff pools occur less often in downstream reaches of Ozark streams (Rabeni and Jacobson 1993a). The spatial location and frequency of bluff pools within the profile of a river may not always be predictable, however, as happenstance contact of a river with valley walls depends on sinuosity, channel migration rates, and the underlying structure (stratigraphy, folds, faults) of basin lithology and valley walls themselves.

Current stream restoration principles emphasize system ecology and benefits for stakeholders. Palmer et al. (2005) proposed five measures of restoration success: 1) restoration project design should be based on a healthy dynamic system that can exist at a site; 2) river ecology (including hyrdogeomorphology) should be improved; 3) the river system must be self-sustaining and resilient to future disturbances; 4) restoration construction should have no lasting, harmful impacts; and 5) pre- and post-project assessment must be completed and data and results made publicly available. Many recent projects have focused on restoring aesthetics and ecology of streams (Moerke and Lamberti 2004), although monitoring of restoration projects has not been frequent (Roni et al. 2002). However, monitoring methods (Roni 2005) are more likely to be implemented when restoring river ecology (versus engineering) is the goal (Bash and Ryan 2002). Project success is often difficult to ensure, however, because stream restoration projects are poorly controlled experimentally, there is little transferability of results from previous projects, and the projects are socially complicated and costly (Shields et al. 2003). Furthermore, reinstating the dynamic equilibrium of rivers often poses a safety risk for project managers who subsequently resort to use of hard engineering (Gillilan et al. 2005). Some of these problems will likely be more difficult to resolve with current practices focusing on larger spatial scales such as watersheds (Williams et al. 1997; Hillman and Brierley 2005).

Conclusions

Streams reflect a multitude of terrestrial and fluvial processes intertwined in a hierarchy of spatial and temporal scales (Frissell et al. 1986). Although study and classification of stream reaches may yield an initial indication of river processes, a full geomorphic analysis of several spatial scales and river history will result in the most complete understanding of factors dictating the success of a restoration project. The suite of habitats used by fishes or other aquatic organisms must also be considered when projects are expected to elicit a biological response. Project success and accountability are important because resources from public entities and private organizations are often used for such activities (Moerke and Lamberti 2004). Failed projects waste monetary resources. This may cause negative perceptions towards the resource agency and future projects (Turner 1997), resulting in fewer resources allocated for future projects.

Therefore, consideration of a full suite of geomorphic and biological factors is crucial to better ensure the success of any stream and river restoration program.

Acknowledgments

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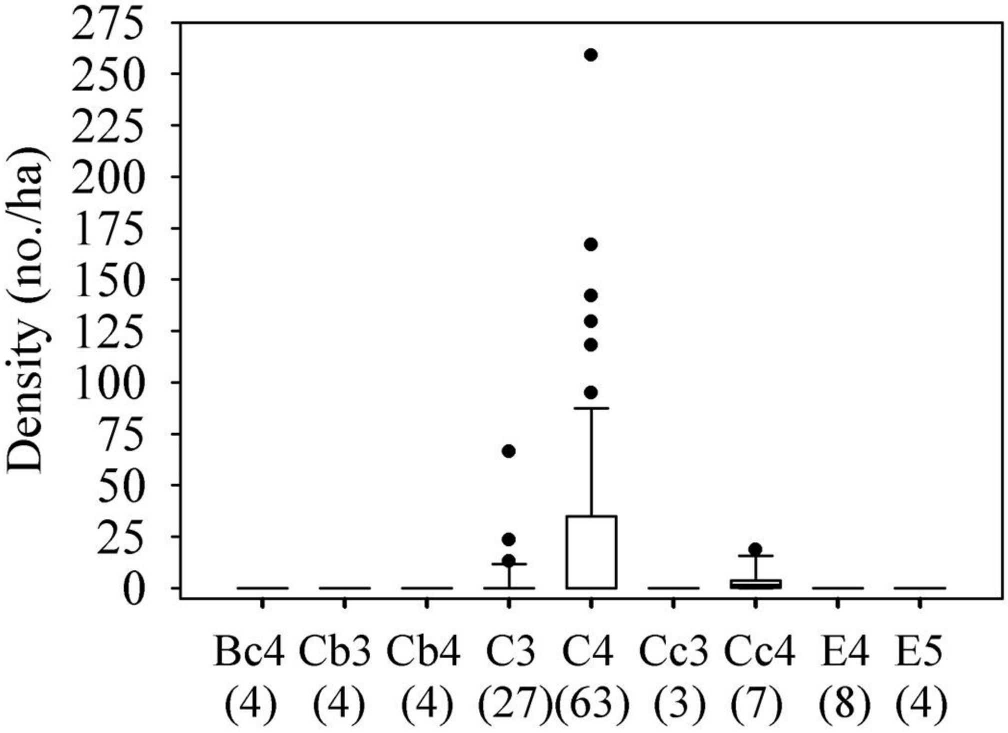
Table 5.1. Number (% total) and mean basin area (range) of Rosgen stream types in a survey of 155 stream reaches the Boston Mountains, Ouachita Mountains, and Ozark Highlands in eastern Oklahoma. Descriptions of stream types designated by letters are given in text, lower case letters indicate higher (b) and lower (c) stream gradients than those without for each type, and numbers indicate dominant substrate type: 2 = boulder, 3 = cobble, 4 = gravel, 5 = sand/silt.

Stream type	Boston Mountains	Ouachita Mountains	Ozark Highlands	Total	Basin area (km^2)
B3	0 (0.0)	0 (0.0)	1 (0.7)	1 (0.7)	1.5
Bc2	0 (0.0)	1 (0.7)	0 (0.0)	1 (0.7)	8.0
Bc4	0 (0.0)	5 (3.2)	1 (0.7)	6 (3.9)	17.8 (2.5-68.0)
C2	0 (0.0)	1 (0.7)	0 (0.0)	1 (0.7)	99.8
C3	2 (1.3)	28 (18.1)	0 (0.0)	30 (19.4)	94.2 (1.2-831.0)
C4	28 (18.1)	21 (13.6)	24 (15.5)	73 (47.1)	87.1 (1.2-951.3)
Cb3	0 (0.0)	4 (2.6)	0 (0.0)	4 (2.6)	5.9 (1.2-15.1)
Cb4	1 (0.7)	3 (1.9)	2 (1.3)	6 (3.9)	19.3 (1.2-104.0)
Cc2	0 (0.0)	1 (0.7)	0 (0.0)	1 (0.7)	235.2
Cc3	0 (0.0)	3 (1.9)	0 (0.0)	3 (1.9)	176.6 (106.5-268.1)
Cc4	3 (1.9)	3 (1.9)	1 (0.7)	7 (4.5)	343.4 (34.9-587.5)
E3	0 (0.0)	1 (0.7)	0 (0.0)	1 (0.7)	35.7
E4	3 (1.9)	7 (4.5)	5 (3.2)	15 (9.7)	36.6 (1.3-258.8)
E5	0 (0.0)	4 (2.6)	1 (0.7)	5 (3.2)	17.5 (3.1-35.9)
Eb4	1 (0.7)	0 (0.0)	0 (0.0)	1 (0.7)	1.2
Total	38 (24.5)	82 (52.9)	35 (22.6)	155 (100.0)	

Table 5.2. Suitability of fish habitat improvement structures by stream type (from Table 8-2a in Rosgen 1996). Exc = Excellent, N/A = not available.

	Stream type								
Structure	B2	B3	B4	C2	C3	C4	E3	E4	E5
Low stage check dam	Exc	Exc	Exc	Good	Good	Fair	N/A	N/A	N/A
Med stage check dam	Exc	Good	Good	Fair	Fair	Poor	Poor	Poor	Poor
Random boulders	N/A	Exc	Exc	N/A	Good	Poor	Poor	Poor	Poor
Bank placed boulders	N/A	Exc	Exc	N/A	Exc	Good	Good	Good	Good
Single wing deflector	Exc	Exc	Exc	Good	Good	Fair	Poor	Poor	Poor
Dbl wing deflector	Exc	Exc	Exc	Good	Good	Fair	Fair	Fair	Fair
Channel constrictor	Exc	Exc	Exc	Good	Good	Fair	N/A	N/A	N/A
Bank cover	Exc	Exc	Exc	Good	Good	Good	N/A	N/A	N/A
Half log cover	N/A	Exc	Exc	N/A	Good	Fair	N/A	N/A	N/A
Floating log cover	N/A	Exc	Exc	Good	Good	Good	N/A	N/A	N/A
Submerged shelter									
Meander	N/A	Good	Good	N/A	Exc	Fair	Good	Good	Good
Straight	N/A	Exc	Exc	N/A	Exc	Good	Good	Good	Good
Migration barrier	Good	Good	Good	Poor	Poor	Poor	Poor	Poor	Poor
Gravel trap, v-shaped	Exc	Good	N/A	Good	Good	N/A	Fair	N/A	Poor
Gravel trap, log sill	Exc	Good	N/A	Good	Good	N/A	Fair	N/A	Poor
Spawning gravel	Fair	Good	N/A	Good	Good	N/A	Fair	N/A	Poor
Cross vane	N/A	Exc	Exc	N/A	Exc	Exc	Good	Good	Good
“W” weir	N/A	Exc	Exc	N/A	Exc	Good	N/A	N/A	N/A
Bank rootwads	N/A	Exc	Exc	Exc	Exc	Exc	Good	Good	Good
J-hook log and rock vanes	N/A	Exc	Exc	Good	Exc	Exc	Good	Good	Good

Figure 5.1. Box plots of age-1+ smallmouth bass densities by Rosgen stream type in stream reaches in eastern Oklahoma. Sample sizes in parentheses. Only stream types represented by more than one stream (not dry) are included.



VITA

Daniel Carl Dauwalter

Candidate for the Degree of

Doctor of Philosophy

Dissertation: RELATIONSHIPS AMONG GEOMORPHOLOGY, HABITAT, AND FISHES IN EASTERN OKLAHOMA STREAMS: IMPLICATIONS FOR STREAM RESTORATION

Major Field: Wildlife and Fisheries Ecology

Biographical: Personal Information: Born in Carver, Minnesota, May 28th, 1977 to Mary Sexton and Roger Dauwalter (deceased).

Education: Received a Bachelor of Arts, double majoring in Biology and Environmental Studies, from Gustavus Adolphus College in May 1999. Received a Master of Science in Aquaculture/Fisheries from University of Arkansas at Pine Bluff in May 2002. Completed requirements for the Doctor of Philosophy degree in May, 2006

Professional Experience: Employed by Carver County Environmental Services as a Water Quality Intern from May to August, 1998. Employed by Biology Department, Gustavus Adolphus College as a Research Technician from August 1998 to May 1999. Employed by South Dakota Cooperative Fish and Wildlife Research Unit as a Fisheries Technician from May 1999 to October 1999. Employed by Department of Aquaculture and Fisheries, University of Arkansas at Pine Bluff as a Graduate Research Assistant from November 1999 to January 2002, and as a Research Associate from January 2002 to July 2002. Employed by the Oklahoma Cooperative Fish and Wildlife Research Unit as a Graduate Research Associate from July 2002 to April 2006.

Professional Memberships: Oklahoma Chapter, Southern Division, and Parent Society of the American Fisheries Society; Oklahoma Academy of Sciences; Sigma Xi; Ecological Society of America.

Name: Daniel Carl Dauwalter Date of Degree: May, 2006

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: RELATIONSHIPS AMONG GEOMORPHOLOGY, HABITAT, AND FISHES IN EASTERN OKLAHOMA STREAMS: IMPLICATIONS FOR STREAM RESTORATION

Pages in Study: 211 Candidate for the Degree of Doctor of Philosophy

Major Field: Wildlife and Fisheries Ecology

Scope and Method of Study: Stream restoration is a multidisciplinary practice aimed at reestablishing disturbed stream ecosystems. Fluvial geomorphology and landscape ecology have been individually incorporated into stream fish ecology. However, they have not been explicitly integrated into stream restoration practices. We used a stream survey to relate geomorphology and habitat to fish species composition and smallmouth bass *Micropterus dolomieu* abundance at several spatial scales in eastern Oklahoma streams. Spatial and temporal changes in stream habitat and population characteristics of smallmouth bass were determined for two eastern Oklahoma streams, and a landscape model was evaluated for smallmouth bass in Baron Fork Creek, Oklahoma.

Findings and Conclusions: Stream survey results elucidated complex relationships between stream geomorphology and stream habitat, and fishes in eastern Oklahoma streams. Geomorphic variables representing stream size best explained variability in fish species composition in both northeastern and southeastern Oklahoma streams. Local channel morphology and substrate characteristics were secondarily important and mostly independent of stream size. Stream size and morphology explained variation in densities of all sizes of smallmouth bass, but channel unit habitat explained additional variation in densities of larger individuals. Stream habitat and smallmouth bass populations in Baron Fork Creek and Glover River were spatially and temporally dynamic. Water temperatures, streamflows, and instream habitat differed between streams and longitudinally within each stream. Abundance, recruitment, and survival of smallmouth bass populations differed between streams and seasons, and longitudinal patterns of these characteristics were unique in each stream. Smallmouth bass showed strong patterns of seasonal habitat complementation and supplementation: different habitats were used for spawning and summer growing periods versus those used for winter thermal refugia. Eastern Oklahoma streams are sensitive to disturbance but naturally resilient. Consideration of geomorphic relationships with fishes and ensuring that all habitats required by fishes are available will best facilitate responses from fish populations during the restoration of eastern Oklahoma streams.

Advisor's Approval: William L. Fisher