Microhabitat Use and Its Effect on Growth of Age-0 Smallmouth Bass in the North Anna River, Virginia

by

Matthew J. Sabo

A dissertation submitted to the faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the
degree of

Doctor of Philosophy
in
Fisheries and Wildlife Sciences

Donald J. Orth

Donald J. Orth
Chair

Paul L. Angermeier

Alan G. Heath

Alan G. Heath

John J. Ney

John J. Ney

Jackson R. Webster

May 1993
Blacksburg, Virginia 24061

Microhabitat use and its effect on growth of age-0 smallmouth bass in the North Anna River, Virginia.

by

Matthew J. Sabo

Committee Chair: Donald J. Orth

ABSTRACT

This study examined the relationship between microhabitat use and growth of age-0 smallmouth bass in the North Anna River. The study objectives were to describe microhabitat use during summer, assess the profitability of microhabitats, and determine if and how microhabitat use could determine which individuals gained a growth advantage.

Age-0 smallmouth bass changed their microhabitat use as they passed through stages of ontogenetic development and became familiar with their environment. More than 30% of the area available to brood larvae contained mean water column velocities greater than 4 cm/s and no cover. More than 80% of larvae observed after dispersing from the nest site occupied areas approximately one m deep with velocities near 0 cm/s, or large cover objects that created low velocity shelters throughout the water column. By six weeks after dispersal (when all juveniles were > 40 mm), more than 50% of juveniles occupied depths less than 60 cm and focal point velocities > 3 cm/s, and microhabitat use by large and small juveniles did not differ. In these shallow microhabitats with moderate to fast current velocities, juveniles foraged at a higher rate (5.1 bites/min on average) than in deeper and slower velocity areas (1.3 bites/min). When these foraging rates were translated into estimates of energetic profit, juveniles in the shallow-fast microhabitats gained approximately 5 j/min more than juveniles foraging in other microhabitats. Microhabitat use

was the only aspect of behavior that affected the foraging rate or energetic profit gained by juvenile smallmouth bass.

I examined daily rings on otoliths to track the growth of individual smallmouth bass through time. Temperature affected growth rates below 22-23°C, so that individuals spawned later grew in warmer thermal regimes and grew relatively fast during early life stages. However, individuals that spawned early and grew slowly in cooler temperatures did not suffer higher mortality and compensated for their slow growth by accumulating growth over a longer period of time. Above 22-23°C, relative growth rates were not consistent through time; a fast growing individual during one life stage could grow relatively slow during the next. If growth above the temperature threshold depended on foraging success and foraging success depended on microhabitat use, then few individuals were consistently occupying the most profitable microhabitats.

In experiments in an artificial stream, juvenile smallmouth bass assessed the potential profitability of an area by the foraging rate they achieved there. They usually did not remain in an area unless they foraged well at the time they searched it, and did not appear to associate habitat characteristics with profitability. In the river, most of the microhabitats available were relatively unprofitable, so an individual that abandoned a profitable area might (depending on its foraging behavior) spend significant time in unprofitable microhabitats and consequently reduce its growth rate. Increasing the availability or density of food resources may improve growth of juvenile smallmouth bass in the North Anna River by increasing the rate at which juveniles encounter profitable microhabitats and elevating their intake rates in profitable areas.

ACKNOWLEDGEMENTS

"Loveliness unfathomable, as ever a lover saw in his young bride's eye! Tell me not of thy teeth-tiered sharks, and thy kidnapping cannibal ways. Let faith oust fact; let fancy oust memory; I look deep down and do believe."

Herman Melville

Plying the hostile waters of smallmouth bass biology would have proved a more harrowing experience without the guidance of Donald Orth, whose advice and friendship fostered my interest in the unfathomable. Additional navigational checks were provided by my advisory committee of Paul Angermeier, Alan Heath, John Ney, and Jackson Webster, who spent many hours critically reviewing my research. I thank the Electric Power Research Institute, and Virginia Power Company for funding this project and allowing me to work with Robert Graham, Donald DeAngelis, Henriette Jager, Ray Newman, Michael Sale, Denise Schmoyer, Webster Van Winkle, and Kirk Winemiller, each of whom contributed to my academic and professional development.

The crew of Robert Easton, Thomas Groshens, Joseph Lukas, Edmund Pert, and Robert Vadas not only helped me collect data, but served as my second (and far more hostile) advisory committee. Thanks dudes. Further assistance in the field and laboratory was provided by Will Adams, Todd Greenwood, Ian Jezorek, Anne Sienwell, and (that most amenable of Jane's Addiction fans) Brian Wells. Peter Arnett and a great guy I know only as Lenny allowed me to access the river from their property, and their cooperation made this whole study possible. Scott Gordon and Joseph Stoeckel were remarkably helpful during the laboratory studies. I thank William Ensign, Yadvendradev Jahla, and

Michael Tonkovich for always coming up with a new way of looking at things, and Renee Speenburgh for feeding me.

My parents gave me life, love, siblings, and several headaches, and I never could have accomplished anything without their support. Many people have put wind in my sails when I sat on a lee shore during the last ten years. Among the most important were Michael and Kathleen Caterina, Tom and Cindy Clements, Leo Francis Faucette Jr., Dr. Ruth Golas, Dr. Evan Heald, William and Vicki Lantz, Laura May (and her menagerie), Kim Mockbee, and Kathy Murphy. I thank them all and salute collectively those who have raised high the banner of ΦUK, subscribing to her high ideals of life, loyalty, and a firm belief in the divinity of Joe Paterno.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION TO THE DISSERTATION

Because streams in the United States frequently have their flows altered by hydropower facilities and off-stream withdrawals, aquatic resources in streams are often threatened by rapidly fluctuating flows, periodic dewatering, and reduced quantity and quality of instream habitat (Bain and Boltz 1989). To reduce the impact of altered stream-flow on fish populations, many resource agencies have used the Instream Flow Incremental Methodology (IFIM) to determine the relationship between discharge and the availability of useable habitat for different species of fish (Bovee 1982). A critical assumption of the habitat simulation component of IFIM is that habitat availability is related to the standing stock of fish. Managers use the results of these simulations to estimate the amount of usable habitat they must preserve to maintain a desired carrying capacity. However, accumulated evidence indicates that the size of a fish population in a stream is not always a simple function of habitat availability (Orth and Maughan 1982, Scott and Shirvell 1987).

Because habitat availability frequently does not relate to population density, some researchers and resource managers have questioned the usefulness of IFIM as a tool for conserving fisheries resources (Granholm et al. 1985, Mathur et al. 1985, Scott and Shirvell 1987). Despite this shortcoming, it is generally agreed that the physical habitat simulation component of IFIM does adequately assess the impacts of flow alterations on the availability of habitat for fish (Orth 1987, Gore and Nestler 1988) and is frequently used for this purpose (Reiser et al. 1989). What the methodology lacks is a firm understanding of how changes in habitat availability directly or indirectly impact population densities.

Most theories that link habitat availability to population regulation assume that habitat selection is an optimal foraging process (Rosenzweig 1991). Fish appear to adhere to this assumption because they tend to occupy habitats where they can maximize feeding rates while minimizing their risk of mortality (Werner et al. 1983a, 1983b). If feeding and mortality rates depend on habitat use, then the carrying capacity of a population will be defined at the life stage where competition for critical habitat is most intense (i.e. when the number of individuals/area of available habitat is maximized), because competition for resources tends to decrease the relative fitness that can be attained in a habitat (Morris 1987, 1988). Among fish, feeding and mortality rates may be most affected by competition during the larval and juvenile life stages (May 1974, Shephard and Cushing 1980, Elliott 1989a, 1989b, 1990), because at that time their densities are highest and individuals are most susceptible to mortality. Therefore, to understand the effect of habitat alterations on population densities of fish it is necessary to examine relationships between habitat availability and first-year recruitment of stream fish.

The smallmouth bass (Micropterus dolomieu) is a relevant fish species to examine in this context. The species commonly occurs in warmwater streams of the United States, and its life history strategy suggests that density-dependent regulation of the spawning stock should occur during the first year of life (Williams 1984, Winemiller and Rose 1992). Furthermore, the microhabitat use of larval and juvenile smallmouth bass differs from the habitat use of adults (Orth and Maughan 1982, Leonard and Orth 1988, Forbes 1989, Aadland et al. 1991). Discharges that reduce habitat availability for age-0 individuals might not reduce availability for adults, so a change in discharge could affect population densities without affecting the amount of living space for adults. To increase spawning populations of smallmouth bass, managers may have to focus their efforts on increasing the amount of microhabitat available to age-0 individuals. But by what mechanism would increasing the availability of microhabitats improve survival of age-0 smallmouth bass?

Modelling simulations indicate that any factor that promotes growth rate of age-0 smallmouth bass should increase their survival through periods of high predation mortality (DeAngelis et al. 1991) and over winter (Shuter et al. 1980). Certain habitat characteristics can promote foraging success of age-0 smallmouth bass (Simonson and Swenson 1990), so individuals that occupy microhabitats with these characteristics should theoretically exhibit higher growth and survival rates than individuals in less suitable areas (Jager et al. in press). By identifying microhabitats that promote growth of age-0 smallmouth bass at each life stage, it may be possible to increase population densities by regulating discharge so that the availability of these profitable microhabitats is increased.

The purpose of this study was to determine how microhabitat use affected growth rates of age-0 smallmouth bass in a warmwater stream. The site selected for this study was the North Anna River, a major tributary of the York River in Eastern Virginia. Detailed descriptions of the river are included in the following sections. The site was selected for several reasons: it supports a reproducing population of smallmouth bass, flows in the river are altered by a dam in the upstream section, and clarity in the river is good, which permitted me to observe behavior of age-0 smallmouth bass in various microhabitats.

The first objective of this study was to accurately describe the microhabitat use by age-0 smallmouth bass from the time they leave the nest until late into their first growing season. By obtaining a detailed description of microhabitat use during all early life stages, I tried to identify habitat characteristics that could affect foraging success, growth, and survival during each stage. My next objective was to assess the profitability of microhabitats occupied by age-0 smallmouth bass. Then I examined growth rates of individuals throughout the summer to determine if growth at any time was related to growth earlier in life. If certain microhabitats were more profitable and certain individuals maintained growth advantages through time, it would imply that a limited amount of profitable microhabitats were available and only a few individuals exploited those areas. Finally, I examined the foraging behavior of age-0 smallmouth bass to determine if aspects of foraging behavior could determine which individuals grew fastest. From all these results I hoped to determine if manipulation of microhabitat availability could increase the growth rates of age-0 smallmouth bass in the North Anna River, and if increasing growth rates would enhance recruitment.

CHAPTER 1

Temporal Variation in Microhabitat Use by Age-0 Smallmouth Bass in the North Anna River, Virginia

Introduction

Fisheries managers try to identify critical instream habitats based on observations of microhabitat use by stream fishes. However, stream fishes may change their microhabitat use during different seasons (Rimmer et al. 1983, 1984, Johnson and Kucera 1985, Grossman and Freeman 1987, Hillman et al. 1987), in response to changes in availability of one or more habitat variables (Morantz et al. 1987, McMahon and Hartman 1989, Shirvell 1990, Burgert et al. 1991), or in response to the presence of predators (Power 1987, Gotceitas 1990, Harvey 1991), or competitors (Fausch and White 1981). Stream fishes may also alter their microhabitat use as they progress through stages of ontogenetic development (Baltz et al. 1991).

For most fishes, rapid anatomical and physiological changes occur during the larval and early juvenile stages of development. These changes alter how larval and juvenile fish function in their environment, and subtle variations in either the rate of ontogenetic development or environmental conditions can correspondingly alter their mortality rates (May 1974, Houde 1989). Larval and juvenile fish do not necessarily remain in prevailing environmental conditions but may actively seek out better nursery habitats where they can most successfully forage and avoid predators (Bohelert and Mundy 1988). Whenever microhabitat characteristics vary spatially and temporally, microhabitat use by larval and juvenile fish could exert a particularly strong influence on growth and survival.

Size affects how larval and juvenile fish function in their environment (Miller et al. 1988) and may therefore affect their microhabitat use. Generally, as fish grow in size their swimming ability improves (Webb and Weihs 1986), vulnerability to predators declines (Luecke et al. 1990), and the size of their preferred prey increases (Crowder et al. 1987). Size could affect microhabitat use of larval and juvenile fish in streams if larger individuals exploited resources in areas that smaller individuals could not enter. In that instance, faster growing individuals could gain a significant growth and survival advantage over the other members of their cohort.

Few examinations of microhabitat use by juvenile fishes in streams have compared use of habitat variables during different periods of ontogenetic development. For example, studies of microhabitat use by smallmouth bass generally assumed all young-of-the-year occupied similar habitats (Sechnick et al. 1986, Bain et al. 1988, Leonard and Orth 1988, Lobb and Orth 1991), or divided age-0 fish into categories based arbitrarily on size (Aadland et al. 1989).

However, age-0 smallmouth bass pass through several stages of morphological development (Meyer 1970) that could affect their preference for certain microhabitat variables. Additionally, during the period when male smallmouth bass guard their progeny, adult habitat preferences may affect microhabitat use by larval smallmouth bass (Ridgeway 1988). No studies have tracked the microhabitat use of a cohort of smallmouth bass from spawning through the first months of the growing season or determined if large and small individuals consistently occupy different microhabitats.

The primary objective of this study was to quantify the microhabitat use by smallmouth bass in the North Anna River, Virginia, during all biologically significant stages of their first growing season. I examined microhabitat use when larvae were guarded by their male parent, after larvae lost the protection of the male, and as juveniles dispersed throughout the river. I also tested the hypothesis that within periods when microhabitat use was sampled, large individuals occupied different microhabitats than small individuals.

Methods

Study Site

The North Anna River forms part of the York River basin and flows through both the Piedmont and Coastal Plain Physiographic Provinces of eastern Virginia (Figure 1.1). In 1972, Virginia Power and Electric Company (VEPCO) impounded the river approximately 64 km from its headwaters to create a cooling-water reservoir (Lake Anna) for a nuclear power plant. The dam maintains a minimum discharge of 1.13 m^3/s from the epilimnion of Lake Anna into the river. This discharge usually becomes the average discharge in the river during the dry summer months. Comparisons of discharge records between the North Anna and the unregulated South Anna River suggest that after heavy rains in the summer, the dam maintains an elevated discharge in the North Anna for several days longer than would naturally occur.

Simmons and Voshell (1978) and Kondratieff and Voshell (1980) described the habitat types, water quality, and benthic macroinvertebrates communities in the river after impoundment. Deciduous trees grow on the river's banks and form a dense, overhanging canopy along most of the shoreline. Immediately below the dam, the river primarily consists of long pools (average width approximately 30 m) underlain with sandy substrate. Largemouth bass (Micropterus salmoides) are the most numerous piscivore in

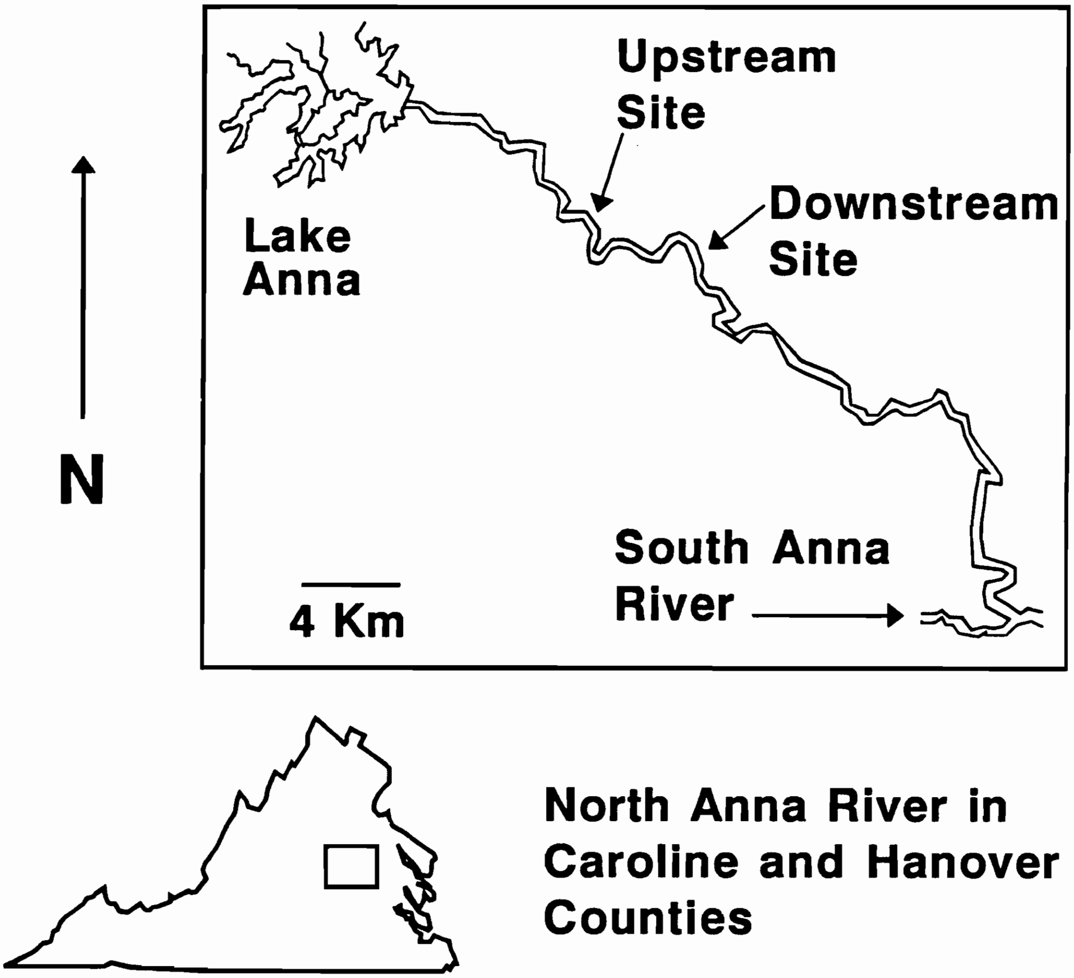


Figure 1.1. Location of study sites on the North Anna River in eastern Virginia. The upstream site was approximately 400 m long, and the downstream site was approximately 650 m long.

this section but smallmouth bass become more numerous approximately 16 km downstream from the dam (VEPCO 1986). At this point the river widens (average width approximately 40 m), and riffle habitats and bedrock substrate occur more frequently than in the upstream section. Smallmouth bass reproduce in this section and their growth rates in the river rank among the highest growth rates recorded for smallmouth bass in Virginia (King et al. 1991).

At minimum discharge, water depths in the river are usually less than 2.5 m but exceed 3.0 m in some pools. Visibility in the river regularly exceeds 3.0 m, and the exceptional clarity promotes growth of attached algae and submerged macrophytes throughout much of the river. The river contains at least 12 species of fish that could serve as prey for most size classes of smallmouth bass, but redbreast sunfish (Lepomis auritus) are the most numerous and widely distributed.

Nesting densities of smallmouth bass were low in the North Anna River during 1990 and 1991, so I searched for broods of larval smallmouth bass throughout a reach of the river that extended 8 km south from the Route 603 bridge in Hanover County. This reach was within the lower section of the river where smallmouth bass were the dominant piscivore. Larvae metamorphosized into juveniles at approximately 20 mm total length, when they acquired their full fin-ray and scale compliment (Meyer 1970), and after they had dispersed from brood sites. After juvenile smallmouth bass dispersed throughout the river, I monitored the microhabitat use of juveniles in two study sites on the river. An upstream site (approximately 405 m long, average width 29 m) was located approximately 0.8 river km downstream from the Route 603 bridge in Hanover County (Figure 1.1). This site lies within the portion of the river where fast water habitats and bedrock substrate increase in abundance. The other site was located approximately 4 km downstream of the first, beginning at the Route 601 Hanover County bridge and extending upstream approximately 640 m (average width 38 m). At this point in the river, bedrock is the most common substrate.

Quantifying microhabitats used by larvae in broods

Quantifying microhabitat use at different larval stages presented some problems because the behavior of male parents determined what microhabitats were available to the larvae. After leaving the nest, larvae occupied an area guarded by the male parent, and he prevented them from leaving that area. Individual larvae did not remain in one place or seek preferred microhabitats within the brood site, but were forced to move throughout the site in response to changes in density of their siblings or the appearance of predators (personal observation). Male parents gradually decrease the intensity with which they guard broods until they abandon their larvae (Ridgeway 1988), and larvae then disperse from the brood site. At dispersal, all microhabitats in the river are (theoretically) available to larvae, and because larvae disperse into a larger area, their microhabitat use is less affected by density of conspecifics. Therefore, my comparison of microhabitat use between brood and dispersed larvae equated to a comparison of what microhabitats were available in brood sites to what microhabitats were used by dispersed larvae outside of the brood area.

Rather than estimating microhabitat availability within brood areas by measuring habitat variables at randomly selected points, I attempted to estimate microhabitat availability based on area. I visually examined brood areas, and delineated blocks within which microhabitat variables did not substantially vary. The method I employed (described below) insured that I could rapidly quantify all visible changes in any microhabitat variable within a brood site without having to measure microhabitat characteristics at a large number of randomly selected points. The time factor was important because broods swam-up during a short period, and I wanted to quantify the available habitat in as many brood sites as possible before larvae dispersed. The method also enabled me to estimate the amount of brood area associated with each incremental change of microhabitat variables. The major disadvantage of this method was that it prohibited direct statistical comparison of the microhabitat availability in brood sites with microhabitat use of dispersed larvae.

I searched for smallmouth bass nests and broods of larvae by snorkeling in the river during the springs of 1990 and 1991. Temperature affects the developmental rate of larval smallmouth bass (Webster 1948, Shuter et al. 1980) and the thermal regime of the North Anna requires larvae to remain on the nest for 3-5 days after hatching. I attempted to quantify the habitat characteristics of these brood areas 3-7 days after larvae first left the nest (swim-up).

When possible I verified the exact date of swim-up by locating a nest prior to swim-up and monitoring it each day until larvae left the nest. From each of these broods I collected 5-10 larvae, preserved them on ice, and measured their total length (TL, mm) the same day using a dissecting microscope equipped with an ocular micrometer. Larvae collected from nests were 9-14 mm in TL, 3-7 days after swim-up. When a brood was not located before swim-up, the brood site habitat was only quantified when the larvae were 9-14 mm in TL.

At each brood site, a snorkeler placed markers at the points furthest upstream and closest to each shore where brood larvae were observed. The points where larvae occurred closest to each shore and furthest downstream were also marked and these points delineated the corners of a four-sided polygon that outlined the brood area. For each corner, the distance and bearing to at least one other corner was recorded, and in each area there was at least one corner for which the distance and bearing to at least two other corners was recorded. These measurements were used later to estimate the size of each brood site and availability of habitat within them.

Transects were oriented along the longest side of the brood site that paralleled stream flow. If the longest side was less than 25 m, transects were placed at 25%, 50%, and 75% of the distance between the upstream and downstream corners on both sides (Figure 1.2). If the longest side was greater than 25 m, transects were placed at 20%, 40%, 60%, and 80% of the distance between the upstream and downstream corners.

I visually inspected microhabitat along each transect and stopped every two meters or at every point where the depth, water velocity, or the substrate noticeably changed. The width of blocks therefore varied depending upon the frequency of changes in microhabitat characteristics. At the center of each block, I recorded the depth (m), mean water column velocity (0.6 of depth, cm/s), and visually described the most common substrate type and all available cover objects in the block. Velocity was measured with a pygmy current meter mounted on a metric wading rod. Substrate descriptions were based on a modified Wentworth scale (Appendix 1) described by Bovee (1982).

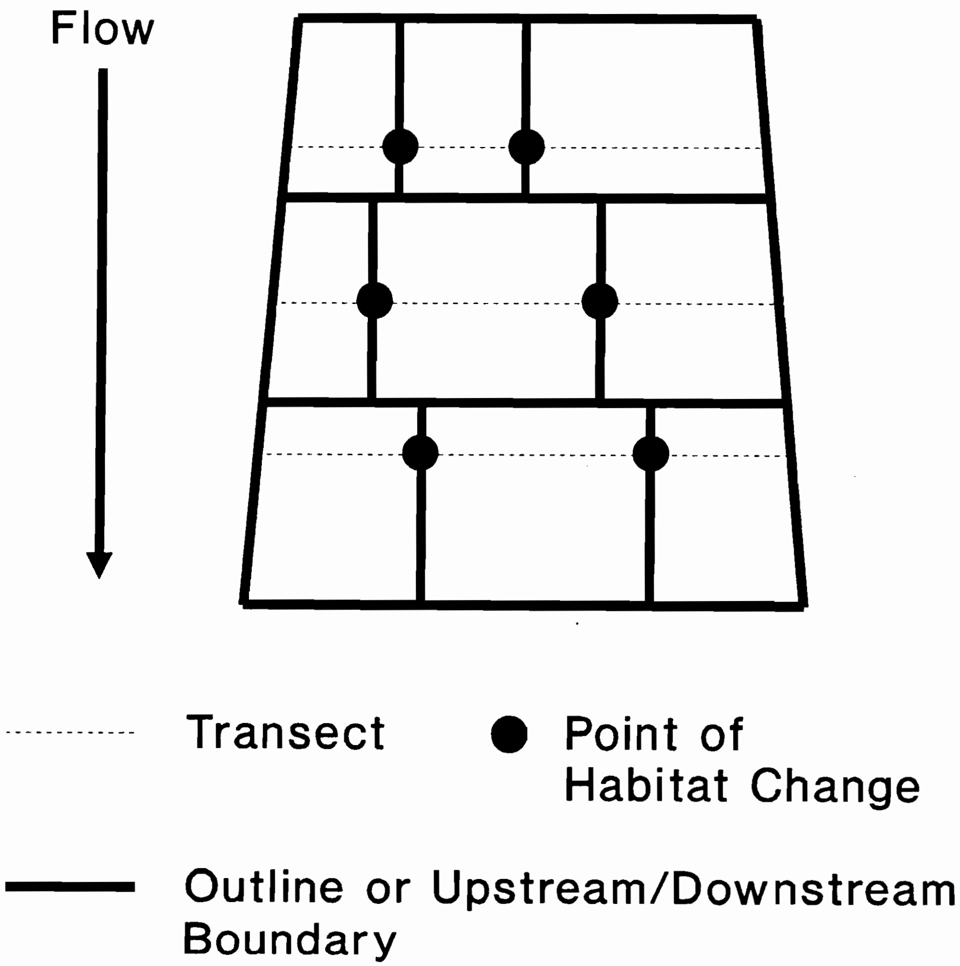


Figure 1.2. Example of habitat quantification in brood sites. Outline of the brood site is based on markers placed at the four corners. Upstream/downstream boundaries divide the brood site into three sections (upstream, middle, downstream). Sections were subdivided laterally at points along transects where noticeable changes in depth, mean velocity, substrate occurred. Area of habitat blocks was used to estimate overall habitat availability.

Microhabitat availability was based on the estimated area of each of these blocks. The outline of each brood site was drawn based on the distances and bearings recorded at the corners. If three transects were placed in the brood area, lines were drawn connecting the sides paralleling the flow at 33% and 66% of the distance between the upstream and downstream corners. If the brood site required four transects then the lines were drawn connecting points at 25%, 50%, and 75% of the distance between the upstream and downstream corners. These lines represented the upstream and downstream boundaries of the blocks identified along each transect. Through each point along a transect where I detected changes in habitat characteristics I drew a vertical line (parallel to the stream flow) that connected the upstream and downstream boundaries and delineated the outline of each habitat block (Figure 1.2).

The area of each block was estimated using a digital planimeter. To determine the percent composition of all brood sites for each microhabitat characteristic, I summed the areas of blocks that contained identical depths, velocities, substrate or cover types and divided these by the total area quantified. The influence (or "weight") of an individual block on the distributions of habitat variables depended on the area the block encompassed.

Quantifying microhabitat use by dispersed larvae.

I revisited broods 3-7 days after male abandonment and quantified the microhabitat used by dispersed larvae. During both 1990 and 1991, spawning densities were low enough that I could always establish the brood from which larvae dispersed (i.e. no two broods were located in close proximity to each other). When I located the larvae that dispersed from a brood, I marked the position of up to 15 individuals per brood and recorded their estimated position in the water column. By limiting the number of larvae sampled per brood, I reduced the influence that the microhabitat use of larvae from any one brood would have on the combined use distribution of all dispersed larvae.

At each point where dispersed larvae were observed, I recorded the depth and mean and focal-point (nose) velocities, and I visually estimated the most common substrate type and all cover objects within a 1-m radius. I collected 2-3 individuals from each brood of dispersed larvae, preserved them on ice, and measured their TL the same day. Total lengths were measured using a dissecting microscope equipped with an ocular micrometer.

Quantifying microhabitat use by juveniles.

Underwater observation is an effective means of locating fish for habitat use studies in clear water and deep habitats (Cunjak et al. 1988, Heggenes et al. 1990), which both commonly occur in the North Anna River. In each of the two study sites, two snorkelers searched for juvenile smallmouth bass two weeks, six weeks, and (in 1991) ten weeks after larvae dispersed from the brood sites. Snorkelers moved upstream and searched for juveniles within three meters on either side of four transects that extended the length of the study site. Of the four total transects, two were located three meters from either shore and two were located nine meters from either shore. Snorkel surveys were only conducted between 0800 and 1200 hours when visibility in the river exceeded 2.5 m, and the dam was releasing 1.13 m^3/s. All four transects could be searched in one morning in the upstream site but only two transects could be searched in one morning in the downstream site.

A numbered marker was placed at the point where each juvenile was first observed and its position in the water column was estimated and recorded. Snorkelers estimated the TL of each juvenile using a calibrated mask bar (Swenson et al. 1988). After snorkelers searched the transects, they revisited the marked positions and recorded the same habitat measurements that were recorded for dispersed larvae.

Additionally, the locations of juveniles in the study site were mapped in relation to reference stakes placed along the shorelines. By mapping the positions of juveniles I could determine if observed changes in microhabitat use were the result of juveniles moving among different portions of the river. In particular, I examined distributions to determine if individuals occupied shorelines or midchannel areas more frequently during different life stages and if individuals changed their use of riffle, run, and pool habitats over time.

Statistical analysis.

I divided the comparisons of habitat use into two groups: comparisons between brood habitats and microhabitat use of dispersed larvae, and comparisons between microhabitat use by dispersed larvae and juveniles. Because the habitat use by brood larvae had to be quantified per m^2, the habitat composition of brood sites could not be statistically compared to point microhabitat measurements made on dispersed larvae. Instead I tried to identify consistent differences in percent composition of brood habitats and percent use of depth, mean velocity, substrate, and cover by dispersed larvae.

I compared microhabitat use by dispersed larvae with use by juveniles observed two weeks after dispersal, and use by juveniles observed two weeks after dispersal with use by juveniles observed six weeks after dispersal. In 1991, I collected data on habitat use of juveniles at 10 weeks after dispersal but did not compare it statistically to samples from other periods because the sample size at 10 weeks was relatively small (N=48).

I was interested in comparing location and dispersion of all habitat use distributions and could therefore not use a multiple comparison test that focused only on location differences (i.e. ANOVA, Kruskall-Wallis tests). Instead I used two-sample, nonparametric analyses to test for overall differences in distributions. Because two comparisons were made for each variable, I set the alpha level for rejection at 0.025 to provide 95% confidence in detected differences for each variable.

Kolomogorov-Smirnov, two-sided tests were used to test for differences among use of depth, distance off the bottom, and velocity variables by dispersed larvae and juveniles observed two, six, and ten weeks after dispersal. I tested for differences in substrate and cover use among stages of dispersed larvae and juveniles using two-sided G-tests.

For each stage of habitat use by juveniles, I compared the use of all habitat variables by the larger and smaller halves of the sample. I tested for differences in depth and velocity variables between periods using two-tailed Kolomogorov-Smirnov tests, and tested for differences in substrate and cover variables using two-tailed G-tests. Alpha levels for rejection were set at 0.025 to provide 95% confidence in detected difference for each variable.

Results

Chronology of spawning and larval dispersal during 1990-91.

Successful spawning in 1990 may have been delayed by a series of high flows and a drop in temperature below 15°C on day 107 (Figure 1.3). Consequently, I did not observe free-swimming larvae in the river until calendar day 139 (19 May). Between days 139 and 146 (26 May), I collected data on five brood sites. Before larvae could disperse from the brood sites, a large flood (> 120 m^3/s) lasting from day 148 (28 May) to day 156 (5 June) destroyed most smallmouth bass larvae in the river. Free swimming larvae were next observed on day 160 (9 June), and between day 160 and 174 (23 June) I collected data on four more brood sites. In total, I quantified microhabitat characteristics of 94 blocks (average area = 4.1 m^2) that comprised 342 m^2 of brood site habitat (average brood area = 37.5 m^2). Between day 171 (20 June), and 181 (30 June) I collected data on 93 larvae that dispersed from these four broods and from two other groups of dispersed larvae that were not located until after their male parent had abandoned the brood site.

On day 105 (15 April) of 1991, I observed smallmouth larvae on three nests but did not quantify habitat in these brood sites or observe free swimming larvae from these nests. Between day 123 (3 May) and 151 (31 May), I collected data on 15 brood sites (average brood area = 63.8 m^2) that covered a total area of 939 m^2 that I divided into 150 blocks of homogeneous microhabitat (average block = 6.3 m^2). Data on 155 dispersed larvae from 10 of those brood sites were collected between days 127 (7 May) and 134 (14 May). I did not observe dispersed larvae from the other five broods.

Habitat use by brood larvae and dispersed larvae.

In both 1990 and 1991, more than 30% of the area in brood sites contained mean velocities higher than 4 cm/s, and no large cover or substrate (Figure 1.4). Less than 7% of the dispersed larvae observed in either 1990 or 1991

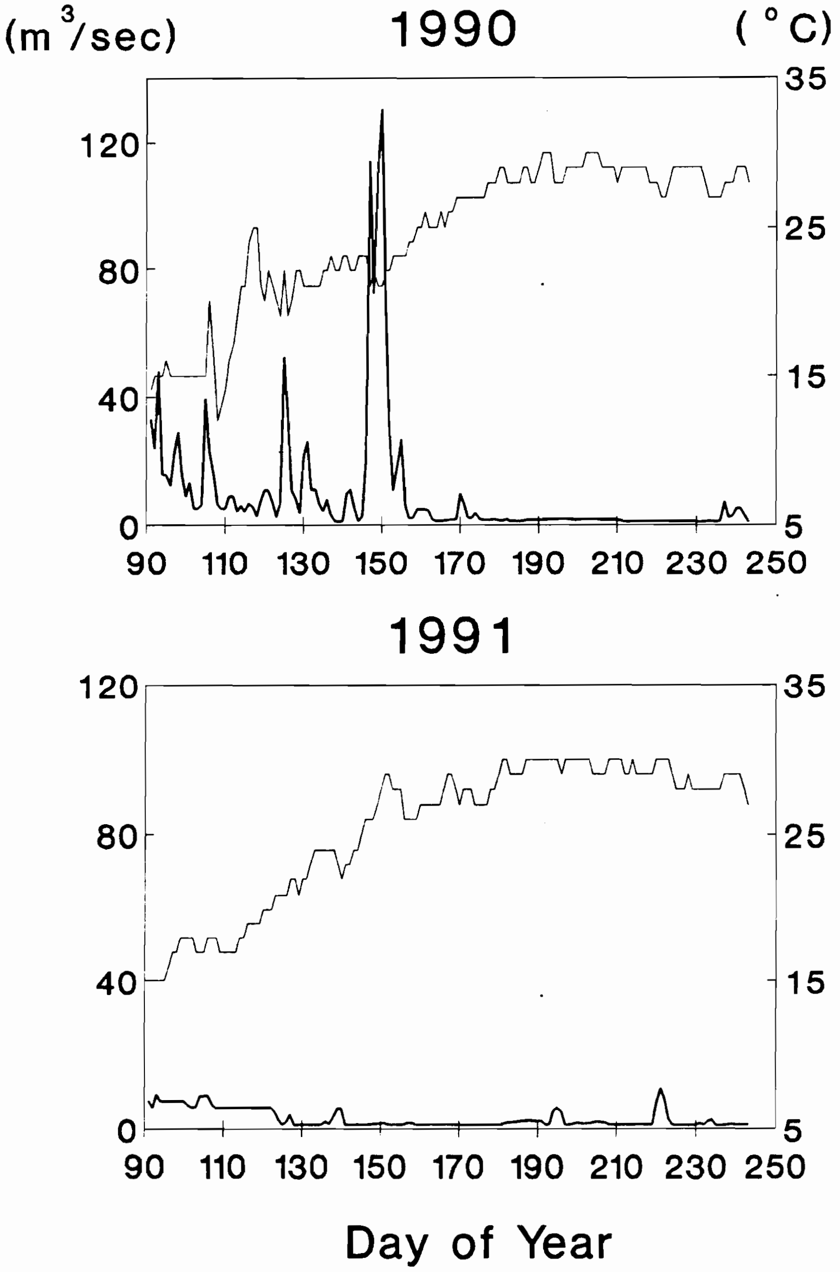


Figure 1.3. Temperature (thin line, °C) and discharge (thick line, m^3/s) in the North Anna River during the growing seasons (April 1 - August 30) of 1990 and 1991.

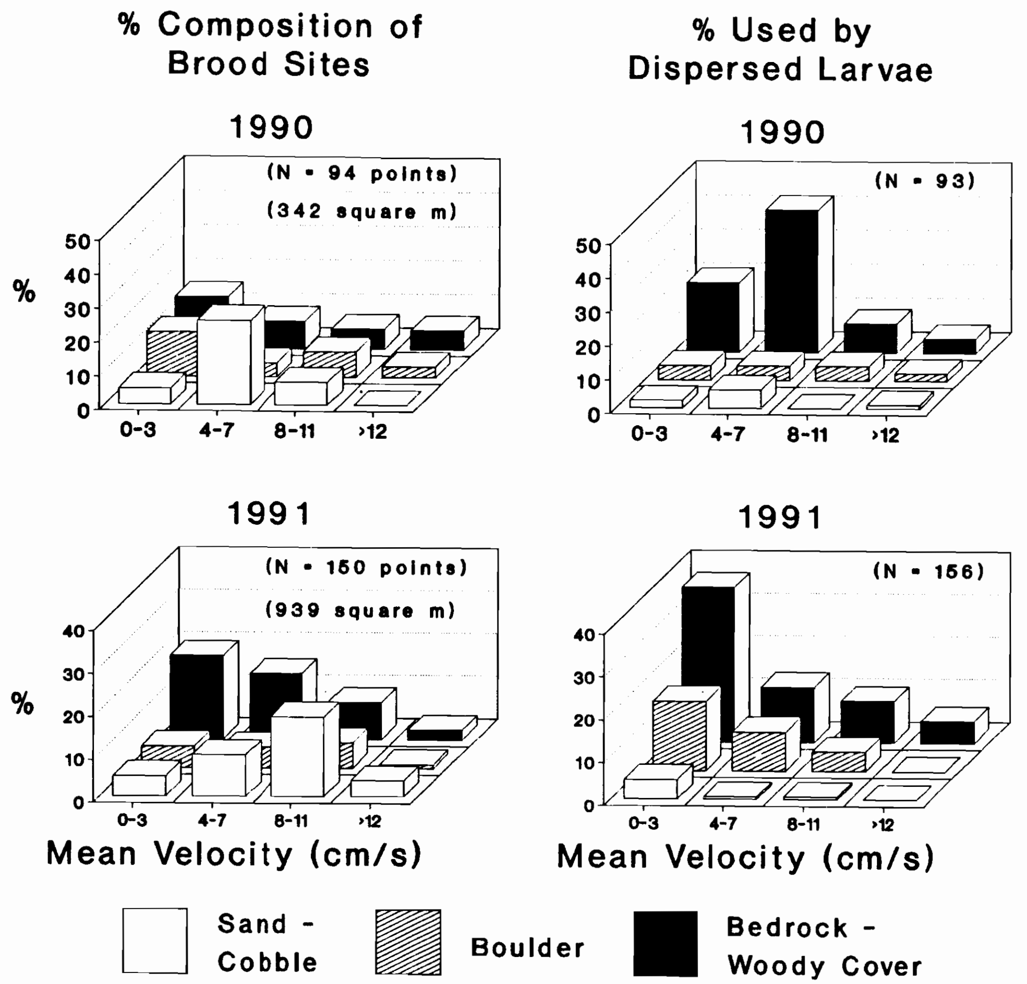


Figure 1.4. Mean velocity (cm/s) and substrate composition of 24 brood sites (9 in 1990, 15 in 1991) compared to mean velocities and substrates used by larval smallmouth bass that had dispersed from brood sites, 1990 and 1991.

occupied microhabitats with all those characteristics. While some dispersed larvae during both years occupied areas with mean velocities greater than 4 cm/s, most of these individuals were sheltered by woody cover or shelves of fractured bedrock.

Less distinct and less consistent differences existed between the depth composition of brood sites and depths used by dispersed larvae. In 1990, 74% of the observed brood area was 76-125 cm deep, but 67% of the dispersed larvae occupied microhabitats that were 126-175 cm deep (Figure 1.5). In 1991, 59% of the brood area observed was greater than 100 cm deep but 80% of the dispersed larvae used depths less than 100 cm. During both years, dispersed larvae occupied a narrower range of depths than was present in the brood sites.

Microhabitat use by dispersed larvae and juveniles.

During both years, I collected data on microhabitats used by smallmouth bass ranging between 15 and 120 mm TL (Figure 1.6). Only 13 juvenile smallmouth bass were observed in the two study sites on day 184 (3 July, approximately two weeks after dispersal). I collected microhabitat data on 30 juveniles observed outside of the study sites during days 186-194 (5-13 July). Between days 195-199 (14-18 July), 77 juveniles were observed in the study sites. The use distributions of habitat variables did not statistically differ (all $P > 0.20$) between juveniles observed during days 185-194 and days 195-199, so I combined all 120 of these juveniles into one sample (the July 1990 sample).

As the growing seasons of 1990 and 1991 progressed, juvenile smallmouth bass moved into shallower microhabitats (Figure 1.7). (See Appendix 2 for box plot format). During

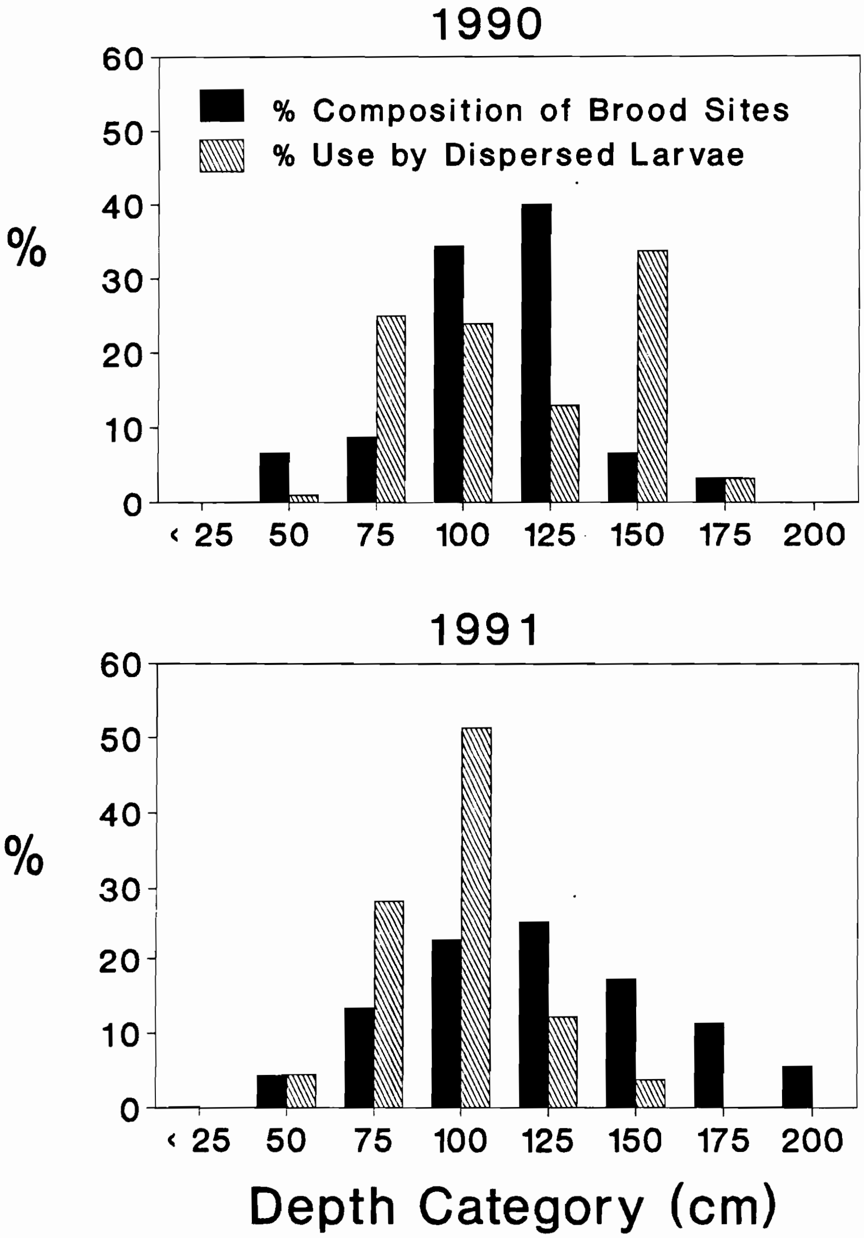


Figure 1.5. Frequency of depths (cm) in brood sites compared to frequency of depths used by larval smallmouth bass that had dispersed from brood sites, 1990 and 1991.

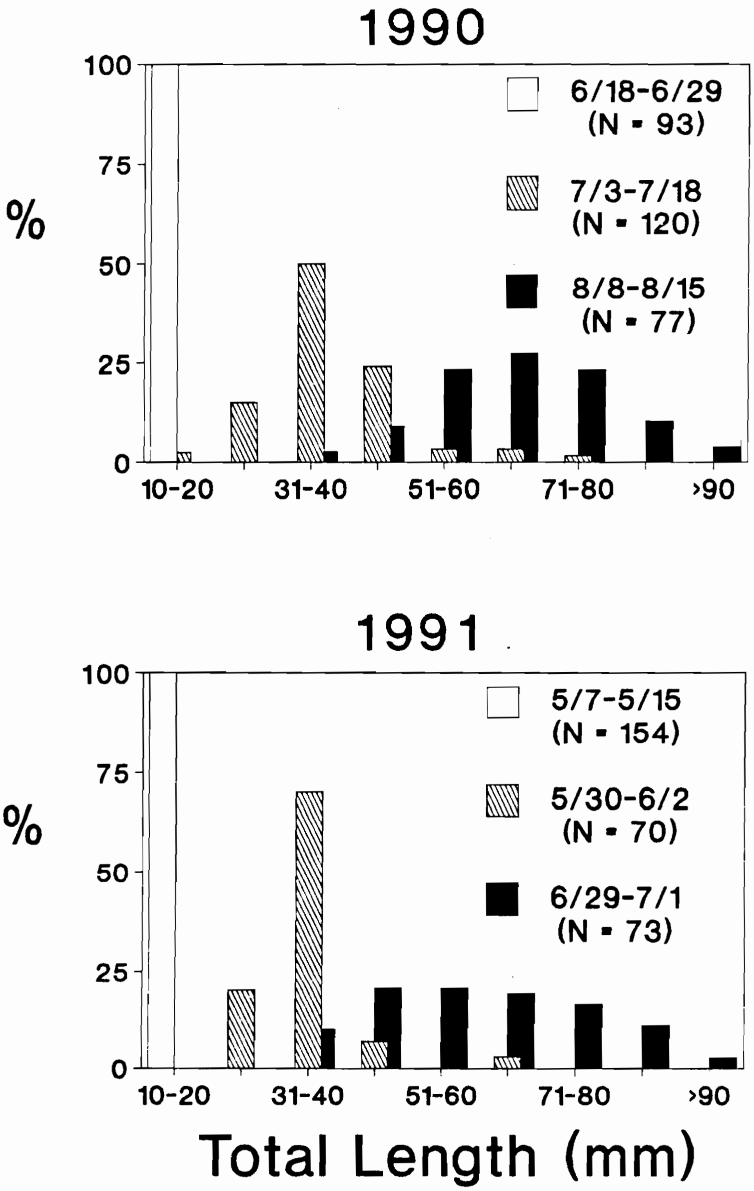


Figure 1.6. Estimated total lengths (mm) of dispersed larval and juvenile smallmouth bass observed during habitat use surveys, 1990 and 1991.

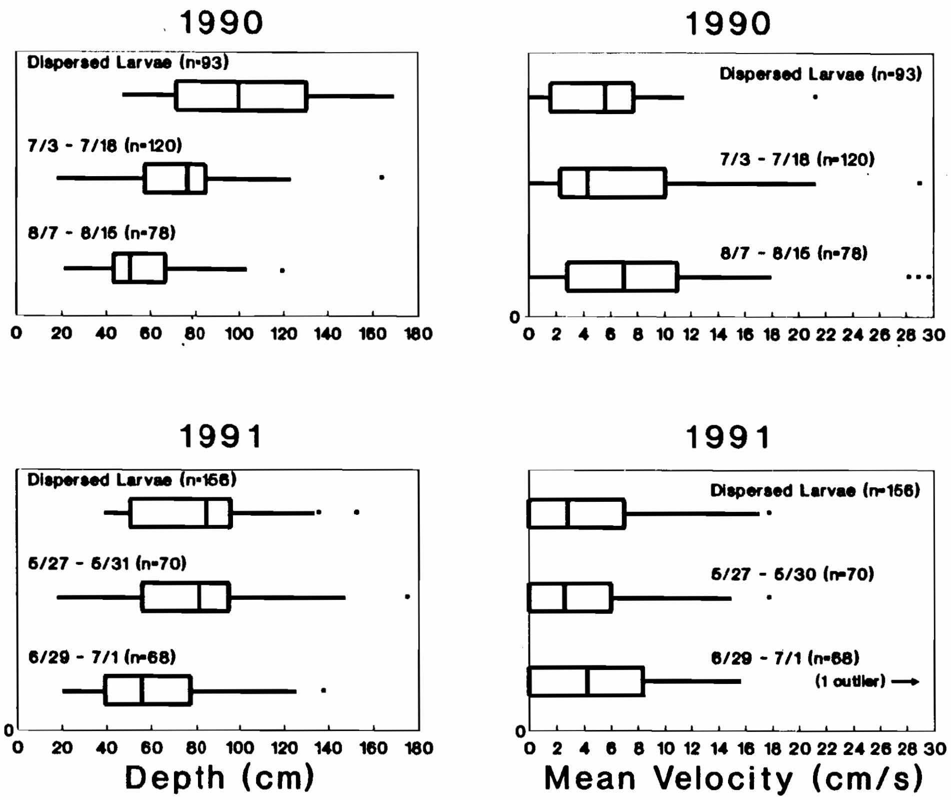


Figure 1.7. Box plots representing distributions of depths (cm) and mean velocities (cm/s) used by dispersed larval and juvenile (all plots not labeled as larval) smallmouth bass, 1990 and 1991.

1990, dispersed larvae occupied a mean depth of 102 cm, while juveniles occupied a mean depth of 74 cm in July and 55 cm in August. The distribution of depths used by juveniles in July differed from the distribution used by dispersed larvae, and the depth distribution in August differed from the distribution used in July (all $P < 0.00001$, Table 1.1). The mean depth used in 1991 also decreased as the growing season progressed (dispersed larvae = 84 cm, May = 83 cm, June = 62 cm), the depth distribution observed in May differed from the distribution for dispersed larvae, and the June distribution differed from the May distribution (all $P < 0.022$).

Juveniles tended to increase the range of mean velocities they used over time (Figure 1.7). All stages of age-0 smallmouth bass generally used mean velocities less than 20 cm/s, but juveniles were observed in mean velocities up to 86 cm/s. The mean velocities used by juveniles in July 1990 differed from the mean velocities used by dispersed larvae that year ($P < 0.022$, Table 1.1), but no other comparisons between mean velocity distributions demonstrated statistical differences for either year (all $P > 0.22$).

Age-0 smallmouth bass typically occupied focal point velocities that were slower than the mean velocity. At some point in both years, juveniles began using faster focal point velocities than they previously used (Figure 1.8). In 1990, the average focal point velocity of 1.4 cm/s for dispersed larvae increased to 3.6 cm/s in July and the distributions of focal point velocities differed between those periods ($P < 0.0009$, Table 1.1). The use of focal point velocities in June 1991 differed from the observed use in May of that year ($P < 0.0004$), with the mean of 1.1 cm/s in May increasing to 5.6 cm/s in June. During all stages,

Table 1.1. Results of statistical tests for differences in use of habitat variables by juvenile smallmouth bass during different periods of the growing seasons of 1990 and 1991 in the North Anna River. The alpha level for rejection of the null hypothesis was set at 0.025.

Comparison	Mean Depth	Water Velocity	Focal Point Velocity	Distance Off Bottom	Substrate	Cover
DL 1990 vs. July 1990	KS=0.46 P<0.001	KS=0.21 P<0.022	KS=0.27 P<0.001	KS=0.33 P<0.001	G=35.06 P<0.001	G=39.7 P<0.001
July 1990 vs. August 1990	KS=0.35 P<0.001	KS=0.12 P>0.49	KS=0.20 P>0.04	KS=0.14 P>0.28	G=10.78 P>0.20	G=14.49 P>0.05
DL 1991 vs. May 1991	KS=0.22 P<0.022	KS=0.14 P>0.34	KS=0.05 P>0.99	KS=0.25 P<0.006	G=15.28 P>0.10	G=10.38 P>0.15
May 1991 vs. June 1991	KS=0.37 P<0.001	KS=0.15 P>0.22	KS=0.35 P<0.001	KS=0.34 P<0.001	G=0.012 P>0.99	G=2.469 P>0.95

DL 1990 = Dispersed Larvae, 1990 (N=93)
July 1990 = 7/3 - 7/18, 1990 (N=120)
August 1990 = 8/7 - 8/15, 1990 (N=78)

DL 1991 = Dispersed Larvae, 1991 (N=155)
May 1991 = 5/27 - 5/30, 1991 (N=70)
June 1991 = 6/29 - 7/1, 1991 (N=68)

Cover Sample Sizes
DL 1990 = 102
July 1990 = 144
August 1990 = 105

DL 1991 = 210
May 1991 = 116
June 1991 = 115

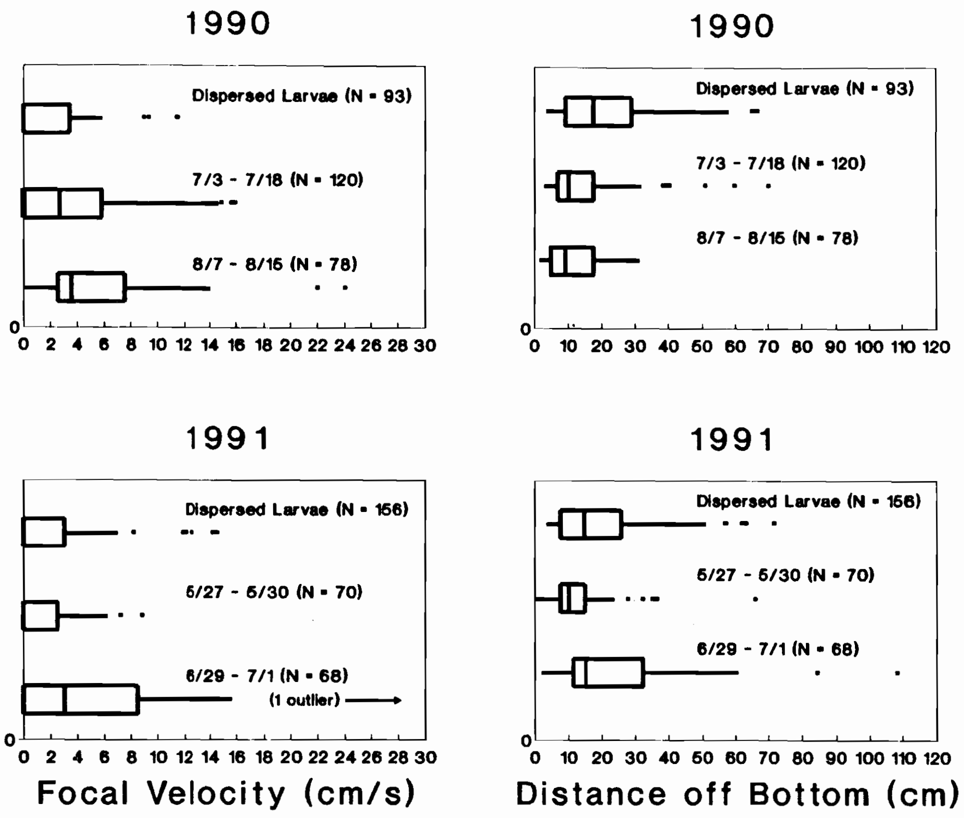


Figure 1.8. Box plots representing distributions of focal point velocities (cm/s) and distance from the bottom (cm) where dispersed larval and juvenile (all plots not labeled as larval) smallmouth bass were observed, 1990 and 1991.

the mean focal point velocities used by age-0 bass indicated that the average individual had to swim one body length/s or less to maintain their position.

During both years, dispersed larvae were found further from the bottom than juveniles observed 14-20 days later (Figure 1.8). In 1990, the mean distance of dispersed larvae from the bottom was 23 cm and juveniles observed two weeks later averaged 14 cm off the bottom. For the same life stages in 1991, average distance off the bottom decreased from 19 to 13 cm. Distributions of distances off the bottom differed between these two life stages in both years (all $P < 0.006$, Table 1.1). By June 1991, the mean distance off the bottom increased to 23 cm and the distribution in June differed statistically from that observed in May ($P < 0.0006$). Age-0 smallmouth bass were occasionally observed at the surface, but more than 90% of all individuals occupied the bottom half of the water column.

Substrate and cover use of age-0 smallmouth bass varied little over time in either year (Figure 1.9). Fractured bedrock/boulder was always the most frequently used substrate type (53-89% of use during all sampling periods) and sand was usually the only other regularly used substrate (5-27% of use). Substrates other than fractured bedrock and sand do not commonly occur in this portion of the river (Groshens 1993). In 1990, 19.6% of the dispersed larvae used points where cobble was the primary substrate, and consequently their substrate and cover use differed from that of juveniles observed in July (both $P < 0.001$). No other comparisons detected differences among age-0 individuals in their substrate or cover use (all $P > 0.05$). Most larvae used microhabitats where rock crevices were present (46.2-95.0% of use during all sampling periods).

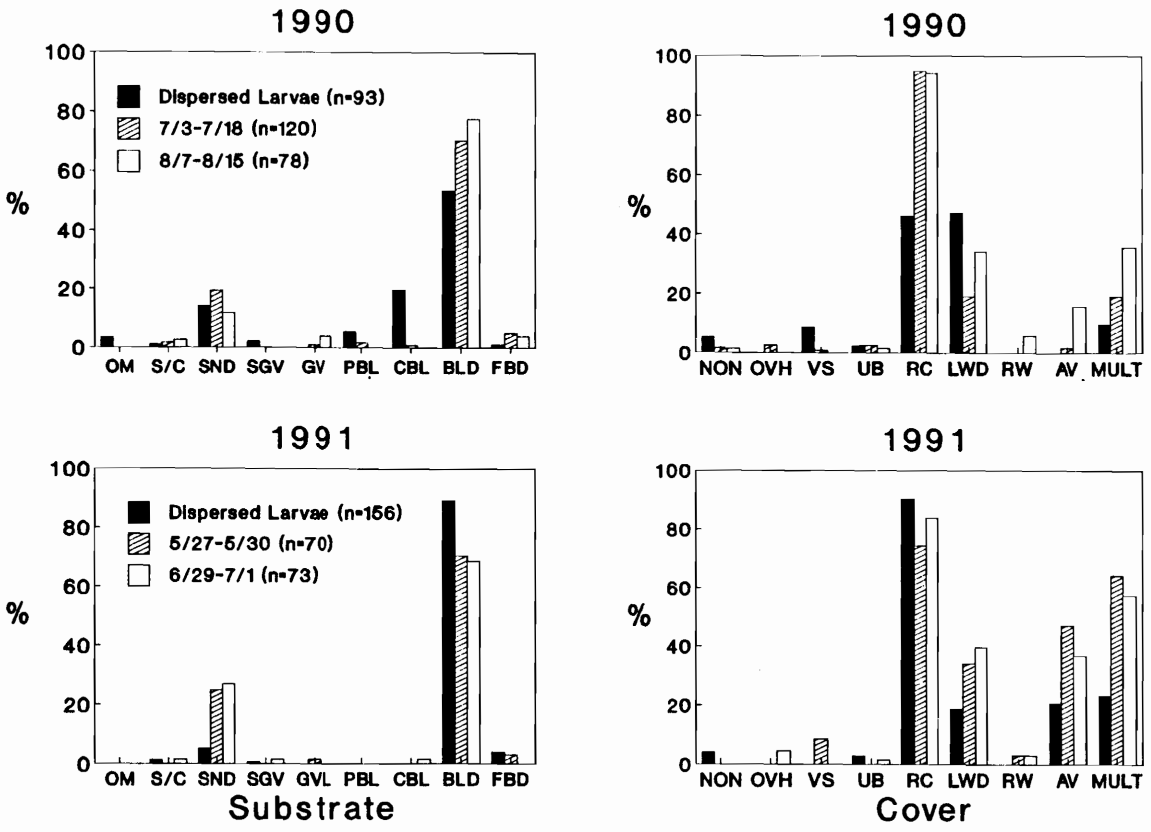


Figure 1.9. Substrate and cover used by dispersed larval and juvenile (all plots not labeled as larval) smallmouth bass, 1990 and 1991. (OM=organic matter, S/C=silt/clay, SND=sand, SGV=small gravel, GVL=gravel, PBL=pebble, CBL=cobble, BLD=boulder/fractured bedrock, FBD=flat bedrock, NON=none, OVH=overhead, out-of-stream, VS=velocity shelter, UB=undercut bank, RC=rock crevice, LWD=large woody debris, RW=rootwad, AV=aquatic vegetation, MULT=multiple).

Large woody debris was frequently used during all sampling periods (18.7-47.3% of use), and in 1991 a high proportion of individuals used aquatic vegetation (20.6-47.1%). A significant number of individuals were observed within 1 m of multiple cover types (9.7-64.3% during all sampling periods).

Microhabitat use by large and small individuals.

During all periods of juvenile microhabitat sampling in 1990 and 1991, the larger half of the age-0 cohort occupied the same depths, mean velocities, and nose velocities as the smallest half of the cohort (all $P > 0.06$, Table 1.2). Neither larger or smaller juveniles exhibited consistent trends in either year for any of these habitat variables (Appendices 3-5).

Comparisons between the largest and smallest 25% of the age-0 cohort indicated that at some time during both years, small juveniles occupied shallower depths than larger juveniles. Depth distributions differed between the largest and smallest 25% of the cohort during July of 1990 ($P < 0.007$) and July of 1991 ($P < 0.03$). Distributions of mean and focal point velocities did not differ between the largest and smallest 25% of the cohort during either year. These results should be interpreted cautiously, because the sample sizes used in the comparisons were relatively small (all $N < 35$). In general, these comparisons indicated that small individuals were not less likely to explore previously unused microhabitats than large individuals were.

Spatial habitat use by juveniles.

During both years, juveniles concentrated in pools during the first 2-4 weeks after dispersal, but 6-8 weeks after dispersal they distributed themselves more evenly

Table 1.2. Results of statistical tests for differences in use of habitat variables by the largest and smallest 50% of observed smallmouth bass during periods of data collection in 1990-1991. The alpha level for rejection of the null hypothesis was set at 0.025.

Comparison	Depth	Mean Velocity	Nose Velocity
July 1990	KS=0.15 P>0.53	KS=0.11 P>0.97	KS=0.10 P>0.98
August 1990	KS=0.10 P>0.98	KS=0.14 P>0.92	KS=0.20 P>0.41
May 1991	KS=0.18 P>0.63	KS=0.26 P>0.19	KS=0.13 P>0.98
June 1991	KS=0.31 P>0.05	KS=0.25 P>0.25	KS=0.25 P>0.19

among habitat types (Figures 1.10 and 1.11). In 1990, 76.1% of the juveniles were in deep pools in July, but in August 58% of the juveniles occupied runs or riffles. In May 1991, 83.9% of juveniles were located in deep pools, but 60.8 % of juveniles in June and 48.9% of the juveniles in August occupied runs and riffle areas. Juveniles did not appear to occupy shorelines more than mid-channel areas in any habitat type. Observed changes in microhabitat use probably occurred because large numbers of juveniles moved out of pools and into riffles and runs.

Discussion

During 1990 and 1991, age-0 smallmouth bass in the North Anna River exhibited two distinct changes in microhabitat use over a relatively short period of time (<10 weeks) during which habitat availability remained constant. First, larvae sought out low velocity microhabitats after dispersal, and 4-6 weeks later most juveniles moved out of those low velocity areas and into shallower microhabitats associated with riffles and runs. Water temperatures varied between the times when microhabitat data was collected (> 5°C) and may have encouraged smallmouth bass to change their microhabitat use. When a wide range of temperatures is available in a stream (e.g. where a cold water tributary joins a warmer stream) fish may occupy microhabitats within a narrow temperature range and demonstrate no preference for other habitat variables (Baltz et al. 1987). Stream fish may also change their microhabitat use when water temperatures drop below or exceed some critical point and subsequently affect fish metabolism or behavior (Rimmer et al. 1983, 1984, Smith and Li 1983, Johnson and Kucera 1985, Hillman et al. 1987). However, I collected microhabitat use data in portions of the river that were downstream from the

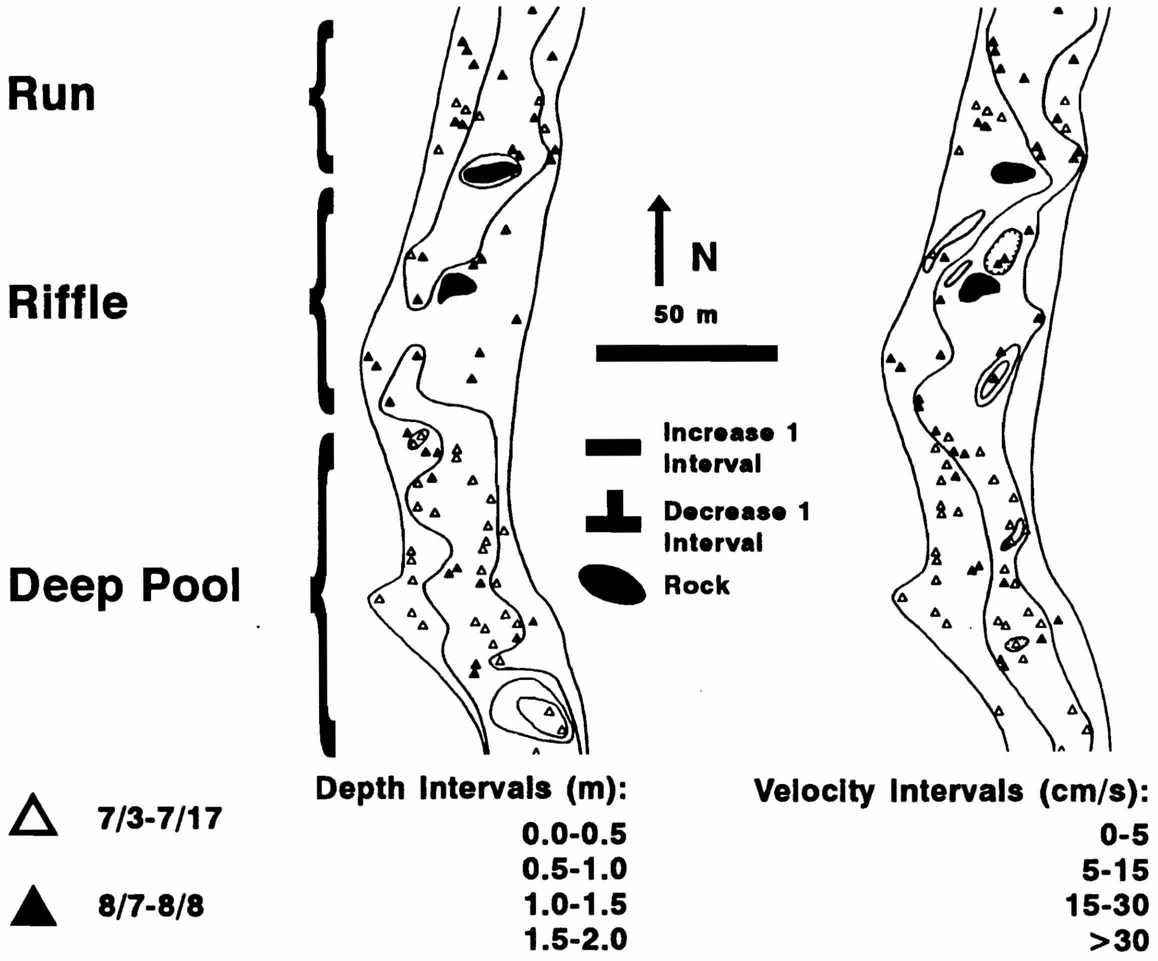


Figure 1.10. Locations of juvenile smallmouth bass in the lowest section of the downstream study site during two periods of the 1990 growing season.

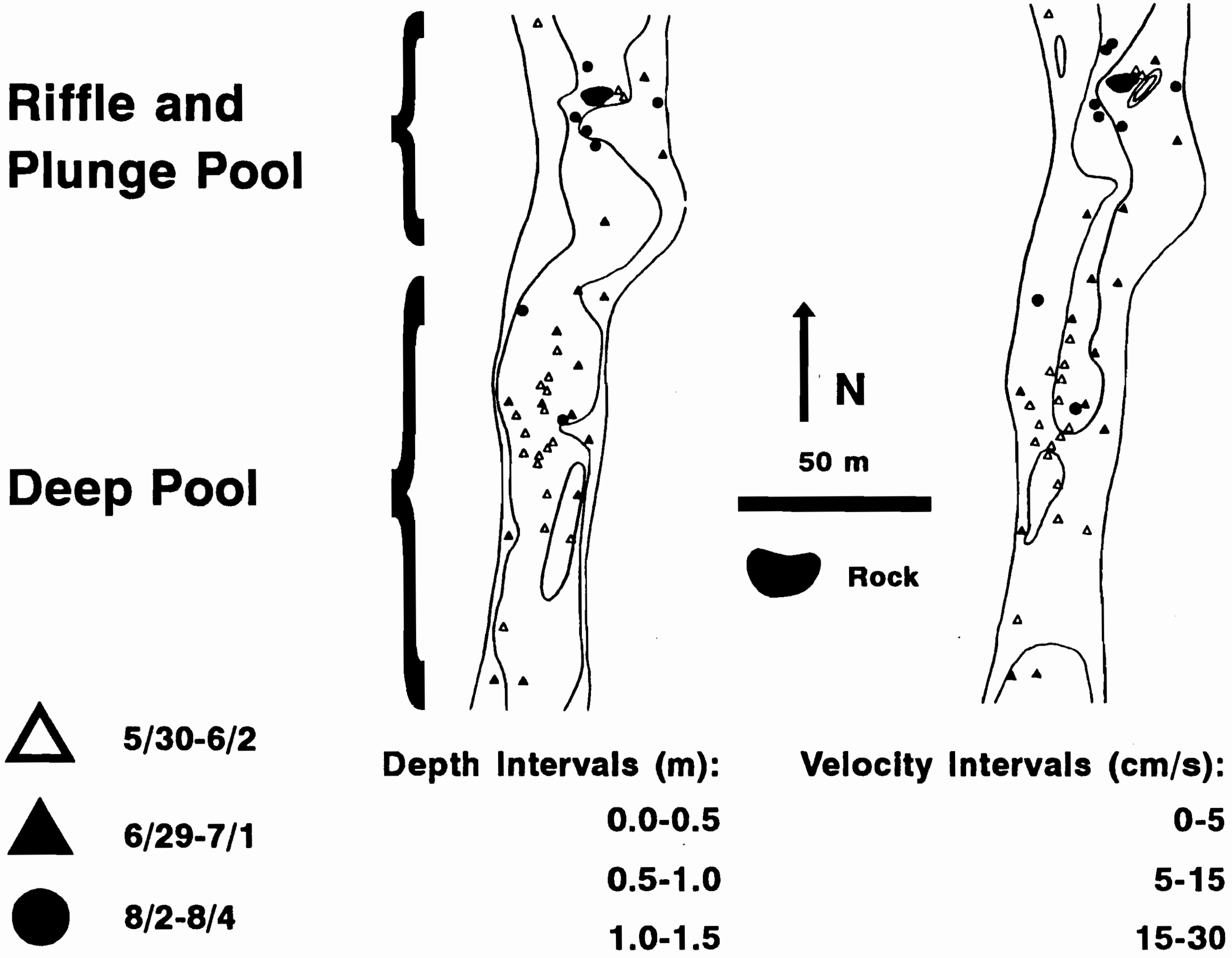


Figure 1.11. Locations of juvenile smallmouth bass in the middle section of the downstream study site during three periods of the 1991 growing season. The bottom of this section adjoins the top of the section in Figure 1.10.

thermal influences of the reservoir, and temperatures in the river varied within the range considered good to optimal for growth of juvenile smallmouth bass (Horning and Pearson 1973, DeAngelis and Coutant 1979, Wrenn 1980). Therefore, it is unlikely that age-0 smallmouth bass altered their microhabitat use in response to changes in temperature. It is more likely that morphological or physiological transitions between stages of ontogenetic development either forced or enabled age-0 smallmouth bass to shift their microhabitat use.

Microhabitat use during larval development.

The most distinct change in microhabitat use that I observed occurred as larval smallmouth bass dispersed from brood sites (when larvae were 14-18 mm, TL). This shift coincided with rapid morphological and physiological changes (Meyer 1970, Wallace 1972), and the shift occurred after male parents abandoned their broods. The combined effects of male abandonment and ontogenetic maturation may have triggered the observed change in larval microhabitat use.

By remaining in the brood site before male abandonment, larvae received protection from predators. Predators can quickly decimate unguarded larvae (Neves 1975) particularly when larvae have been freely swimming for less than one week (Brown 1984). While much of the area in brood sites contained no cover, the microhabitats used by dispersed larvae were usually associated with fractured bedrock or large woody debris. After losing the protection of their male parent, larval smallmouth bass may have congregated around large cover objects to avoid predators.

Most dispersed larvae used large cover outside of the brood site rather than objects within the brood site. Agonistic interactions among larvae in the brood site may have necessitated dispersal. Previous research identified aggressive behavior as a factor associated with dispersal of larval salmonids (Chapman 1962) and centrarchids (Elliot 1976, Brown 1985). Agonistic behavior began soon after swim-up and forced many larvae to abandon low velocity areas associated with cover in the brood site (personal observation). After losing the protection of the male parent, larvae may have benefitted by moving far from their siblings. I identified one group of 26 larvae that in three days dispersed over a wide area approximately 150 m upstream from their brood site.

Large cover objects not only provided protection from predators but also created unique microhabitats associated with the cover (Shirvell 1990). Larvae may have been attracted to these microhabitats for reasons other than protection, specifically low water velocities throughout much of the water column. I frequently observed dispersed larvae using as much as 50% of the water column in their chosen microhabitats. Larvae would have had limited mobility in the water column in portions of brood sites where velocities exceeded 4 cm/s (Larimore 1975).

Because larval smallmouth bass dispersed over long distances to seek out low velocity habitats, I drew some contradictory conclusions about their swimming ability. Before dispersal, larvae attained a size (average TL = 16 mm) where their swimming abilities allowed them to move through areas with mean water-column velocities greater that 15 cm/s. Yet smallmouth bass as large as 20 mm TL have limited mobility in the water column when velocities exceed 4 cm/s (Larimore 1975), so larvae were probably restricted to the bottom of the water column when moving through areas containing velocities 4 cm/s or higher. My results indicated that while dispersed larvae were capable of occupying and moving through relatively high velocities (by restricting movement to the bottom of the water column), they primarily used areas where they could move vertically throughout much of the water column.

A change in foraging ability may have encouraged larvae to use habitats where they could move easily throughout the water column. By the time they dispersed, most larvae could eat invertebrates that were two mm wide (Easton and Orth 1992) which meant they were no longer restricted to only small invertebrate prey (e.g. chironomids). Additionally, their ability to pursue and capture mobile prey had probably improved (Drost et al. 1988, Osse and Drost 1989). When larvae occupied portions of the brood site where high velocities restricted them to the bottom, they could encounter small, slow moving chironomids (Ward 1992). Microhabitats containing slow velocities throughout a large section of the water column attract larger microcrustaceans and larval insects (Brown et al. 1989, Shiozawa 1991). In a lotic environment, larval smallmouth bass less than 15 mm TL (average TL at dispersal = 16 mm) consume primarily chironomids, but they eat more copepods and larval insects after they exceed 15 mm TL (Easton 1992).

Brood site habitats in the North Anna River were deeper and contained faster velocities than are typically reported in studies of microhabitat use by larval smallmouth bass (Dowling 1987, Aadland et al. 1989, Simonson and Swenson 1990). The vast majority of dispersed larvae occupied microhabitats that more closely match literature descriptions: low velocity habitats with large substrate or cover objects present. Contrary to some reports, brood and dispersed larvae were frequently observed in the midchannel and not exclusively in vegetated shoreline habitats near where they were spawned (Floyd et al. 1984).

Microhabitat use by juveniles.

Previous studies of habitat use by juvenile smallmouth bass have classified them as occupants of moderately deep run habitats (Leonard and Orth 1988), shallow, slow habitats (Sechnick et al. 1986), shallow habitats of variable velocity (Aadland et al. 1991), and shallow, slow margins of riffles and pools (Bain et al. 1988, Lobb and Orth 1991). These descriptions may have differed because microhabitat availability and the size or developmental stage of juvenile smallmouth bass varied among studies. I tracked age-0 smallmouth bass throughout their ontogenetic development and observed them inhabiting shallow, slow microhabitats but only after they spent several weeks occupying deeper habitats earlier in their development. Until approximately four weeks after dispersal, juveniles were observed both along the river's margin and in mid-channel pool areas using microhabitats that resembled those occupied by dispersed larvae.

Juveniles may have gained an energetic advantage by changing their habitat use. When juveniles moved into shallower microhabitats, they frequently used locations that bordered high velocity areas (i.e. riffles and runs). These areas probably contained higher densities of aquatic insect larvae from the Order Ephemeroptera (Simmons and Voshell 1978, Georgian and Thorp 1992, Ward 1992), which have been identified as the primary prey of juvenile smallmouth bass during late summer (Stewart 1978, Angermeier 1982, Easton and Orth 1992).

Juveniles expanded the range of focal point velocities they occupied in these microhabitats, but throughout all their stages of development swam in velocities that required them (on average) to move one body length/s to maintain position. As juvenile smallmouth bass grow their swimming ability improves (Simonson and Swenson 1990) and the use of higher focal point velocities probably reflects this improvement. After experiencing an improvement in swimming ability, juvenile smallmouth bass probably occupied higher velocities without expending more energy than they expended in slower velocities.

Size is considered an important factor affecting microhabitat use for several species (Heggenes 1988, Shirvell 1990, Baltz et al. 1991). Smallmouth bass used different habitats at different sizes over time but large and small juveniles observed during the same period generally occupied the same types of microhabitats. The lack of a sized-based difference in microhabitat use suggested that juvenile smallmouth bass employed a complicated process for selecting microhabitats. As their swimming and foraging abilities improved, juveniles did not immediately explore unfamiliar microhabitats. Habitat availability, location of juveniles, and the predisposition of juveniles to abandon known areas could all affect the probability that any individual would encounter shallow habitats on the margins of riffles and runs. Of these three factors, only the predisposition to move was likely to have been affected by size, and studies of salmonids indicated that size may not affect how likely a fish is to abandon a known area (Grant and Noakes 1987).

Fish location could have been affected by a size-based dominance hierarchy, but juvenile stream fishes do not always establish hierarchies based on size (Fausch 1984). Additionally, densities of age-0 smallmouth bass in the river were low relative to the amount of habitat available during both years, so juveniles would probably gain little energetic advantage by defending their hierarchical status (Feldmeth 1983) or fighting over available resources (Mesick

1988). Therefore, the pattern of microhabitat use I observed probably resulted from active habitat selection rather than forced use in response to aggression from conspecifics, and apparently large and small juveniles did not select different microhabitats to occupy.

The pattern of microhabitat use that age-0 smallmouth bass exhibited might be interpreted as that of a habitat specialist (constrained by limited swimming ability) that gradually becomes more of a generalist. Juveniles expanded the range of mean and focal point velocities they occupied and became less dependent on large cover objects. The observed decrease in depth use primarily resulted from movement of juveniles out of pools and into riffles and runs. However, juveniles never completely abandoned pools. In order to further understand the consequences of habitat selection and the details of habitat partitioning by juvenile smallmouth bass, the variation of energetic profitability and their process of habitat evaluation must be explored in greater detail. In Chapter 2 I explore whether microhabitats differ in their energetic profitability to determine if juvenile smallmouth bass enacted their final habitat shift because that shift was energetically profitable.

Implications of results.

The observed tendency of age-0 smallmouth bass to change their microhabitat use over a relatively short time may necessitate some changes in our concept of stream habitat management for the species. Most instream-flow assessments that include smallmouth bass (e.g. Leonard and Orth 1988, Aadland et al. 1991) attempt to identify flows that insure adequate recruitment by providing enough critical habitat so that resource competition within the age-0 cohort is minimized. The results of this study suggested that smallmouth bass occupy a variety of microhabitats throughout their first growing season. It is impractical to suggest monitoring age-0 development and altering flows to provide critical microhabitat for each life stage. Therefore, managers may have to identify flow regimes that support a variety of microhabitats so age-0 smallmouth bass can effect microhabitat shifts at critical stages of development.

CHAPTER 2

Energetic Profitability of Microhabitats Used by Age-0 Smallmouth Bass in the North Anna River, Virginia

Introduction

In streams, complex interactions of water velocity with depth and substrate cause the physical environment and availability of resources to vary in space and time (Statzner et al. 1988). Fish occupying different microhabitats in streams must contend with dissimilar physical stresses, so individuals of the same species that use dissimilar microhabitats can exhibit considerable variation in their behavior and physiological performance. Some physical habitat characteristics (e.g. temperature or oxygen tension) delineate constraints within which a fish can function metabolically (Ultsch et al. 1978, Crowder and Magnuson 1983), but within those constraints, other habitat attributes affect the energetic profit that individuals can obtain (Fausch 1984, Facey and Grossman 1990). Therefore, selection of microhabitats can substantially influence the energy gain of individual stream fish and may rank among the most important factors affecting growth of stream fishes.

However, physical variables interact with biological factors to influence the relative energetic profitability of microhabitats. Some fish species exhibit morphological adaptations that reduce the energetic cost of occupying habitats with high water velocities (Weihs and Webb 1983, Facey and Grossman 1992). Stream fish also modify their foraging behavior in different microhabitats in order to stabilize metabolic costs (Godin and Rangely 1989), or exploit different resources (Grant and Noakes 1987). Because some fish can change strategies to improve their foraging success in a variety of microhabitats, it is possible that some stream fish may forage equally well in all microhabitats where temperature, oxygen constraints, or high water velocities do not exclude them. If this were true it would not mean that all microhabitats were equally profitable because profitability would still be affected by variation in food availability and the presence of competitors (Werner et al. 1983b). However, if individuals forage at similar rates and with similar metabolic costs in all microhabitats, then other factors (e.g. protection from predators) may affect their microhabitat use more than energetic profit does.

In the previous chapter, I described how age-0 smallmouth bass in the North Anna River gradually move out of deep pools and into shallow microhabitats during the first 4-6 weeks after they leave their nests. The observed shift appeared to occur as age-0 smallmouth bass abandoned relatively unprofitable pools where they began life, and began occupying areas close to relatively productive riffles and runs. It is also possible that the observed microhabitat shift was induced by predators or occurred as individuals developed morphologically and entered areas that they previously could not inhabit. Each of these mechanisms would link microhabitat use to subsequent growth or survival of age-0 smallmouth bass, but the outcomes could differ significantly depending on whether one or all of these mechanisms actually motivated movement.

Understanding the adaptive significance of the observed microhabitat shift could reveal links between habitat selection and recruitment success of smallmouth bass in the North Anna River. If juvenile bass were moving into more profitable areas, then the availability of profitable microhabitats could determine how many age-0 smallmouth bass could exist in this system (Morris 1988, Kwak et al. 1992).

If juvenile smallmouth bass obtained equal energetic gains in all microhabitats, then the shift may be a survival response, and the abundance of predators or competitors may influence carrying capacity along with microhabitat availability.

The objective of this study was to determine the relative energetic profit obtained by age-0 smallmouth bass foraging in different microhabitats of the North Anna River. The null hypothesis I tested was that all individuals could obtain similar energetic gains in all microhabitat types. If this hypothesis were rejected, then it is possible that juvenile smallmouth bass shifted their use of microhabitats because they sought higher energetic profits. In the course of evaluating the relative profitability obtained in various habitats, I monitored the foraging behavior of juvenile smallmouth bass to determine if behavioral adaptations enabled individuals to obtain similar energetic profits in different microhabitats.

Methods

Study Site.

Data for this study were collected from observations of 43 juvenile smallmouth bass videotaped in the North Anna River, Virginia, between July 19 and August 21, 1991. The hydrology and biological characteristics of the North Anna River were discussed in the methods section of Chapter 1. All observations were filmed in a reach of the river extending 640 m upstream from the 601 Hanover County bridge. The river averaged 38 m wide in this section, maximum depth was 2.5 m, and bedrock, boulders, and sand were the most common substrate types. The study site was divided into eight sections based on general habitat characteristics (4 pools, 3 riffles, and 1 run).

Field observations of foraging and habitat use.

A section of the study site was randomly selected and a snorkeler searched that section for juvenile smallmouth bass. After locating a juvenile, the snorkeler observed the individual for at least one minute before videotaping. Preliminary observations indicated that juveniles generally ignored snorkelers after 30 seconds of visual contact, and their behavior after 1 minute of underwater observation did not differ from their behavior after 10 minutes of observation. The snorkeler would visually estimate the total length (TL) of the juvenile to within 5 mm. During the period of data collection, 80% of the juveniles in this site were between 60 and 90 mm TL. A comparison of length estimates to actual lengths of fish that were captured by electroshocking indicated that snorkelers could classify juveniles into the correct 5-mm category 90% of the time.

After one minute of visual contact, the snorkeler would begin recording the actions of the selected juvenile. Observations were videotaped with a remote video system which consisted of a remote camera and a surface monitor. The remote camera was encased in a camouflaged, waterproof housing and recorded 30 frames/s through a 6-mm wide-angle lens. The time and date of the observation were recorded on videotape at the start of each observation. The snorkeler followed the juvenile with the remote camera while another observer watched the surface monitor and told the snorkeler how to move the camera to keep the juvenile centered in the picture. The surface observer also took notes defining the boundaries of the area that the juvenile occupied during the observation. If the snorkeler lost contact with the juvenile before taping for five minutes, then the observation was discarded. If contact was maintained for five minutes, then videotaping of the juvenile continued for a maximum of another five minutes (10 minutes total) or until visual contact was lost.

After videotaping, I marked four corners of the area occupied by the juvenile, and then marked the corners of blocks within that area that visibly differed in habitat characteristics (i.e. depth, water velocity, and substrate type). During preliminary investigations, I determined that by stratifying sampling among visibly different areas and quantifying habitat variables at one point/m^2 in a 25-m^2 area, I obtained means and variances that were not significantly different from means and variances obtained from nonstratified random sampling of five points/m^2 (all $P > 0.50$). I measured the distance to the nearest 0.5 m, and bearing to the nearest degree between the corners of habitat blocks. Each block was later drawn based on these measurements, and the total area of the blocks was estimated with a digital planimeter. Areas of all habitat blocks were added to obtain a total estimate of the area used by each juvenile during filming.

Immediately after videotaping, habitat variables were quantified at randomly selected points (a stopwatch simulated a random number generator) along randomly placed transects within each habitat block. Transects were placed perpendicular to the flow at randomly selected points along the longest side parallel to the flow. An initial sample point was randomly selected within the first meter of each transect, and remaining samples were taken at 1-m intervals along each transect. I selected one point for every m^2 in areas estimated to be less than 25 m^2, and selected 25 points in areas larger than 25 m^2. At each randomly selected point, I measured the depth (cm), mean water column velocity, and described the dominant substrate type. Mean water column velocity was measured using a pygmy current meter at 0.6 of depth from the surface. Substrate types were divided into a categories based on a modified Wentworth scale described in the Methods section of Chapter 1 (Appendix 1).

Analysis of foraging activity.

To determine where juveniles obtained their highest foraging success, two observers reviewed each taped observation and recorded where and how each juvenile used different portions of the water column. Recorded sequences were viewed at normal speed (30 frames/s), and observers recorded the duration of sequences during which juveniles remained in the view of the camera and occupied the same position in the water column. I considered juveniles to be using the bottom of the water column when they were within 0.25 body lengths of the substrate or when they were oriented downward with their eyes searching the substrate. When juveniles were within 0.25 body lengths of the surface or searching the surface, I recorded that they were using the top of the water column. At all other times I considered juveniles to be using the middle of the water column.

After recording the duration of each sequence, we rewound the tape to the beginning of the sequence, reviewed all possible feeding attempts at 0.1 normal speed, and counted the total number of bites. While juveniles may not have ingested prey each time they took a bite, the number of feeding attempts taken by a fish is correlated with the amount of prey in its stomach (Grant 1990). For each observation we calculated the total time the juvenile spent at the top, middle, and bottom of the water column, the total number of bites in each portion, and the bites/minute in each portion.

Analysis of energy intake and expenditure.

The energetic profitability of a microhabitat depends on the number of prey that an individual can consume while in that microhabitat and the amount of energy that the individual must expend while foraging (Fausch 1984, Kacelnik and Houston 1984). For fishes that feed on benthic or water column invertebrates, a significant proportion of the energy expended while foraging may be attributable to activity costs (Boisclair and Leggett 1989). To determine if the energetic profitability gained by juvenile smallmouth bass varied among microhabitats, I subtracted an estimate of the energy that juveniles expended while foraging from an estimate of the total energy ingested during the same period.

The duration of each filmed observation varied (because the time each fish was out of view varied), so I reduced estimates of total energetic profit gained to profit gained/min. Energetic profit obtained by each juvenile during the time they were filmed was estimated using a formula adapted from a generalized bioenergetics model for fish (Rice et al. 1983):

$$G = [C\cdot(1-(R_{SDA}+F+U))-R_{(S+A)}]/t \tag{1}$$

where G = rate of energy gain (J/min), C = total consumption during the observation (J), R_{SDA} = the proportion of consumption used for specific dynamic action, F = the proportion of consumed energy egested, U = the proportion of consumed energy excreted, $R_{(S+A)}$ = energy used for standard and active metabolism (J), and t = time observed (min). I used constant values for R_{SDA} (0.17), F (0.15), and U (0.088), and based my estimates on values reported for species that were fed invertebrate diets because I assumed juveniles only ate invertebrates (see below). Roell and Orth (in press) used the value of 0.17 for R_{SDA} of smallmouth bass based on the value determined for bluegills (*Lepomis macrochirus*) eating mayfly nymphs (Pierce and Wissing 1974). Elliott (1976) reported that the value of F for brown trout (*Salmo trutta*) eating invertebrates was 0.15, and Rice et al. (1983) derived a value of 0.088 for U of largemouth bass.

Energy lost to standard and active metabolism was estimated for each juvenile using a formula adapted for predicting daily respiratory losses of age-0 smallmouth bass by Simonson and Swenson (1990):

$$R_{(S+A)} = a \cdot W^{(b+1)} \cdot e^{mT} \cdot e^{gs} \cdot (t/1440) \cdot 4{,}184\,(J/g) \qquad (2)$$

where a = intercept for respiration ($0.03\ g \cdot g\ ww^{-1} \cdot d^{-1}$), W = wet weight (g), b = weight-dependent exponent for respiration (-0.21/g ww), m = temperature-dependent coefficient for respiration (0.0313/°C), T = water temperature (°C) on the day of the observation, g = coefficient for swimming speed dependence of respiration (0.0196 s/cm), and s = average swimming speed (cm/s) during the observation. All constants were derived for juvenile smallmouth bass (Shuter and Post 1990) except m and g which were derived for juvenile largemouth bass (Rice et al. 1983). The coefficients of equation 2 applied to a 24-h (1440 min) day, so I multiplied the initial result by the proportion of the day that I observed the juvenile on videotape. Mean daily water temperatures used in equation 2 were measured by a thermograph maintained approximately 3 km upstream from the study area. Temperatures varied between 25 and 30°C. Weight of each juvenile was estimated from a length-weight relationship ($P < 0.0001$, $R^2 = 0.89$) developed from 80 juveniles (27-70 mm TL) that were collected between June 1 and July 9, 1991. The resulting formula was:

$$W = 0.00026 \cdot L^{2.21} \qquad (3)$$

where $\underline{W}$ = wet weight (g), and $\underline{L}$ = estimated total length (mm).

Tail-beat frequencies have been used to estimate the energetic cost of activity for several species (Feldmeth and Jenkins 1973, Feldmeth 1983, Puckett and Dill 1984, 1985) and I used this technique to estimate the swim speed variable ($\underline{s}$) of equation 2. During the initial review of the films, observers classified sequences as episodes where fish were foraging (i.e. searching the surface or substrate, or drift feeding at a point in the water column) or cruising (i.e. moving without specifically searching for food). Because swimming speeds may vary during these two types of movement, I randomly selected 20, 2-s segments from the foraging and cruising segments of each observation. I reviewed each frame of the 2-s segments and counted the number of tail-beats taken. The number of tail-beats taken was determined by counting the number of times the trailing edge of the caudal fin passed through the midline of the body and dividing that number by two. If an individual spent less than 40 s either foraging or cruising I counted all tail-beats taken while foraging or cruising. The average tail-beat frequency for other juveniles was estimated as:

$$\underline{T}_t = [(\underline{T}_f \cdot \underline{f}_t)+(\underline{T}_c \cdot \underline{c}_t)/(\underline{f}_t+\underline{c}_t)] \qquad (4)$$

where $\underline{T}_t$ = tail-beat frequency (beats/s) during the total observation, $\underline{T}_f$ = average tail-beat frequency while foraging (beats/s), $\underline{f}_t$ = total time spent foraging (s), $\underline{T}_c$ = average tail-beat frequency while cruising (beats/s), and $\underline{c}_t$ = total time spent cruising.

I estimated the swimming speed term of equation 2 using the formula developed by Bainbridge (1958):

$$\underline{s} = 0.075 \cdot \underline{L} \cdot (\underline{T}_t - 1.33) \qquad (5)$$

where $\underline{L}$ = total length (mm), and $\underline{T}_t$ = tail-beat frequency (beats/s) during the observation. This formula accurately predicted the swimming speed of a variety of species (e.g. *Carasius auratus* and *Oncorhynchus mykiss*) of all size classes (e.g. juveniles and adults) from observed tail-beat frequencies. Puckett and Dill (1984) verified that the formula accurately predicted the swim speed of juvenile coho salmon (*Oncorhynchus kisutch*), but the formula has not been verified for juvenile centrarchids.

To estimate the total joules each juvenile consumed while being filmed, I multiplied the total number of bites by an estimate of the average joules contained in a single prey item. I assumed juveniles ate only microcrustaceans or larval aquatic insects (because I did not observe them eating either fish, crayfish, or mollusks) and ate one prey item each time they took a bite. I estimated the percentage of four categories of aquatic invertebrates that occurred in the diet of juvenile smallmouth bass collected from the New River, West Virginia (Easton 1992). Prey were grouped into four categories based on differences in their caloric content, average volume, or frequency of occurrence in the diets of juvenile smallmouth bass (Table 2.1). The average energetic content of a prey item was calculated as a weighted average of the four categories:

$$\underline{K} = [\sum_{i=1}^{4} \underline{a}_i \cdot \underline{V}_i \cdot \underline{k}_i \cdot \underline{E}_i] \cdot 4.184 (J/kcal) \qquad (6)$$

where $\underline{K}$ = joules contained in the average prey item consumed, i = the category of aquatic invertebrate, $\underline{a}_i$ = the average proportion of category i in the diet, $\underline{V}_i$ = the average wet volume (mm^3) of a prey item in category i, $\underline{k}_i$ = specific constant for converting wet volume to dry weight

Table 2.1. Values of variables (and sources) used to calculate the average energetic content of a prey item ingested by a juvenile smallmouth bass.

Category of Invertebrates	Percentage in Diet[2]	Average Volume (mm^3)[3]	mg/mm^3 Dry Weight	Average Kcal/mg
Chironomidae	17	0.15	0.2[4]	5.248[6]
Other Aquatic Insects[1]	70	1.66	0.1[5]	5.200[7]
Amphipoda and Isopoda	7	1.39	0.1[5]	3.776[8]
Microcrustacea	6	0.18	0.1[5]	5.335[9]

[1] Includes larval: Ephemeroptera, Odonata, Hemiptera, Megaloptera, Trichoptera, Coleoptera, and Diptera other than Chironomidae.

[2] Easton 1992.

[3] Easton (unpublished data).

[4] Stites and Benke 1989.

[5] Cummins and Wuycheck 1971.

[6] Cummins and Wuycheck 1971. Mean of eight species.

[7] Cummins and Wuycheck 1971. Mean of 31 species.

[8] Cummins and Wuycheck 1971. Mean of four species.

[9] Cummins and Wuycheck 1971. Mean of 27 species.

(mg), and $\underline{E}_i$ = energetic content (Kcal/mg) of a prey item in category i.

I estimated average volumes from measurements taken on 500 prey items removed from the stomachs of juvenile smallmouth bass (Easton, unpublished data), obtained estimates of mg wet-weight/mm^3 from Cummins and Wuycheck (1971) and Stites and Benke (1989), and used caloric values reported in Cummins and Wuycheck (1971). My calculations determined that $\underline{K}$ = 2.82 J, and therefore the consumption term of equation 1 was estimated as:

$$\underline{C} = 2.82 \cdot \underline{B} \qquad (7)$$

where $\underline{B}$ = the number of bites taken during the observation.

Statistical Analyses.

Effect of confounding variables.

Differences in estimates of energetic profitability could have been caused by factors associated with data collection. Water temperature or fish size could have directly affected foraging rates or fish activity. Additionally, the duration of each observation could have influenced estimates of foraging rate or swim speed, with brief observations influenced more by short term variation, and longer observations dampening the effects of extreme variation. I used least squares regressions and multiple regressions to determine if temperature, total length, and duration of observations affected estimates of foraging rate or tail-beat frequency. If no relationship existed I assumed temperature, fish size, and duration of observation did not consistently bias my estimates of net energetic gain.

Relationship between microhabitat and energetic profit.

I used least-squares regression and multiple regression analyses to test the null hypotheses that the rate of energetic profit gained by each individual was not related to habitat variables. Factors that affect energetic profitability could relate to individual habitat variables, multiple habitat variables, or hydraulic characteristics that are a function of habitat variables. Therefore, I executed three sets of analyses that examined relationships between my estimates of energetic profitability and the habitat characteristics listed above. Each set of analyses examined relationships between habitat characteristics and variables that directly affected my estimates of profitability: foraging rate, respiratory rate, and tail-beat frequency.

Microhabitat data collected for each individual was summarized by determining the mean, variance, and maximum of depth and velocity measurements and the modal substrate type. To determine the effect of individual habitat variables on energetic profit, I tested for linear relationships between energetic profit gained by juveniles and the mean value of depth and velocity measurements in the areas they occupied. Because most of the river is underlain by bedrock (see Chapter 1), substrate type by itself was unlikely to affect rates of energetic gain, so I did not include substrate type as an independent parameter in regression analysis.

When summary statistics were examined together they could differentiate several types of lotic microhabitats. However, collinearity among habitat variables complicated the use of regression analysis to examine the relationship of energetic profit to multiple habitat characteristics. Other than modal substrate, all of the summary statistics (mean, variance, and maximum) calculated from depth and velocity measurements were highly correlated (all Pearson's $r > 0.59$) with at least one other summary statistic. Rather than using correlated summary statistics as independent variables in multiple regressions, I used principal components to summarize multivariate differences among microhabitats, and examined linear relationships between principal components and energetic profitability.

Principal components analysis (PCA) was used to create artificial variables that described larger proportions of the overall microhabitat variation than any one of the summary statistics (Johnson and Wichern 1988). Principal components were uncorrelated, and each component incorporated summary statistics that varied along the same multivariate plane. All components with eigenvalues greater than 1.0 (meaning they explained more variation than any one of the original variables) were retained. The original summary statistics were multiplied by scoring coefficients generated by the PCA to create a data set of factor scores representing linear combinations of the coefficients and the summary statistics. Each of the retained components was used as an independent variable, and their corresponding factor scores were the data points used to relate habitat variables to energetic gain or respiratory rate. Mallow's Cp criterion (Daniel and Wood 1980) was used to determine which combination of independent variables best explained the relationship between energetic profitability and the principal components.

I used two hydraulic ratios that incorporated depth and velocity to describe the relationship between the inertia of flowing water and inertia-eroding forces within a habitat (Vogel 1981). Both of the ratios were calculated for each point where habitat was quantified, and mean ratios were calculated for each individual based on their habitat use. The ratio of inertial forces to viscous forces (Reynolds number) was calculated as:

$$\underline{Re} = \underline{pdU}/\mu \tag{8}$$

and the ratio of inertial forces to gravitational forces (Froude number) was calculated as:

$$\underline{Fr} = \underline{U}^2/\underline{gd} \tag{9}$$

where $\underline{U}$ = the mean water-column velocity (m/s), $\underline{d}$ = depth (m), $\underline{p}$ = density of water (kg/m^3), μ = kinematic viscosity of water (m^2/s), and $\underline{g}$ = the gravitational constant (9.81 m/s^2). Both $\underline{p}$ and μ were adjusted for differences in water temperature (Streeter and Wylie 1985).

Reynolds number increases as either depth or velocity increases, and microhabitats with high Reynolds numbers have a large mass of water flowing through them and high turbulence throughout the water column. The Froude number increases as velocity increases or depth decreases, and high Froude numbers occur in microhabitats where surface turbulence and water momentum is high (relative to the force or gravity). Therefore, microhabitats with very different depths or mean water column velocities may have similar Reynolds or Froude numbers because their hydraulic characteristics are similar. I used these ratios as independent variables in simple linear regressions to test for relationships between the hydraulic characteristics and energetic profitability.

Relationship between behavior and energetic profit.

Besides microhabitat, the energetic profit gained by an individual could have been affected by the area (m^2) they searched, or the percent time they spent actively foraging or moving throughout the water column. I used least squares regression to test the null hypothesis that these behavioral variables were not related to the estimates of energetic profit. As with the analyses described earlier, I also examined how behavioral variables related to foraging rate, respiration rate, and tail-beat frequency.

Results

Juvenile use of the water column.

All individuals spent the majority of their time in the middle or at the bottom of the water column (Figure 2.1). Only 12 individuals used the top of the water column and none of those remained near the surface for long durations. Most juveniles that ventured to the surface fed at relatively high rates, but because they remained there for short periods the estimated amount of food they ingested at the surface was relatively low. Juveniles located most of the food they ingested by searching the substrate or vegetation attached to the substrate. Juveniles rarely fed in the middle of the water column, and when they did they primarily fed on items attached to leaves of rooted macrophytes.

Summary of factors affecting rate of energetic gain.

Juveniles ranged between 45-100 mm in TL (mean = 77.1), observed foraging rates varied between 0-20 bites/min (mean = 2.1), and tail-beat frequencies ranged between 65-255 beats/min (mean = 178, Table 2.2). Foraging rates translated to energetic intake rates between 0-56.4 J, and estimated swim speeds from observed TL's and tail-beat frequencies ranged from 0-23 cm/s. Estimates of respiratory rates ranged from 0.3-1.2 J (mean = 0.73), and estimates of net energy gained ranged from -1.2-36.7 J/min (mean = 3.32).

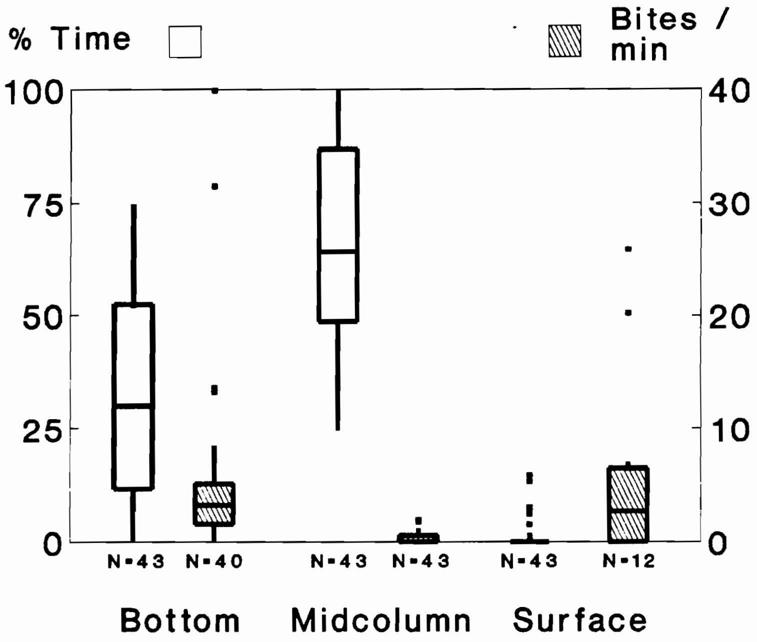


Figure 2.1. Box plots of percent time occupied and foraging rates (bites/min) at the bottom, middle, or surface portions of the water column. Individuals that did not enter the bottom or surface portion of the water column were not included in the box plots of foraging rates.

Table 2.2. Observed values of morphological and behavioral variables used to estimate energetic profit for 43 fish and characteristics of the microhabitats they occupied during observations (μ = sample mean, s^2 = sample variance, MVel = mean water-column velocity).

TL (mm)	Bites (#/min)	Tail-beats (#/min)	μ of Depth (cm)	μ of MVel (cm/s)	s^2 of Depth (cm)	s^2 of MVel (cm/s)	Maximum Depth	Maximum Mvel	Modal Substrate
70	2.3	65.0	78.6	0.0	1198.9	0.0	115	0	Bedrock
65	3.0	143.0	61.7	3.4	179.4	2.1	86	6	Bedrock
65	5.1	128.5	78.0	4.0	547.9	14.5	108	11	Bedrock
65	0.3	220.0	73.2	10.3	331.8	8.5	106	16	Bedrock
90	0.2	133.5	73.2	10.3	331.8	8.5	106	16	Bedrock
45	3.2	194.0	40.3	5.2	243.4	6.5	72	10	Bedrock
80	3.3	255.0	76.3	19.8	738.6	18.2	121	31	Bedrock
55	0.5	195.0	41.8	1.3	489.3	2.6	70	4	Bedrock
65	0.4	149.0	41.8	1.3	489.3	2.6	70	4	Bedrock
55	1.7	159.0	37.9	0.0	110.4	0.0	54	0	Bedrock
85	0.1	166.0	37.9	0.0	110.4	0.0	54	0	Bedrock
70	2.4	220.0	51.6	16.6	445.3	55.0	80	30	Bedrock
85	1.6	179.0	54.8	5.6	332.4	17.2	82	15	Bedrock
65	5.9	204.0	49.2	10.1	172.5	78.3	67	33	Bedrock
75	0.4	229.5	58.3	11.9	403.4	18.1	85	17	Bedrock
70	1.1	167.5	68.3	1.5	251.4	2.6	90	3	Bedrock
75	2.8	130.5	52.6	6.2	126.6	4.2	68	11	Sand
85	2.1	228.0	69.8	4.2	1193.8	11.8	110	11	Sand
90	20.0	247.0	49.1	13.6	151.3	118.0	67	41	Bedrock
70	3.6	178.5	32.8	36.5	31.4	305.1	41	56	Boulder
100	1.5	110.0	102.9	4.3	173.8	2.9	117	7	Bedrock
90	1.2	163.0	68.2	3.8	194.4	6.6	90	12	Bedrock
70	1.9	154.0	64.8	2.8	159.8	3.0	82	7	Bedrock
85	0.3	156.0	50.9	6.1	171.7	19.2	75	12	Bedrock
95	1.0	126.0	86.2	3.8	155.5	3.5	103	6	Gravel
70	1.6	146.0	39.9	6.2	204.5	8.2	64	12	Bedrock
85	2.0	212.0	61.4	21.5	135.6	54.1	76	27	Bedrock
90	4.4	159.5	50.8	12.8	464.4	67.5	90	26	Bedrock
75	5.9	205.0	49.5	17.0	161.5	19.4	73	23	Bedrock
95	0.0	271.0	56.4	11.2	634.0	55.7	86	25	Bedrock
75	0.0	208.0	56.4	11.2	634.0	55.7	86	25	Bedrock
85	1.3	200.0	52.7	16.3	135.2	43.6	64	25	Boulder
70	0.1	65.0	48.3	0.7	122.2	1.6	60	3	Boulder
80	4.3	220.0	28.1	13.7	59.1	63.8	41	27	Bedrock
70	1.2	243.0	80.1	11.6	272.1	13.8	109	18	Bedrock
85	2.0	222.0	52.7	17.3	168.0	29.5	64	25	Boulder
95	0.3	187.0	49.1	8.6	58.8	3.4	67	12	Bedrock
90	1.5	177.0	53.6	8.1	55.6	2.8	67	11	Boulder
95	0.6	147.0	45.3	5.9	437.5	15.7	84	13	Sand
70	0.2	170.0	68.3	6.2	318.8	11.9	100	14	Bedrock
75	1.5	116.0	63.1	2.8	200.7	1.4	85	5	Sand
70	0.0	220.0	48.8	1.9	287.4	12.1	72	11	Bedrock
75	3.7	253.0	46.8	16.3	408.6	25.1	70	24	Bedrock

Tests of possible confounding variables.

Water temperatures during the study ranged from 25-30°C. Temperature, total length, and the total time each juvenile was observed did not linearly relate to foraging rate or tail-beat frequency when examined independently or as multiple independent variables (all $P > 0.27$). Feeding rates varied throughout the day but did not consistently increase at any particular time of day (Figure 2.2), although they may have decreased some after 1600 hours. In general, the manner in which data were collected did not consistently bias the results in a way that could alter relationships detected between net energy gain and habitat or behavioral variables.

Summary of habitat variables.

Most of the areas occupied by juvenile smallmouth bass were underlain by bedrock, but depths and velocities varied more noticeably among occupied areas (Table 2.2). Mean depths ranged between 28.1-102.9 cm (mean = 56.9) in microhabitats, and the mean of velocity measurements varied from 0-36.5 cm/s (mean = 8.7). In three cases, habitat variables were identical for two juveniles because both were observed using approximately the same areas.

Independent habitat variables and energetic profit.

Mean depth was not linearly related to foraging rate, tail-beat frequency, respiratory rate, or energetic profit gained by individuals (all $P > 0.23$). Mean velocity was positively related to foraging rate, tail-beat frequency, and respiration rate (all $P < 0.05$, Table 2.3), but was not related to energetic profit ($P > 0.05$). These results indicated that juveniles fed more frequently, and increased their activity and respiration rates in microhabitats with

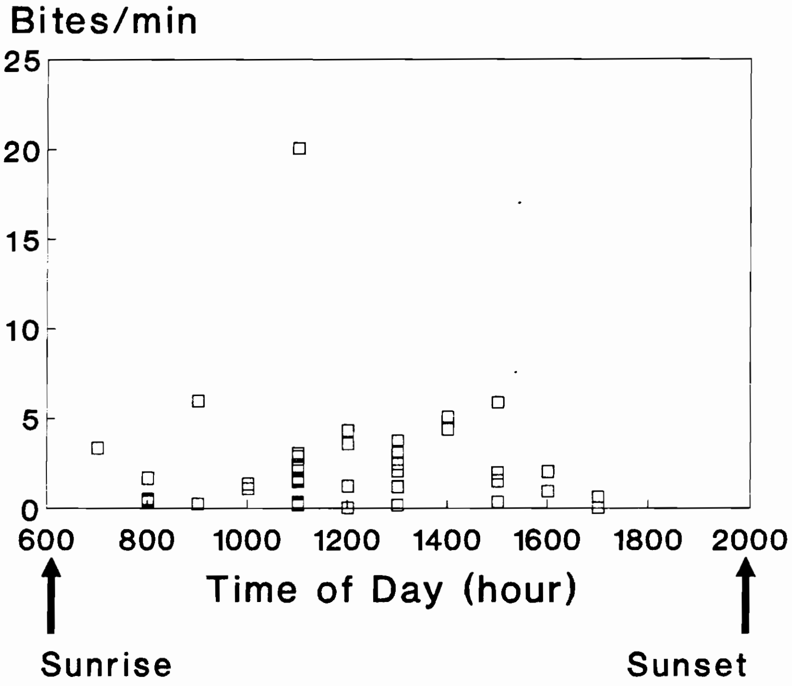


Figure 2.2. Foraging rates of individuals observed at different times of the day.

Table 2.3. Significant linear relationships detected between variables describing habitat characteristics (mean depth, mean velocity, principal components, Reynolds number, and Froude number) and estimates of energetic profit gained in a microhabitat or factors affecting estimates of energetic profit (foraging rate, tail-beat frequency, respiration rate). Principal components are explained in Table 2.4.

Habitat Variable	Energetic Variable	Relationship	$P <$	R^2
Velocity (cm/s)	Foraging Rate (bites/min)	1.00+0.13V	0.05	0.09
	Tailbeats (#/min)	0.65+0.009V	0.04	0.10
	Respiration (J/min)	150.00+3.42V	0.0004	0.27
Principal Component 1	Profit (J/min)	2.85+2.17PC1	0.007	0.17
	Foraging Rate (bites/min)	2.14+1.32PC1	0.006	0.17
	Tailbeats (#/min)	179.6+19.92PC1	0.006	0.17
Principal Component 2	Respiration (J/min)	0.73+0.07PC2	0.04	0.11
Froude	Tailbeats (#/min)	154.2+622.15F	0.0009	0.24
Reynolds	Tailbeats (#/min)	146.3+(6.20E-7)R	0.01	0.14
	Respiration (J/min)	0.63+(1.95E-9)R	0.0002	0.30

higher velocities, but did not acquire more net energy by entering higher velocities.

Principal components and energetic profit.

The PCA extracted three components that explained 85% of the total variation within the summary statistics that quantified microhabitat characteristics. The first of these components (PC1) was positively related to all velocity variables and negatively related to all depth variables (Table 2.4). The second component (PC2) was positively related to all depth and velocity variables (though weakly so) and the third component (PC3) was positively related to the modal substrate type. When viewed on a scatter plot, areas that scored high on PC1 tended to contain shallower depths and higher water column velocities (Figure 2.3), and areas that scored high on PC2 tended to be deeper and contained a wide range of velocities.

Foraging rate and net energy gain were positively related to PC1 (both $P < 0.007$, Table 2.3), indicating that juveniles occupying the shallowest, highest velocity microhabitats (and the microhabitats that varied most in depth and velocity) foraged most frequently and gained the highest energetic profit (Figure 2.4a). No other single component or combination of principal components improved the fit of the model to estimates of energetic profit. The rate of net energy gain was very highly correlated with foraging rate (Pearson's $r = 0.99$, $P < 0.001$), which suggested that the estimates of energetic profit were primarily a function of intake rate (Figure 2.4b).

If I deleted the individual that gained an estimated 32 J/min from the sample, the regression analysis still detected a significant positive relationship between the first principal component and the rate of net energetic gain

Table 2.4. Factor pattern of the three components retained by the principal component analysis performed on statistics summarizing habitat data (N=43).

Statistic	Component 1	Component 2	Component 3
Mean Depth	-0.638	0.619	0.067
Mean Velocity	0.802	0.508	0.002
Depth s^2	-0.443	0.549	-0.061
Velocity s^2	0.854	0.342	-0.067
Maximum Depth	-0.702	0.682	0.086
Maximum Velocity	0.830	0.510	0.049
Modal Substrate	0.092	-0.070	0.989
Eigenvalues	3.165	1.788	1.001
Proportion of s^2 Explained	0.452	0.256	0.143

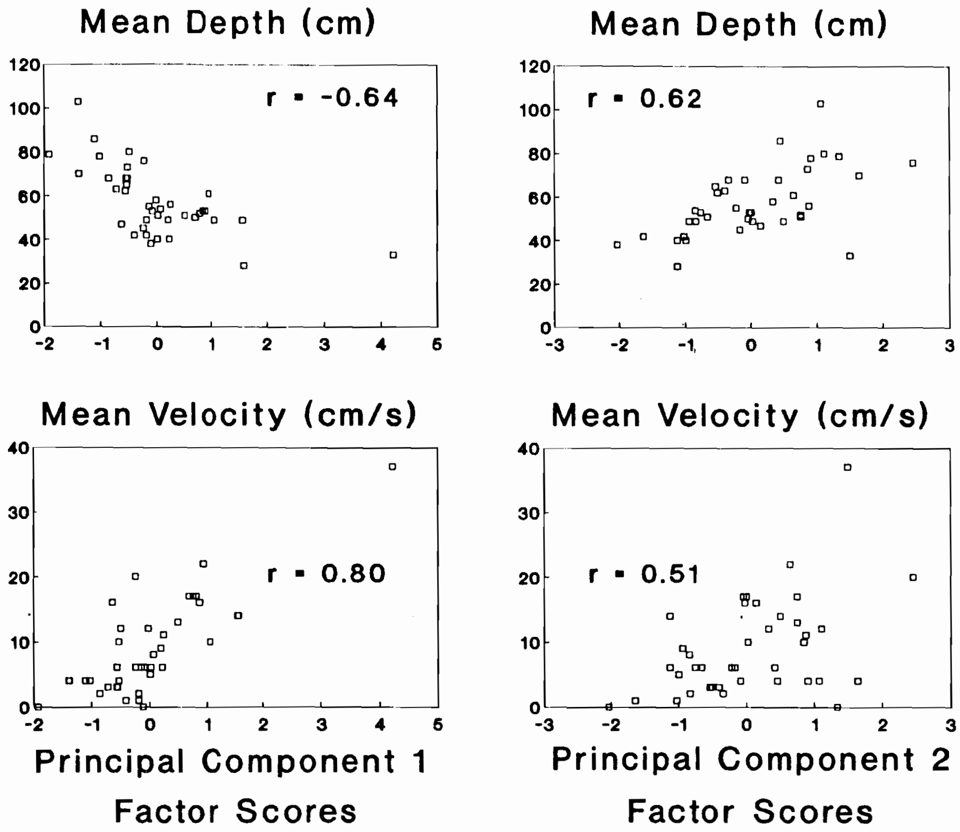


Figure 2.3. Relationship of factor scores generated from the principal component analysis on all habitat variables to the mean values of depth and mean water column velocity in areas occupied by juvenile smallmouth bass.

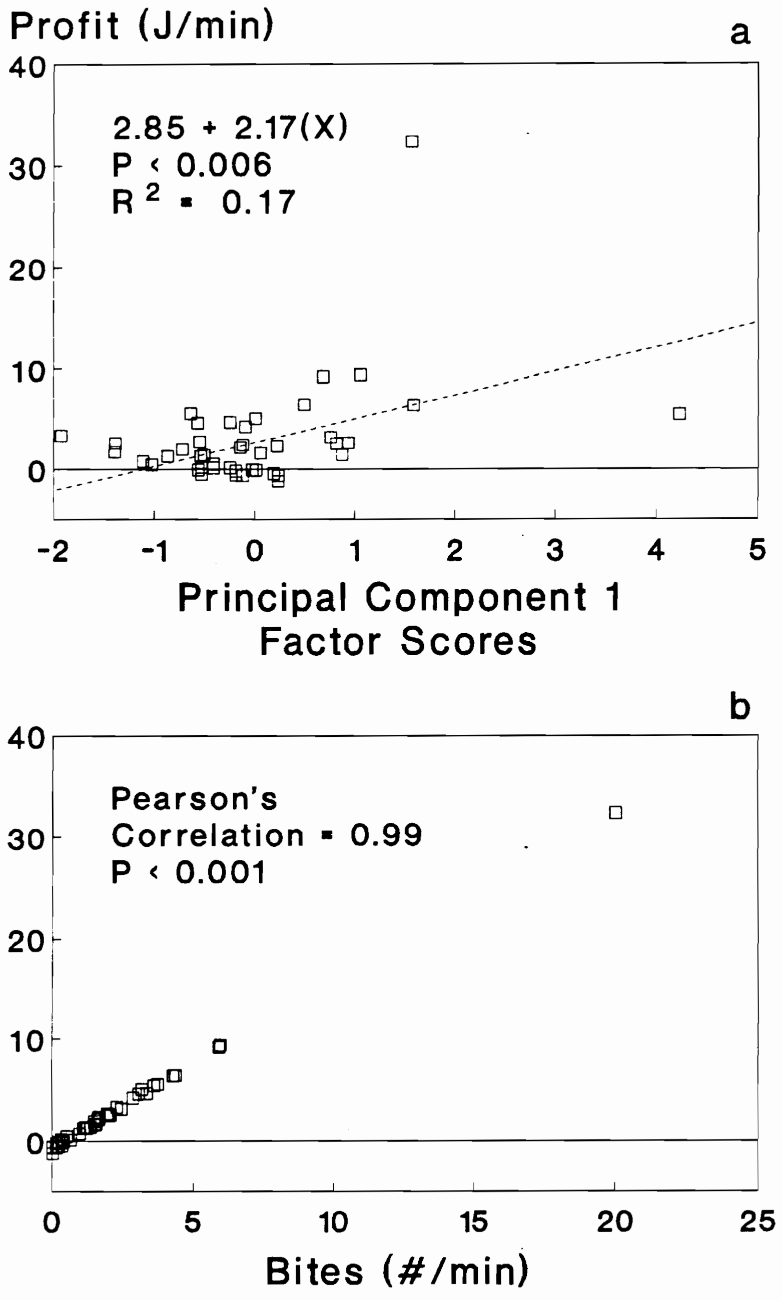


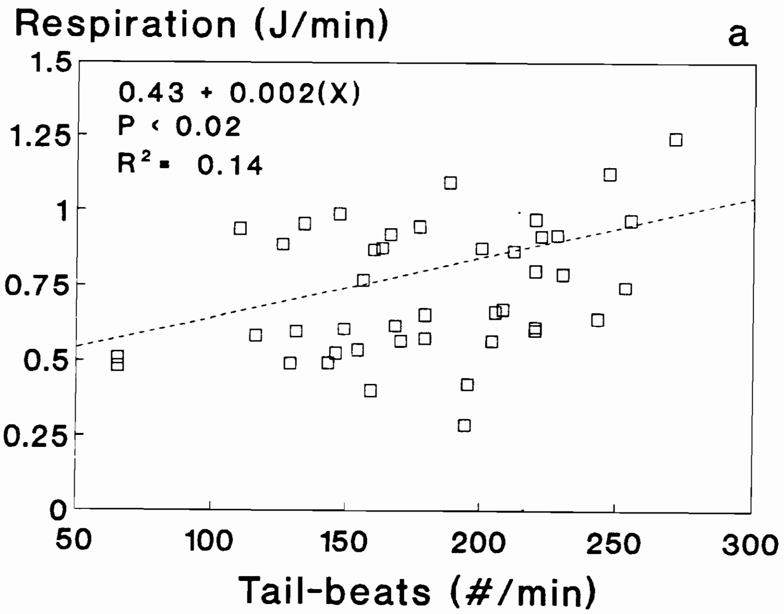
Figure 2.4. a) Scatter plot of estimated rates of net energy gained (J/min) versus factor scores generated from the first principal component. b) Scatter plot of foraging rate (bites/min) versus net energy gained.

($P < 0.007$, $R^2 = 0.17$). Whether computed with the outlier included or not, the regression predicted net energy gained equally well for all values of the first component. Therefore, the detected increase in the rate of energy gain in shallow, fast habitats was not dependent on a single influential observation or a tight cluster of samples at the extreme values of the first principal component.

Because the estimates of net energetic gain were highly dependent on estimates of consumption, the detected relationship between energy gain and PC1 depended on the assumption that one food item was consumed each time a juvenile took a bite. The relationship remained positive if I assumed that the 22 juveniles with the highest PC1 scores ate a food item during only 66% of their bites ($P < 0.03$). No relationship was detected if I assumed the same group of juveniles ate an item during 50% of their bites ($P > 0.10$).

While tail-beat frequencies increased in shallow, fast habitats ($P < 0.006$, Table 2.3), respiratory rates did not ($P > 0.39$). This result was somewhat confusing, because both variables increased in high velocity microhabitats. However, while respiration estimates increased with increasing tail-beat frequencies ($P < 0.02$), the relationship did not explain a large proportion of the variation in respiration rates ($R^2 = 0.14$, Figure 2.5a), so the two variables could relate to habitat characteristics differently.

This interpretation was reinforced by the significant relationship detected between respiration rate and PC2 ($P < 0.04$, Table 2.3). The relationship indicated that respiration increased as both depth and velocity increased (Figure 2.5b), although tail-beat frequency did not ($P > 0.07$). Net energy gain and foraging rate were not related



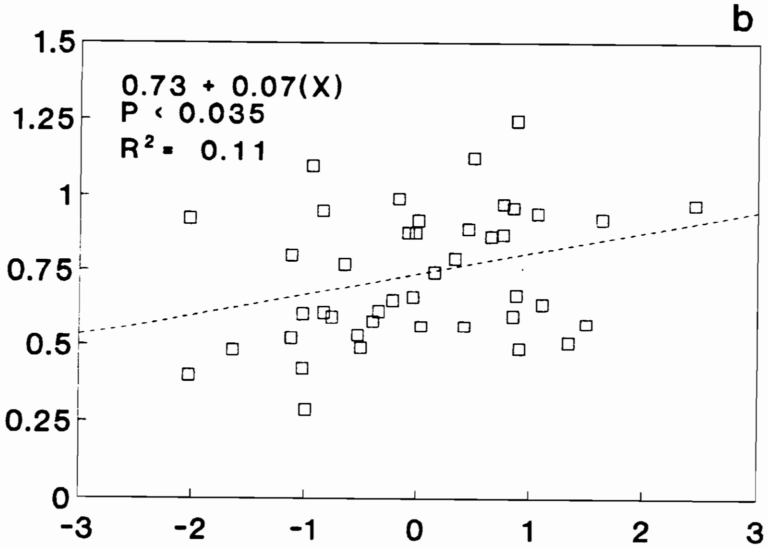


Figure 2.5. a) Scatter plot of observed tail-beat frequencies versus estimated respiration rates (J/min). b) Scatter plot of factor scores generated from the second principal component versus respiration rates.

to PC2 (both $P > 0.38$), and none of the energetic variables were related to PC3 (all $P > 0.50$).

Hydraulic ratios and energetic profit.

Reynolds numbers ranged between $0-1.82 \cdot 10^8$ (mean = $5.37 \cdot 10^7$), and Froude numbers ranged between 0-0.20 (mean = 0.04). Mean velocity was highly correlated with both Reynolds ($r=0.89$, $P < 0.01$) and Froude numbers ($r=0.98$, $P < 0.01$), and energetic variables exhibited relationships with these hydraulic characteristics that were similar to those exhibited with mean velocity. Neither hydraulic variable was related to net energetic gain or foraging rate (all $P > 0.05$), but both were positively related to tail-beat frequency (both $P < 0.0009$, Table 2.3). Additionally, Reynolds numbers were related to respiration rates ($P < 0.01$, Table 2.3). Log transformation of Reynolds numbers did not improve any of the regressions involving that variable. These results indicated that in the microhabitats where I observed juvenile smallmouth bass, these hydraulic indices did not account for energetic profitability of microhabitats.

Behavioral variables and energetic profit.

Juveniles exhibited wide variation in the area they occupied (range: 2.3-65.3 m^2, mean = 16.9 m^2), and percent time they spent moving among foraging sites (range: 22-100%, mean = 57%), or actively searching for food (range: 0-79%, mean = 43%). However, none of the energetic variables were related to these behavioral characteristics (all $P > 0.06$). These results indicated that searching the benthos for food could be as energetically costly as moving through the water column among foraging sites, and that foraging success did not necessarily depend on foraging (i.e. searching) effort.

Discussion

Factors determining energetic profit of microhabitats.

The juvenile smallmouth bass observed in this study primarily fed on benthic prey or prey attached to rooted vegetation. However, foraging strategies varied among individuals, in terms of the microhabitats they occupied, their average swimming speed, the size of the area they moved within, and the time they actively searched for food. While variation in any one of these aspects might affect either intake rate or energy expenditure, microhabitat use was the only factor in this study that consistently influenced the estimated rates of net energy gain. Different modes of benthic foraging (e.g. spending a long period searching a small area as opposed to searching several smaller, dispersed areas over the same period of time) could net similar energetic gains depending on the characteristics of the microhabitat in which they were employed.

This study was not specifically designed to define the characteristics of profitable and unprofitable microhabitats in the North Anna River, but the data suggested some generalizations. Juveniles that occupied areas less than 60 cm deep with average velocities higher than 10 cm/s always attained positive rates of net energetic gain, so areas with these characteristics might be considered profitable. Juveniles that occupied areas greater than 70 cm deep and containing average velocities less than 5 cm/s always attained positive net energy gains as well. However, juveniles in the shallow, fast microhabitats (n=9) averaged 7.86 J/min of net energy gain, while those in the deep, slow microhabitats (n=7) averaged 2.13 J/min. The difference in the magnitude of energetic gain indicated that the microhabitats meeting the shallow, fast criteria were the most energetically profitable microhabitats in the river. These microhabitats have also been identified as the areas that support the highest densities of larval aquatic insects in streams (Kondratieff and Voshell 1980, Gore and Judy 1981, Orth and Maughn 1983).

A significant result of this study was that the relative profitability of microhabitats could only be predicted if both depths and water velocities were examined. I attempted to account for variation in depth and velocity using hydraulic ratios and principal components, but Froude and Reynolds numbers did not relate to net energetic gain because they did not incorporate the effects of depth adequately. The first principal component (PC1) was the only variable that differentiated between deep microhabitats with slow velocities and shallow microhabitats with higher velocities, and it was the only habitat variable that was related to estimates of energetic profit.

Juveniles foraged more frequently in high velocities (regardless of depth), but not frequently enough to indicate that energetic profitability was associated with velocity alone. It is possible that profitability did not directly relate to velocity because energy lost to respiration also increased in higher velocities, thereby nullifying gains amassed through increased foraging. This explanation is intuitively appealing; juveniles increased their tail-beat frequencies when swimming in high water velocities, and the corresponding increase in respiratory costs nullified energetic gains achieved through elevated consumption.

However, other results raised some doubt about the simple explanation that juveniles had to swim faster and expended more energy in faster velocities. While tail-beat frequency was related to respiration rate, it did not explain a large proportion of the variation in respiration.

In fact, respiratory estimates did not increase in shallow-fast microhabitats (i.e. areas with high PC1 scores), even though tail-beat frequencies were significantly higher in those areas. Therefore, it is possible that increased respiratory estimates in high-velocity microhabitats were not entirely caused by elevated tail-beat frequencies, but were more consistently affected by a factor such as juvenile size.

Additionally, all estimates of respiration rate were less than 1.3 J/min, which suggested that respiratory losses in all microhabitats were low relative to many of the estimates of consumption. Therefore, the profitability of habitats for juvenile smallmouth bass primarily depended on foraging rates and not respiratory losses. Foraging rates certainly increased in higher velocities, but they increased more significantly in high-velocity microhabitats that were also shallow. This relationship between habitat variables and energetic profit for juvenile smallmouth bass was not exactly identical to the conceptual model of microhabitat profitability developed for drift-feeding salmonids in streams.

Profitability of microhabitats for drift-feeding salmonids and benthic feeding smallmouth bass.

The energetic profitability of a microhabitat is defined as the trade-off between energy expended while foraging in the microhabitat and the resulting intake rate (Jenkins et al. 1970, Bachman 1984, Crowder and Magnuson 1983, Fausch and White 1981, Fausch 1984). For drift-feeding salmonids, rates of both intake rate and energy expenditure depend on the velocity they occupy. Both juvenile and adult salmonids increase their intake rate of drifting invertebrates as they occupy increasingly faster water velocities (Smith and Li 1983, Fausch 1984, Hughes and Dill 1990), and expend more energy to maintain their feeding position (Brett 1973, Puckett and Dill 1984, Dabrowski 1986, Facey and Grossman 1990). However, both adult and juvenile salmonids decrease their attack distance in high velocities, so by moving into higher velocities salmonids generally increase their energetic intake more than their energy expenditures (Godin and Rangely 1989, Hughes and Dill 1990). Therefore, the profitability of microhabitats for drift-feeding salmonids, like benthic-feeding smallmouth bass, is defined by the consumption rate achieved in the microhabitat.

But the habitat characteristics associated with profitability for juvenile smallmouth bass differed from those associated with profitability for drift-feeding salmonids. Juvenile smallmouth bass netted their highest energetic profit in areas that were both shallow and contained high velocities, not areas that simply contained high velocities. Shallow-fast microhabitats may have been most profitable for juvenile smallmouth bass because submerged vegetation grew well in those areas, and this vegetation frequently supports high densities of benthic invertebrates (Ward 1992). The presence or proximity of aquatic vegetation may therefore be an important variable to include in future evaluations of microhabitat use by age-0 smallmouth bass.

Another difference between smallmouth bass and salmonids was that juvenile smallmouth bass exhibited similar foraging behavior (i.e. benthic foraging) in dissimilar microhabitats, suggesting that they maintained similar respiratory costs in all microhabitats without modifying their behavior. Similar results have been observed for other benthic-feeding species (Facey and

Grossman 1992), so the relationship between velocity and energy expenditure for fish that are primarily benthic foragers may differ from the relationship observed for salmonids. Salmonids appear to shift between drift feeding and benthic foraging depending upon the microhabitat they occupy (Grant and Noakes 1987).

Assumptions affecting estimates of energetic profit.

The assumptions I made in the course of estimating energetic profit are certainly subject to dispute. Estimates of respiratory costs depended on estimates of average swimming speed during the observation, but it was evident that swimming speed varied substantially within each observation period. The swimming-speed method of estimating respiratory costs is typically applied to species that exhibit steady swimming (e.g. Dabrowski 1986, Facey and Grossman 1990, Kaufmann 1990), and the actual metabolic costs of non-steady swimming may be much higher than my estimates (Webb 1991). However, all the swim speed estimates were less than 3.0 body-lengths/s, which is considered a sustainable speed for most fishes (Videler and Wardle 1991), and probably represents a relatively small metabolic cost.

Estimates of energetic profit also depended on the estimated energetic content of the average food particle, which in turn assumed that food habits of juvenile smallmouth bass in the North Anna River resembled those of juveniles in the New River. Studies of the food habits of age-0 smallmouth bass from throughout eastern and midwestern U.S. (Lachner 1950, Stewart 1978, George and Hadley 1979, Angermeier 1982, Buynak et al. 1982) have reported varying percentages of aquatic invertebrates in the diets. However, all studies suggested that larval aquatic insects were the most frequently occurring food item in late summer, and chironomids and microcrustaceans were a more minor component of the diet. Therefore, the relative proportions I assumed for each category in the diet were supported by data collected in a number of systems throughout the geographic range of smallmouth bass.

If it were not valid, the assumption that one item was ingested with each bite could also affect the estimates of energetic intake. Comparison of observed foraging rates with estimates of foraging rates necessary to obtain maximum consumption suggested that this assumption was at least possible. For the average sized juvenile I observed (80 mm TL), the maximum consumption possible in a day was 0.67 g/day (Shuter and Post 1990). If the average prey item weighed 0.132 mg (based on the data in Table 2.1), and an individual consumed an average of one item per bite, then the individual would have to average 5.9 bites/min for 14 hours to achieve maximum consumption. Only one individual observed in this study exceeded that rate, and the average foraging rate (2.1 bites/min) was well below the rate necessary to reach maximum consumption in a 14 hour day. This comparison suggested that the juvenile smallmouth bass I observed were not consuming more food than they could consume based on my estimates of foraging rates and the energy consumed during an average bite. Additionally, the estimate of 5.9 bites/min for a juvenile to achieve maximum consumption was similar to the mean foraging frequency observed for juvenile smallmouth bass feeding in the Mississippi River (5 bites/min) and growing at a rate considered near "optimal" (Simonson and Swenson 1990).

The relationship between energetic profit and PC1 remained positive when the intake rate for juveniles in the 22 areas that scored highest on PC1 was lowered to two items for every three bites. This test indicated that foraging rates in shallow-fast microhabitats were high enough to make those habitats more profitable, even if the number of bites taken was negatively related to the rate of energetic intake. This is significant because evidence indicates that the number of bites taken was positively related to energetic intake. Not only do fish that bite more frequently tend to consume more prey items (Grant 1990), but the juveniles I saw biting more frequently were foraging in shallow-fast microhabitats containing more larval Ephemeroptera and Trichoptera (Ward 1992), which contained more energy/individual than other food items (Table 2.1).

When drift feeding, juvenile smallmouth bass concentrate their foraging efforts at dawn and dusk when the concentrations of drift are highest (Stewart 1978). Because I could not video-tape juveniles at dawn and dusk (due to low light levels), I can not definitely state that juvenile smallmouth bass in the North Anna River never switched to a drift feeding mode at dawn or dusk. However, I observed juvenile smallmouth bass at dusk on several occasions and never noticed them moving into new microhabitats or switching foraging modes as would be expected if they were drift feeding.

Implications for microhabitat use.

Given that shallow-fast microhabitats yielded a higher energetic gain to juvenile smallmouth bass, optimal foraging theory would predict that juveniles should occupy shallow, fast microhabitats more frequently than deep, slow habitats (Crowder and Magnuson 1983, Werner et al. 1983b). The results presented in Chapter 1 support this prediction because juveniles increased their use of shallow microhabitats and expanded the range of velocities they occupied as the summers of 1990 and 1991 progressed. The chronology of microhabitat use suggested that some individuals entered the most profitable habitats earlier than others but after several weeks of evaluating available microhabitats the majority of juveniles entered areas that were likely to yield relatively high energetic profits.

The results of this study indicated that microhabitat use by juvenile smallmouth bass could directly affect their growth rate during the first year. Age-0 smallmouth bass that grow quickly increase their chances of surviving to maturation and subsequently increase their fitness within the population (Werner et al. 1983a, Rozenweig 1991), so an individual's fitness may depend upon its ability to identify and occupy profitable habitats. Accumulated evidence indicates that this is the case for drift-feeding salmonids. Salmonids establish dominance hierarchies where dominant individuals exclude competitors from the most profitable positions, subsequently grow faster, and maintain that growth advantage by increasing their size and swimming ability so they can be the first to invade even more profitable positions in higher velocities (Wankowski and Thorpe 1979, Abbot et al 1985).

But a key difference between benthic-feeding smallmouth bass and drift-feeding salmonids is that salmonids identify and defend specific focal points in a stream that convey food at relatively stable rates, and they occupy those positions for long periods of time (McNicol and Noakes 1981, Bachman 1984, Fausch 1984, Stradmeyer and Thorpe 1987). The size of defended feeding territories can vary with changes in food abundance (Dill et al. 1981), or changes in the density of competitors (Li and Brocksen 1977, Fausch and White 1981) but the relative focal points remain the same.

While drifting food resources are replenished continuously at a focal point, it may take several days to replenish depleted benthic resources. Therefore, benthic food resources in all microhabitats fluctuate both spatially and temporally (Angermeier 1985), and benthic feeders can not concentrate their efforts in a small area for an extended time. As benthic feeders, juvenile smallmouth bass tend to employ the mobile strategy described by Grant and Noakes (1987) in which individuals do not focus their efforts on a single position but instead search a wide area.

Juveniles could improve their foraging success by concentrating their efforts in areas with profitable habitat characteristics, but competitors or abiotic factors could cause food resources to vary so much that typically profitable areas frequently become unprofitable (Werner and Hall 1979, Peckarsky 1983, Poff and Ward 1989). If microhabitat profitability varied, juveniles may have reentered microhabitats that were typically less profitable (i.e. deep pools) as they searched for another area where they could forage successfully (Werner et al. 1983b). Therefore, the probability that a mobile, benthic feeding juvenile would gain a growth advantage becomes a function of microhabitat availability, spatial and temporal variability of the food resource, and the behavioral mechanisms employed while searching for a patchy resource. If the availability of food resources was extremely variable (even in profitable microhabitats), then it is possible that all individuals would experience periods of slow growth, and stochastic abiotic factors could determine which (if any) individuals gain a growth advantage.

CHAPTER 3

Effect of Early Growth Rate on Subsequent Growth and Survival of Age-0 Smallmouth Bass

Introduction

Larval and juvenile fish typically experience high mortality rates, but larval cohorts that grow at different rates experience dissimilar survival rates (Houde 1989, Luecke et al. 1990). Individual larvae that grow relatively fast may gain a survival advantage over slower growing members of their cohort (Miller et al. 1988, Persson and Diehl 1990). This early growth advantage may result from initial size differences of larvae at the time of hatching (West and Larkin 1987) or from individual differences in foraging success or prevailing environmental conditions. However, the duration of time that individual larvae and juveniles maintain growth advantages is a subject of speculation.

During their first growing season, individuals that gain an early growth advantage usually begin feeding on high-energy prey items (e.g. larval fish) sooner and thereby further increase their growth rate (Keast and Eadie 1985). Additionally, large individuals are frequently the first members of a cohort that are morphologically capable of exploiting new habitats in which they may forage more efficiently (Layzer and Clady 1987, Ehlinger 1990). Small individuals may lock themselves into a cycle of slow growth by specializing on small, low-energy prey items which promote slower growth and this subsequently increases the time that these individuals are morphologically unable to capture high-energy prey (Walton et al. 1992). These results suggest that individuals that gain an early growth advantage are likely to maintain that advantage, reduce their susceptibility to predation and starvation mortality, and subsequently are more likely to recruit to the spawning population.

However, much of the evidence supporting size-dependent growth and mortality of age-0 fish does not consider how environmental stochasticity affects these processes. In a heterogeneous environment, large individuals may have their competitive advantages eliminated by spatial and temporal shifts in food resources. In such cases, foraging success may depend more on the ability of individuals to locate resources (an ability that is not necessarily size dependent) rather than the ability to capture or defend resources (abilities that are frequently size-dependent). Age-0 fish in streams may be particularly susceptible to these influences because streams are highly variable environments (Angermeier 1985, Statzner et al. 1988), and many stream fish demonstrate limited mobility (and therefore limited ability to search for resources) during their first growing season (Shuck 1945, Heggenes et al. 1991).

In Chapters 1 and 2, I demonstrated that age-0 smallmouth bass change their use of microhabitats in the North Anna River as they progress through stages of ontogenetic development. The first individuals to enter previously unused (and energetically profitable) habitats may gain a growth advantage over the rest of the age-0 cohort. Alternatively, it is also possible that individuals gain only short-term growth advantages when they enter profitable habitats because of environmental stochasticity.

Growth advantages may also result less from the actions of juveniles than from behavioral decisions made by spawning adults. Adults that spawn early may provide their offspring with a size advantage over the rest of the cohort during an early period of development. Conversely, warmer thermal regimes may provide late-spawned larvae with a growth advantage that overwhelms the growth head-start that early-spawned individuals gained or the growth advantages amassed by individuals occupying the most profitable habitats. Understanding the factors that determine how some individuals gain a size advantage during their first growing season may improve management efforts to stabilize recruitment of smallmouth bass populations.

The primary objective of this study was to quantify and compare growth rates of individual smallmouth bass in the North Anna River during early life stages. By examining daily rings deposited on otoliths (Brothers et al. 1976), I was able to compare the relative growth rates of individuals through time. I also tried to determine whether individual differences in growth rate were influenced more by individual differences in consumption and energy expenditure or by variation in thermal regime. Finally, I examined the effect of growth rate on larval survival, to determine if fast growing larvae were more likely to survive through the period of mass mortality that occurs after larvae disperse from their brood sites.

Methods

Site Description.

Larval and juvenile smallmouth bass used in this study were collected from the North Anna River in eastern Virginia. A complete description of the river is included in Chapter 1. All collections were taken from a reach of the river extending approximately seven km downstream from the Route 603 bridge in Hanover County and encompassing both the study sites described in Chapter 1. Larvae were collected from all areas where I observed smallmouth bass nests in this reach, but juveniles were only collected from areas outside of the two study sites described in Chapter 1, to insure that I did not directly affect juvenile densities in those sites.

Sample collection.

Collections were timed to coincide with life stages during which age-0 smallmouth bass exhibited distinctive behaviors, food habits, and habitat use. Brood larvae were collected to estimate the distribution of individual growth rates that existed before mass mortality occurred at dispersal. A sample of juveniles was collected two weeks after dispersal to represent individuals that had survived dispersal, were morphologically capable of eating a wide variety of prey items (Easton and Orth 1992), and were beginning to explore previously unoccupied habitats (see Chapter 1). Juveniles were sampled again six weeks after dispersal, when most individuals were occupying previously unused habitats.

Between May 24 and June 29, 1990, I collected 78 larvae that swam off the nest at least six days earlier but still occupied their brood sites. I collected a maximum of 10 larvae from each brood (eight broods total) with an aquarium net, preserved them on ice, and transported them back to the laboratory where their total length (TL, mm) was measured the same day using a dissecting microscope equipped with an ocular micrometer. Also in 1990, I collected 38 juvenile smallmouth bass during July 11-26, and 16 juveniles during August 14-17. Juveniles were collected using a backpack electroshocker, their TL was measured immediately after capture, and they were preserved on ice until transported to the laboratory. Because ethanol degrades otolith microstructure of smallmouth bass (R. J. Graham, D. J. Orth, M. J. Sabo, R. S. Easton, and B. Wells, personal observation), larvae and juveniles were frozen to preserve them until I could begin age and growth analyses.

In 1991 I obtained samples of larval and juvenile smallmouth bass at life stages similar to those sampled in 1990. I collected 73 larvae from eight broods during May 8-15, 38 juveniles during June 4-5, and 38 additional juveniles during July 2-9. Sampling methods were identical to those used in 1990.

Otolith removal and preparation.

Larval and juvenile smallmouth bass were dissected, and their sagittal otoliths were removed and mounted in thermoplastic cement on glass slides. I used an adapted metallurgical jig (Neilson and Geen 1981) to grind otoliths level along the anterior-posterior plane, using an alternate convex-concave grinding procedure (Graham and Orth 1987). Based on the morphology of smallmouth otoliths, the anterior-posterior plane is the ideal plane for growth analyses because the distance between rings is largest along this plane (Panfili and Ximenes 1992).

Procedures for counting and measuring.

I covered larval otoliths with immersion oil and counted their rings by examining them with a compound microscope at 200X power. The diameter (μm) and longest radius (μm) of larval otoliths along their anterio-posterior plane were measured with an ocular micrometer. Magnified images of juvenile otoliths were projected, and their diameters and long radii were measured using a metric ruler. Measurements in mm were converted to μm based on comparisons of diameters for 10 otoliths measured with both the ocular micrometer and from projected images. Diameter measurements on five projected images predicted the diameter measurements obtained with the ocular micrometer within 1 μm.

Ring counts do not differ between the left and right sagittae of individual smallmouth bass (Graham and Orth 1987), so only one otolith from each individual was used to estimate age and growth. Rings were counted until I obtained the same ring count three consecutive times and concurrently identified ring numbers 6, 12, 24, and 50 at the same positions. Weakly defined rings that disappeared when followed into the lateral field were considered subdaily rings (Miller and Storck 1982) and were not counted. If an otolith had seven rings I only established the position of ring 6, if it only had 13 rings I established the position of rings 6 and 12, etc. The longest radius to each of these rings was measured. These rings were chosen as bench-marks of growth, based upon observations of distinct differences among life stages. The first otolith ring is formed at the time of swim-up, and between swim-up and day six larvae only occupied the brood site. Larvae dispersed from the brood site between days 6 and 12, and metamorphosize before day 24. By day 50, most juveniles have begun occupying previously unoccupied habitats.

Estimating growth.

Smallmouth bass deposit rings daily (Graham and Orth 1987), and current evidence indicates that these rings are deposited even during periods of extremely slow growth (Wright et al. 1991). The relationship between otolith growth and somatic growth is particularly strong before otolith morphology changes towards the end of the first growing season (Rice et al. 1985, Wright 1990). Therefore, measurements of radii at specified rings should provide comparable estimates of growth rates over standardized periods early in life.

However, the procedure used to estimate growth rates can significantly affect the results. Different methods yield different back-calculated estimates of TL though all methods are equally plausible under most circumstances (Francis 1990). Back-calculated length estimates are highly sensitive to investigator errors when the objective is to estimate changes in length over short periods of time (Rice 1987). Additionally, estimates of larval growth rates are affected by random error when the size of the larvae at the formation of the first ring is variable and independent of otolith size (Titus and Mosegaard 1991). Because I was estimating growth rates over a small number of days and was unable to predict the size of larval smallmouth bass at swim-up, I chose to compare otolith growth rates as a surrogate for growth of fish in TL. To validate the assumption that otolith growth was related to growth in TL, I used least squares regression to determine if an otolith's long radius was linearly related to the TL of the fish from which it was taken. The assumption was tested for each year and separately for larvae and juveniles to insure that the assumption applied to both life stages during both years. The alpha level of rejection equaled 0.05 for each of these comparisons (and for all subsequent analyses used in this study).

I calculated absolute otolith growth (OG, microns accumulated on the long radius over a specified period) from swim-up to day 6, days 6-12, days 12-24, and days 24-50. The radius of the sagittal centrum was subtracted from the absolute growth estimate for days 1-6 to insure that only growth accumulated after swim-up was considered. For each year, OG during days 1-6 was compared between larval and juvenile samples to determine if individuals that grew quickly as larvae were more likely to survive to the juvenile stage. I used two-sample t-tests to compare sample means of these variables and two-sample F-tests to compare the dispersion of distributions observed for larvae and juveniles collected each year. Pearson correlation analyses were used to determine if individuals that grew quickly during early life stages were likely to grow quickly during subsequent life stages.

These analyses did not resolve whether variation in growth rates was caused by environmental or behavioral differences among individuals. Specifically, because smallmouth bass swam off nests on different dates (and were exposed to different temperature regimes), I wanted to determine if temperature regime was the primary factor affecting growth rates, or if the rate of food intake and energy expenditure could override the effects of temperature (Radtke 1989). I estimated the mean water temperature experienced by each individual during each period by relating water temperature data collected by a thermograph installed at the Route 603 Hanover County bridge to each individual's swim-up date. Pearson correlations were used to determine if individuals that grew in higher temperatures were more likely to grow quickly. This comparison was made for each life stage during each year.

A final correlation analysis was used to compare the TL of juveniles at the time of capture to their date of swim-up and accumulated degree-days. This comparison demonstrated whether the largest juveniles at the times of collection were individuals that were spawned earliest or those that experienced the warmest thermal regimes. It also revealed if thermal advantages were gained by juveniles that accumulated degree-days over a longer period of growth, or by juveniles that grew for a shorter period but in a warmer thermal regime.

The analyses described so far examined characteristics of growth during the first two months after larvae began to swim off the nest. I used estimates of TL collected during the August underwater surveys described in Chapter 1 to compare the results of growth at a time near the end of the summer during both years. Juveniles observed underwater during 7-15 August, 1990, and 2-4 August, 1991, were classified into 5-mm categories based on TL estimates obtained with calibrated mask bars (Swenson et al. 1988), and then grouped as small, medium, or large juveniles (each group encompassed five 5-mm length categories). I used a chi-squared contingency test to determine if these size distributions differed. This comparison revealed whether the factors that affected growth rates early in the growing season resulted in significant differences in the size of juveniles near the end of the summer.

Results.

Spawning chronology and general characteristics of growth.

According to estimates of swim-up days from larval and juvenile otoliths, smallmouth bass spawned later in the year in 1990 than in 1991. These estimates concurred with observations reported in Chapter 1, and the difference was probably attributable to differences in the hydrologic regimes of the river during those years (Figure 3.1). In 1990, spawning occurred during a period of relatively low flow beginning soon after day 130 (10 May), but most swim-up larvae from that spawn did not survive a large flood that occurred about day 145 (25 May). Most successful spawning occurred during the subsequent low-flow period that began on Day 155 (5 June). Flows were relatively low throughout the

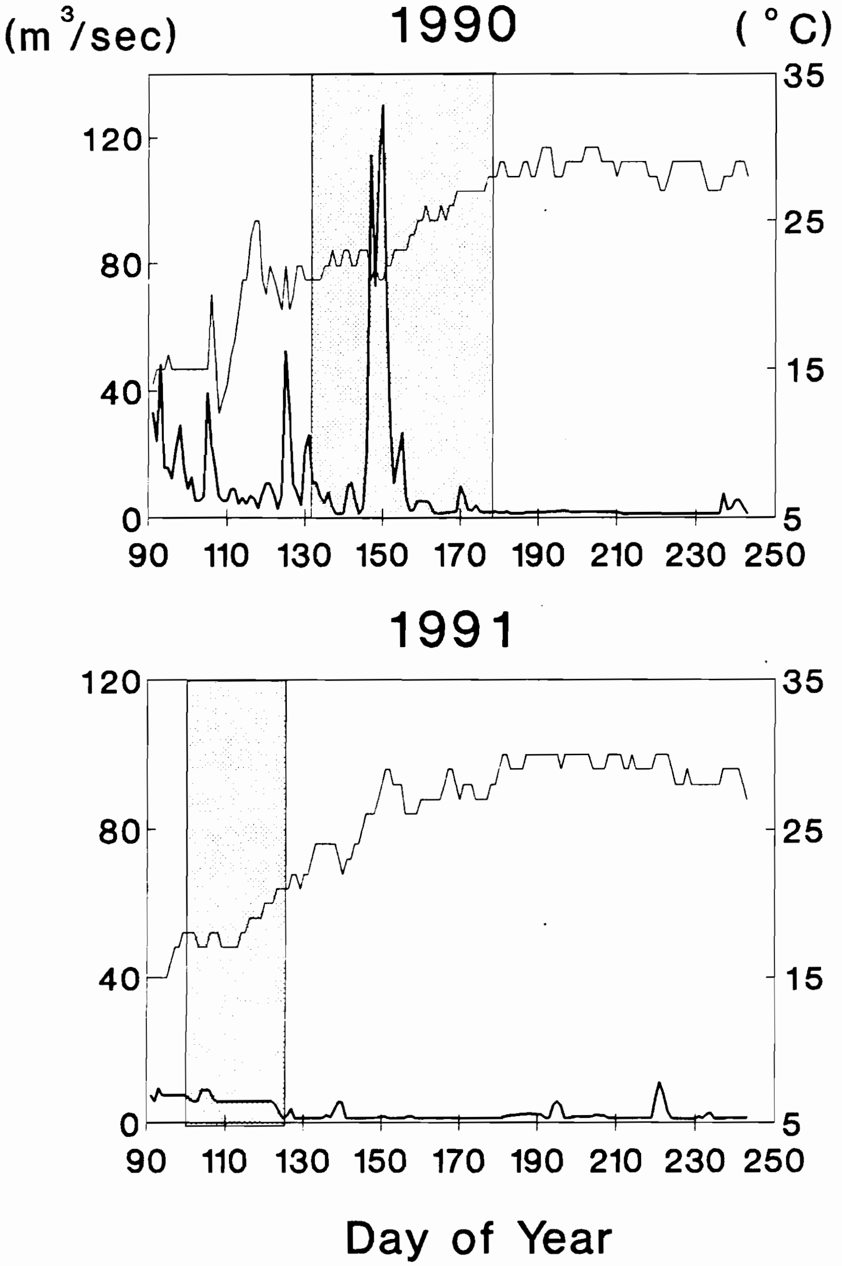


Figure 3.1. Water temperature (thin line, °C) and discharge (thick line, m^3/s) in the North Anna River, during the 1990 and 1991 growing season (April 1 - August 30). Shaded regions define when larval smallmouth bass swam-up.

growing season of 1991, and most spawning occurred during a relatively short period between days 100-128 (10 April-8 May).

Because successful spawning occurred later in the year in 1990 than in 1991, age-0 smallmouth bass experienced different thermal regimes during much of the two growing seasons. In general, larvae and juveniles experienced warmer thermal regimes and exhibited faster otolith growth during all life stages in 1990 (Figure 3.2), and juveniles collected in 1990 were larger than juveniles collected during corresponding periods in 1991 (Table 3.1). During both years, there was some variation in otolith growth that did not appear to be solely attributable to differences in thermal regimes.

Relationship between otolith size and length.

During both years, the length of the otolith radius was linearly related to TL of larval and juvenile smallmouth bass (all $P < 0.00001$, Table 3.2). All regression models explained variation in TL from otolith radius well (all $R^2 \geq 0.89$, and all MSE < 1% of mean squared regression). These results indicated that otolith growth approximated growth in TL and conclusions drawn from examinations of otolith growth could be extended to growth in TL.

Relationship between larval growth and survival.

Individual smallmouth bass in 1990 tended to have higher OG between days 1-6 than individuals collected in 1991 (Figure 3.3). In 1990, the mean OG during days 1-6 observed among larval smallmouth bass (mean=72.4) did not differ ($P > 0.49$) from the mean OG observed among juveniles (mean=71.19). Individuals that survived to the juvenile stage showed more variation in OG during days 1-6 (s^2=110.3)

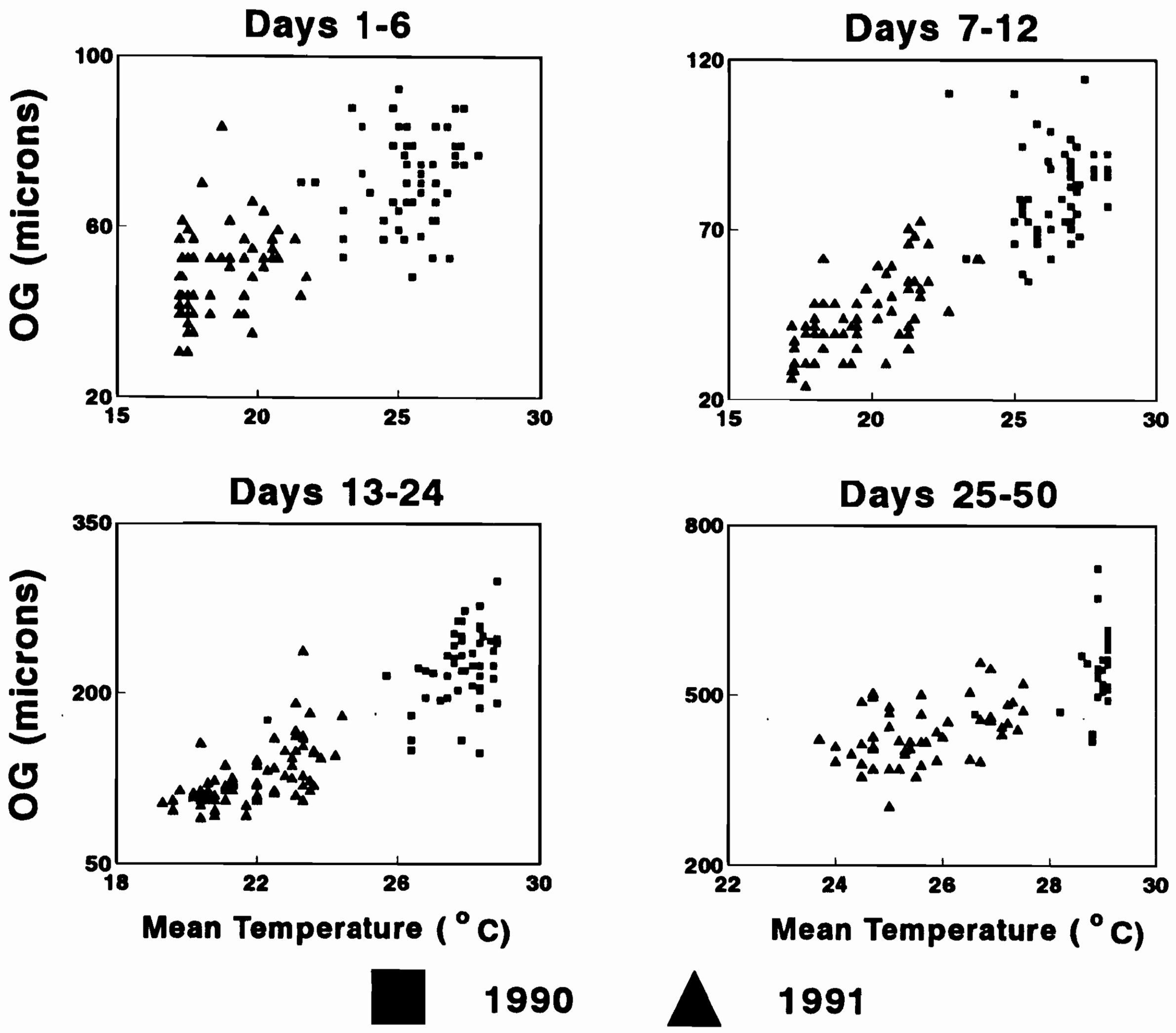


Figure 3.2. Range of absolute otolith growth (OG) and mean temperatures experienced during each growth period by age-0 smallmouth bass that survived to the juvenile stage, 1990 and 1991.

Table 3.1 Summary statistics of total length (mm) and weight (g) for juvenile smallmouth bass collected from the North Anna River during 1990 and 1991.

Year	Sample Period	N	Total Length (mm) Mean	SD	Range	Weight (g) Mean	SD	Range
1990	7/11-7/26	38	53.1	12.70	30-92	2.01	1.37	0.5-7.9
	8/14-8/17	16	67.6	8.65	48-82	3.32	1.08	1.3-5.3
1991	6/4-6/5	38	39.4	6.03	27-57	0.86	0.28	0.4-1.7
	7/2-7/9	38	58.2	5.77	47-70	2.23	0.62	1.1-3.8

Table 3.2. Linear regressions describing relationship between the long radius of the otolith (OR, microns) and total length (TL, mm) of smallmouth bass that otoliths were removed from (all P<0.00001). Separate models were developed for larval (8-19 mm TL) and juvenile smallmouth bass (23-118 mm TL) collected during 1990 and 1991.

Year	Life Stage	N	Model	r^2	MSE	MSR
1990	Larvae	55	TL=5.36+0.04OR	0.90	0.19	80.3
1990	Juvenile	54	TL=2.62+0.06OR	0.89	19.60	8429.0
1991	Larvae	69	TL=5.17+0.04OR	0.89	0.89	457.4
1991	Juvenile	76	TL=5.94+0.05OR	0.90	13.09	8346.5

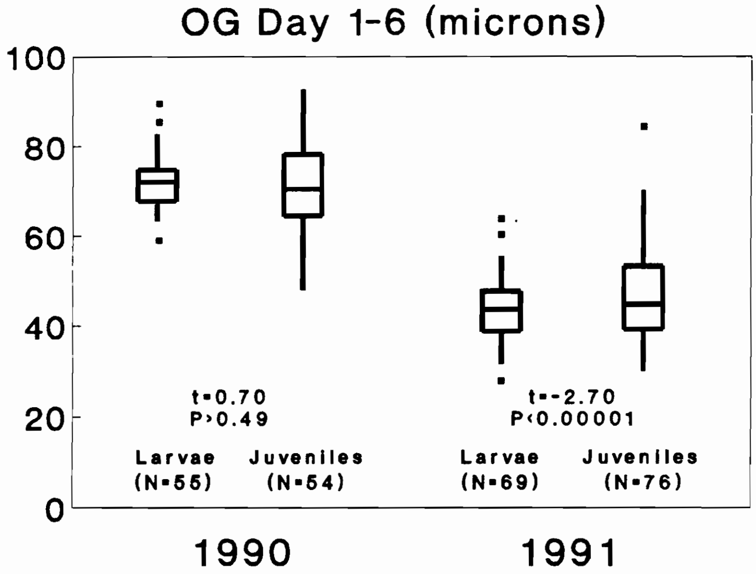


Figure 3.3. Absolute growth of otoliths compared between larvae collected before mass mortality occurred and age-0 juveniles collected later in the growing season, 1990 and 1991.

than larvae (s^2=49.7) in 1990, and the variances statistically differed ($P < 0.002$). These analyses indicated that during 1990 individuals that grew faster between days 1-6 were not more likely to survive through dispersal, and some very slow-growing individuals actually survived. Juveniles collected in 1991 tended to have higher (mean=47.7) and more variable (s^2=86.5) OG between days 1-6 than larvae (mean=44.3, s^2=32.7) and the means and variances exhibited during each life stage statistically differed (both $P < 0.008$). Therefore, in 1991, individuals that grew faster between days 1-6 were more likely to survive through dispersal. However, the difference between mean OG of larvae and juveniles was only three microns (which equated to 0.15 mm of TL based on regression presented in Table 3.2), and some juveniles grew as slowly as the slowest-growing larvae.

Correlation of OG among periods.

In 1990, OG during days 7-12 was negatively correlated with OG during days 25-50 ($r=-0.43$, $P<0.02$, Table 3.3) but was not significantly positively correlated between any two periods (all $r < 0.22$, all $P > 0.10$). In 1991, OG was positively (though weakly) correlated among all adjacent periods (all $r > 0.32$ and < 0.57, all $P < 0.02$) and between days 1-6 and days 13-24 ($r = 0.35$, $P < 0.01$). Comparisons between all other periods did not yield significant correlations ($P > 0.05$). These results indicated that fast-growing individuals during early periods in 1990 were not more likely to grow fast during later periods. In 1991, the fastest growers during any period were somewhat more likely to grow fast during the next period, but that advantage generally did not extend further into time.

Table 3.3. Results of Pearson's correlation analysis of absolute otolith growth among growth periods during 1990 and 1991.

1990

	Day 1-6 (n=54)	Day 7-12 (n=54)	Day 13-24 (n=54)	Day 25-50 (n=26)
Day 1-6	r=1.00	r=-0.05 P>0.20	r=0.20 P>0.10	r=-0.09 P>0.20
Day 7-12		r=1.00	r=0.10 P>0.20	r=-0.43 P<0.02
Day 13-24			r=1.00	r=0.22 P>0.20
Day 25-50				r=1.00

1991

	Day 1-6 (n=76)	Day 7-12 (n=76)	Day 13-24 (n=76)	Day 25-50 (n=53)
Day 1-6	r=1.00	r=0.44 P<0.01	r=0.35 P<0.01	r=0.25 P>0.05
Day 7-12		r=1.00	r=0.56 P<0.01	r=0.26 P>0.05
Day 13-24			r=1.00	r=0.32 P<0.02
Day 25-50				r=1.00

Relationship of OG and mean temperature.

In 1990, OG during days 13-24 was positively correlated with the mean temperatures individuals experienced during that period ($r = 0.44$, $P < 0.01$), but the two variables were not significantly correlated during any other period (all $P > 0.10$, Table 3.4). In 1991, OG and mean temperature were correlated during all periods (all $r > 0.37$, all $P < 0.01$, Table 3.4). These results indicated that fast-growing individuals in 1990 did not always experience the warmest thermal regimes, but warm temperatures did promote faster growth in 1991.

Relationship of degree days and growth with swim-up date.

During both years, total degree-day accumulation was negatively correlated with swim-up date ($r < -0.71$, $P < 0.01$) at the time of the first collection (Table 3.5) and at the time of the second collection ($r < -0.67$, $P < 0.01$). Also during both years, TL at the time of collection was negatively correlated with swim-up date at the time of the first collection ($r < -0.43$, $P < 0.01$) and uncorrelated at the time of the second collection (all $P > 0.05$).

These results indicated several interactions between swim-up date and growth rate. Although late spawned individuals in both years accumulated more degree-days/growth period (Figure 3.1), they generally did not overcome the total degree-days accumulated by early spawned individuals. In 1990, the degree-days accumulated by early-spawned individuals did not guarantee that they would maintain the growth advantaged achieved by being spawned earlier. Temperature and OG were not closely related that year, so the probability of an individual being a large juvenile at the end of the summer did not appear to depend on the time of spawning or the thermal regime experienced.

Table 3.4. Pearson correlation coefficients resulting from comparisons between absolute otolith growth with mean temperature during each growth period during 1990 and 1991. During each year, the sample sizes for the first three growth periods were equal (n=54 in 1990, n=76 in 1991), but were lower for comparisons during Days 25-50 (n=26 in 1990, n=53 in 1991).

	Growth Period (Mean Temperature)			
Year	Days 1-6	Days 7-12	Days 13-24	Days 25-50
1990	0.18 (P>0.10)	0.17 (P>0.20)	0.44 (P<0.01)	0.31 (P>0.10)
1991	0.37 (P<0.01)	0.64 (P<0.01)	0.61 (P<0.01)	0.45 (P<0.01)

Table 3.5. Results of Pearson's correlation analyses of swim-up date with total degree days accumulated, and total length (TL) of juveniles at the time of collection. Comparisons were made among juveniles collected during each sampling period (indicated by month) of 1990 and 1991.

	1990		1991	
	July (n=38)		May (n=38)	
	Degree Days	TL	Degree Days	TL
Swim-up date	r=-0.72 P<0.01	r=-0.55 P<0.01	r=-0.94 P<0.01	r=-0.44 P<0.01
	August (n=16)		June (n=38)	
	Degree Days	TL	Degree Days	TL
Swim-up date	r=-0.68 P<0.01	r=-0.43 P>0.05	r=-0.71 P<0.01	r=0.01 P>0.20

In 1991, early and late spawned individuals had an equal probability of being large at the time of the second collection because late spawned individuals consistently grew more quickly in warmer thermal regimes. So while early-spawned individuals accumulated more degree-days over time, individuals spawned later accumulated more growth/degree-day in the warmer thermal regimes.

Juvenile size near the end of the growing season.

The distribution of TL observed for juveniles in August 1990 (n=77) did not differ from the distribution observed for juveniles in 1991 (n=48, $X^2 = 4.63$, $P > 0.09$). The proportion of medium-sized juveniles (55-75 mm TL) in samples were nearly identical for both years (Figure 3.4). Although the 1990 sample was collected approximately one week later in August than the 1991 sample, juveniles in 1990 were only off the nest 7-8 weeks while juveniles in 1991 left the nest 11-12 weeks before sampling. Therefore, the results indicated that juveniles spawned in 1990 and 1991 were approximately the same size at the end of their first summer, despite the fact that juveniles spawned in 1991 effectively had a longer growing season.

Discussion

Larval smallmouth bass (and larval fish in general) are thought to experience lower mortality rates when they grow fast (Miller et al. 1988) and are therefore more likely to survive through their first growing season. Furthermore, age-0 smallmouth bass that grow fast early in life are generally assumed to maintain higher rates of growth than the rest of their cohort (DeAngelis et al. 1991) and are considered more likely to survive their first winter (Oliver et al. 1979). Given these premises, individual smallmouth

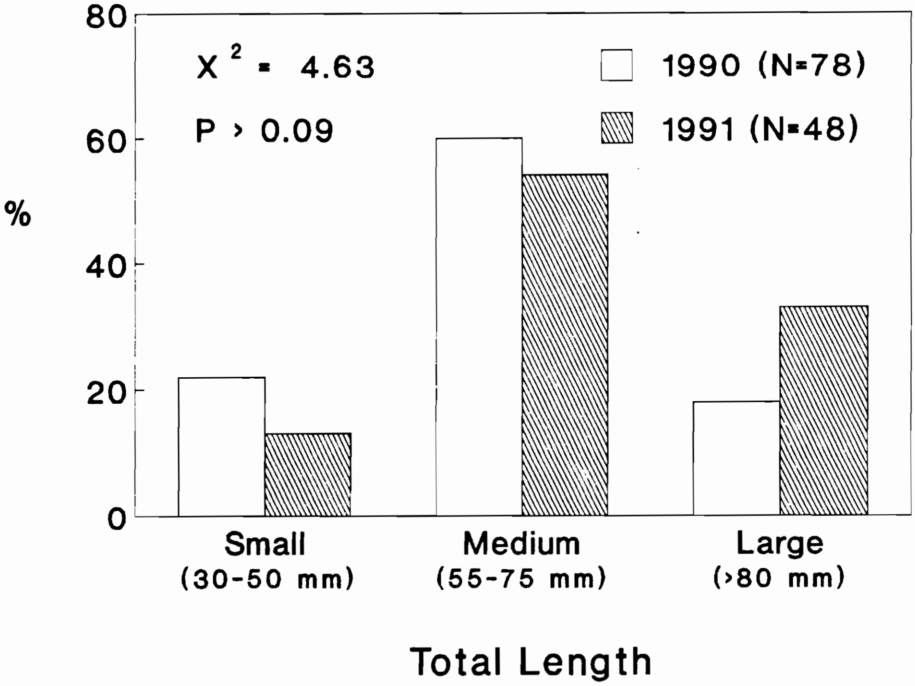


Figure 3.4. Size distributions of juvenile smallmouth bass observed between August 7-15, 1990, and August 2-4, 1991. Juveniles were grouped in 5-mm categories based on their estimated total length.

bass would benefit from any factor that promotes their growth early in life.

This study was designed to examine each how well those premises applied to age-0 smallmouth bass in the North Anna River. The results suggested several general conclusions. First, fast growing larvae were not more likely to survive to the juvenile stage. Next, when temperatures remained below 22-23°C, individuals that grew in warmer temperatures grew faster during comparable life stages. Above 22-23°C, variation in growth was not related to temperature, and was also unrelated to previous growth rates. Finally, individuals that gained a growth advantage were not insured of attaining a size advantage by the middle of the growing season.

In the following sections, I will discuss the evidence that supports these conclusions and the consequences they allude to. The general idea I will try to communicate is that individual age-0 smallmouth bass did not necessarily benefit from high growth rates during their early stages of life. Instead, timing of spawning, prevailing thermal regimes, and individual variation in temperature-independent growth rates interacted to give all individuals an equal chance of being among the largest or smallest members of the cohort by the middle of the growing season.

Larval growth and survival.

The results of this study indicated that larger brood larvae were not more likely to survive to the juvenile stage. The mean OG during days 1-6 differed slightly between larvae and juveniles in 1991 (equating to a small difference in TL), and the mean radii of otoliths from juveniles were smaller than that of larvae in 1990. In both years, OG before day 6 varied substantially more among juveniles than among larvae. This suggested that no portion of the size-range of brood larvae was excluded from surviving to the juvenile stage.

It is possible that size-dependent mortality occurred before day 6 and was therefore not detectable with collections of larvae made after day 6. However, in all cases larvae were guarded by the male parent between swim-up and day 6. Parental defense greatly decreases the susceptibility of larvae to predation (Neves 1975, Ridgeway 1988), so it is more likely that most larval mortality occurred after dispersal from the brood site. The results of this study indicated that mortality during dispersal was probably not dependent on size.

The relationship between survival and growth rate of larval fish is apparently strongest when larval densities are high (Elliott 1989a, 1989b, Houde 1989). Nesting densities of smallmouth bass during 1990 and 1991 were low (approximately 1/150 m of stream length) relative to densities reported in other studies (Pflieger 1966, Goff 1985, Hoff 1991, Reynolds and O'Bara 1991) which suggested that larval densities were low, and may explain why growth rates were not closely related to larval survival.

Timing, temperature, and growth rates.

I examined two years that exhibited very different interactions among prevailing environmental conditions and growth rates. Therefore, I will discuss the results of 1990 and 1991 separately. Afterward, I will discuss how such different years could produce juvenile cohorts with almost identical size distributions at the end of the growing season.

1990.

In 1990, most successful spawning occurred after temperatures exceeded the threshold of 22-23°C. The fastest growing individuals during any life stage were not necessarily growing in higher temperatures and were not necessarily the fastest growers during any previous life stage. The probability that an individual would be among the largest members of the cohort at the end of any life stage was primarily a function of their growth rate during that life stage and not previous growth. Therefore, the individual that grew slowest as a larvae could potentially be the largest member of the cohort by the end of the summer. This year represented a scenario where most age-0 growth occurred in optimal temperatures, and differences in growth rate at each life stage were probably attributable to difference in foraging success (Figure 3.5).

Model simulations of first-year growth and survival of smallmouth bass (DeAngelis et al. 1991) predicted that individuals that gained an early growth advantage would maintain relatively high growth rate, consistently occupy the largest portion of the size distribution, and be more likely to survive throughout the growing season. However, these individuals occurred more frequently in simulations that assumed age-0 densities were high (> 300 juveniles/ha). In these simulations, larger individuals were assumed to be better competitors for resources (Miller et al. 1988, Miller et al. 1992) and more likely to survive periods of resource scarcity (Elliott 1990). In contrast, I never observed more than 30 juveniles/ha in transect counts that covered 80% the area in study sites used in Chapter 1, so I would assume that juvenile densities in the North Anna River during 1990 and 1991 were low relative to those examined in the model simulations. Fast growers may not have been consistently

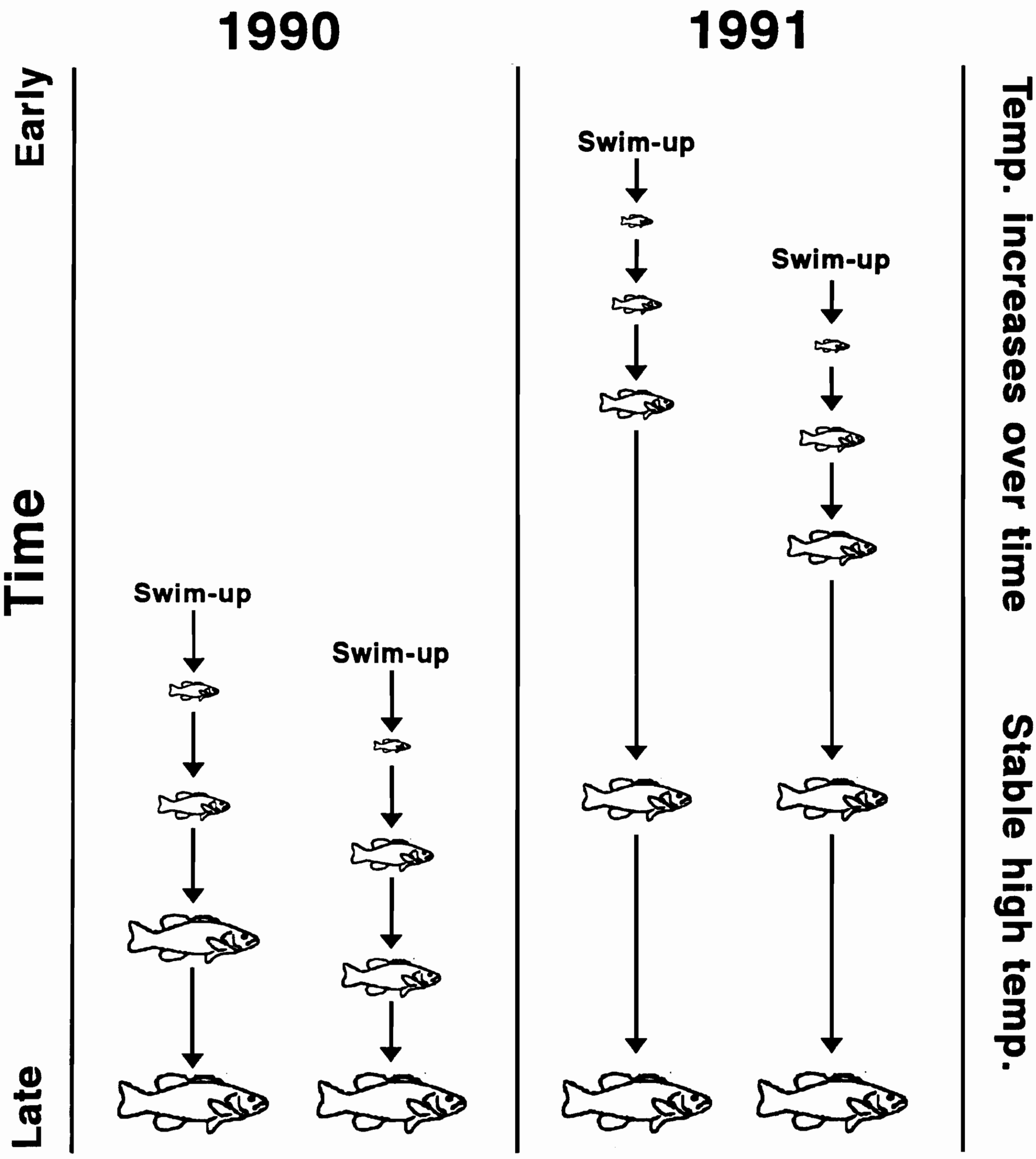


Figure 3.5. In 1990, spawning occurred when temperatures had stabilized above 25°C. Growth rates were high and unrelated to thermal regime. In 1991, bass spawned when temperatures were low and increasing. Growth was slow and individuals experiencing the warmest thermal regimes grew fastest, but early spawned juveniles accumulated slow growth over time. Rapid growth in 1990 compensated for the longer growing season of 1991.

better competitors for resources in these low densities. Instead, all individuals had an equal chance of locating stores of resources and temporarily benefitting from their exploitation.

I developed this explanation by examining some of the evidence presented in Chapter 2. Age-0 smallmouth bass were feeding on benthic invertebrates, which vary in density both spatially and temporally (Angermeier 1985). Therefore, an individual's ability to exploit food resources depended heavily on its ability to consistently locate areas with high densities of benthic invertebrates. Individuals may have improved their chances of finding profitable areas by recognizing habitat characteristics associated with profitability, or their chances may have depended upon their location in the river at a point in time and the availability of profitable areas around them. Neither mechanism is size-dependent, so all individuals in the cohort had the potential of finding and exploiting profitable resources.

1991.

In 1991, all successful spawning occurred in temperatures below the threshold of 22-23°C. During each life stage, early spawned individuals consistently grew in colder temperatures than those spawned later. Consequently, individuals growing in cold temperatures consistently grew more slowly during each life stage. By the middle of the growing season (the time of the second collection), early and late spawned individuals had an equal chance of being among the largest members of the cohort. Those spawned early had accumulated more days of growth, and those spawned later grew at higher rates for shorter periods of time. This year represented a scenario where temperature regimes maintained consistent differences in relative growth rates among individuals, but timing of spawning and size-independent mortality allowed slow-growers to attain the same size as fast-growers by accumulating growth over a longer period of time (Figure 3.5).

Previous investigators concluded that temperature does significantly affect the growth of juvenile smallmouth bass. The growth rate of a juvenile smallmouth bass increases asymptotically with increases in water temperature until achieving a maximum potential growth rate at approximately 26°C (Horning and Pearson 1973) and maintaining high, though variable growth rates until reaching 33°C (DeAngelis and Coutant 1979, Wrenn 1980). This would explain why growth rates increased with increasing mean temperature in 1991 but not in 1990.

The initiation of spawning for smallmouth bass spawn is triggered by changes in both photoperiod and temperature (Cantin and Bromage 1991), but they generally begin to spawn in the North Anna River soon after temperatures exceed 15°C (Lukas 1993). It seems strange that smallmouth bass should begin spawning that early because their offspring would grow slowly in such low temperatures. Among other species that spawn in thermally dynamic habitats, individuals that spawn early are less likely to successfully reproduce because their offspring grow slowly and experience higher mortality rates (Rice et al. 1987). The difference in the North Anna River was that fast growth was not associated with higher survival. Therefore, all individuals had an equal opportunity to survive and continue to grow over time.

Results of these scenarios and a conceptual model of growth.

The size distributions of juvenile smallmouth bass in August generally did not differ between the two years. I observed proportionally more large individuals (> 80 mm TL) in 1991 than in 1990, but the majority of juveniles observed during both years were medium sized (55-75 mm TL). Because the time of spawning differed between the two years but temperature regimes were fairly similar, this result suggests that most of the early growth accumulated by age-0 smallmouth bass in 1991 was relatively insignificant. Individuals in 1990 were able to attain as much growth in a shorter (though consistently warmer) growing season.

This result suggests that timing of spawning, thermal regime, and mortality interact to determine the characteristics of the age-0 smallmouth bass that survive to the end of their first growing season. In streams and lakes where mortality is not size based, the individuals surviving to the end of the growing season could have been spawned early and grown slowly for a long period of time, or spawned later and grown relatively fast for a shorter time (Figure 3.6). In systems where mortality was strongly dependent on size, the characteristics of juveniles at the end of the growing season would depend on when spawning occurred. If spawning occurred while temperatures were below 22-23°C and increasing, early spawned individuals would suffer higher mortality, and most juveniles surviving to the end of the growing season would probably have been spawned relatively late and grown in warmer temperatures. If spawning occurred after temperatures exceeded 22-23°C, then the juveniles that survived to the end of the summer were probably better foragers or were initially placed in more profitable areas, but did not necessarily grow in higher temperatures.

This conceptual model imparts some important management implications for smallmouth bass in the southern portion of their range. The results of this study indicate that in the southern portion of their range, age-0

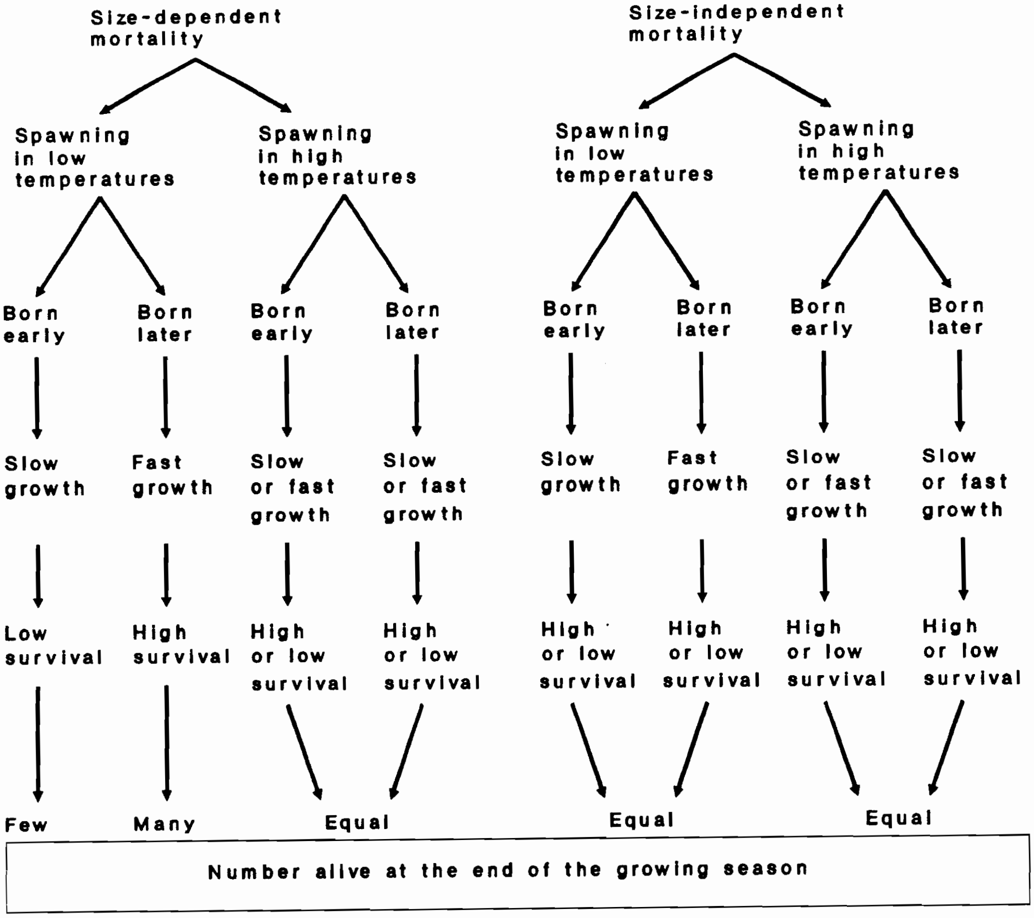


Figure 3.6. Conceptual model of how the mechanism of mortality, time of spawning, and temperature regime interact to affect the probability that individuals will survive to the end of their first growing season. In systems where larval mortality depends on size, larvae that grow fast should experience less mortality. If spawning occurs while temperatures are less than 22-23°C, individuals that grow in the coldest temperatures (typically spawned earliest) should grow slowest and experience the highest mortality. If spawning occurs in temperatures higher than 22-23°C, then growth does not depend on temperature, and either early or late spawned individuals may grow fast and survive. In systems where mortality does not depend on size, all individuals have an equal chance of surviving to the end of the growing season regardless of when they were spawned or how fast they grew.

smallmouth bass can achieve good growth even in a year when spawning is delayed. Additionally, in the North Anna River, it was unusual for any individual to attain a growth advantage that extended through time. Therefore, in southern rivers with low density populations of smallmouth bass, management efforts designed to encourage spawning early in the season (e.g. stabilizing flows in regulated rivers, special harvest regulations in early spring) may not improve recruitment success. However, smallmouth bass are distributed widely throughout North America, and their natural range extends into Quebec. In these northern areas, where the growing season is short and water temperatures rarely reach the optimal range for growth of smallmouth bass, a delay in initiation of spawning can result in poor recruitment because juveniles do not reach the minimum size needed to survive their first winter (Oliver et al. 1979, Shuter 1980).

CHAPTER 4

Effect of Foraging Success and Hunger on Foraging Behavior of Juvenile Smallmouth Bass

Introduction

The premises of optimal foraging theory suggest that animals can improve their foraging success by increasing the profitability of items in their diet (Werner and Hall 1974), selecting the most profitable patches to forage in (Smith and Dawkins 1971), abandoning searches in unprofitable patches sooner than in profitable patches (Krebs et al. 1974), and increasing their encounter rate with profitable patches and profitable items in a patch (Beukema 1968, Thomas 1974). Individuals that successfully accomplish any or all of these should improve their ability to exploit scarce resources and increase their fitness within the population. However, if the relative profitability of specific actions varies in space and time, then foraging success may depend on an individual's ability to react to environmental cues that signal a change in the relative profitability of an action (Krebs and Inman 1992).

These tenants of optimal foraging theory provide a conceptual framework for understanding the consequences of habitat use. Indeed, much of the application of this theory to fish has involved trying to predict their habitat use and determining the long-term consequences of habitat selection (Fraser and Sise 1980, Werner et al. 1983a, 1983b, Persson and Greenberg 1990). For example, drift-feeding salmonids typically try to occupy the habitats in a stream where they can maximize the difference between their intake rate and the energy they expend to maintain position (Fausch 1984, Hughes and Dill 1990). If only a limited number of these profitable positions are available, salmonids establish social hierarchies that prohibit subordinate individuals from entering areas where they would gain their maximum energetic profit (Abbot et al. 1985, Grant 1990, McNicol and Noakes 1981). Dominant individuals change positions as points of maximum food delivery change within streams (Gotceitas and Godin 1992) but subordinates remain in unprofitable locations. Therefore, the carrying capacity of salmonids in a stream is thought to be at least partially determined by the availability of microhabitats where they can forage most optimally (Chapman 1966, Horwitz 1978, Bachman 1984, Morhardt and Mesick 1988).

This hierarchy is established among salmonids very early in their development (Wankowski and Thorpe 1979, Grant and Noakes 1988, Gotceitas and Godin 1992), and because very few individuals move more that 50 m during their first growing season (Heggenes et al. 1991) the first individuals to establish dominance may gain an advantage that subordinates cannot compensate for. Therefore, the keys to foraging success in juvenile salmonids are the ability to recognize the characteristics of profitable positions in a local area and the ability to maximize the time they spend in these positions by excluding competitors. Individuals that succeed in these actions establish and maintain a growth advantage over other individuals in their population.

Some of the same principles that apply to juvenile salmonids may also apply to age-0 smallmouth bass feeding on benthic invertebrates. In Chapter 2, I determined that juvenile smallmouth bass feeding on benthos could improve their foraging success by occupying shallow microhabitats (< 60 cm) with moderate to fast current velocities (> 10 cm/s). This result suggested that individuals would benefit if they recognized the characteristics of profitable microhabitats. The results of Chapter 3 indicated that when age-0 smallmouth bass gained a growth advantage early in life they did not necessarily maintain that advantage through time. This suggested that the juveniles that occupied profitable areas at one point in time could occupy relatively unprofitable areas at a later time, either because the profitability of the area they were in decreased or because they were forced to abandon their profitable area. Therefore, juvenile smallmouth bass would also benefit from search behaviors that minimized the amount of time they spent in unprofitable patches and increased their encounter rate with profitable patches.

Because food resources vary both spatially and temporally in streams, the behaviors that juvenile smallmouth bass employ while searching for profitable patches may determine which individuals will find food most frequently. Specifically, the ability to recognize profitable habitats may be the most significant aspect of a profitable search. However, it is likely that this ability varies among individuals (Ringler 1983) because individuals vary in their age and experience (Godin 1978), internal factors that motivate foraging (e.g. hunger, Bryan 1974, Milinski 1985), and in inherited traits that affect foraging ability (Trexler 1990). It is also possible that the availability of their food resource is so inherently variable that the profitability of decisions made by juvenile smallmouth bass is essentially a matter of chance.

By examining the results of Chapters 1, 2, and 3, I formed some hypotheses about the foraging behavior of age-0 smallmouth bass in the North Anna River. The assumption underlaying these hypotheses was that growth rate depended on foraging success. The empirical evidence indicated that foraging success was a function of microhabitat use (Chapter 2), not all juveniles were occupying profitable habitats

(Chapter 1), and the same individuals were not always occupying profitable habitats (Chapter 3). While a number of factors could force individuals into a profitable area (e.g. competition with conspecifics, presence of predators), I hypothesized that juvenile smallmouth bass have inherent characteristics of their foraging behavior that cause them to move out of profitable patches. I also thought it possible that hungry individuals might forage differently from satiated juveniles and thereby increase their chances of foraging successfully. In this way, all juveniles would experience periods of successful and unsuccessful foraging, and rapid and slow growth, and the cause would lie within the inherent behavior of the individual.

The primary objective of this study was to determine the effect of foraging success on foraging behavior of juvenile smallmouth bass. I was particularly interested in how foragers searched for food in a patchy environment and the effect of success on foraging behavior. I attempted to reproduce the consequences of the habitat shift I observed in the river by restricting age-0 smallmouth bass to habitats with relatively uniform depths and low velocities for an extended period and then forcing them to enter a habitat with variable depths and higher velocities in order to find food. With this experimental design, I hoped to determine if juveniles could learn to identify a new habitat as a more profitable foraging site and how likely they were to occupy that habitat when they no longer obtained food there. If juveniles did not necessarily associate habitat variables with increased foraging success, then they would not be able to recognize certain microhabitats as inherently more profitable and therefore would occupy unprofitable areas on occasion.

A secondary objective was to test the effect of hunger on foraging strategies. If hungry individuals were more likely to search an area in a manner that increased their chances of encountering a profitable patch, then short-term foraging success might well be a function of hunger. In such a case, individuals that had foraged poorly most recently might be more likely to inhabit the most profitable areas of the stream in a short time.

Methods

Fish Collection and Maintenance

Larval smallmouth bass (12-18 mm) were collected with dip nets from three broods in the North Anna River on 19 and 28 May, 1992, and transferred to the laboratory where they were placed in 38-L aquaria that were individually aerated. Temperatures in the aquaria were allowed to vary with ambient air temperature but always ranged between 19-25°C, which should have supported intermediate or good growth rates for juvenile smallmouth bass (Horning and Pearson 1973). Each smallmouth bass was fed 10 live tubifex worms twice each day, and all were raised in aquaria for at least 34 days before I used them in experiments. Total lengths of juveniles used in experiments ranged between 25-48 mm.

The bottoms of all aquaria were covered with gravel (0.5-2 cm in diameter) to a depth of 2-3 cm. Each aquarium was divided in half with a piece of opaque, perforated plexiglass, and one juvenile was placed in each half. Visual contact among juveniles provoked agonistic behaviors, so aquaria were surrounded with black plastic to visually isolate juveniles from each other and from activity outside of the aquaria. Light entered aquaria through the top only, and all aquaria received 14 hours of light each day.

Experimental Stream

Behavioral experiments were conducted in a circular laboratory stream (Figure 4.1) that was divided into 12 habitat patches. Patches were smaller than natural habitats, but previous studies revealed that fish placed in this artificial stream exhibited similar behaviors to fish observed in natural streams (Angermeier 1992). Temperature in the stream was allowed to fluctuate with ambient air temperature (range 19-25°C) and overhead fluorescent lights provided illumination. I attempted to create an environment where habitat patches were visually isolated from each other, so that when juveniles decided to abandon a patch they had to enter another patch in order to inspect it. There were three categories of habitat patches available in the stream: pools, mazes, and riffle-pool complexes.

The bottoms of all habitat patches were covered with 2-3 cm of gravel. There were four pools in the tank; one was located at each bend in the stream. Each pool was 1.2 m wide, 40 cm deep, covered approximately 2.0 m^2, and contained mean water column velocities that ranged between 0-4 cm/s (mean of 12 measurements = 0.1 cm/s). The longest (2-m) straight sections of the tank were converted into two riffle-pool complexes that covered approximately 1.7 m^2. The upper halves of these sections were constricted to a channel 0.6 m wide and 12 cm deep, and the lower halves were 1.2 m wide and 40 cm deep. Water drawn from outflow vents on the bottom of two pool sections was injected through six jets into the upper half of each riffle/pool complex. This process increased the range of mean water-column velocities in the upper halves of the complexes to 4-31 cm/s (mean of 16 points = 13 cm/s). Mean velocities in the lower halves of the complexes ranged between 0-13 cm/s (mean of eight points = 3 cm/s). To provide cover in these patches, I

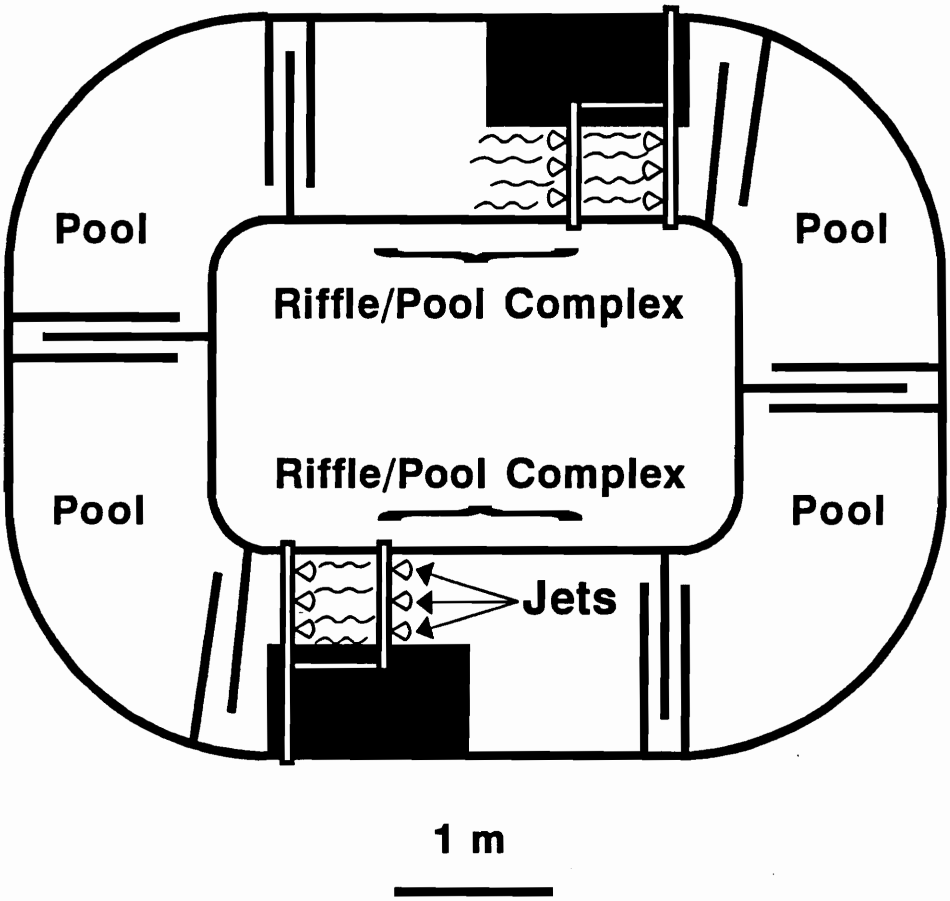


Figure 4.1. Experimental arena for testing the effects of foraging success on search strategy of juvenile smallmouth bass. Pools approximated the low-velocity conditions of the tanks in which juveniles were held before being placed in the arena. The large black boxes represent obstructions I placed in the arena to reduce the width and depth of the adjacent section of the stream channel. Velocities were raised in these constricted sections of the riffle-pool complexes by spraying water from the jets.

placed a concrete block (19 cm X 19 cm X 40 cm) in each pool and in the lower halves of the riffle-pool complexes.

Mazes were located at each end of all pools and riffle-pool complexes. The entrances to mazes were 15 cm wide and adjoined the inside wall of the tank, and the maze channel (20 cm wide) passed through one 180° turn between entrances. The entrances to each maze could be blocked with a screen that allowed water to flow through but prevented juveniles from moving among patches. Water depth in all mazes was 34 cm, and mean velocities ranged between 0-13 cm/s (mean of 16 points = 6 cm/s). Mazes visually isolated each patch from all others, but I also considered them a separate habitat type because their shaded channels and unique hydrologic characteristics could have attracted juvenile smallmouth bass (Sechnick et al. 1986).

Clear plexiglass panels lined the inside wall of the stream and provided a full view of the water column. An opaque blind was suspended within the inner wall of the stream, extending from 0.5 m above the tank downward to the floor. I only observed fish in the stream when I was within this blind. I could observe fish in pool and maze sections by peering over the blind, but observed fish in riffle sections by looking at the plexiglass panels through slits in the blind.

1. Effect of foraging success on foraging behavior.

Experimental trials. I randomly assigned 20 juveniles to either control or treatment groups (n=10 for each group) for the first experiment. Only one fish occupied the artificial stream each day during this experiment. Each fish was put through two trials of the experiment in one day.

The night before an experimental trial, one juvenile was transferred from an aquarium to a pool in the artificial stream. Transfer at night was less stressful for the fish than transfer during the daytime because juveniles were generally lethargic at night. I transferred juveniles in plastic bags filled with water from their aquaria, and allowed bags to float in the stream for ten minutes to acclimate juveniles to the stream temperature before releasing them. Fish experience physiological stress from handling of this type (Mazeaud et al. 1977) but they can usually recover from the perturbation of homeostasis within five hours if handling is minimized (Wedemeyer 1972).

Screens at the maze entrances prevented the juvenile from leaving the pool until trials began on the morning after a transfer. At the start of a trial, screens were removed from the mazes adjoining the pools, and the juvenile was allowed free access to two pools, three mazes, and one riffle-pool complex (i.e. half the stream) for two hours. I recorded the time juveniles spent in each patch and what patch they entered each time they exited a patch. After two hours, I used a dip net to guide the juvenile into a pool in the other half of the stream, and blocked the maze entrances so that the juvenile could not leave that pool. Another two-hour trial was conducted 2-3 hours later. After the second trial the juvenile was netted and returned to the aquarium.

Juveniles in the control group did not receive food in any patch during either the morning or afternoon trial. During the morning trials, juveniles in the treatment group received food immediately upon entering a riffle-pool complex and at five-minute intervals as long as they remained in the riffle-pool complex. The ration size was five live tubifex worms released from overhead and approximately 0.1 m upstream of the juvenile. Treatment group fish did not receive food in any patch during the afternoon trial.

Food was added to only the riffle-pool complex for several reasons. The juveniles used in this study had only occupied environments (in both the river and the laboratory) that contained relatively uniform depths and low velocities. Therefore, they had only foraged in environments with those characteristics. In order to find food in this experiment they would have to enter a habitat with variable depths and higher velocities (i.e. a novel habitat). With this experimental design, I hoped to determine if juveniles could learn to identify a new habitat as a foraging site and how likely they were to occupy that habitat when they no longer obtained food there. By comparing how juveniles in treatment and control groups used riffle-pool complexes I also hoped to determine if juveniles innately preferred or avoided these novel habitats.

Foraging indices and statistical analyses. I assessed the effect of foraging success on three aspects of foraging behavior: the number of patches juveniles used, the number of times they changed their patch use, and the percent of time they occupied riffle-pool complexes. The number of patches used provided insight into how widely juveniles ranged when searching for food, and the number of switches between patches indicated how long juveniles occupied patches. Because riffle-pool complexes were the only patches that I released food into, the percent of time juveniles spent in those patches indicated how foraging success affected patch use.

I compared the observed trends in all three variables between the first and second hour of each trial for juveniles in the control and treatment groups. The purpose of this analysis was to determine if characteristics of foraging behavior changed as juveniles became familiar with their environment. While all foraging behaviors would prove equally unsuccessful for trials with control group fish, individuals in the treatment group would profit by gradually narrowing their search during the morning trial to only the riffle-pool complex. During the afternoon trial, all foraging behaviors would prove equally unsuccessful for treatment group fish but only one patch contained the habitat variables they most recently associated with foraging success. I used two-tailed, paired t-tests (alpha level = 0.05 for all tests) to detect if individuals in the control or treatment groups demonstrated consistent increases or decreases between hours in the number of patches searched, frequency of patch switching, and percent use of riffles.

I also compared the foraging behavior (in terms of the three variables mentioned above) of control and treatment fish during the second hour of each trial. If juveniles in control and treatment groups foraged differently during the second hour of the morning trial, it would indicate that spatial variability of the food resource affected foraging strategies. Differences between the behavior of control and treatment groups during the second hour of the afternoon trial would suggest that juveniles can associate habitat variables with foraging success. I used two-sample t-tests to compare the mean values of the variables and two-sample F-tests to compare variances of the three variables between control and treatment groups.

2. Effect of hunger on foraging behavior.

Experimental Trials. The primary hypothesis that was tested in this experiment was that hunger level could affect search behavior and use of profitable and unprofitable patches in a heterogeneous environment. I randomly assigned 28 juveniles (from the same group used in the previous experiment) into two treatment groups (n=14 in each group) representing two different hunger levels. Each fish was held in the aquaria for at least 14 days between experiments, so I considered that when juveniles were placed in the arena for either experiment they were being placed in an unfamiliar habitat.

For two days before they were placed in the stream for a trial, juveniles in one group (the satiated group) were fed twice their normal ration (40 tubifex worms/day). Juveniles in the other group (the hungry group) were fed half their normal ration (10 tubifex worms/day) two days before they were placed in the stream, and 10% of their normal ration (2 worms/day) the day before their transfer.

In this experiment, two fish (one from each treatment group) occupied the stream during each trial, and one trial was conducted for each treatment group in one day. Juveniles were kept separate from each others at all times while in the stream. On the night before trials, I transferred juveniles from the aquaria into separate pools in the stream. I used the same transfer procedures that were described earlier. Entrances to the mazes adjoining the pools were blocked so that juveniles could not leave the pools.

The next morning I randomly selected which juvenile would be tested first. Screens were removed from the pool containing that juvenile and it was allowed to move among all patches except the pool containing the other juvenile. I released five tubifex worms into the riffle immediately after a juvenile entered the riffle-pool complex and every five minutes thereafter as long as they remained in the complex. I recorded the amount of time juveniles spent in each patch and where they moved when they abandoned a patch.

After one hour, the first juvenile was guided back into the pool it was originally placed in and the entrances to that pool were blocked. Screens were removed from the pool containing the second juvenile and the trial was repeated. Both fish were removed from the stream at the end of the trials.

If differences in search pattern or riffle use existed between treatment groups they should have been easiest to detect during the first hour of searching. Therefore, I only examined the first hour of patch use by each juvenile. I did not repeat trials for the juveniles in the afternoon because their feeding in the morning affected the difference in hunger levels between groups.

Foraging indices and statistical analysis. I used the same variables that were used in the previous analysis to determine the effect of hunger on foraging behavior. I tested for differences between satiated and hungry juveniles by comparing the means (two-sample t-test) and variances (two sample F-test) observed for each variable by the two groups. Differences would indicate if hunger level affected the range of patches juveniles searched, and their duration in patches while searching for food. The comparisons would also indicate if hunger level affected how quickly juveniles could locate and exploit food resources that were only available for a limited time.

I also examined how long it took juveniles to abandon the patch where they began a trial. This comparison indicated if either group was more likely to abandon a familiar habitat and move to unseen habitats. I used a two-sample t-test to test for differences between the mean time it took juveniles in each treatment group to abandon the first patch.

Results

General description of foraging behavior.

Juveniles varied in the way they searched the arena and used the available patches (Table 4.1). During the first experiment, juveniles occupied 1-6 patches/hour (median = 3), switched their patch use 0-31 times each hour (median = 6), and spent 0-100% of their time each hour in riffle-pool complexes (median = 28%).

More patches were available during the second experiment (although in the same proportion), so the ranges for each of the statistics mentioned differed from what was observed during the first experiment (Table 4.2). Juveniles occupied 1-11 patches/hour (median = 4), enacted 0-16 switches/hour (median = 6), and spent 0-78% of their time in riffle pool complexes (median = 9%). Time to first movement between patches varied from 1-60 minutes (median = 9).

Some foraging characteristics remained constant during both experiments. Juveniles were always able to detect tubifex worms when I released worms into the riffle-pool complex, and always ate at least one of the worms when they were released. Juveniles spent much of their time in pools and mazes inspecting the walls of the arena, and in riffle-pool complexes they primarily inspected the substratum or maintained position at a focal point. Most individuals used cover objects infrequently and rarely hid in shaded maze habitats. However, some juveniles did spend a significant portion of their time searching the walls of mazes.

Table 4.1. Mean number of patches used each hour, switches made each hour, and percent time spent in riffle-pool complexes during each hour of each trial for juveniles in control and treatment groups of Experiment 1. Variances associated with means are presented in parentheses.

		Trial 1[a]		Trial 2[b]	
Group	Variable	Hour 1	Hour 2	Hour 1	Hour 2
Control (n=10)	Patches	3.0 (3.11)	3.1 (3.66)	4.1 (3.66)	3.9 (2.77)
	Switches	7.4 (59.82)	8.8 (99.51)	7.8 (33.29)	10.2 (56.18)
	% Riffle	19.5 (564.63)	33.1 (1180.13)	22.2 (491.38)	24.5 (270.57)
Treatment (n=10)	Patches	3.3 (1.79)	2.7 (1.79)	3.2 (3.50)	4.0 (2.43)
	Switches	6.7 (17.34)	3.8 (9.96)	7.2 (63.96)	10.4 (76.27)
	% Riffle	29.5 (694.64)	62.3 (1426.50)	24.2 (743.11)	38.7 (887.03)

[a] Trial 1 - juveniles in treatment group were fed in riffle-pool complex during both hours.

[b] Trail 2 - juveniles in both groups received no food in any patches during either hour.

Table 4.2. Mean number of patches used each hour, switches made each hour, percent time in riffle-pool complexes, and time to first switch observed for satiated and hungry juveniles in Experiment 2. Variances associated with means are presented in parentheses.

Variable	Treatment Group	
	Satiated (n=14)	Hungry (n=14)
Patches	4.9 (7.15)	3.6 (1.63)
Switches	7.3 (29.30)	7.0 (15.38)
% Riffle	16.8 (448.80)	25.6 (1095.10)
First Move (min)	16.6 (354.87)	14.6 (280.56)

1. Effect of foraging success on foraging strategy.

Number of patches used. Fish in the control group did not change the number of patches they used between the first and second hours during either the morning ($t = -0.20$, $P > 0.84$) or afternoon trials ($t = 0.80$, $P > 0.44$). Juveniles used between 1-6 patches during each hour of the control trials (Figure 4.2), and medians ranged between 2.5-4 during all hours. Similarly, during the morning trial, treatment-group fish did not use a different number of patches during the first hour than they used during the second hour ($t = 1.33$, $P > 0.20$) although juveniles occupied a smaller range of patches during the second hour (Figure 4.2). During the afternoon trial, juveniles in the treatment group increased their patch use during the second hour of the experiment (by 0.7 patches on average, $t = -2.45$, $P < 0.04$), although juveniles used between 1-6 patches in both hours.

Juveniles in the control and treatment groups used the same number of patches (on average) during the second hour of both the morning ($t = -0.54$, $P > 0.59$) and afternoon trials ($t = 0.14$, $P > 0.89$). Additionally, variation in the number of patches used did not differ between groups during the morning ($F = 2.04$, $P > 0.15$) or afternoon trials ($F = 1.13$, $P > 0.43$). These results implied that juveniles did not change the number of patches they used when all patches became unprofitable. Juveniles in the treatment group did not alter the number of patches they used when food was released into the riffle-pool complex, but after all patches became unprofitable again they increased the number of patches used to a number similar to that exhibited by the control group.

Number of switches between patches. Individuals in the control group maintained (on average) the same rate of

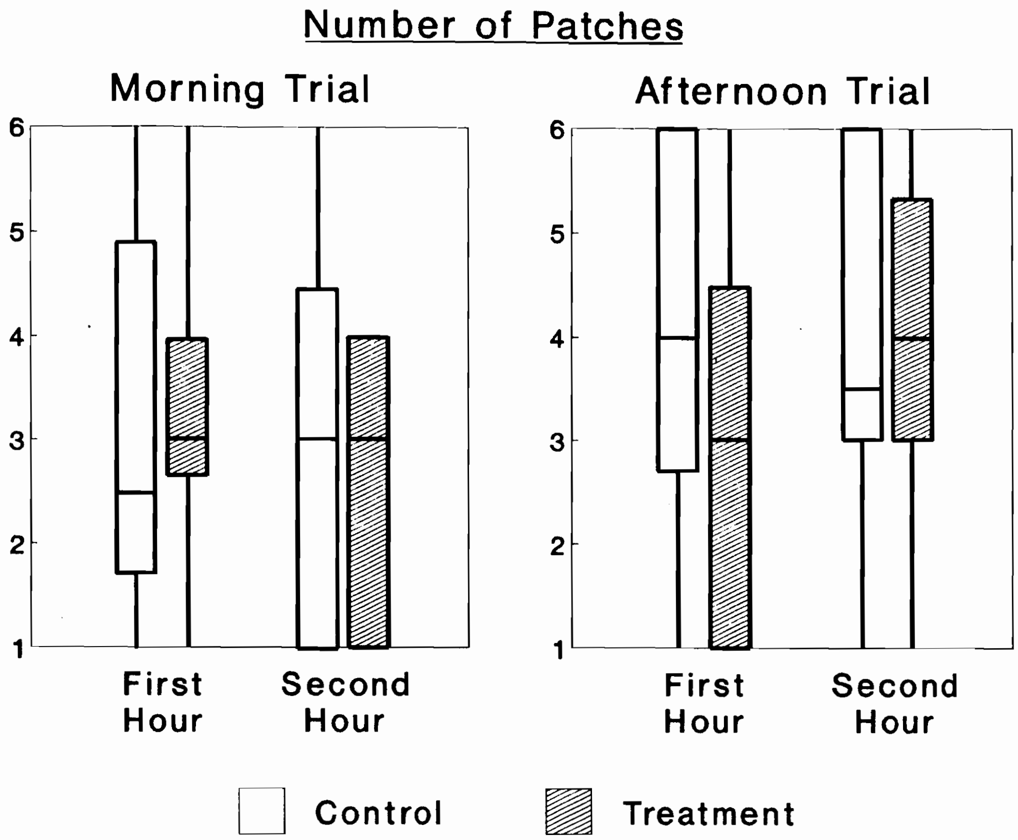


Figure 4.2. Box plots of number of patches used by juvenile smallmouth bass during control- and treatment-group trials of Experiment 1 (n=10 for both groups). Treatment-group juveniles received food in riffles during the morning trial, but received no food in any patch during the afternoon trial.

switching between patches during both hours of the morning ($t = -0.65$, $P > 0.53$) and afternoon trials ($t = -1.98$, $P > 0.07$). The narrowest range of switches made during any hour by juveniles in the control group was 0-16, and the maximum range was 0-30 (Figure 4.3). During the morning trial, juveniles in the treatment group decreased the number of switches they enacted (mean decrease = 2.9) between the first and second hours ($t = 3.06$, $P < 0.02$). Treatment group juveniles increased the number of patch switches they made (mean = 3.2) between the first and second hour of the afternoon trial ($t = -3.64$, $P < 0.006$).

Treatment and control groups enacted the same number of switches (on average) during the second hour of both the morning ($t = -1.51$, $P > 0.05$) and afternoon trials ($t = 0.10$, $P > 0.95$). The rate of patch switching was significantly more variable within the control group than within the treatment group during the second hour of the morning trial ($F = 10.00$, $P < 0.001$). During the afternoon trial, variances did not significantly differ between control and treatment groups ($F = 1.36$, $P > 0.33$). These results indicated that successful foraging caused juveniles to reduce their rate of patch switching. When all patches became unprofitable, the rate and variation of patch switching among treatment group juveniles increased to levels similar to the control group.

Use of riffle-pool complexes. Juveniles in the control group spent the same percentage of time in riffle-pool complexes during the first and second hours of both the morning ($t = -1.33$, $P > 0.21$) and afternoon trial ($t = -0.37$, $P > 0.71$). The range of times that control-group juveniles occupied riffles generally decreased throughout the day (Figure 4.4), from a maximum of 0-90% during the

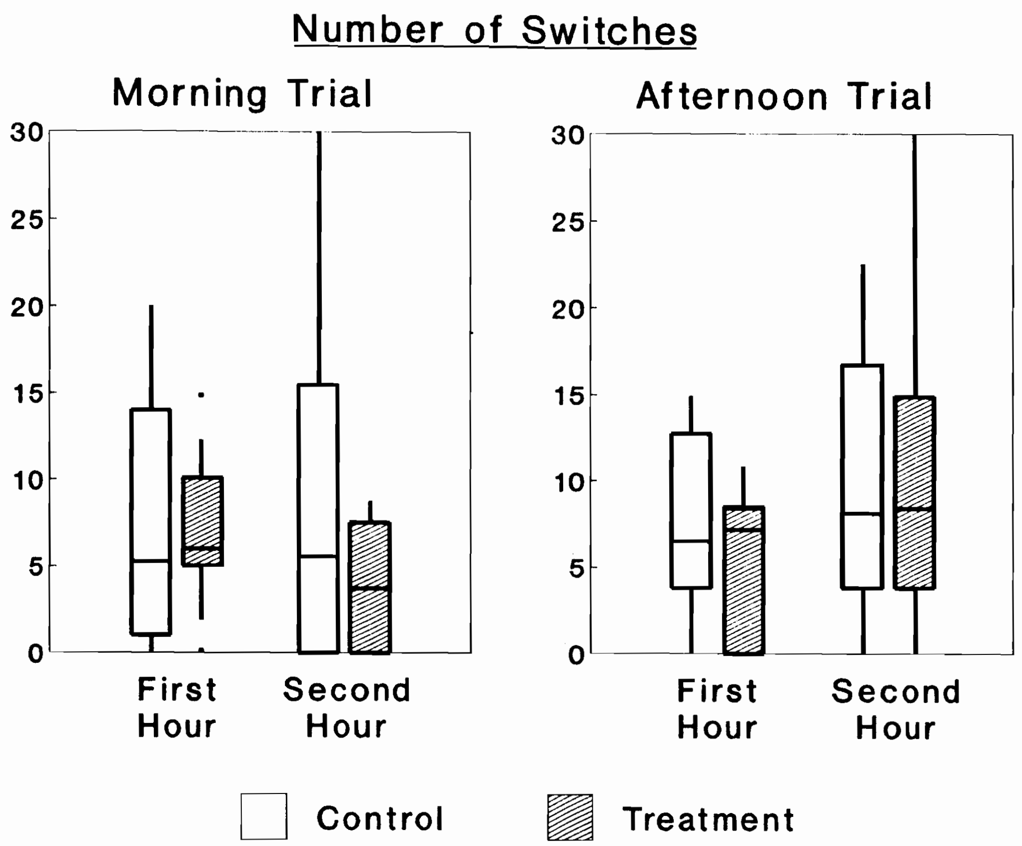


Figure 4.3. Box plots of number of switches between patches made by juvenile smallmouth bass during control- and treatment-group trials of Experiment 1 (n=10 for both groups). Treatment-group juveniles received food in riffles during the morning trial, but received no food in any patch during the afternoon trial.

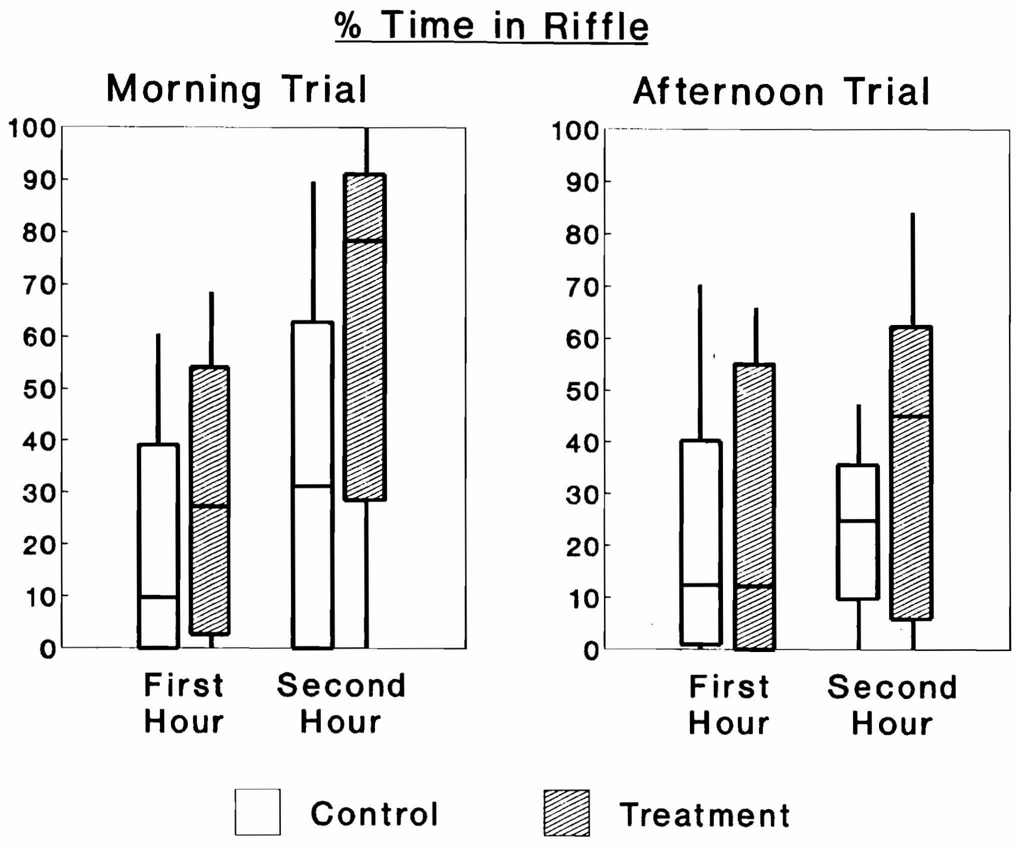


Figure 4.4. Box plots of percent time spent in riffle-pool complexes by juvenile smallmouth bass during control- and treatment-group trials of Experiment 1 (n=10 for both groups). Treatment-group juveniles received food in riffles during the morning trial, but received no food in any patch during the afternoon trial.

second hour of the morning trial to a minimum range of 0-40% during the second hour of the afternoon trial. Treatment-group fish increased their use of riffle-pool complexes by an average of 32.9% ($t = -3.25$, $P < 0.01$) during the morning trial. During the afternoon trial, juveniles in the treatment group did not change the amount of time they spent in riffles between the first and second hours ($t = -1.35$, $P > 0.21$), and individuals displayed wide variation (0-65% in first hour, 0-83% in second hour) in their use of riffles.

While treatment-group individuals increased their use of riffles during the morning trial, their use of riffles during the second hour of that trial was not significantly different ($t = 1.81$, $P > 0.08$) or more variable ($F = 1.21$, $P > 0.39$) than the use of riffles by juveniles in the control group. Mean use of riffles did not significantly differ between treatment and control groups during the afternoon trial, but the treatment group did exhibit more variable use of riffles than the control group ($F = 3.28$, $P < 0.05$). Therefore, foraging success in riffle-pool complexes caused juveniles to increase their use of riffle-pool complexes over time. When riffles became unprofitable, juveniles varied in their use of riffles. Some individuals exhibited an initial preference for riffles even when riffles were not profitable, but all individuals generally decreased their use of riffles if they remained unprofitable.

2. Effect of hunger on foraging behavior.

Satiated juveniles did not differ from hungry juveniles in the mean number of patches used ($t = -1.62$, $P > 0.10$), mean number of switches ($t = -0.84$, $P > 0.40$) or mean percent of time in riffles ($t = -0.16$, $P > 0.87$). Hungry individuals displayed a smaller range than satiated individuals did in the number of patch switches made (Figure

4.5). However, only the variance in the number of patches used differed between hungry and satiated groups ($F = 4.38$, $P < 0.006$) and not variance in the number of switches ($F = 2.44$, $P > 0.06$) or percent time in riffles ($F = 1.90$, $P > 0.12$). Other than a tendency for satiated fish to vary more in the amount of area they searched, there was little evidence that differences in hunger level promoted differences in foraging strategy in the tank.

On average, individuals in the satiated group took longer to abandon their original patch than individuals in the hungry group did (Table 4.2) but the difference was not statistically significant ($t = 0.36$, $P > 0.76$; equal s^2, $P > 0.34$). The minimum time to patch abandonment was one minute in both treatment groups, and both groups had individuals that did not abandon the original patch after 60 minutes (Figure 4.5). Other than their slightly lower time to abandonment, fish in the hungry group did not exhibit a greater disposition towards patch abandonment than satiated fish did.

Discussion

These experiments were designed to determine if characteristics of foraging behavior could explain some of the temporal variation in growth observed among age-0 smallmouth bass (Chapter 3). I hypothesized that aspects of microhabitat selection could account for some of the observed variation because both microhabitat use and energetic profitability of microhabitats varied in the North Anna River (Chapters 1 and 2). This hypothesis depended on the assumption that smallmouth bass would occasionally abandon the most profitable microhabitats, enter unprofitable areas, and consequently suffer a period of poor growth. The results of this experiment indicated that

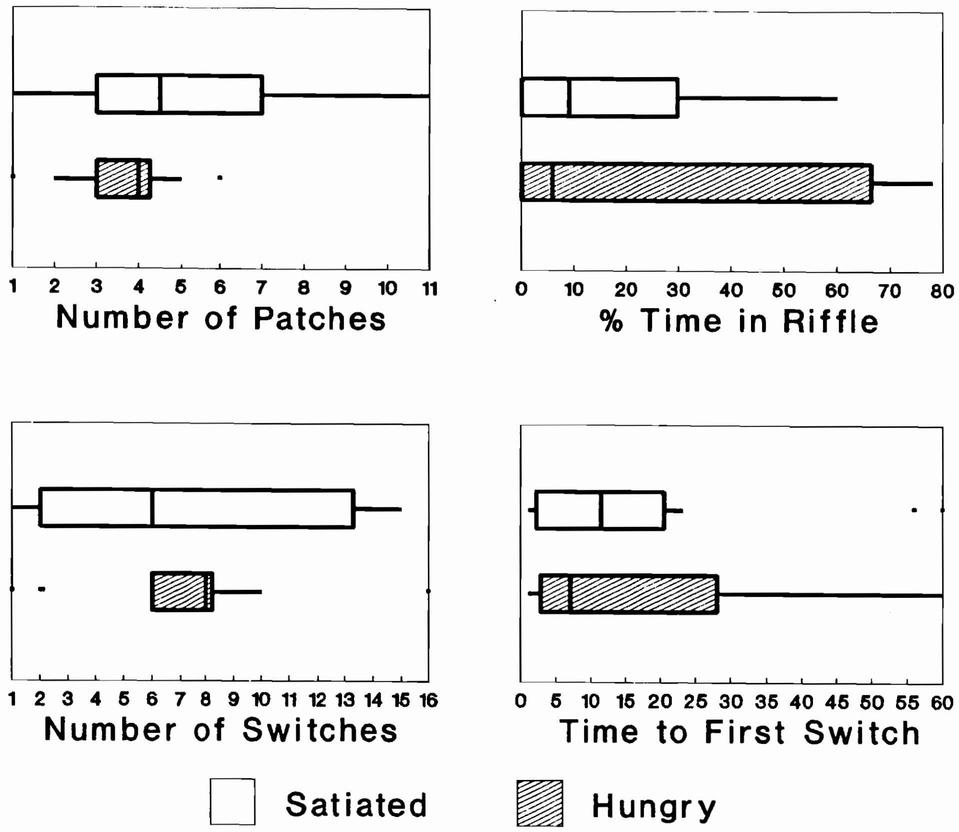


Figure 4.5. Box plots of the number of patches used, switches enacted, percent time spent in riffle-pool complexes, and time of first switch observed for satiated and hungry juveniles during Experiment 2 (n=14 for both hungry and satiated groups).

variation in food availability coupled with individual variation in foraging behavior could cause smallmouth bass to abandon profitable habitats. This finding does not imply that juveniles only move among microhabitats in response to foraging success, only that inherent characteristics of their foraging behavior make if difficult for individuals to consistently forage in the most profitable areas when availability of their food resource varies.

Optimal policies have the property that "whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision" (Bellman 1957). Given this context, the inherent characteristics of foraging employed by juvenile smallmouth bass frequently cause individuals to deviate from optimality over the long term. The erroneous decisions that juveniles make appear to result from spatial and temporal variation in food availability in their environment and individual differences in foraging behavior. Over time, the cumulative effect of poor foraging decisions could lead to short periods of slow growth that commonly occurred among smallmouth bass in the North Anna River.

Spatial and temporal variation in food availability.

In Experiment 1, juveniles were allowed to access six patches in the morning but only received food when they entered one patch. In the afternoon, juveniles did not receive food in any patch. When juveniles located the profitable patch in Experiment 1, they usually stayed in it, which indicated most juveniles were trying to use habitats that promoted faster growth. When all patches became unprofitable, juveniles did not consistently occupy a patch with the same habitat characteristics as the patch that had been profitable earlier. They did generally revert to the same search pattern they used earlier in the day. These results indicated that when food resources varied spatially and temporally, juveniles may sometimes have foraged in areas that are consistently unprofitable because they did not associate habitat characteristics with profitability (McNamara and Houston 1985, Green and Nuñez 1986).

Fish can be conditioned to recognize certain environmental cues as rewarding (Gleitman and Rozin 1971), so why did the juvenile smallmouth bass in this experiment not associate variable depths and high velocities with food? A possible explanation is that while some species of fish respond to conditioning training quickly, smallmouth bass do not. In one negative-reenforcement conditioning experiment, adult smallmouth bass exhibited the correct response at most only 44% of the time (Coble et al. 1985). Additionally, in the experiment I conducted, juvenile smallmouth bass were not presented with a simple choice between positive-negative reenforcement. Instead their choice was complicated by maintaining no reward in two types of patches, and making the reward inconsistent in the third type.

In the North Anna River, the choice becomes even more complex, as juveniles must decide between a number of microhabitats that support different probabilities of foraging success. While an individual may benefit most by concentrating its efforts in only one type of microhabitat, there will be times when that microhabitat yields no reward. In such circumstances, fish do not concentrate their efforts in a profitable area to the exclusion of all others, but instead respond to the most recent positive or negative reenforcement (Bitterman et al. 1958, Behrend and Bitterman 1961, 1966). Therefore, in an environment where food resources vary both spatially and temporally, juvenile smallmouth bass could be expected to occasionally abandon consistently profitable areas. Depending on the juxtapositioning of microhabitats in the river and their preferred search pattern (see next section), it may take a significant amount of time for a juvenile to encounter another high profit area.

Fish may cause their food resources to vary both spatially and temporally in streams by depleting local prey densities (Angermeier 1985). Because the juveniles I observed in the river primarily fed on benthos (Chapter 2), it is possible that they temporarily eradicated food resources in areas where they had been foraging, thereby creating frequent variation in availability. Similar changes in availability also result when prey organisms alter their behavior in the presence of a predator (Stein 1979, Persson and Diehl 1990). Because these sources of short-term variation occur in stream systems, juvenile smallmouth bass may have difficulty associating habitat characteristics with energetic profitability in natural environments. Ringler (1979) proposed that similarly frequent, short-term changes in food availability caused brown trout to occasionally deviate from a profitable diet.

The effects of food availability on habitat selection can also be affected by an environment's spatial organization. Modelling analyses have demonstrated that if the area within a predator's daily home range varies only slightly in profitability, but varies widely over a larger scale, the predator cannot always assess what area it should occupy to optimize their energy intake (Bernstein et al. 1991). While I did not examine this principle in the laboratory study (juveniles could easily enter and assess all available habitats within the experimental time limit) it could apply in the North Anna River, where pool habitats 100 m long are not uncommon.

In the river, juvenile smallmouth bass searched for food in one area for a short time and then moved to a new foraging location (Chapter 2). This strategy of saltatory searching has been documented for many predators (O'Brien et al. 1990, O'Brien and Evans 1991, Browman and O'Brien 1992) and results in sampling of microhabitats within a larger habitat block. Because of the limited availability of riffle and run habitats (the most profitable habitat) in the river, juveniles would only sample them infrequently, perhaps only once every few days. When they did enter riffles and runs, juveniles might remain there longer because of their higher profitability (Thomas 1974, Brown 1982, Turchin 1991), but a short-term decline in profitability could cause them to reenter the pool habitats they previously abandoned.

This scenario could explain both the observed habitat distribution of juveniles and their occasional periods of poor growth. During early life stages, age-0 smallmouth bass were not familiar with large sections of the river, and once they abandoned a riffle or run they may have taken several days to locate a similar habitat (assuming random movement). Therefore, while juveniles were most frequently observed in riffles and runs because they were less likely to abandon those profitable habitats, they could remain in pools several days (and grow slowly as a consequence) while they searched for more profitable habitats.

Individual variation in foraging strategy.

During Experiment 1, searching behavior varied more among individuals when they did not receive food in any patch than when they received food in one patch, and this variation provided insight into how individuals searched for food in unprofitable areas. There were always some juveniles in the control group that used all available patches and some that never exited the original patch. Likewise, in all trials there were some individuals that approached one patch switch per minute and some that never moved between patches. This suggested that some individuals waited for conditions in a patch to change, while others made cursory searches for food in all available patches, and the rest adopted an intermediate strategy.

Consider how these various search strategies might affect an individual's foraging success in the North Anna River. As I mentioned earlier, most of the available microhabitats in the river were relatively unprofitable. An individual that thoroughly searched each area would probably have a long residence time in profitable microhabitats and consequently would enjoy a long period of good growth. However, if it abandoned the profitable area, it could take a relatively long time to locate another profitable site, and its growth rate would decline in the interim. An individual that searched microhabitats more cursorily might encounter profitable areas more frequently but would probably also abandon them more rapidly. Either case would cause an individual to exhibit alternating periods of relatively fast and slow growth.

Juveniles in the control group of Experiment 1 initially varied in their use of riffle sections, but usage became more similar among individuals over time. Even during control trials there were always some individuals that remained in the riffle for a higher proportion of time than suggested by its availability (approximately 33% of the tank area), and some individuals that did not enter the complex. Therefore, some individuals may have innately preferred habitat variables in the riffle-pool complex, while others avoided those variables if no food was present. Individuals that previously fed in riffles were more likely to remain in the riffle than those that never fed in that patch (personal observation).

When food was added to the riffle-pool complex, the variation among individuals declined because most moved into the complex and remained there. However, even during these trials there were some individuals that would occasionally abandon the riffle complex and search adjoining patches for brief periods. Additionally, some individuals never entered the riffle-pool complex and, therefore, could not discover that food was present.

Differences in age and experience may explain some of the variation in the search strategies employed by juveniles in this study and in the river (Godin 1978, Colgan et al. 1986). However, all individuals used in these experiments were approximately the same age and fed on the same diet within similar habitat conditions for a minimum of four weeks prior to the trials. Therefore, I attribute the observed variation in foraging in this study and in the river to heritable traits that predispose how individuals will forage (Trexler 1990) or to what Thomas (1977) characterized as "internal state and motivational factors". The latter could include hunger (see discussion below), but also include differences in experience (Brown 1982, Thomas 1974) or positions in social hierarchies (Grant and Noakes 1987, Nielsen 1992). Because juveniles did not interact with each other in holding tanks or the experimental arena, it is unlikely that they established hierarchical systems in this study. However, behavioral characteristics that contribute to the establishment of hierarchies may predispose individuals to exhibit particular foraging behaviors.

In some circumstances, hunger may affect the physiological performance of fish (Dabrowski 1986, Mikheev et al. 1992) or otherwise motivate individual fish to employ different search patterns (Bryan 1974, Laurence 1972, Milinski 1985), but the results of Experiment 2 did not indicate that hungry and satiated juveniles foraged differently. While hungry juveniles varied less in terms of number of patches used, they did not show a greater propensity towards abandoning unprofitable patches or remaining in profitable ones. However, this experiment only examined differences in foraging behavior that occurred over a relatively short time and at a small spatial scale. Experimentation on the long term effects of hunger on foraging strategy may detect relationships that my experimental design could not discern. But at the spatial and temporal scale I examined, it appeared that hunger did not significantly affect foraging behavior.

Individual specialization on prey or foraging strategies have been documented for a variety of stream fishes and this specialization might cause some individuals to forage less efficiently than others. Individual brook trout (Salvelinus fontinalis) specialize on specific food items and are reluctant to feed on other prey even when the relative availability of their preferred food declines (Bryan and Larkin 1972, Allan 1981). Some juvenile smallmouth bass also exhibit narrow diet breadth (Easton 1992). Additionally, cyprinids occasionally abandon profitable feeding positions to enter unprofitable areas without being influenced by the density or aggression of conspecifics (Fraser and Sise 1980, Freeman and Grossman 1992).

If food resources vary in space and time, a behavior that appears profitable at one point in time may prove unprofitable at other times. Therefore, stream fish may frequently deviate from a behavior considered "optimal", when foraging in heterogeneous environments (Ringler 1979, 1983). Changing foraging tactics may not substantially improve foraging success unless individuals can quickly assess food availability and rapidly modify their behavior. Recent studies of coho salmon suggest that few individuals in a population are capable of this kind of behavioral plasticity (Nielsen 1992). Additionally, occasional inspection of patches that are normally unprofitable can increase foraging success when the result is exploitation of resources that would not be available unless they abandoned consistently profitable areas (Fraser and Sise 1980, Krebs and Inman 1992).

Conclusions.

The clearest implication of this study was that juvenile smallmouth bass exhibited a variety of search patterns while searching for food in patches of varying profitability. Individuals varied in their ability to associate certain habitat characteristics with profitability but generally did not prefer patches with those characteristics after they no longer received food there. Starved and satiated juveniles exhibited few differences in their foraging behavior, suggesting that the use of particular search patterns are affected more by innate differences in behavioral predispositions among individuals. An individual's foraging success may depend upon an interaction of the variability of food resources in their environment and the foraging behavior they employ. In extremely variable environments, all search patterns could prove unprofitable at some times and profitable at others. In such a case, the availability of consistently profitable habitats in a lotic environment may significantly affect the growth rates of juvenile smallmouth bass.

The results of this study suggest that conclusions generated from studies of drift-feeding salmonids (e.g. Fausch 1984, Hughes and Dill 1990) may not be applicable to other species of fish. Juvenile smallmouth bass in the North Anna River relied on benthic food resources, and the densities of benthic invertebrates in streams were affected by discharge in a way that is different from the effect of discharge on densities of drifting invertebrates (Gore and Judy 1981, Orth and Maughan 1983, Ward 1992). While the location of profitable drift-feeding stations changes almost instantaneously as discharge changes, the densities of benthic invertebrates in microhabitats occurs over a longer time scale and may relate back to biological or environmental factors that were present weeks or even months earlier. Therefore, at a given discharge, juvenile smallmouth bass cannot depend on a single microhabitat as always being profitable but must search areas and rely on their ability to appraise the profitability of microhabitats at a given moment.

SUMMARY AND MANAGEMENT IMPLICATIONS

The results of this study established that the growth of age-0 smallmouth bass in the North Anna River was directly affected by their microhabitat use. Age-0 smallmouth bass used shallower habitats and occupied higher velocities more frequently as the summer progressed, and these were the most energetically profitable microhabitats in the river. Because there were always some individuals using less profitable areas, it was possible that there was only a limited amount of profitable microhabitat available. If so, only a fraction of age-0 cohort could occupy the most profitable areas. These individuals could achieve and maintain a growth advantage over all other members of the cohort, and they would be more likely to survive through the rest of the growing season and over winter. In this way, the carrying capacity of the population could conceivably have depended on the profitable microhabitat available to the age-0 cohort.

However, the growth rate of age-0 smallmouth bass during any life stage was typically not related to growth during a previous life stage. The exception to this rule was that below a threshold of 22-23°C, individuals that grew in warmer thermal regimes grew fastest. This growth advantage did not continue after temperatures stabilized above the threshold. The data suggested that most individuals grew relatively fast at some stage in their development but did not necessarily maintain that growth advantage through all subsequent life stages. Assuming that a period of fast growth was associated with high foraging success and foraging success depended on microhabitat use, then it would appear that most individuals used profitable microhabitats at some point in their life but that few consistently occupied profitable areas.

Characteristics of their foraging behavior and food resource may explain the tendency of age-0 smallmouth bass to abandon profitable microhabitats and experience a period of poor growth. In the North Anna River, age-0 smallmouth bass were feeding on benthic invertebrates. Environmental stochasticity coupled with losses to predation could cause densities of benthic invertebrates to vary in even the most profitable microhabitats. In laboratory microhabitats, age-0 smallmouth bass tended to assess the potential profitability of an area by the foraging rate they achieved there. They did not linger in an area unless they foraged well at the time they searched it and did not appear to identify sites as potentially profitable based on their physical characteristics. In the river, most of the microhabitats available were relatively unprofitable, so an individual that abandoned a profitable area might (depending on its foraging strategy) spend a significant time in unprofitable microhabitats and consequently reduce its growth rate.

Based on these results, I drew several conclusions about how growth of age-0 smallmouth bass in the North Anna River and similar systems could be enhanced through regulation of discharge. Because age-0 smallmouth bass occupy a variety of microhabitats through their first growing season, they might benefit from flows that maintained a variety of microhabitats. However, managers should consider that age-0 smallmouth bass attained their best foraging success in only a subset of usable microhabitats. First-year growth rates might be increased by making the most profitable microhabitats more available. In this way, age-0 smallmouth bass would encounter profitable microhabitats more frequently regardless of the search strategy they employed.

However, the physical characteristics of a river may limit the effectiveness of this strategy. For example, in the North Anna River, the shallow, high-velocity microhabitats that are the most profitable foraging locations can only occur (no matter what the flow is) within short sections where the gradients change rapidly. Therefore, the amount of profitable microhabitat changes only slightly over a wide range of discharges.

Manipulating flows to increase the overall productivity of benthic invertebrates may improve the growth rates of age-0 smallmouth bass in warmwater streams. Flow regimes can directly affect densities of benthic invertebrates in streams (Gore and Judy 1981, Orth and Maughan 1983), so managers could develop strategies of flow manipulation that increase the food resource (rather than living space) available to age-0 smallmouth bass. In the North Anna River, most of the change in benthic densities that would result from flow manipulation would probably occur in shallow, high-velocity areas (i.e. the most profitable microhabitats). This strategy would probably not increase the availability of profitable microhabitats or the probability that age-0 smallmouth bass would encounter a profitable microhabitat. Instead, this strategy would attempt to increase the amount of successful foraging and residence time of age-0 smallmouth bass in profitable microhabitats. This would increase the growth rates they attained while they occupied profitable areas and increase the duration of time they achieved high growth rates.

I would not predict that improving growth rates of age-0 smallmouth bass would necessarily improve their recruitment in the North Anna River or in any other system supporting low densities of smallmouth bass. Based on my observations, most of the mortality appeared to occur soon after larvae dispersed from the nest, so the causes of mortality at that time must be studied in more detail before a strategy can be developed to increase the number of juvenile smallmouth bass in the river. However, individuals that grow well in their first year will retain more stored energy over winter and begin consuming more profitable prey (e.g. fish, crayfish) sooner that individuals that grow more slowly. Therefore, enhancing the growth of age-0 smallmouth bass could still improve the recreational value of smallmouth bass fisheries by improving growth rates early in life.

LITERATURE CITED

Aadland, L. P., C. M. Cook, M. T. Negus, H. G. Drewes, and C. S. Anderson. 1991. Microhabitat preferences of selected stream fishes and a community-oriented approach to instream flow assessments. Minnesota Department of Natural Resources, Section of Fisheries, Investigational Report No. 406. 125 pp.

Abbot, J. C., R. L. Dunbrack, and C. D. Orr. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (Salmo gairdneri). Behaviour 92:241-253.

Allan, J. D. 1981. Determinants of diet of brook trout (Salvelinus fontinalis) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184-192.

Angermeier, P. L. 1982. Resource seasonality and fish diets in an Illinois stream. Environmental Biology of Fishes 7:251-264.

_____. 1985. Spatio-temporal patterns of foraging success for fishes in an Illinois stream. American Midland Naturalist 114:342-359.

______. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. Environmental Biology of Fishes 34:171-180.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69:382-392.

______, and J. M. Boltz. 1989. Regulated streamflow and warmwater stream fish: A general hypothesis and research agenda. U.S. Fish and Wildlife Service, Biological Report 89(18). Washington, D.C.

Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. Journal of Experimental Biology 35:109-133.

Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Transactions of the American Fisheries Society 116:12-20.

______, B. Vondracek, L. R. Brown, and P. B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Transactions of the American Fisheries Society 120:166-176.

Behrend, E. R., and M. E. Bitterman. 1961. Probability-matching in the fish. American Journal of Psychology 74:542-551.

______. 1966. Probability-matching in the goldfish. Psychonomic Science 6:327-328.

Bellman, R. E. 1957. Dynamic Programming. Princeton University Press, Princeton, New Jersey.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. Journal of Animal Ecology 60:205-225.

Beukema, J. J. 1968. Predation by the three-spined stickleback (Gasterosteus aculeatus L.): the influence of hunger and experience. Behaviour 30:1-126.

Bitterman, M. E., J. Wodinsky, and D. K. Candland. 1958. Some comparative psychology. American Journal of Psychology 71:94-110.

Boehlert, G. W., and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Pages 51-67 in M. P. Weinstein editor. Larval fish and shellfish transport through inlets, American Fisheries Society Symposium 3, American Fisheries Society, Bethesda, Maryland.

Boisclair, D., and W. C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Canadian Journal of Fisheries and Aquatic Sciences 46:1859-1867.

Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. U.S. Fish and Wildlife Service, Instream Information Paper, 12, FWS/OBS-82/26. Washington, D.C.

Brett, J. R. 1973. Energy expenditure of sockeye salmon, Oncorhynchus nerka, during sustained performance. Journal of the Fisheries Research Board of Canada 30:1799-1809.

Brothers, E. B., C. P. Matthews, and R. Lasker. 1976. Daily growth increments in otoliths from larval and juvenile fishes. Fishery Bulletin 74:1-8.

Browman, H. I., and W. J. O'Brien. Foraging and prey search behaviour of golden shiner (Notemigonus crysoleucas) larvae. Canadian Journal of Fisheries and Aquatic Sciences 49:813-819.

Brown, A. V., R. L. Limbeck, and M. D. Schram. 1989. Trophic importance of zooplankton in streams with alluvial riffle and pool geomorphometry. Archives für Hydrobiologie 114:349-367.

Brown, J. A. 1984. Parental care and the ontogeny of predator-avoidance in two species of centrarchid fish. Animal Behaviour 32:113-119.

______. 1985. The adaptive significance of behavioural ontogeny in some centrarchid fishes. Environmental Biology of Fishes 13:25-34.

Brown, M. J. 1982. Foraging by burbot, Lota lota L.: search tactics and the use of a behavioral patch. Masters Thesis, State University of New York, Syracuse, New York. 46 pp.

Bryan, J. E. 1974. Hunger and the capture of grayling and char. Journal of the Fisheries Research Board of Canada 31:1945-1948.

______, and P. A. Larkin. 1972. Food specialization by individual trout. Journal of the Fisheries Research Board of Canada 29:1615-1624.

Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120:474-485.

Buynak, G. L., A. J. Gurzynski, and H. W. Mohr, Jr. 1982. Comparison of the food habits of smallmouth bass (Micropterus dolomieui) at two stations on the Susquehanna River. Proceedings of the Pennsylvania Academy of Science 56:127-132.

Cantin, M., and N. Bromage. 1991. Environmental control of the timing of smallmouth bass reproduction. pp. 73-75 in D. C. Jackson, editor. First international smallmouth bass symposium. Mississippi State University, Mississippi State, Mississippi.

Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board of Canada 19:1047-1080.

______. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345-357.

Coble, D. W., G. B. Farabee, and R. O. Anderson. 1985. Comparative learning ability of selected fishes. Canadian Journal of Fisheries and Aquatic Sciences 42:791-796.

Colgan, P. W., J. A. Brown, and S. D. Orsatti. 1986. Role of diet and experience in the development of feeding behaviour in largemouth bass, Micropterus salmoides. Journal of Fish Biology 28:161-170.

Crowder, L. B., and J. J. Magnuson. 1983. Cost-benefit analysis of temperature and food resource use: A synthesis with examples from the fishes. pp. 189-221 in W. P. Aspey and S. I. Lustik, editors, Behavioral energetics: The cost of survival to vertebrates. Ohio State University Press, Columbus, Ohio.

______, M. E. McDonald, and J. A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: The importance of size-based interactions between fish and zooplankton. Canadian Journal of Fisheries and Aquatic Sciences 44:141-147.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 18:1-158.

Cunjak, R. A., R. G. Randall, and E. M. P. Chadwick. 1988. Snorkeling versus electrofishing: A comparison of census techniques in Atlantic salmon rivers. Le Naturaliste Canadien 115:89-93.

Dabrowski, K. R. 1986. A new type of metabolism chamber for the determination of active and postprandial metabolism of fish, and consideration of results for coregonid and salmon juveniles. Journal of Fish Biology 28:105-117.

Daniel, C., and F. Wood. 1980. Fitting equations to data. John Wiley and Sons, New York.

DeAngelis, D. L., and C. C. Coutant. 1979. Growth rates and size distributions of first-year smallmouth bass populations: Some conclusions from experiments and a model. Transactions of the American Fisheries Society 108:137-141.

______, L. Godbout, and B. J. Shuter. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. Ecological Modelling 57:91-115.

Dill, L. C., R. C. Ydenberg, and A. G. H. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (Oncorhynchus kisutch). Canadian Journal of Zoology 59-1801-1809.

Dowling, D. C. 1987. Population dynamics of, and habitat utilization by, young-of-the-year rock bass (Ambloplites rupestris) and smallmouth bass (Micropterus dolomieui). Masters Thesis, Michigan State University, Lansing, Michigan. 99 pp.

Drost, M. R., J. W. Osse, M. Muller. 1988. Prey capture by fish larvae, water flow patterns and the effect of escape movements of prey. Netherlands Journal of Zoology 38:23-45.

Easton, R. S. 1992. Feeding ecology of age-0 smallmouth bass in the New River, West Virginia. Masters Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 99 pages.

______, and D. J. Orth. 1992. Ontogenetic diet shifts of age-0 smallmouth bass (Micropterus dolomieu Lacepède) in the New River, West Virginia, USA. Ecology of Freshwater Fish 1:86-98.

Ehlinger, T. J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. Ecology 71:886-896.

Elliot, G. V. 1976. Diel activity and feeding of schooled largemouth bass fry. Transactions of the American Fisheries Society 105:624-627.

Elliott, J. M. 1976. Energy losses in the waste products of brown trout (Salmo trutta L.). Journal of Animal Ecology 45:561-580.

______. 1989a. The critical period concept for juvenile survival and its relevance for population regulation in young sea trout, Salmo trutta. Journal of Fish Biology 35A:95-98.

______. 1989b. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. I. The critical time for survival. Journal of Animal Ecology 58:987-1001.

______. 1990. Mechanisms responsible for population regulation in young migratory trout, Salmo trutta. II. Fish growth and size variation. Journal of Animal Ecology 59:171-185.

Facey, D. E., and G. D. Grossman. 1990. The metabolic cost of maintaining position for four North American stream fishes: Effects of season and velocity. Physiological Zoology 63:757-776.

______. 1992. The relationship between water velocity, energetic costs, and microhabitat use in four North American stream fishes. Hydrobiologia 239:10-6.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

______, and R. J. White. 1981. Competition between brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Feldmeth, C. R. 1983. Costs of aggression in trout and pupfish. Pages 119-138 in W. P Aspey, and S. I. Lustik, editors, Behavioral energetics: the cost of survival to vertebrates. Ohio State University Press, Columbus, Ohio.

______, and T. M. Jenkins, Jr. 1973. An estimate of energy expenditure by rainbow trout (Salmo gairdneri) in a small stream. Journal of the Fisheries Research Board of Canada 30:1755-1759.

Floyd, K. B., R. D. Hoyt, S. Timbrook. 1984. Chronology of appearance and habitat partitioning by stream larval fishes. Transactions of the American Fisheries Society 113:217-223.

Forbes, A. M. 1989. Population dynamics of smallmouth bass (Micropterus dolomieui) in the Galena (Fever) River and one of its tributaries. Wisconsin Department of Natural Resources, Technical Bulletin No. 165, Madison, Wisconsin.

Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36:883-902.

Fraser, D. F., and T. E. Sise. 1980. Observations on stream minnows in a patchy environment: A test of a theory of habitat distribution. Ecology 61:790-797.

Freeman, M. C., and G. D. Grossman. 1992. Group foraging by a stream minnow: shoals or aggregations? Animal Behaviour 44:393-403.

George, E. L., W. F. Hadley. 1979. Food and habitat partitioning between rock bass (Ambloplites rupestris) and smallmouth bass (Micropterus dolomieui) young of the year. Transactions of the American Fisheries Society 108:253-261.

Georgian, T., and J. H. Thorp. 1992. Effects of microhabitat selection on feeding rates of net-spinning caddisfly larvae. Ecology 73:229-240.

Gleitman, H., and P. Rozin. 1971. Learning and memory. pp. 191-278 in W. S. Hoar, and D. J. Randall, editors. Fish physiology, Volume VI: Environmental relations and behavior. Academic Press, New York, New York.

Godin, J. J. 1978. Behavior of juvenile pink salmon (Oncorhynchus gorbuscha Walbaum) toward novel prey: influence of ontogeny and experience. Environmental Biology of Fishes 3:261-266.

______, and R. W. Rangeley. 1989. Living in the fast lane: effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. Animal Behaviour 37:943-954.

Goff, G. P. 1985. Environmental influences on annual variation in nest success of smallmouth bass, Micropterus dolomieui, in Long Point Bay, Lake Erie. Environmental Biology of Fishes 14:303-307.

Gore, J. A., and R. D. Judy Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. Canadian Journal of Fisheries and Aquatic Sciences 38:1363-1370.

______, and J. M. Nestler. 1988. Instream flow studies in perspective. Regulated Rivers 2:93-101.

Gotceitas, V. 1990. Foraging and predator avoidance: a test of a patch choice model with juvenile bluegill sunfish. Oecologia 83:346-351.

______, and J. J. Godin. 1992. Effects of location of food delivery and social status on foraging-site selection by juvenile Atlantic salmon. Environmental Biology of Fishes 35:291-300.

Graham, R. J., and D. J. Orth. 1987. Otolith aging of young-of-the-year smallmouth bass. pp 483-491 in R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. The Iowa State University Press, Ames, Iowa.

Granholm, S., S. Li, and B. Holton. 1985. Warning: Use IFIM and HEP with caution. Hydro Review 4:22-28.

Grant, J. W. A. 1990. Aggressiveness and the foraging behaviour of young-of-the-year brook charr (Salvelinus fontinalis). Canadian Journal of Fisheries and Aquatic Sciences 47:915-920.

______, and D. L. G. Noakes. 1987. Movers and stayers: Foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. Journal of Animal Ecology 56:1001-1013.

______, and D. L. G. Noakes. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). Behavioral Ecology and Sociobiology 22:435-445.

Green, R. F., and A. T. Nuñez. 1986. Central-place foraging in a patchy environment. Journal of Theoretical Biology 123:35-43.

Groshens, T. P. 1993. An assessment of the transferability of habitat suitability criteria for smallmouth bass. M. S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 103 pp.

Grossman, G. D., and M. C. Freeman. 1987. Microhabitat use in a stream fish assemblage. Journal of the Zoological Society of London 212:151-176.

Harvey, B. C. 1991. Interaction of abiotic and biotic factors influences larval fish survival in an Oklahoma stream. Canadian Journal of Fisheries and Wildlife Sciences 48:1476- 1480.

Heggenes, J. 1988. Physical habitat selection by brown trout (*Salmo trutta*) in riverine systems. Nordic Journal of Freshwater Research 64:74-90.

______, Å. Brabrand, and S. J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. Transactions of the American Fisheries Society 119:101-111.

______, T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:757-762.

Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116:185-195.

Hoff, M. H. 1991. Effects of increased nesting cover on nesting and reproduction of smallmouth bass in northern Wisconsin lakes. pp. 39-43 _in_ D. C. Jackson, editor. First international smallmouth bass symposium. Mississippi State University, Mississippi State, Mississippi.

Horning, W. B., and R. E. Pearson. 1973. Growth temperature requirements and lower lethal temperatures for juvenile smallmouth bass (_Micropterus_ _dolomieui_). Journal of the Fisheries Research Board of Canada 30:1226-1230.

Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fish. Ecological Monographs 48:307-321.

Houde, E. D. 1989. Subtleties and episodes in the early life of fishes. Journal of Fish Biology 35(Supplement A):29-38.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: Model and test for arctic grayling (_Thymallus_ _arcticus_) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039-2048.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. Van Winkle, D. D. Schmoyer, M. J. Sabo, D. J. Orth, J. A. Lukas. In Press. An individual-based model for smallmouth bass reproduction and young-of-the-year dynamics in streams. Rivers.

Jenkins, T. M., C. R. Feldmeth, and G. V. Elliot. 1970. Feeding of rainbow trout (_Salmo_ _gairdneri_) in relation to drifting invertebrates in a mountain stream. Journal of the Fisheries Research Board of Canada 27:2356-2361.

Johnson, J. H., and P. A. Kucera. 1985. Summer-autumn habitat utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 63:2283-2290.

Johnson, R. A., and D. W. Wichern. 1988. Applied multivariate statistical analysis. Prentice-Hall International Limited, London.

Kacelnik, A., and A. I. Houston. 1984. Some effects of energy costs on foraging strategies. Animal Behaviour 32:609-614.

Kaufmann, R. 1990. Respiratory cost of swimming in larval and juvenile cyprinids. Journal of Experimental Biology 150:343-366.

Keast, A., and J. McA. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114:204-213.

King, M. A., R. J. Graham, and W. S. Woolcot. 1991. Comparison of growth of smallmouth bass from two tributaries of the York River, Virginia. Pages 6-13 in D. C. Jackson, editor. Proceedings of the first international smallmouth bass symposium, Mississippi Agricultural and Forestry Experiment Station, Mississippi State University, Starkville, Mississippi.

Kondratieff, C., and J. R. Voshell. 1980. Life history and ecology of Stenonema modestum (Banks) (Ephemeroptera: Heptageniidae) in Virginia, USA. Aquatic Insects 2:177-189.

Krebs, J. R., and A. J. Inman. 1992. Learning and foraging: Individuals, groups, and populations. The American Naturalist 140:S63-S84.

______, J. C. Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study in patch use by chickadees. Animal Behaviour 22:953-964.

Kwak, T. J., M. J. Wiley, L. L. Osborne, and R. W. Larimore. 1992. Application of diel feeding chronology to habitat suitability analysis of warmwater stream fishes. Canadian Journal of Fisheries and Aquatic Sciences 49:1417-1430.

Lachner, E. A. 1950. Food, growth and habits of fingerling northern smallmouth bass, Micropterus dolomieu dolomieu Lacépède, in trout waters of western New York. Journal of Wildlife Management 14:50-57.

Larimore, R. W. 1975. Visual and tactile orientation of smallmouth bass fry under floodwater conditions. Pages 323-332 in H. Clepper, editor. Black bass biology and management, Sport Fishing Institute, Washington, D.C.

Laurence, G. C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (Micropterus salmoides). Journal of Fish Biology 4:73-78.

Layzer, J. B., and M. D. Clady. 1987. Phenotypic variation of young-of-the-year bluegills (Lepomis macrochirus) among microhabitats. Copeia 3:702-707.

Leonard, P. L., and D. J. Orth. 1988. Use of habitat guilds of fishes to determine instream flow requirements. North American Journal of Fisheries Management 8:399-409.

Li, H., and R. W. Brocksen. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (Salmo gairdneri). Journal of Fish Biology 11:329-341.

Lobb, M. D., and D. J. Orth. 1991. Habitat use by and assemblage of fish in a large warmwater stream. Transactions of the American Fisheries Society 120:65-78.

Luecke, C., J. A. Rice, L. B. Crowder, S. E. Yeo, F. P. Binkowski. 1990. Recruitment mechanisms of bloater in Lake Michigan: an analysis of the predatory gauntlet. Canadian Journal of Fisheries and Aquatic Sciences 47:524-532.

Lukas, J. A. 1993. Factors affecting reproductive success of smallmouth bass and redbreast sunfish in the North Anna River, Virginia. M. S. Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 71 pp.

Mathur, D., W. H. Bason, E. J. Purdy, and C. A. Silver. 1985. A critique of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825-831.

May, R. C. 1974. Larval mortality in marine fishes and the critical period concept. pp. 3-19 in J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, Berlin.

Mazeaud, M. M., F. Mazeaud, and E. M. Donaldson. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Transactions of the American Fisheries Society 106:201-212.

McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 46:1551-1557.

McNamara, J. M., and A. I. Houston. 1985. Optimal foraging and learning. Journal of Theoretical Biology 117:231-249.

McNicol, R. E., and D. L. G. Noakes. 1981. Territories and territorial defense in juvenile brook charr, Salvelinus fontinalis (Pisces: Salmonidae). Canadian Journal of Zoology 59:22-28.

Mesick, C. F. 1988. Effects of food and cover on numbers of Apache and brown trout establishing residency in artificial stream channels. Transactions of the American Fisheries Society 117:421-431.

Meyer, F. A. 1970. Development of some larval centrarchids. The Progressive Fish Culturist 32:130-136.

Mikheev, V. N., D. S. Pavlov, and D. Pakulska. 1992. Swimming response of goldfish, Carassius auratus, and the tetra, Hemigrammus caudovittatus, larvae to individual food items and patches. Environmental Biology of Fishes 35:351-360.

Milinski, M. 1985. The patch choice model: no alternative to balancing. The American Naturalist 125:317-320.

Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Transactions of the American Fisheries Society 111:527-530.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: towards a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.

______, L. B. Crowder, J. A. Rice, and F. P. Binkowski. 1992. Body size and the ontogeny of the functional response in fishes. Canadian Journal of Fisheries and Aquatic Sciences 49:805-812.

Morantz, D. L., R. K. Sweeney, C. S. Shirvell, and D. A. Longard. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 44:120-129.

Morhardt, J. E., and C. F. Mesick. 1988. Behavioral carrying capacity as a possible short term response variable. Hydro Review 7:32-40.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology 1:379-388.

______. 1988. Habitat-dependent population regulation and community structure. Evolutionary Ecology 2:253-269.

Neilson, J. D., G. H. Geen. 1981. Method for preparing otoliths for microstructure examination. The Progressive Fish Culturist 43:90-91.

Neves, R. J. 1975. Factors affecting fry production of smallmouth bass (Micropterus dolomieui) in South Branch Lake, Maine. Transactions of the American Fisheries Society 103:83-87.

Nielsen, J. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617-634.

O'Brien, W. J., and B. I. Evans. Saltatory search behavior in five species of planktivorous fish. Internationale Vereinigung für Theoretishe und Angewandte Limnolgie Verhandlungen 24:2371-2376.

______, H. I. Browman, and B. I. Evans. 1990. Search strategies of foraging animals. American Scientist 78:152-160.

Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers 1:171-181.

______, and O. E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. Transactions of the American Fisheries Society 111:413-445.

______, and O. E. Maughan. 1983. Microhabitat preferences of benthic fauna in a woodland stream. Hydrobiologia 106:157-168.

Osse, J. W., and M. R. Drost. Hydrodynamics and mechanics of fish larvae. Polish Archives of Hydrobiologie 36:455-465.

Panfili, J., and M.-C. Ximenes. Measurements on ground or sectioned otoliths: possibilities of bias. Journal of Fish Biology 41:201-207.

Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. pp. 303-324 in T. D. Fortaine and S. M. Bartell, editors, Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Persson, L., and S. Diehl. 1990. Mechanistic individual-based approaches in the population/community ecology of fish. Annales Zoologici Fennici 27:165-182.

______, and L. A. Greenberg. 1990. Optimal foraging and habitat shift in perch (Perca fluviatilis) in a resource gradient. Ecology 71:1699-1713.

Pflieger, W. L. 1966. Reproduction of smallmouth bass (Micropterus dolomieui) in a small Ozark stream. American Midland Naturalist 76:410-418.

Pierce, R. J, and T. E. Wissing. 1974. The energy cost of food utilization in the bluegill Lepomis macrochirus. Transactions of the American Fisheries Society 103:38-45.

Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: Importance of stream depth and prey size. Pages 333-351 _in_ W. C. Kerfoot and A. Sih, editors. Predation: Direct and indirect impacts on aquatic communities, University Press of New England, Hanover and London.

Puckett, K. J., and L. M. Dill. 1984. Cost of sustained and burst swimming to juvenile coho salmon (_Oncorhynchus kisutch_). Canadian Journal of Fisheries and Aquatic Sciences 41:1546-1551.

______, and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (_Oncorhynchus kisutch_). Behaviour 92:97-111.

Radtke, R. L. 1989. Larval fish age, growth, and body shrinkage: information available from otoliths. Canadian Journal of Fisheries and Aquatic Sciences 46:1884-1894.

Reiser, D. W., T. A. Wesche, and C. Estes. 1989. Status of instream flow legislation and practices in North America. Fisheries 14:22-29.

Reynolds, C. R., and C. J. O'Bara. 1991. Reproductive ecology and spawning habitat of smallmouth bass in two streams of the Tennessee River System. pp. 61-65 _in_ D. C. Jackson, editor. First international smallmouth bass symposium. Mississippi State University, Mississippi State, Mississippi.

Rice, J. A. 1987. Reliability of age and growth-rate estimates derived from otolith analysis. pp. 167-176 in R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. Iowa State University Press, Ames, Iowa.

______, J. E. Breck, S. M. Bartell, and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes 9:263-275.

______, L. B. Crowder, and F. P. Binkowski. 1985. Evaluating otolith analysis for bloater _Coregonus hoyi_: Do otoliths ring true? Canadian Journal of Fisheries and Aquatic Sciences 114:532-539.

______, L. B. Crowder, and M. E. Holey. 1987. Exploring of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116:703-718.

Ridgeway, M. S. 1988. Developmental stage of offspring and brood defense in smallmouth bass (Micropterus dolomieui). Canadian Journal of Zoology 66:1722-1728.

Rimmer, D. M., U. Paim, and R. L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon (Salmo salar) in a small river. Canadian Journal of Fisheries and Aquatic Sciences 40:671-680.

_____, U. Paim, and R. L. Saunders. 1984. Changes in the selection of microhabitat by juvenile Atlantic salmon (Salmo salar) at the summer-autumn transition in a small river. Canadian Journal of Fisheries and Aquatic Sciences 41:469-475.

Ringler, N. H. 1979. Prey selection by drift-feeding brown trout (Salmo trutta). Journal of Fisheries Research Board of Canada 36:392-403.

______. 1983. Variation in foraging tactics of fishes. pp. 159-171 in D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, and J. A. Ward, editors, Predators and prey in fishes. Dr. W. Junk Publishers, Boston.

Roell, M. J., and D. J. Orth. In press. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: The search for mechanism. The American Naturalist 137:S5-S28.

Scott, D., and C. S. Shirvell. 1987. A critique of the Instream Flow Incremental Methodology with observations on flow determination in New Zealand. pp. 27-43 in B. Kemper, and J. F. Craig, editors. Regulated streams: Advances in ecology. Plenum Press, New York.

Sechnick, C. W., R. F. Carline, R. A. Stein, and E. T. Rankin. 1986. Habitat selection by smallmouth bass in response to physical characteristics of a simulated stream. Transactions of the American Fisheries Society 115:314-321.

Shephard, J. G., and D. H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Journal du Conseil 39:160-167.

Shiozawa, D. K. 1991. Microcrustacea from the benthos of nine Minnesota streams. Journal of the North American Benthological Society 10:286-299.

Shirvell, C. S. 1990. Role of instream rootwads as juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (O. mykiss) cover habitats under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47:852-861.

Shuck, H. A. 1945. Survival, population density, growth and movement of the wild brown trout in Crystal Creek. Transactions of the American Fisheries Society 73:209-230.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

______, and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Simmons, G. M., and J. R. Voshell. 1978. Pre- and post-impoundment benthic macroinvertebrate communities of the North Anna River. Pages 45-61 in J. Cairns Jr., E. F. Benfield and J. R. Webster, editors. Current perspectives on river-reservoir ecosystems. North American Benthological Society.

Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young-of-the-year smallmouth bass in relation to habitat use. Transactions of the American Fisheries Society 119:902-909.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, Salmo gairdneri. Pages 173-180 in D. L. G. Noakes, D. G. Lingquist, G. S. Helfman, and J. A. Ward, editors. Predators and prey in fishes. Dr. W. Junk, The Hague, The Netherlands.

Smith, J. N. M., and R. Dawkins. 1971. The hunting behavior of individual great tits in relation to spatial variations in their food density. Animal Behaviour 19:695-706.

Statzner, B., J. A. Gore, and V. H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of the North American Benthological Society 7:307-360.

Stein, R. A. 1979. Behavioral response of prey to fish predators. pp. 343-355 in H. Clepper, editor, Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D. C.

Stewart, J. I. 1978. Daily feeding chronology of young smallmouth bass in the Snake River, Minnesota. M. S. Thesis, University of Minnesota, Saint Paul, Minnesota. 71 pp.

Stites, D. L., and A. C. Benke. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P:B ratios. Limnology and Oceanography 34:1278-1289.

Stradmeyer, L., and J. E. Thorpe. 1987. Feeding behavior of wild Atlantic salmon, Salmo salar L., parr in mid- to late summer in a Scottish river. Aquaculture and Fisheries Management 18:33-49.

Streeter, V. L., and E. B. Wylie. 1985. Fluid mechanics. Eighth edition. McGraw-Hill, New York. 586 pp.

Swenson, W. A., W. P. Gobin, and T. D. Simonson. 1988. Calibrated mask-bar for underwater measurement of fish. North American Journal of Fisheries Management 8:382-385.

Thomas, G. 1974. The influence of encountering a food object on the subsequent searching behaviour in Gasterosteus aculeatus L. Animal Behaviour 22:941-952.

______. 1977. The influence of eating and rejecting prey items upon feeding and food searching behaviour in *Gasterosteus aculeatus* L. Animal Behaviour 25:52-66

Titus, R. G., and H. Mosegaard. 1991. Selection for growth potential among migratory brown trout (*Salmo trutta*) fry competing for territories: Evidence from otoliths. Canadian Journal of Fisheries and Aquatic Sciences 48:19-27.

Trexler, J. C. 1990. Genetic architecture of behavior in fishes and the response to selection. Annales Zoologici Fennici 27:149-163.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253-1266.

Ultsch, G. R., H. Boschung, and M. J. Ross. 1978. Metabolism, critical oxygen tension, and habitat selection in darters (*Etheostoma*). Ecology 59:99-107.

Videler, J. J., and C. S. Wardle. 1991. Fish swimming stride by stride: speed limits and endurance. Reviews in Fish Biology and Fisheries 1:23-40.

Virginia Electric and Power Company. 1986. North Anna power station Section 316(a) demonstration - Environmental studies of Lake and the lower North Anna River. VEPCO, Richmond, Virginia. 1339 pp.

Vogel, S. 1981. Life in moving fluids. Princeton University Press, Princeton, New Jersey. 352 pp.

Wallace, C. R. 1972. Embryonic and larval development of the smallmouth bass at 23°C. The Progressive Fish Culturist 34:237-239.

Walton, W. E., N. G. Hairston, Jr., J. K Wetterer. 1992. Growth related constraints on diet selection by sunfish. Ecology 73:429-437.

Wankowski, J. W. J. 1979. Behavioural aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate, drifting prey. Animal Behaviour 29:557-571.

______, and J. E. Thorpe. 1979. Spatial distribution and feeding in Atlantic salmon, Salmo salar L. juveniles. Journal of Fish Biology 14:239-247.

Ward, J. V. 1992. Aquatic Insect Ecology: Biology and Habitat. John Wiley and Sons, Inc., New York. 438 pp.

Webb, P. W. 1991. Composition and mechanics of routine swimming of rainbow trout, Oncorhynchus mykiss. Canadian Journal of Fisheries and Aquatic Sciences 48:583-590.

______, and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Transactions of the American Fisheries Society 115:115-127.

Webster, D. A. 1948. Relation of temperature to survival and incubation of the eggs of smallmouth bass (Micropterus dolomieui). Transactions of the American Fisheries Society 75:43-47.

Wedemeyer, G. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 29:1780-1783.

Weihs, D., and P. W. Webb. 1983. Optimization of locomotion. Pages 339-371 in P. W. Webb, and D. Weihs, editors, Fish biomechanics. Praeger Publishers, New York.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.

______, and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256-264.

______, J. F. Gilliam, D. J. Hall, and G. G. Mittlebach. 1983a. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540-1548.

______, G. G. Mittlebach, D. J. Hall, and J. F. Gilliam. 1983b. Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. Ecology 64:1525-1539.

West, C. J., and P. A. Larkin. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (Oncorhynchus nerka) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44:712-721.

Williams, F. M. 1984. A fish population model for instream flow assessment. LW-8401. Institute for Research on Land and Water Resources, The Pennsylvania State University, University Park, Pennsylvania.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: Implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196-2218.

Wrenn, W. B. 1980. Effects of elevated temperature on growth and survival of smallmouth bass. Transactions of the American Fisheries Society 109:617-625.

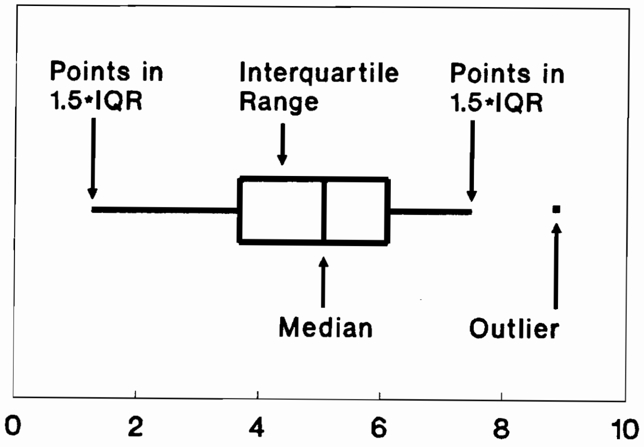
Wright, P. J., N. B. Metcalfe, and J. E. Thorpe. 1990. Otolith and somatic growth rates in Atlantic salmon parr, Salmo salar L.: evidence against coupling. Journal of Fish Biology 36:241-249.

______, D. Rowe, and J. E. Thorpe. 1991. Daily growth increments in the otoliths of Atlantic salmon parr, Salmo salar L., and the influence of environmental factors on their periodicity. Journal of Fish Biology 39:103-113.

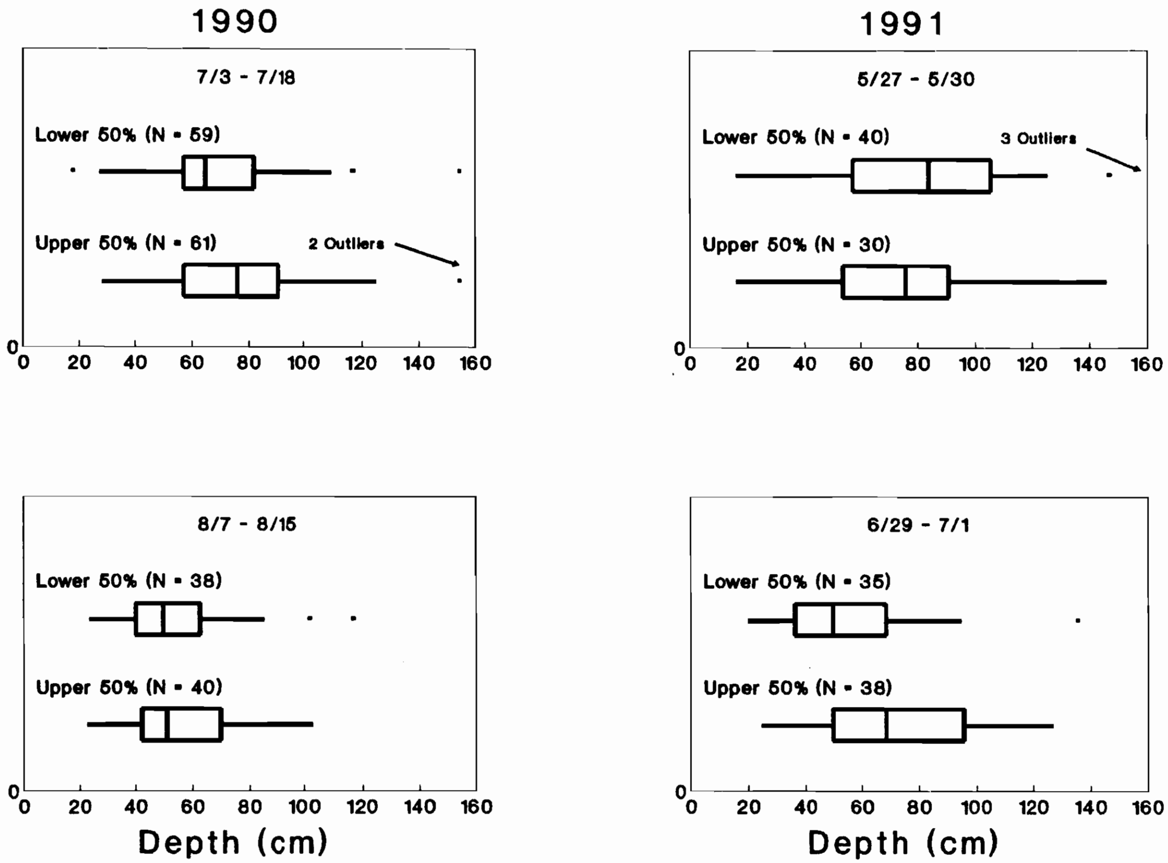
APPENDICES

Appendix 1. Size ranges of substrate categories used in microhabitat descriptions.

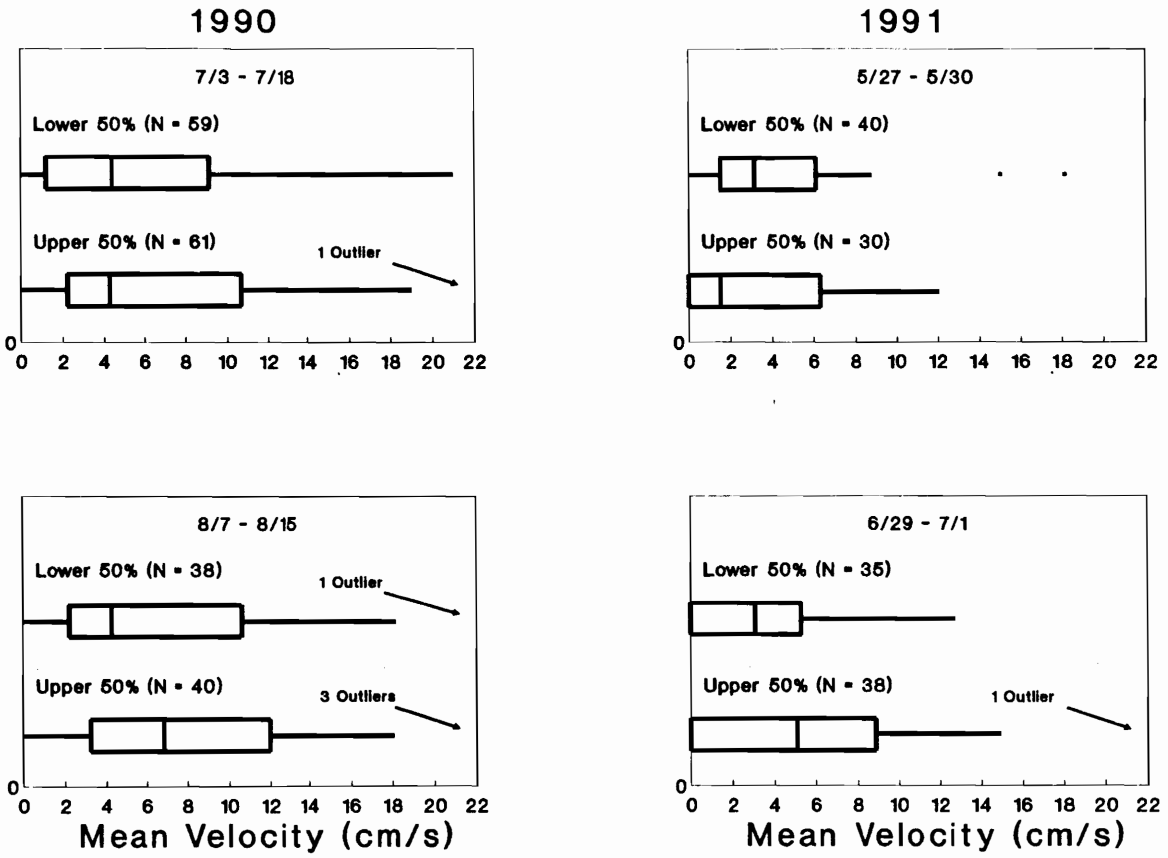
Substrate Category	Size Range
Silt/Clay	< 0.5 mm
Sand	0.5-2.0 mm
Small Gravel	2-8 mm
Gravel	8-32 mm
Pebble	32-64 mm
Cobble	64-150 mm
Boulder	150-1000 mm
Flat bedrock	Flat plane
Fractured bedrock	Extending into Water Column



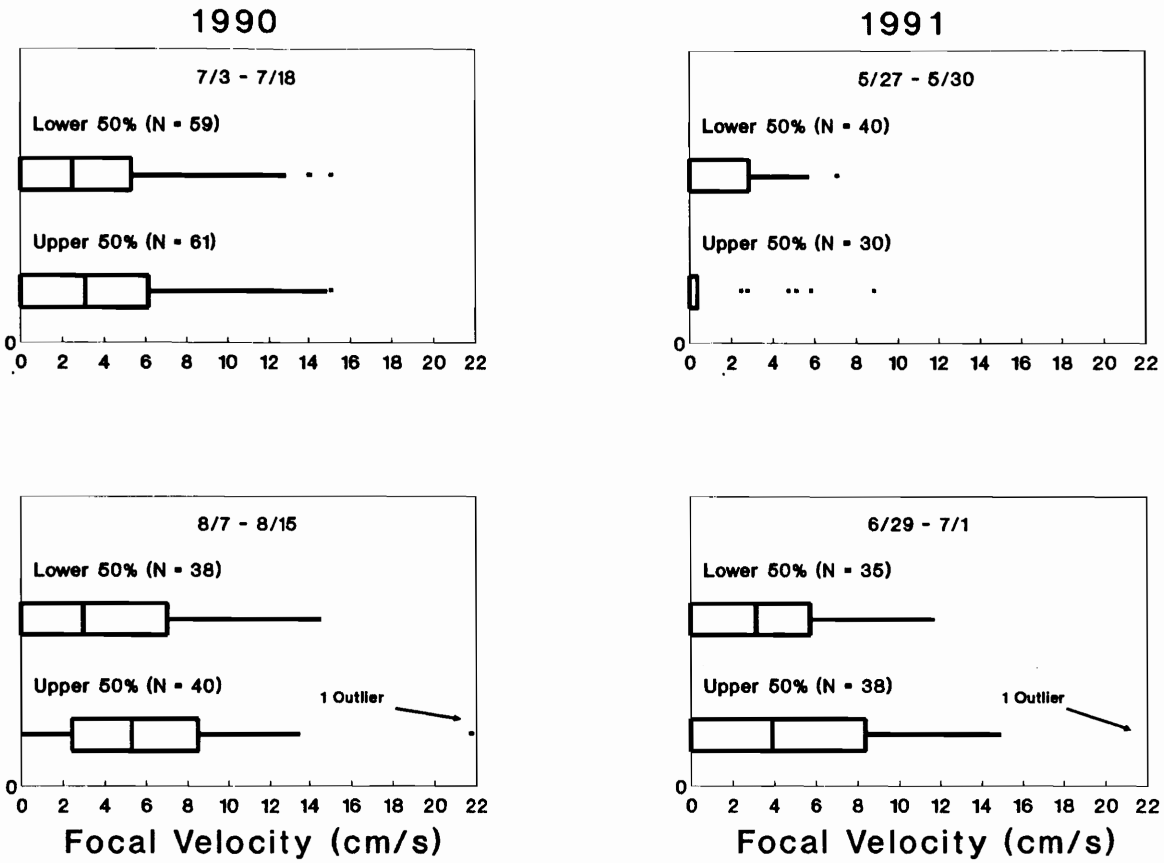
Appendix 2. Format for box plots. The box represents the interquartile range (IQR) and the vertical line designates the median. The horizontal lines cover all data points within the range of 1.5 times the IQR added to the upper and lower boundaries of the IQR. Dots designate points outside this range.



Appendix 3. Box plots of depths (cm) used by the largest and smallest half of observed juvenile smallmouth bass during July and August 1990, and May and June 1991.



Appendix 4. Box plots of mean water-column velocities (cm/s) used by the largest and smallest half of juvenile smallmouth bass observed during July and August 1990, and May and June 1991.



Appendix 5. Box plots of focal point velocities (cm/s) used by the largest and smallest half of juvenile smallmouth bass observed during July and August 1990, and May and June 1991.

VITA

Matthew James Sabo was born on March 15, 1965 and for the first 18 years of his life he resided in West Middlesex, Pennsylvania. He graduated from Kennedy Christian High School in 1983 and enrolled in The Pennsylvania State University, where he earned a Bachelor of Science degree in Wildlife Science in 1987. At that time, his primary research interest was the sociobiology of timber wolves, so he logically enrolled in Louisiana State University where he studied larval fish in the Mississippi River. After graduating from LSU in 1989 with a Master of Science degree in Fisheries Science, he decided to continue investigating the nursery habitats of fish and enrolled in Virginia Polytechnic Institute and State University as a doctoral candidate in Fisheries Science. In June 1993, he joined the faculty of Louisiana State University as an Assistant Professor of Fisheries Science.

Matthew James Sabo