INTER-SEASONAL MOVEMENTS OF ETHEOSTOMATINAE DARTERS IN YELLOW CREEK AND WHITEOAK CREEK, TENNESSEE

Mark S. Hoger

Inter-seasonal movements of Etheostomatinae darters in

Yellow Creek and Whiteoak Creek, Tennessee

A thesis

Presented to

The College of Graduate Studies

Austin Peay State University

In Partial Fulfillment

Of the Requirements for the Degree
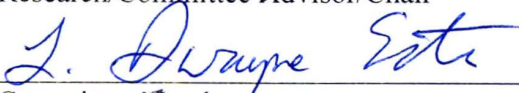
Master of Science in Biology

Mark S. Hoger

May, 2012

To the College of Graduate Studies:

We are submitting a thesis written by Mark S. Hoger entitled "Inter-seasonal movements of Etheostomatinae darters in Yellow Creek and Whiteoak Creek, Tennessee." We have examined the final copy of this thesis for form and content. We recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science in Biology.
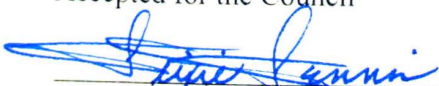
_____
Research/Committee Advisor/Chair

_____
Committee Member

_____
Committee Member

_____
Committee Member

Accepted for the Council

_____
Dean, College of Graduate Studies

Statement of Permission to Use

In presenting this thesis in partial fulfillment of the requirements for the Master of Science in Biology at Austin Peay State University, I agree that the library shall make it available to borrowers under the rules of the library. Brief quotations from this field study are allowable without special permission, provided that accurate acknowledgement of the source is made.

Permissions for extensive quotation or reproduction of this field study may be granted by my major professor, or in his/her absence, by the Head of the Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

_____
Signature

6 APRIL 2012
Date

To my wife, Emily,

for encouraging me to pursue my passions

LIST OF TABLES

ACKNOWLEDGEMENTS

ABSTRACT

MARK S. HOGER. Inter-seasonal movements of Etheostomatinae darters in Yellow Creek and Whiteoak Creek, Tennessee (under the direction of DR. REBECCA JOHANSEN.)

Although movements of some fishes have been extensively studied, limited focus has been given to small, non-game fishes such as darters. Previous studies have demonstrated the need to incorporate multiple scales, taxa, and life histories to provide better insight into the movements of darters. A multi-season, mark-recapture study was conducted with darters at two Highland Rim streams of central Tennessee. A total of 10,136 individuals (12 species) were marked and 849 (8.5%; 8 species) recaptured.

Frequency and distance of movement varied among species and an atypical, downstream directional bias was observed. The extent of movement was generally greater than previous studies of darters with respect to both frequency of movement (16.6%) and average distance traveled (247.1 m). This is likely due to the inclusion of multiple seasons, among which movement significantly varied. Overall, males traveled longer distances than females during the pre-spawning season.

Two corridor-specific factors had notable impacts on darter movement. First, higher average corridor depth limited the distance traveled. Also, darters that attach their eggs showed particular sensitivity to increased predator densities by showing significant reduction in their movement rate through corridors with high predator density. Inverse relationships were observed between seasons with respect to movement rate and darter size, indicating a probable shift in ecological pressures. Overall, individuals moved more frequently when congeneric density was high.

Darters with increased reproductive investment moved more frequently but traveled shorter distances overall. However, during the spawning season, darters with decreased reproductive investment moved more frequently, demonstrating a strong seasonal effect on movement. A reduction in distance traveled in species with high reproductive investment is consistent with previous research which shows reduced gene flow in species with small clutches and large eggs.

Although limited in its ability to detect long-range movements, this study provides a baseline for darter movement patterns across spatial and temporal scales, taxa, and life history characteristics. The potential impacts of habitat degradation, fragmentation, and loss as they relate to movements are discussed in addition to the use of results from focal species to infer movement patterns and potential conservation implications for imperiled species with comparable life histories.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER I

Introduction

One of the most diverse groups of North American vertebrates is the darters, diminutive members of the family Percidae. Endemic to North America, these benthic fishes have a reduced or absent swimbladder that is an adaptation to a benthic lifestyle. This adaptation also makes them particularly suited to living in riffles, the preferred habitat of many darters (Page, 1983). Riffles are areas of streams typically characterized by shallower depths, higher velocity, increased turbulence, and clean coarse substrates. The preference of darters for riffles, which have high prey (benthic arthropods) and low predator abundances, has likely contributed to their evolutionary success (Page and Swofford, 1984). Furthermore, their association with various benthic habitats has led to a wide range of reproductive and life history strategies (Page and Swofford, 1984).

Riffles are patchily distributed throughout streams, alternating with runs and pools that are characteristically different habitats. Pools, in particular, are deeper, have lower velocity, finer substrates, and often higher predator abundances. Due to their reduced or absent swimbladder, darters are relatively poor swimmers, which potentially limits their ability to traverse intervening pools and runs. The ability of darters to move between riffle patches has important ecological implications with respect to population dynamics (Slack et al., 2004). Because of specific habitat requirements, darters are susceptible to habitat alteration. Habitat degradation, fragmentation, and loss lead to increased patchiness of riffle habitat and may lead to isolation of populations and loss of gene flow. Currently 44% of darter species are imperiled (Jelks et al., 2008). Thus,

understanding the limitations of darter movements relative to abiotic and biotic habitat features is crucial to their conservation.

Early research on stream fish movement found that many species exhibit restricted movements of 20-50 m (reviewed in Gerking, 1959). The designs of many of these studies, however, were potentially biased toward detecting limited movement by focusing recapture efforts in the area of release (Gowan et al., 1994; Rodriguez, 2002). Furthermore, these studies were almost exclusively conducted on larger-bodied, non-benthic fishes that have increased vagility relative to darters. Funk (1957), in an attempt to use a less-biased recapture method, counted only recaptures collected by fisherman, and found a much higher incidence of long distance movement. He concluded that fish populations were comprised of groups of sedentary and mobile individuals and implied that an individual fish fits into one category or the other. Harcup et al. (1984) provided evidence that fish shift between sedentary and mobile states. Recent work has continued to support stream fishes as more mobile than originally proposed (Gowan and Fausch, 1996; Rodriguez, 2002).

Less restricted movement, or frequent exploratory movement, is often suggested in studies of fish recolonization. Experimentally or naturally defaunated areas are often reinhabited within several days (Power, 1984; Peterson and Bayley, 1993). Power (1984) observed recolonization patterns of Central American catfish (Loricariidae) after the creation of new habitat from events such as flooding. When new habitat was created, colonization occurred within weeks. Recolonization after experimental removal of fish was also studied, and was even quicker. Colonization models by Peterson and Bayley (1993) indicated that 90% of the original fish abundance would be reached in 100-270

hours after experimental removal from a locality. Variation in the colonization rates among lizards shows the importance of including multiple species to account for differences in vagility and habitat preferences (Hoger, 1976).

The basis for these conclusions, however, comes primarily from the study of larger-bodied fishes from the families Centrarchidae and Salmonidae, which comprise a small percentage of freshwater stream fishes and represent a limited portion of the life history variation seen in fishes. In contrast, groups containing the great majority of North American fish diversity (i.e., Cyprinidae and Percidae) have received relatively little attention. These smaller-bodied fishes also exhibit a wide range of life history variation (Etnier and Starnes, 1993). Minnows (Cyprinidae) have been observed to show restricted movement with respect to both movement rate (Smithson and Johnston, 1999; Walker, 2011) and home range (Hill and Grossman, 1987; Goforth and Foltz, 1998). Similarly, darter movements outside the riffle of release have been found to be infrequent (Reed, 1968; Scalet, 1973; Mundahl and Ingersoll, 1983; Roberts et al., 2008) and distances traveled short (most movements to the next riffle; Roberts and Angermeier, 2007b; Schwalb et al., 2011).

Lonzarich et al. (1998) found that large fish (>100mm) recolonize areas more quickly than small fish, indicating that larger fish are more mobile. Small benthic fish, however, have also been shown to recolonize rapidly. Population density and size structure of *Cottus girardi* recover 30 days after removal from an area (Hudy and Shiflet, 2009). Additionally, some darters quickly reinvade streams that are dry part of the year (Winn, 1958). Although rapid recolonization may indicate high mobility (Sheldon and Meffe, 1995), it could also be the result of long distance dispersal of a small portion of

the population (Hudy and Shiflet, 2009). Furthermore, factors such as proximity (Detenbeck et al., 1992; Lonzarich et al., 1998) and density (Sheldon and Meffe, 1995) of source populations are known to affect recolonization rates.

Sculpins (Cottidae), benthic fish that are often syntopic with darters, have been shown to be exceptionally sedentary. Brown and Downhower (1982) found that during the summer, adults moved an average of only 1.2 m (max 14.3 m), with over 50% of individuals found under the same tile throughout the season. Studies that have incorporated other seasons or methods (i.e., genetic approaches), have found sculpins to be somewhat more mobile suggesting frequency and distance moved may vary by season or that traditional mark-recapture studies may underestimate movements (Natsumeda, 1999; Hudy and Shiflet, 2009; Lamphere and Blum, 2012).

Movement is generally considered to increase in the spring (Funk, 1957; Gatz and Adams, 1994), which is the spawning season for many fishes—including darters (Funk, 1957; Etnier and Starnes, 1993). Most darter movement studies, however, have been conducted in the summer or fall. Only two studies have examined movements of darters through spawning and non-spawning seasons. In an 18-month study, Freeman (1995) found *Percina nigrofasciata* more likely to make long distance movements in the spring. Labbe and Fausch (2000) noted directional trends from a year-long movement study of *Etheostoma cragini* in an intermittent stream. Additional insight can be obtained by comparing similar studies done in different seasons. Ingersoll et al. (1984) found a higher movement rate for *Etheostoma nigrum* (24%) and *E. flabellare* (19%) in the spring than Mundahl and Ingersoll (1983) did in the fall (3% and 13%, respectively). This trend has also been documented for other benthic (Natsumeda, 1999) and small (Goforth and Foltz,

1998) stream fishes. In addition to frequency, direction of movement can also vary by season. Winn (1958) observed that darters moved upstream prior to spawning and downstream to deeper water after spawning.

Both biotic and abiotic parameters are known to influence the movements of small-bodied stream fishes such as darters. Flow (Albanese et al., 2004; Petty and Grossman, 2004), time of day (Natsumeda, 1998; Breen et al., 2009), riffle isolation, loss of shallow microhabitat (Roberts and Angermeier, 2007b), microhabitat diversity (Albanese et al., 2004; Roberts and Angermeier, 2007b), cover throughout a corridor (Roberts and Angermeier, 2007a), and intermittency (Albanese et al., 2004; Walker, 2011) have all been shown to influence frequency of movement. In addition to direct movement studies, analysis of allozymes has also suggested that variation in habitat can influence gene flow (Faber and White, 2000).

Conspecific and predator densities are two biotic parameters that have been shown to affect darter movements (Roberts and Angermeier, 2007b). These factors, in addition to food resource availability, have been observed to influence other benthic (Petty and Grossman, 2004; Lamphere, 2005) and small-bodied fishes (Gilliam and Fraser, 2001). Lamphere (2005) found that the response to these biotic parameters varies seasonally. Several studies have revealed variations in movement with respect to age class and individual size (Labbe and Fausch, 2000; Petty and Grossman, 2004; Roberts and Angermeier, 2007b; Walker, 2011).

As stated earlier, darters are one of the most speciose groups of North American vertebrates (Page, 1983). Within this diversity, darters exhibit extensive life history variation (Bart and Page, 1992). Turner and Trexler (1998) used allozymes to study gene

flow in 15 species of darters and found relationships between gene flow and life history traits. Most notably, they observed that darters with high fecundity and small eggs had increased gene flow when compared to those with low fecundity and large eggs. Work by Faber and White (2000) support these conclusions, as they found genetic structure within *Etheostoma flabellare* (low fecundity and larger eggs) populations and no structure within *E. blennioides* (high fecundity and smaller eggs) populations.

In addition to variation in fecundity and egg size, another notable difference in the life history of darters is the larval phase of development. Upon hatching from the egg, larval darters spend varying amounts of time in the water column before settling to the bottom (Simon and Wallus, 2006). During this time, they are susceptible to downstream drift. Upstream migration compensates for this downstream drift (Hall, 1972). Paine (1984) contended that a decrease in drift dispersal is associated with decreased gene flow promoting speciation. Turner (2001) showed larval transport was negatively associated with egg size but did not find a significant relationship between larval drift and gene flow. Similar relationships between life history traits (i.e., body-size, fecundity, and larval dispersal) and gene flow have been recorded in marine shore fishes (Waples, 1987). Variations in the significance of the ecological factors outlined above (Roberts and Angermeier, 2007b) as well as opposite responses occur (Albanese et al., 2004) among different species. Unfortunately, because most studies on the movement of darters are single-species studies, the relationship between movement and these life history traits has not been explored.

Understanding the relationship between life history variables and movement patterns of darters is essential to the development and implementation of effective

conservation practices. Patterns of movement and their correlation with various factors help predict the outcomes of events such as habitat degradation, fragmentation, and loss. A species, for instance, that is unable or unwilling to migrate readily may be more greatly impacted and need more carefully planned conservation efforts. By studying movement in multiple darters with different life history characteristics, predictions can be made on the impacts of a wide range of other darters with similar life histories.

Roberts and Angermeier (2007b) expressed the need for more research incorporating multiple scales, taxa, and life histories to provide better insight into the movements of darters. This study was undertaken to fill the gaps left by single-season and single-species studies that dominate the literature. The objectives of this study were to (1) monitor inter-seasonal movements of multiple darter species that possess different life history strategies and (2) relate movements to life history and abiotic and other biotic factors. The potential impacts of habitat degradation, fragmentation, and loss as they relate to movements, and the use of results from focal species to infer movement patterns and potential conservation implications for imperiled species with comparable life histories will also be discussed.

Based on the findings from previous fish movement studies and established ecological theories, it was predicted that species movements would vary and correlate with aspects of life history. More specifically, that reproductive investment and extent of movement would be inversely related. Also, darter movement would be greater in the upstream direction and in those with longer larval drift phases, as a compensatory mechanism for downstream drift. It was further expected that larger individual size, smaller stream size (i.e., depth, width), lower predator corridor density and riffle area

stability, and higher riffle congeneric density would result in greater darter movement. Finally, as reported in many other fishes and specifically in darters, it was expected that movements would be greatest prior to and during the spawning season.

CHAPTER II

Materials and Methods

Study sites

Two streams, Whiteoak Creek and Yellow Creek, were selected to conduct this study. Both are perennial streams located within the Western Highland Rim of the Interior Highlands in north-central Tennessee (Figure 1). The Whiteoak Creek (Tennessee R.) site was located at the crossing of Tennessee Ridge Rd. (36.227159°, -87.766670°), Humphreys County, approximately 12.0 km southwest of Erin, TN. Total length of the site was 525.6 m (307.2 m above and 218.4 m below the bridge, Figure 2). The Yellow Creek (Cumberland R.) site was located at the crossing of Highway 13 (36.348734°, -87.538749°), Montgomery County, 25.7 km southwest of Clarksville, TN. Total length of the site was 1,837.3 m (1,525.6 m above and 311.7 m below the bridge, Figure 3). Each site contained six riffle habitats with varying distances between them (corridors). Despite both being third order streams, the Yellow Creek site was much larger than the Whiteoak Creek site. Discharge values were not available for the two study sites but measurements over the course of the study indicate that Yellow Creek is roughly 35% wider and runs and pools are 50% deeper.

Species studied

The Cumberland and Tennessee River systems are the two most diverse river systems with respect to darters (Page, 1983). Streams in these systems were selected, to incorporate this great diversity. All darter species present at each site were included in the study, representing three genera (*Etheostoma, Nothonotus,* and *Percina*) and five

subgenera (*Etheostoma, Oligocephalus, Catonotus, Ulocentra,* and *Percina*). Species present at the two sites are *E. bison, E. blennioides, E. blennius, E. caeruleum, E. crossopterum, E. flabellare, E. flavum, E. occidentale, E. oophylax, E. smithi, N. rufilineatus,* and *P. caprodes. Percina burtoni* was also observed during snorkel surveys at Whiteoak Creek but was never collected during sampling efforts. In addition to diversity with respect to species, a wide range of reproductive behaviors, larval stages, body sizes, and other life history traits are present (Table 1). Furthermore, despite being part of separate river systems, there is sufficient overlap of fauna at the two sites to allow for replication within the study (Table 1).

Field procedures

As stated above, darters generally prefer riffle habitat (Page, 1983), which occurs patchily throughout streams. To analyze darter movements, their occurrence in this preferred habitat was tracked. Riffle habitat was sampled in two passes using a backpack electrofisher (Smith-Root Model 15-C, Smith-Root, Inc.) and 12 ft x 4 ft seine. Individuals ≥ 30 mm were selected for this study, roughly representing adults of all species (Etnier and Starnes, 1993). Darters were held in 5-gallon buckets with battery-powered aerators. Icepacks were used during the warm seasons to keep the water cool and reduce mortality. Tricaine methanesulfonate (Tricaine-S, Western Chemical, Inc.) at a concentration of 60 mg/L was used to anesthetize the fish.

Once anesthetized, each darter was given a riffle- and season-specific mark using fluorescent, visible implant elastomer (VIE) dye (Northwest Marine Technology, Inc.) to allow tracking throughout multiple recaptures. Fluorescent VIE has been shown to be an

effective long-term marker (Labbe and Fausch, 2000), and has better retention than injectable photonic dye (Roberts and Angermeier, 2004) and some colors of latex paint (Goforth and Foltz, 1998). The four interior riffles at each site were designated as marking riffles and assigned a specific color (red, yellow, blue, or orange; Figures 2 and 3). A different ventral marking location (breast, anterior belly, posterior belly, or along anal fin insertion) was used for each marking event (Figure 4). Ventral marks were used to eliminate the possibility of increased predation (Roberts and Kilpatrick, 2004) or interference with visual cues associated with mating (Page, 1983). Additionally, marking ventrally allowed for quick identification of marked individuals using a container with a clear bottom. After marking, fish were revived in aerated buckets of clean water until fully recovered from anesthesia, and then released into the center of the riffle from which they were collected.

Initial marking took place between 4 February and 13 February 2011, just prior to spawning. Recapture and remarking rounds were conducted 24 April to 24 May, 1 August to 15 August, 3 December to 15 December, and 3 February to 8 February 2012. Periods between mark-recapture rounds represented pre-spawning, spawning, post-spawning, and non-spawning seasons. Figure 5 shows mark-recapture periods and their relation to known darter spawning periods. While most darter spawning takes place from late February through May, *Nothonotus rufilineatus* spawns from May to August (Etnier and Starnes, 1993). For this reason, calendar seasons could not be broadly associated with reproductive seasons. Instead recapture periods were classified as reproductive seasons on a species-by-species basis. The interval from round two to round three was classified

as the spawning season for *N. rufilineatus* while that from round one to round two was classified as the spawning season for all other darters in the study.

All four original riffles plus one additional upstream and downstream riffle at each site were included in the recapture efforts to document fish movements. All new captures as well as recaptures were marked with a season- and riffle-specific mark. Recaptured fish were identified to species (Etnier and Starnes, 1993), enumerated, sex was determined (Kuehne and Barbour, 1983), and total length (TL) was measured.

Life history information was obtained from the literature. Data sources included Cooper (1978), Keevin et al. (1989), Bart and Page (1992), Etnier and Starnes (1993), Page and Knouft (2000), and Simon and Wallus (2006). Whenever possible, life history information was used from the source whose study was conducted nearest geographically to the study locations to account for possible intraspecific variation in traits. For analysis, life history information was consolidated into life history categories. These categories were largely based on reproductive behaviors and egg sizes of the focal fishes. Variation of other life history traits was accounted for indirectly due to the high correlation of these traits (Page, 1983; Turner and Trexler, 1998). Categories were ranked based on relative reproductive investment. Darters laying larger eggs were considered to have higher input than those laying smaller eggs. Burying eggs represented the behavior with least investment, followed by attachment of eggs (to specific substrate or vegetation), and clustering and guarding of eggs. Recaptured darter species fell into one of four categories: buriers with small eggs, buriers with big eggs, attachers (small eggs), and clusterer-guarders (big eggs; Table 2). These life history groupings are largely conserved within darter subgenera and have been used as a basis for their classification (Page, 1983;

Bart and Page, 1992). Larval drift phases were also ranked with respect to susceptibility to downstream drift. Pelagic larvae were classified as most susceptible followed by epibenthic and demersal larvae (Simon, 1994).

In addition, several habitat variables were measured to test for their potential influence on darter movements. When possible, these measurements were recorded for each sampling round to account for seasonal variation. Discharge values were obtained from the Ellis Mills USGS gaging station (USGS 2012) on Yellow Creek, located 5.2 river kilometers upstream from the Yellow Creek study site. Maximum daily values were averaged over each season to provide relative flow during those periods. Corridor-predator density (CPD) was defined as density of predators in habitats between sample riffles (i.e., pools and runs), and was calculated as fish per m^2. Snorkel surveys were conducted to quantify predator presence. Only species that are known piscivores and fish that were of adequate size were counted. Congeneric density (CGD) of riffles was also calculated as number of fish per m^2. Areas for the preceding calculations were derived by multiplying the average of the measured widths by the length. Riffle area stability (RAS) was quantified by calculating change in riffle area between sampling periods. Riffle area was calculated by multiplying riffle length by the average of widths taken at the head, middle, and end of the riffle. Average corridor width (ACW) was the average of widths taken every 50-100m, depending on the length of the corridor. Average corridor depth (ACD) was the average of multiple depth profiles taken throughout the corridor at the same frequency and location of the widths. Maximum corridor depth (MCD) was the largest depth measured for each corridor. Corridor length (CL), the distance between riffles, was determined using GPS coordinates (± 4m) and following the path of the

stream on Google Earth. With the exception of MCD, corridor variables were averaged when fishes crossed multiple corridors. When darters did not move, the corridor measures on either side of the riffle were averaged and recorded. Distance traveled (D) was measured as distance from the end of the starting riffle to the beginning of the ending riffle. For darters found in the same riffle, D=0. Direction (upstream or downstream) was recorded for darters that were recaptured in a different riffle.

Analysis

Data were organized in Excel 14.1.0 (Microsoft, Inc., 2010) and analyzed in JMP 9.0.0 (SAS Institute, Inc., 2010). One exception was that Fisher's exact tests on contingency tables larger than 2x2 were performed with RxC (Miller, 1997). Movements were quantified in two ways: frequency of movement and distance traveled when movement occurred. Influences on the direction of movement were also examined. Analysis of binomial responses (frequency of movement and direction of movement) to categorical data was performed through the use of Pearson's chi-squared tests (goodness of fit and tests of independence). When expected frequencies ≤ 5 exceeded 20% of the cells in a contingency table, Fisher's exact tests were used in place of Pearson's chi-squared tests. Analysis of binomial response to continuous data was completed with logistic regression. To examine relationships between distance moved and categorical variables, non-parametric Mann-Whitney U and Kruskal-Wallis tests were used instead of t-tests and ANOVAs because of violations of the assumption of normality. Linear regression was used to test distance moved against continuous variables. No statistical procedure was available to test the ordinal life history data against the movement

responses while maintaining the directional relation between categories; however, variation among the groups was tested and results were graphed to reveal directional relationships. For all tests, statistical significance was considered at $P < 0.05$.

Because most darters did not move (see results), only darters that moved were included in the analyses of distance moved. In some cases, this limited the ability to perform analysis of seasonal variation of relationships due to low sample sizes. Because some darters went multiple recapture rounds before being recaptured, it was sometimes unclear when a darter moved. Thus, analyses that were sensitive to time of movement—seasonal analyses, habitat measures, and densities—were conducted with only recaptures for which the timing of movement was known (i.e., darter was captured previous round of collecting). Tests performed, sample sizes, and full results are summarized for all tests in APPENDIX A.

Table 1. Life history information for all darters found in Whiteoak Creek (Tennessee R.) and Yellow Creek (Cumberland R.), Tennessee. Darters collected represent three genera (*Etheostoma, Nothonotus,* and *Percina*) and five subgenera (*Etheostoma, Oligocephalus, Catonotus, Ulocentra,* and *Percina*). If appropriate, data from closely related species were used when data were not available for a given species. MS = maximum size (mm TL). SM = size at maturity (mm SL - female), SL = spawns/life, MO = number of mature ova. ES = egg size (mm in diameter).

	MS	SM	SL	MO	ES	Reproductive Behavior	Larval Drift Phase
Whiteoak Creek							
E. bison[1]	74	35	3	109	1.4	Burying	Demersal
E. blennius	82	43	2	56	2.1	Burying	Unknown
E. oophylax[2]	84	35	3	178	2.2	Clustering	Demersal
E. smithi	64	31	2	38	2.2	Clustering	Demersal
Both locations							
E. blennioides	166	50	4	228	2.0	Attaching	Pelagic
E. caeruleum	80	28	3	65	1.7	Burying	Demersal
E. flabellare	95	30	2	49	2.4	Clustering	Demersal
E. flavum	71	27	3	141	1.1	Attaching	Epibenthic
N. rufilineatus	98	39	3	77	2.2	Burying	Pelagic
P. caprodes	165	71	3	300	1.2	Burying	Pelagic
Yellow Creek							
E. crossopterum	110	35	3	178	1.8	Clustering	Demersal
E. occidentale[3]	76	44	2	138	1.2	Attaching	Epibenthic

[1] Species information used from *E. spectabile*
[2] Species information other than MS and ES used from *E. crossopterum*
[3] Species information used from *E. atripinne*
Data sources: Cooper (1978), Keevin et al (1989), Bart and Page (1992), Etnier and Starnes (1993), Page and Knouft (2000), Simon and Wallus (2006)

Table 2. Life history categories of recaptured species created for analysis of life history traits with respect to movement during the mark-recapture study at Whiteoak Creek and Yellow Creek, Tennessee. Subgenera (or genus if no subgenus) listed to show that life history categories fall mainly in line with these taxonomic groups. Life history categories are listed in increasing order of reproductive investment.

Life History Category	Species Represented	Genera (G)/Subgenera (SG) Represented
Buriers of small eggs	*Etheostoma caeruleum*	*Oligocephalus* (SG)
Buriers of big eggs	*E. blennius* *Nothonotus rufilineatus*	*Etheostoma* (SG) *Nothonotus* (G)
Attachers (small eggs)	*E. flavum, E. occidentale*	*Ulocentra* (SG)
Clusterer-guarders (big eggs)	*E. crossopterum, E. flabellare, E. oophylax*	*Catonotus* (SG)
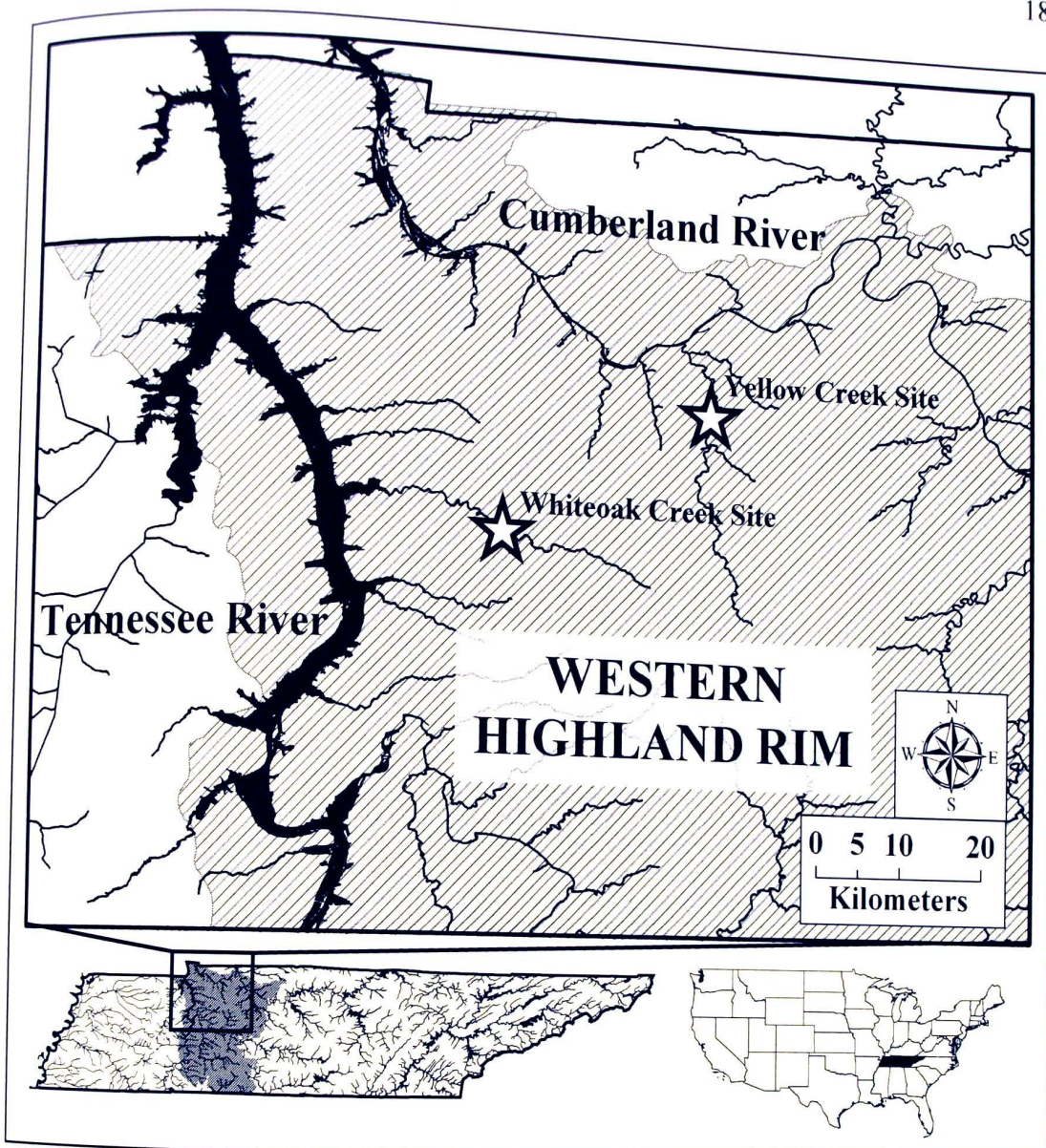
Figure 1. Location of the two study sites, Whiteoak Creek and Yellow Creek, in the north-central portion of Tennessee. Both sites are contained within the Western Highland Rim of the Interior Highlands. Whiteoak Creek is a tributary to the Tennessee River in Humphreys County. Yellow Creek is a tributary to the Cumberland River in Montgomery County.
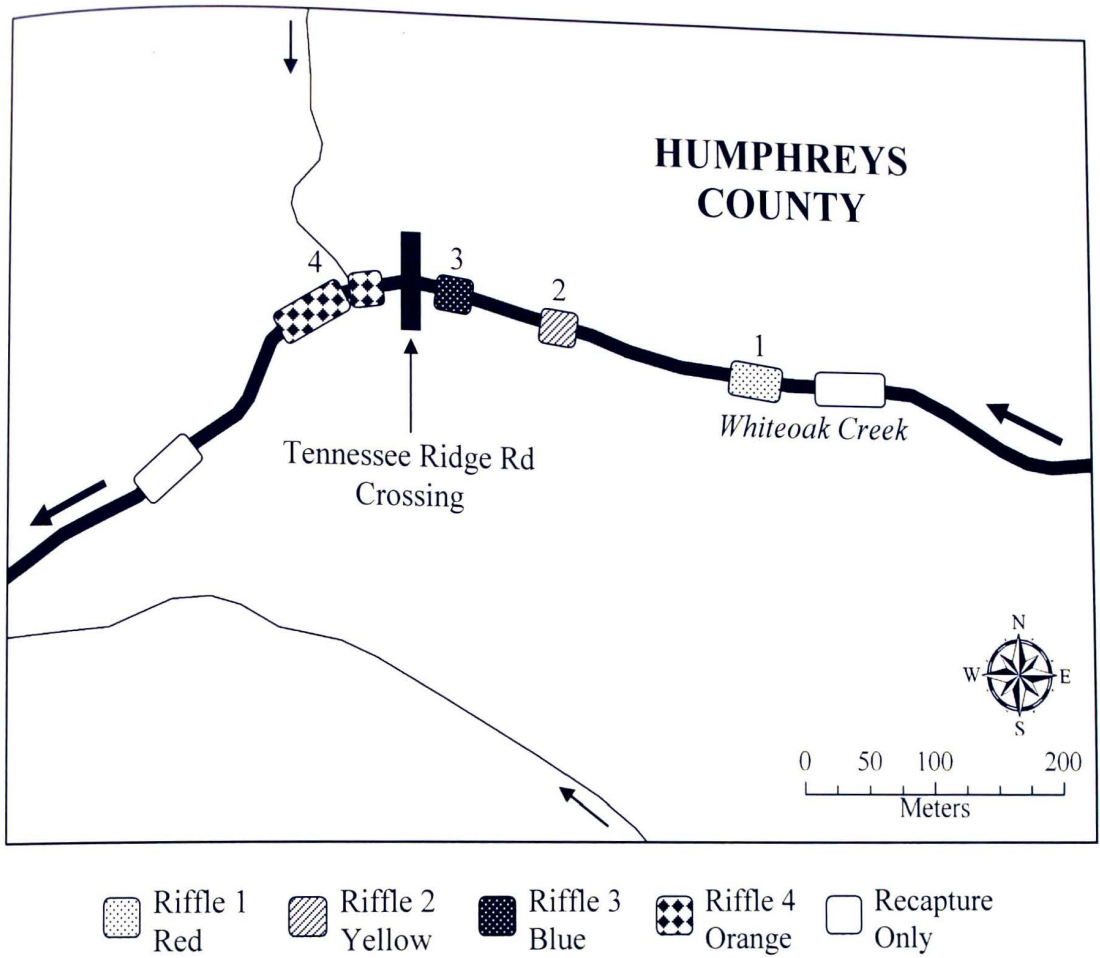
Figure 2. Map of the Whiteoak Creek study site in Humphreys County, Tennessee. Rectangles represent the riffles included in the study. Each of the four interior riffles were assigned a specific color of VIE dye that was used to mark captured fish. The two outer riffles were recapture only riffles. Riffle length (length of boxes) and spacing are to scale. Riffle 1 was not present during the August and December samplings. Arrows indicate direction of stream flow.
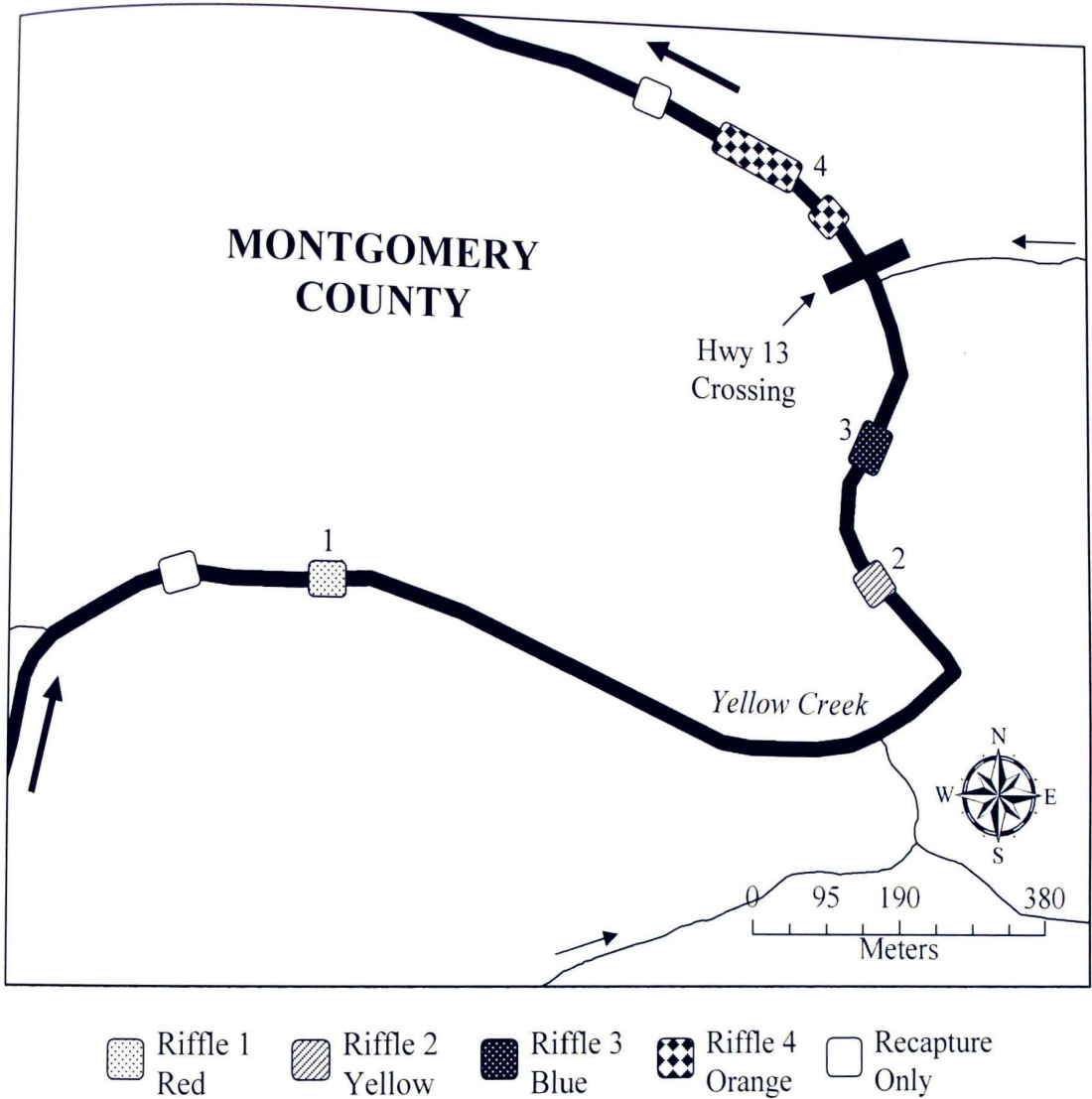
Figure 3. Map of the Yellow Creek study site in Montgomery County, Tennessee. Rectangles represent the riffles included in the study. Each of the four interior riffles were assigned a specific color of VIE dye that was used to mark captured fish. The two outer riffles were recapture only riffles. Riffle length (length of boxes) and spacing are to scale. Arrows indicate direction of stream flow.
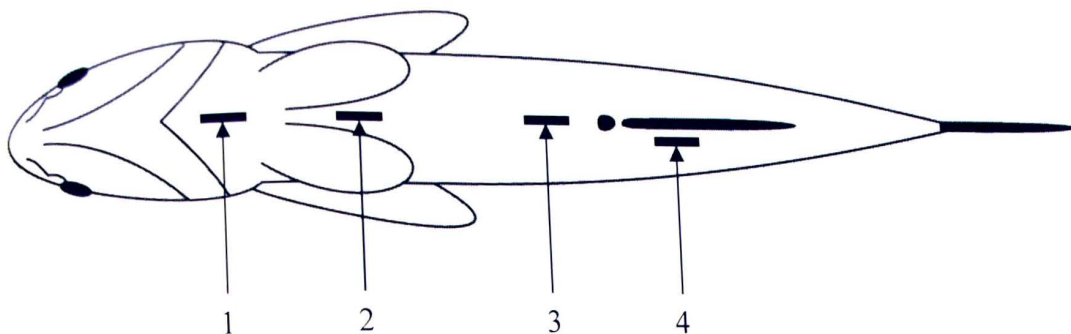
Figure 4. Illustration of marking locations on darters at Whiteoak Creek and Yellow Creek, Tennessee. All marks were made ventrally with VIE. Body location of marks indicated when the darter was marked (1 = February; 2 = April/May; 3 = August; 4 = December). Color of VIE indicated the riffle from which the darter was collected (see Figures 2 and 3).
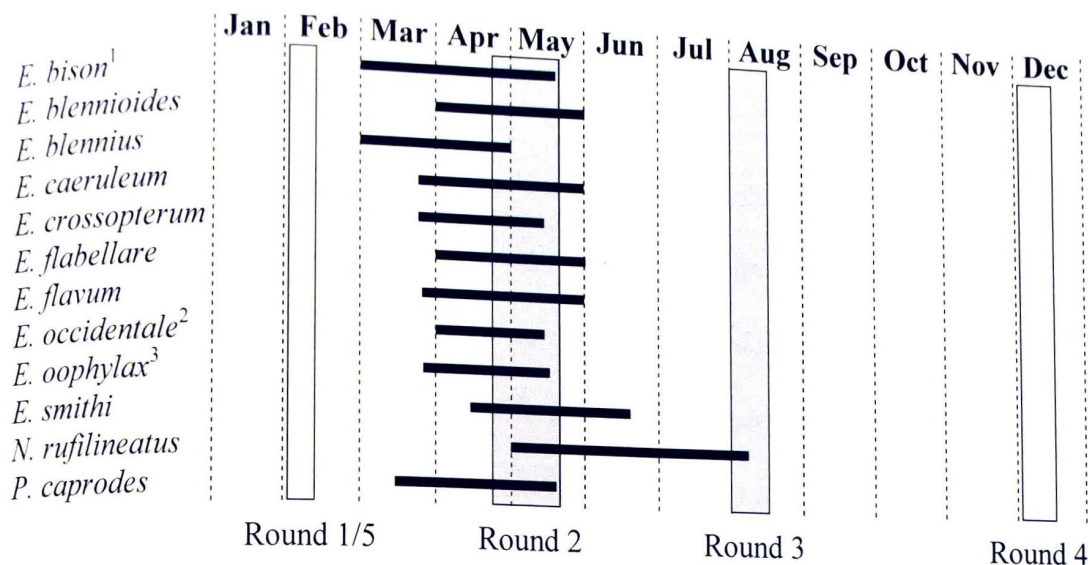
Figure 5. Known spawning periods for the species of darters found during mark-recapture study at Whiteoak Creek and Yellow Creek, Tennessee. Periods between mark-recapture rounds were designated as one of four reproductive seasons (pre-spawning, spawning, post-spawning, or non-spawning) based on the known reproductive season of the species. For all species other than *Nothonotus rufilineatus* (see text), Round 1 to 2 was the spawning season, Round 2 to 3 was post-spawning, Round 3 and 4 was non-spawning, and Round 4 to 5 was pre-spawning. The spawning season for *N. rufilineatus* was between Round 2 and 3, with other seasons shifted accordingly. The three genera represented are *Etheostoma*, *Nothonotus* and *Percina*.

Data source: Etnier and Starnes (1993)

CHAPTER III

Results

Over the course of the study, 10,136 darters, representing 12 species, were marked (Table 3). *Nothonotus rufilineatus* (n = 6,299), *Etheostoma flavum* (n = 1,516), *E. flabellare* (n = 1,137), and *E. caeruleum* (n = 870) comprised the majority of the fishes marked. A total of 849 (8.4%) recaptures from 8 species (2 genera and 4 subgenera) were recorded. Of those recaptures, 573 were marked the previous study period and could be used for the seasonal analyses as described above. Recapture rate was consistently fairly low across most species (4-10%) with the exception of *E. blennius* (35%). Because of the low number of recaptures for other species (*E. occidentale*, *E. crossopterum*, and *E. oophylax*), they were not included in individual species analyses.

Overall movement rate from the riffle of release was 17%. This rate was lowest in *N. rufilineatus* and *E. caeruleum* (both 14%), highest in *E. blennius* (63%), and intermediate in *E. flabellare* and *E. flavum* (27% and 25%, respectively). Of those movements, 27% moved more than one riffle, and average distance moved was 247.1 m. *Etheostoma flabellare* (54.5%) and *E. blennius* (50%) made the most frequent multi-riffle movements, while *N. rufilineatus* (287.0 m) and *E. caeruleum* (293.6 m) had the highest mean distances moved. More females were marked than males ($P < 0.0001$), however the numbers of each sex recaptured were not significantly different ($P = 0.6067$).

Mean distance traveled for darters that moved at Yellow Creek (404.0 m) was significantly greater than at Whiteoak Creek (105.0 m; $P < 0.0001$). This result is likely an artifact of the difference in the length of the two study sites (Schwalb et al., 2011), but is important to note for the additional analyses below. Movement rate was higher at

Whiteoak Creek, but not significantly ($P = 0.0503$). Significant difference ($P < 0.0001$) in corridor length (CL) at the two sites likely contributed to this observed trend, as movements across short distances of unpreferred habitat are presumably successful more frequently than those across long distances of unpreferred habitat. Mean CL over the course of the study was 68.9 m (min = 35.3, max 161.6) at Whiteoak Creek and 301.7 m (min = 63.3, max = 872.7) at Yellow Creek. Variation between sites is shown by species in Table 4.

Variation in movement rate was observed among the reproductive seasons ($P = 0.0028$) with pre-spawning and spawning seasons (both 24%) having roughly twice the rate of movement seen in post-spawning (11%) and non-spawning (13%) seasons (Figure 6); however, no significant difference in the mean distances moved was observed among the reproductive seasons ($P = 0.2289$). An overall trend toward downstream movement was seen (76 downstream, 65 upstream) but was not significant ($P = 0.3543$; Figure 7). Differences in the directional biases were not statistically significant among the reproductive seasons ($P = 0.4883$). The downstream bias in the non-spawning season was significant ($P = 0.0285$). Mean distance traveled in the upstream direction was larger than that in the downstream direction but this difference was not statistically significant ($P = 0.2045$). Further seasonal and directional analysis was performed with respect to other variables and is contained within those sections below.

Movement with respect to size and sex

Mean distances moved across all species did not differ significantly between sexes overall ($P = 0.4713$). However, when examining the data by reproductive season,

mean distance traveled by males was significantly greater than females during the pre-spawning season ($P = 0.0348$; Figure 8). Males also tended to travel greater distances in the spawning season but this difference was not significant ($P = 0.0517$). Movement rates did not differ between sexes overall ($P = 0.6215$) or within reproductive seasons (Figure 9). Directional ratios of movement between sexes were also not significant ($P = 0.1980$) nor were the directional biases of females (59% downstream, $P = 0.1176$) and males (51% upstream, $P = 0.8137$).

Overall, there was no significant relationship between movement rate and darter size (TL; $P = 0.6851$). During the pre-spawning season, however, larger darters tended to move more frequently ($P < 0.0001$), and post-spawning smaller darters moved more frequently ($P = 0.0095$; Figure 10). Mean distance moved did not significantly relate to darter size overall ($P = 0.6803$) or within reproductive seasons. Furthermore, no relation was found between total length and direction of movement ($P = 0.5041$).

Movement with respect to abiotic variables

Riffle size varied throughout the study with the largest values in April/May and the smallest in August (Table 5). Riffles at Yellow Creek were typically wider and longer than those at Whiteoak Creek, but depths were similar. Due to the ever-changing nature of streams, a few notable variations occurred throughout the study. The furthest upstream marking riffle (see Figure 2, red riffle) at Whiteoak Creek disappeared as a riffle for the August and December recapture events but reappeared, slightly upstream, during the February 2012 recapture. Additionally, on multiple occasions, original riffles at both sites had new riffle habitats appear that were connected by short runs. In these circumstances

the total riffle habitat was sampled and measured, excluding the intervening run habitat. A significant, positive relationship was seen between distance moved and riffle area stability (RAS; $r^2 = 0.14$, $P = 0.0001$). Logistic regression of movement rate by RAS was positive but was not significant ($P = 0.0861$). Finally, as RAS decreased, darters were more likely to move upstream, while as RAS increased darters were more likely to move downstream ($P = 0.0061$).

Similarly to riffles, corridors were largest in April/May with respect to depth and width (Table 6). However, as riffle lengths increased during this period, corridor lengths decreased. Pool measurements were not taken at Yellow Creek for the December sample nor at either site for the February 2012 sample due to low temperatures and the depth and time in the water required to take the measurements. No relationship was seen between movement rates and either average corridor depth (ACD) or maximum corridor depth (MCD; $P = 0.2797$ and $P = 0.6266$, respectively). A non-significant trend ($P = 0.0588$) toward greater movement rate with increased average corridor width (ACW) was observed. Because of site variation with respect to study site length (allowing for longer distances to be recorded at Yellow Creek) and size of stream, distance analysis with respect to corridor variables was conducted independently for each site. Only depth measures at Yellow Creek showed significant linear regressions with distance moved. However, ACD was negatively related to distance moved ($r^2 = 0.15$, $P = 0.0393$) while MCD was positively related to distance moved ($r^2 = 0.14$, $P = 0.0450$).

Discharge at the Ellis Mills USGS gaging station on Yellow Creek varied significantly among seasons ($P < 0.0001$). Average maximum daily discharge was

greatest in the spring (561 cfs), intermediate in winter (248 cfs), and smallest in fall (73 cfs) and summer (56 cfs; Figure 11).

Movement with respect to biotic variables

Congeneric density (CGD) varied by season and site (Table 7). Both sites had the lowest CGD in April/May, and highest in August at Yellow Creek and in December at Whiteoak Creek. Logistic regression showed that as CGD increased, darters were more likely to move ($P = 0.0030$). This trend was particularly strong during the post-spawning season ($P < 0.0001$) while other seasons showed no significant trend. The positive relationship between CGD and movement rate was seen in three of the four life history categories (buriers of both big and small eggs and attachers) although only significantly so in buriers with big eggs ($P = 0.0093$). CGD appeared to have no affect on movement rate in clusterer-guarders ($P = 0.9834$). Mean CGD varied significantly between sites ($P < 0.0001$); therefore, sites were analyzed independently with respect to distance moved. No significant relationships, however, were observed between CGD and distance moved.

Several piscivorous species of fish were encountered during snorkeling surveys to assess predator density including *Micropterus salmoides*, *M. punctulatus*, *M. dolomieu*, *Ambloplites rupestris*, *Lepisosteus osseus*, *Pylodictus olivaris*, *Ictalurus punctatus*, *Lepomis cyanellus*, *L. macrochirus*, *L. megalotis*, and *L. microlophus*. Corridor predator density (CPD) was similar in both seasons recorded at Yellow Creek but was notably higher in August than in April at Whiteoak Creek (Table 7). Overall relationships between CPD and distance moved, and CPD and movement rate were not significant ($r^2 = 0.01$, $P = 0.4085$ and $P = 0.1658$, respectively). CPD did, however, influence

movement rate within the life history categories. Attachers were more likely to move (or had more frequent successful movement) across corridors with low CPD ($P = 0.0047$). Other life history categories showed the opposite trend, but because of low sample sizes it was significant only in buriers of big eggs ($P = 0.0185$).

Movement with respect to life history characteristics

Variations in movement rates among the life history categories were not significant ($P = 0.0741$); however, movement rate was higher in life history categories with increased reproductive investment (i.e., attachers and clusterer-guarders; Figure 12). Additional trends appear when looking at this data by reproductive season (Figure 13). The same positive relationship between movement rate and reproductive investment is seen in the pre-spawning and post-spawning seasons ($P = 0.0365$ and $P = 0.0022$), while the inverse relationship was observed in the spawning season ($P = 0.2426$). All life history categories had low movement rates during the non-spawning period ($P = 0.8956$). Seasonal trends in the movement rates varied among life history categories (Figure 14). Buriers of both egg sizes had highest movement rates during the spawning season. Attachers had the highest rate of movement in the post-spawning season and clusterer-guarders had the highest rate in the pre-spawning season. Variation in movement rates among reproductive seasons was significant in buriers of big eggs and attachers ($P = 0.0002$ and $P = 0.0334$, respectively).

When darters did move, mean distance moved ($P = 0.0012$) and direction ($P = 0.0402$) varied significantly among life history categories. While movement rate increased with increasing reproductive investment, distance moved was greater in darters

exhibiting less reproductive investment (Figure 15). A trend in directional bias was also seen with respect to reproductive investment (Figure 16). Buriers had a slight downstream bias over the course of the study, which was significant in those that bury large eggs ($P = 0.0477$). Attachers had a slight upstream bias (57%) and cluster-guarders exhibited a significant upstream bias (82%; $P = 0.0348$).

Darters with pelagic larval drift phases moved greater distances on average than those with epibenthic or demersal phases ($P = 0.0001$; Figure 17) Movement rate also varied significantly among the larval drift phases ($P = 0.0273$). Darters with epibenthic larvae moved most frequently (24%) and those with pelagic larvae moved least frequently (14%; Figure 18). The post-spawning season was the only season for which there was a significant difference among the phases ($P = 0.0002$). During this season, the epibenthic category exhibited an especially high movement rate (75%) and the pelagic category a particularly low rate (3%; Figure 19). Because of these extreme values during the post-spawning season, epibenthic and pelagic categories had significant variation in movement among seasons ($P = 0.0334$ and $P < 0.0001$) while the demersal category did not ($P = 0.8342$). With increasing susceptibility to downstream drift as larvae, a shift from an upstream bias to a downstream bias was observed in the movements of the adult darters ($P = 0.0503$; Figure 20). The downstream bias observed in darters with pelagic larvae was significant ($P = 0.0350$).

Table 3. Number of marked and recaptured darters and basic movement data for each species collected during mark-recapture study at Whiteoak Creek and Yellow Creek, Tennessee. The three genera represented are *Etheostoma*, *Nothonotus* and *Percina*. Species are listed in order of number of recaptures.

	Number Marked	Number Recaptured (%)	Number Moved (%)	Percent Multi-Riffle Movement	Mean Distance Moved (m)
N. rufilineatus	6,299	650 (10)	90 (14)	21.1	287.0
E. flavum	1,516	84 (6)	21 (25)	23.8	184.1
E. caeruleum	870	49 (6)	7 (14)	28.6	293.6
E. flabellare	1,137	41 (4)	11 (27)	54.5	133.5
E. blennius	55	19 (35)	12 (63)	50.0	134.4
E. occidentale	187	4 (2)	0 (0)	-	-
E. crossopterum	6	1 (17)	0 (0)	-	-
E. oophylax	12	1 (8)	0 (0)	-	-
E. bison	1	0	-	-	-
E. blennioides	40	0	-	-	-
E. smithi	4	0	-	-	-
P. caprodes	9	0	-	-	-
Totals	10,136	849 (8)	141 (17)	27.0	247.1

Table 4. Movement frequency and mean distance moved for darter species examined at each study site, Whiteoak Creek and Yellow Creek, to show variation between the two sites. The difference in mean distances traveled between the two sites was significant ($P < 0.0001$) but was not significant for movement frequency ($P = 0.0503$).

	Whiteoak Creek		Yellow Creek	
	Percent Movement	Mean Distance Moved	Percent Movement	Mean Distance Moved
Nothonotus rufilineatus	12.7	106.2	14.5	377.4
Etheostoma flavum	28.8	65.7	16.0	686.9
E. caeruleum	12.5	96.1	17.7	557.0
E. flabellare	31.4	133.5	0.0	-
E. blennius	63.2	134.4	-	-
E. oophylax	0.0	-	-	-
E. crossopterum	-	-	0.0	-
E. occidentale	-	-	0.0	-
Overall	**19.4**	**105.0**	**14.4**	**404.0**

Table 5. Physical measurements of riffle habitats at the study sites for each of the five mark-recapture events.

	Width (m)	Length (m)	Area (m²)	Depth (m)
Whiteoak Creek				
February 2011	16.1	24.3	377.8	0.39
April 2011	18.3	29.7	533.7	0.55
August 2011	6.7	22.0	204.8	0.20
December 2011	13.7	22.0	379.9	0.31
February 2012	16.0	21.2	298.0	0.24
Averages	*14.1*	*23.8*	*358.8*	*0.34*
Yellow Creek				
February 2011	17.9	51.2	882.2	0.39
May 2011	23.5	61.8	1359.4	0.38
August 2011	10.3	31.6	338.0	0.33
December 2011	14.7	44.4	761.0	0.34
February 2012	14.0	41.1	406.9	0.28
Averages	*16.1*	*46.0*	*749.5*	*0.34*

Table 6. Physical measurements of corridors at the study sites. Measurements were not completed for all seasons due to low water temperatures.

	Average Depth (m)	Maximum Depth (m)	Average Width (m)	Length (m)
Whiteoak Creek				
April 2011	0.72	1.48	18.8	53.3
August 2011	0.57	1.28	15.0	83.1
December 2011	0.89	1.43	18.5	79.8
Averages	*0.73*	*1.39*	*17.4*	*72.1*
Yellow Creek				
May 2011	1.18	2.94	24.0	284.5
August 2011	1.09	2.37	23.7	308.6
December 2011	-	-	-	-
Averages	*1.14*	*2.65*	*23.8*	*296.5*

Table 7. Congeneric densities of darters in riffles and predator densities of corridors at Whiteoak Creek and Yellow Creek, Tennessee, during the course of the mark-recapture study. Predator density assessment, conducted via snorkeling, was not completed during the winter months due to low water temperatures.

	Total Darters	Total Riffle Area (m^2)	Darter Density (fish/m^2)	Total Predators	Total Corridor Area (ha)	Predator Density (fish/ha)
Whiteoak Creek						
February 2011	707	1,511.0	0.468	-	-	-
April 2011	813	2,134.9	0.381	43	0.50	85.6
August 2011	394	819.4	0.481	214	0.50	430.2
December 2011	1,003	1,519.6	0.660	-	-	-
Yellow Creek						
February 2011	2,563	3,528.8	0.726	-	-	-
May 2011	1,319	5,437.4	0.243	697	3.42	204.1
August 2011	1,149	1,351.9	0.850	688	3.65	188.4
December 2011	2,188	3,043.8	0.719	-	-	-
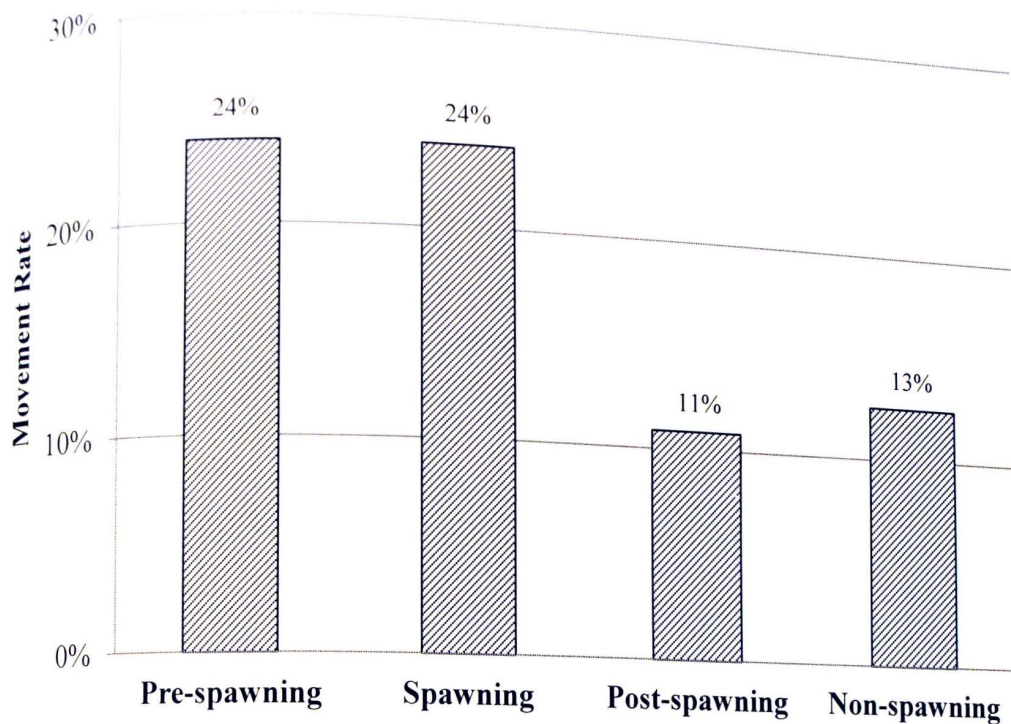
Figure 6. Movement rate (% found in riffle other than that of release) by reproductive season of darters at Whiteoak Creek and Yellow Creek, Tennessee. Differences in the movement rates were significant among the four reproductive seasons ($P = 0.0028$).
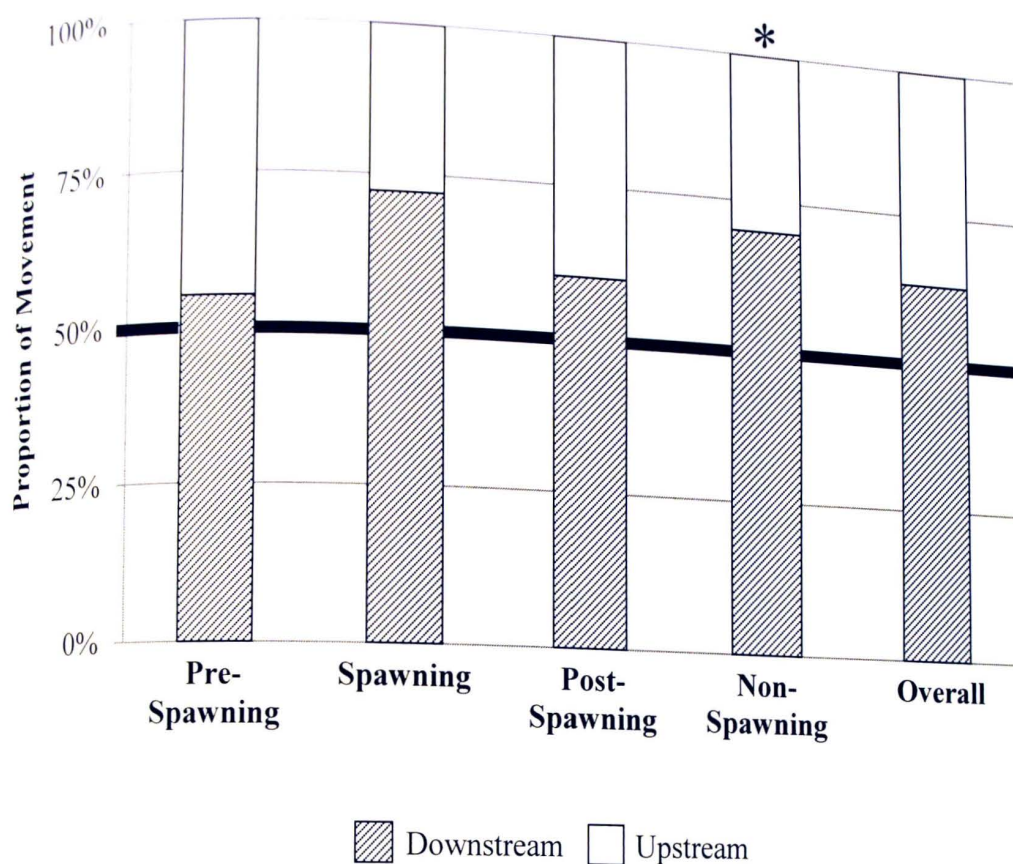
* Significant directional bias in individual ratio ($P < 0.05$)

Figure 7. Directional movement for each reproductive season and overall for darters at Whiteoak Creek and Yellow Creek, Tennessee. The 50% gridline is bolded and is the point at which upstream and downstream movements were equal. No significant variation was observed in the direction moved among the seasons ($P = 0.4883$).
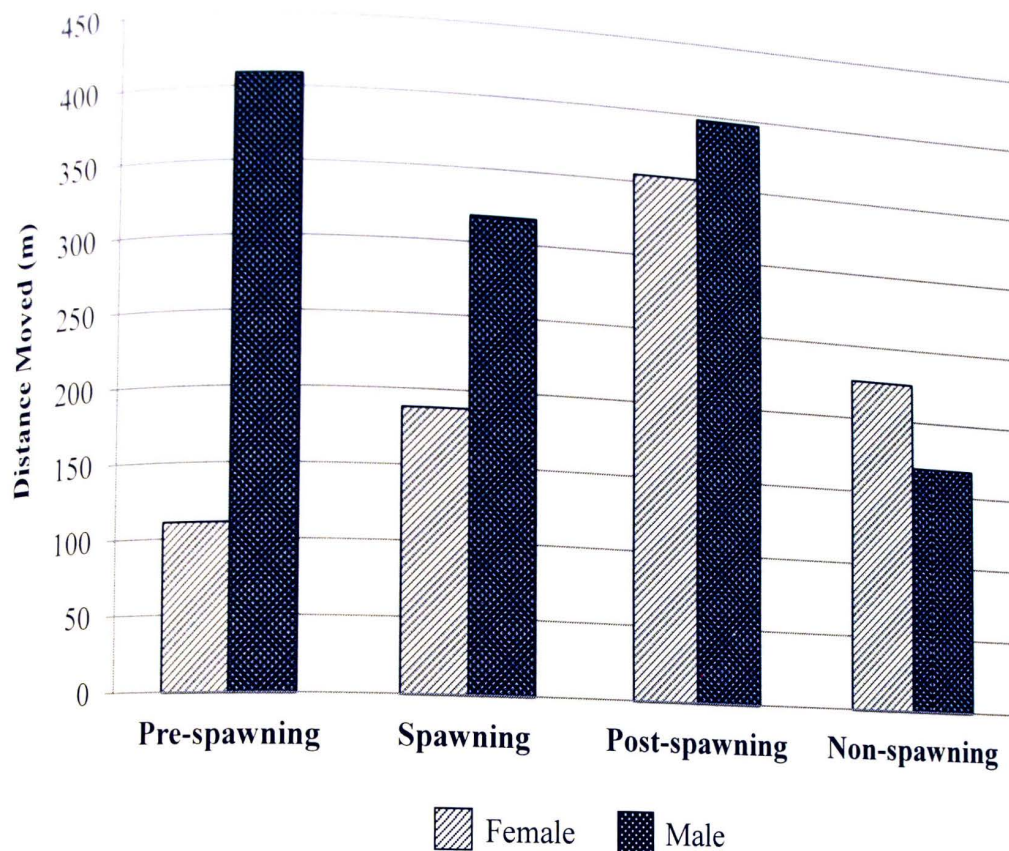
* $P < 0.05$ within reproductive season

Figure 8. Mean distances moved (m) between sexes within reproductive seasons of darters at Whiteoak Creek and Yellow Creek, Tennessee. No significant difference was observed between the sexes in overall distances moved ($P = 0.4713$).
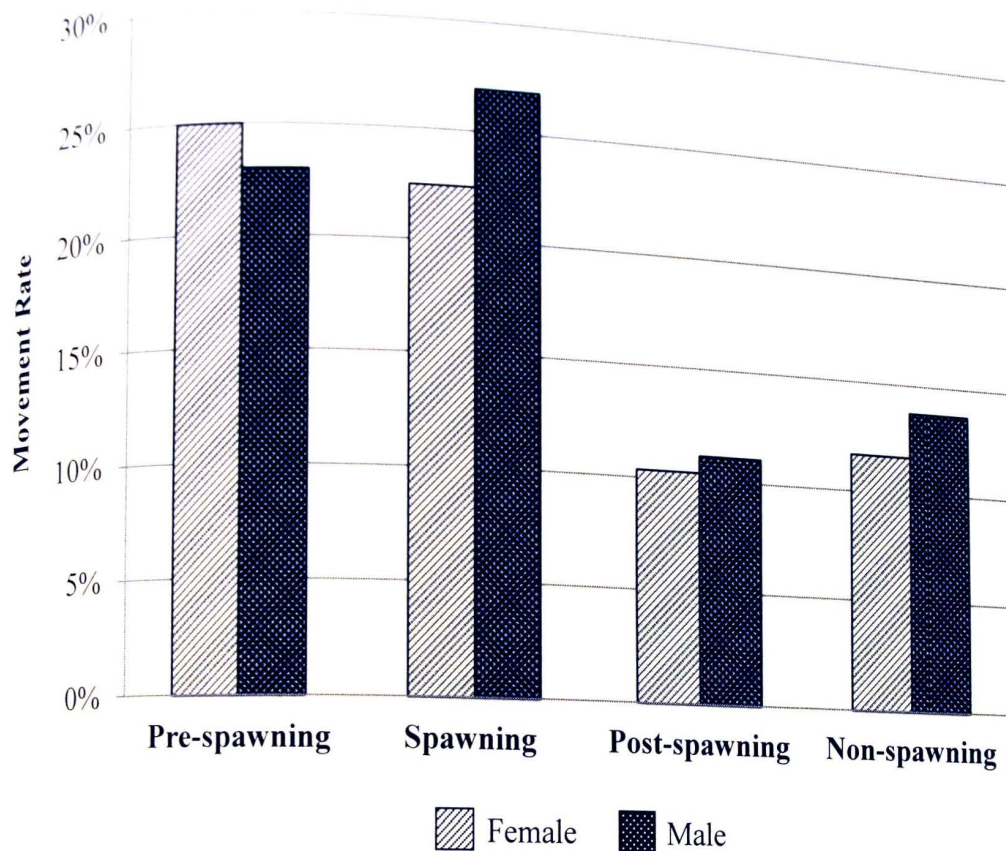
Figure 9. Movement rates (% found in riffle other than that of release) between sexes within reproductive seasons of darters at Whiteoak Creek and Yellow Creek, Tennessee. No significant difference was observed between the movement rates of males and females overall ($P = 0.6125$) or between the sexes within the reproductive seasons.
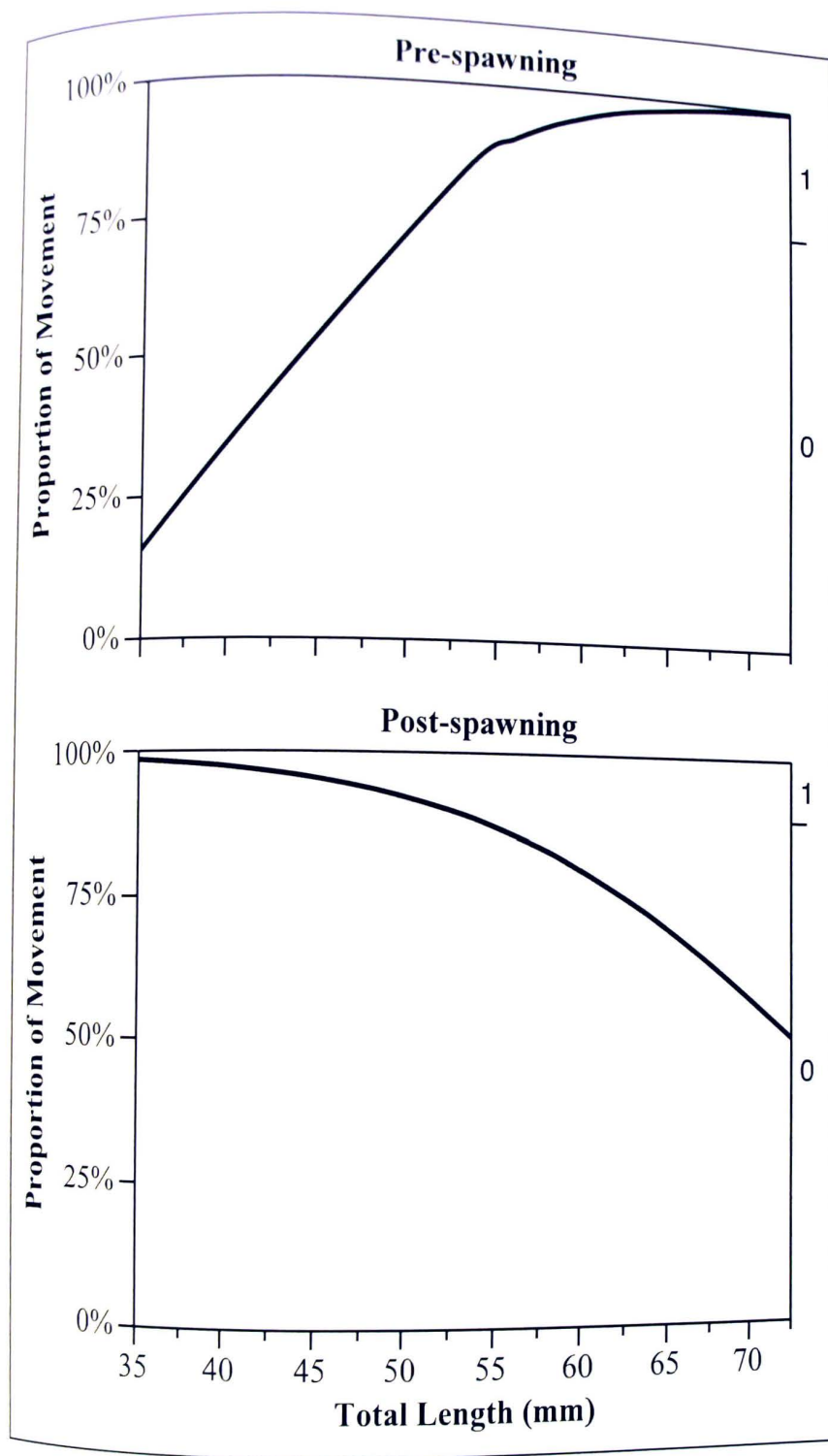
Figure 10. Logistic regression of movement rate (% found in riffle other than that of release) and total length of darters during the pre-spawning and post-spawning seasons at Whiteoak Creek and Yellow Creek, Tennessee ($P < 0.0001$ and $P = 0.0095$, respectively).
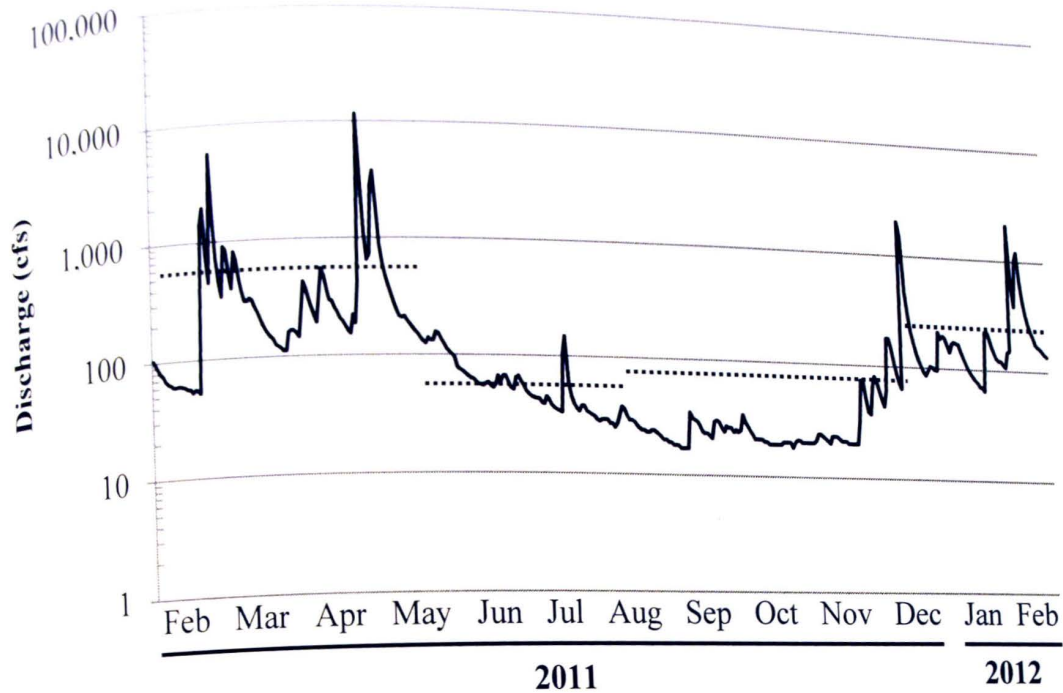
Figure 11. Maximum daily discharge values at Ellis Mills USGS gaging station, located 5.2 river kilometers upstream from the Yellow Creek study site. Mean discharge over each recapture period is indicated by horizontal dotted line. Vertical axis is displayed in base 10 logarithmic scale. Data obtained from USGS (2012).
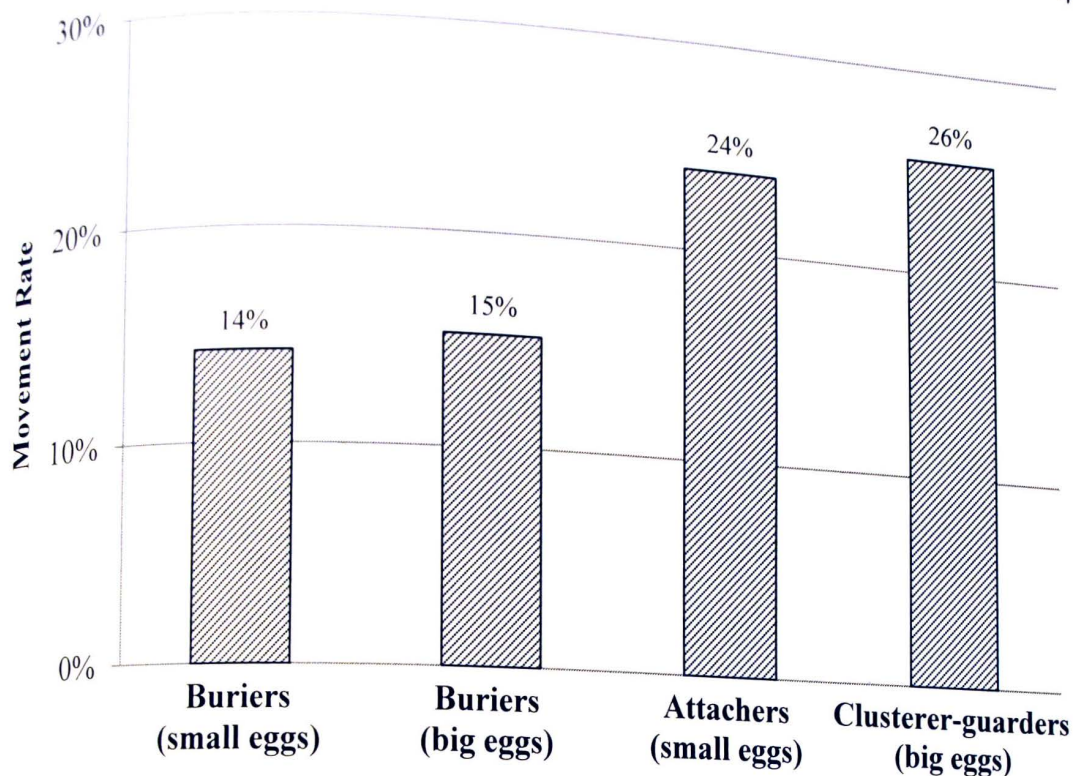
Figure 12. Movement rate (% found in riffle other than that of release) by life history categories of darters at Whiteoak Creek and Yellow Creek, Tennessee. Life history categories are displayed in increasing order of reproductive investment to show the trend of increasing movement rate with increased investment. The difference among the four categories was not significant ($P = 0.0741$).

* No data
** $P < 0.05$ within reproductive season
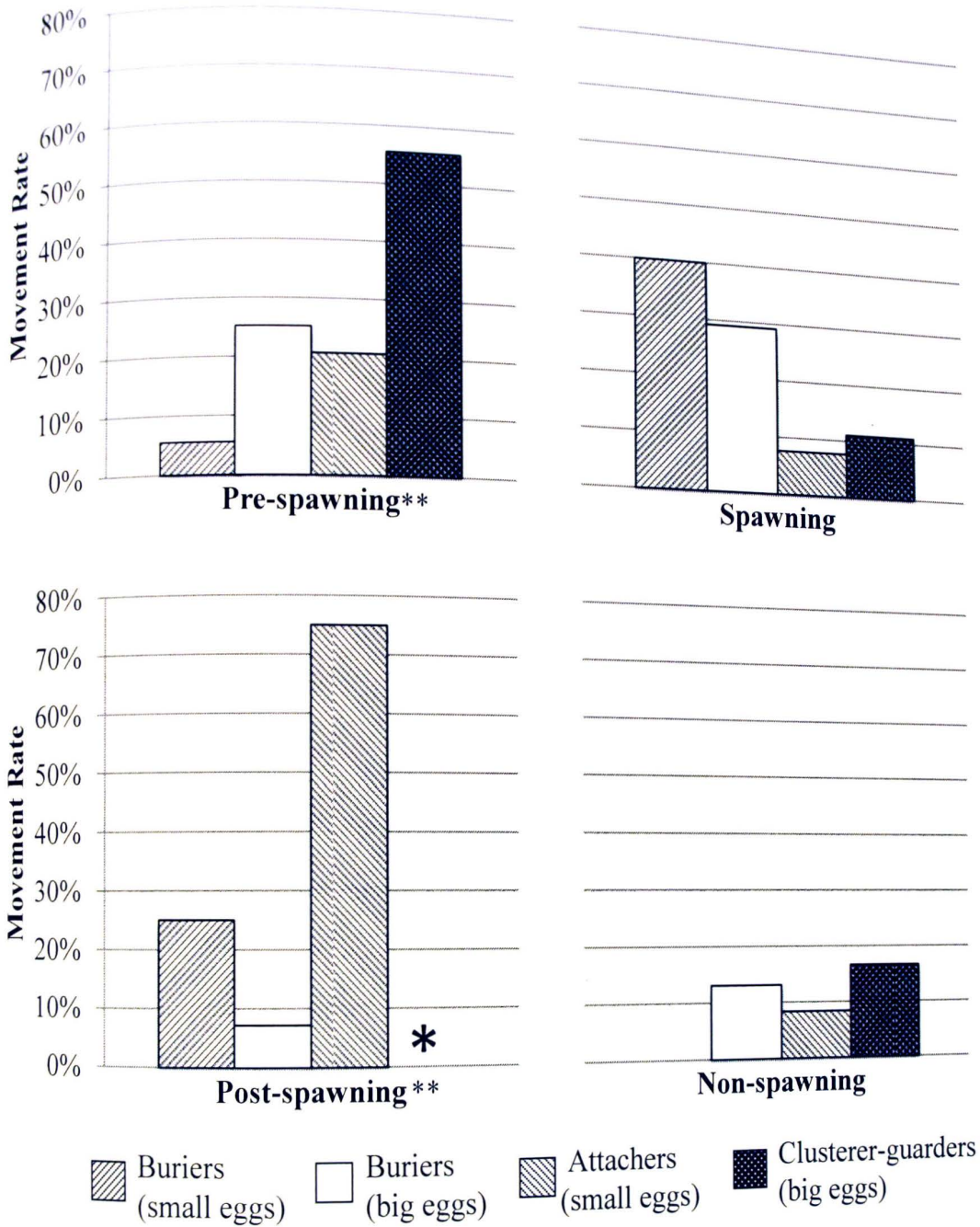
Figure 13. Movement rates (% found in riffle other than that of release) within life history categories by reproductive seasons of darters at Whiteoak Creek and Yellow Creek, Tennessee. Life history categories are displayed in increasing order of reproductive investment to show the relationship of movement rate and reproductive investment within each season.
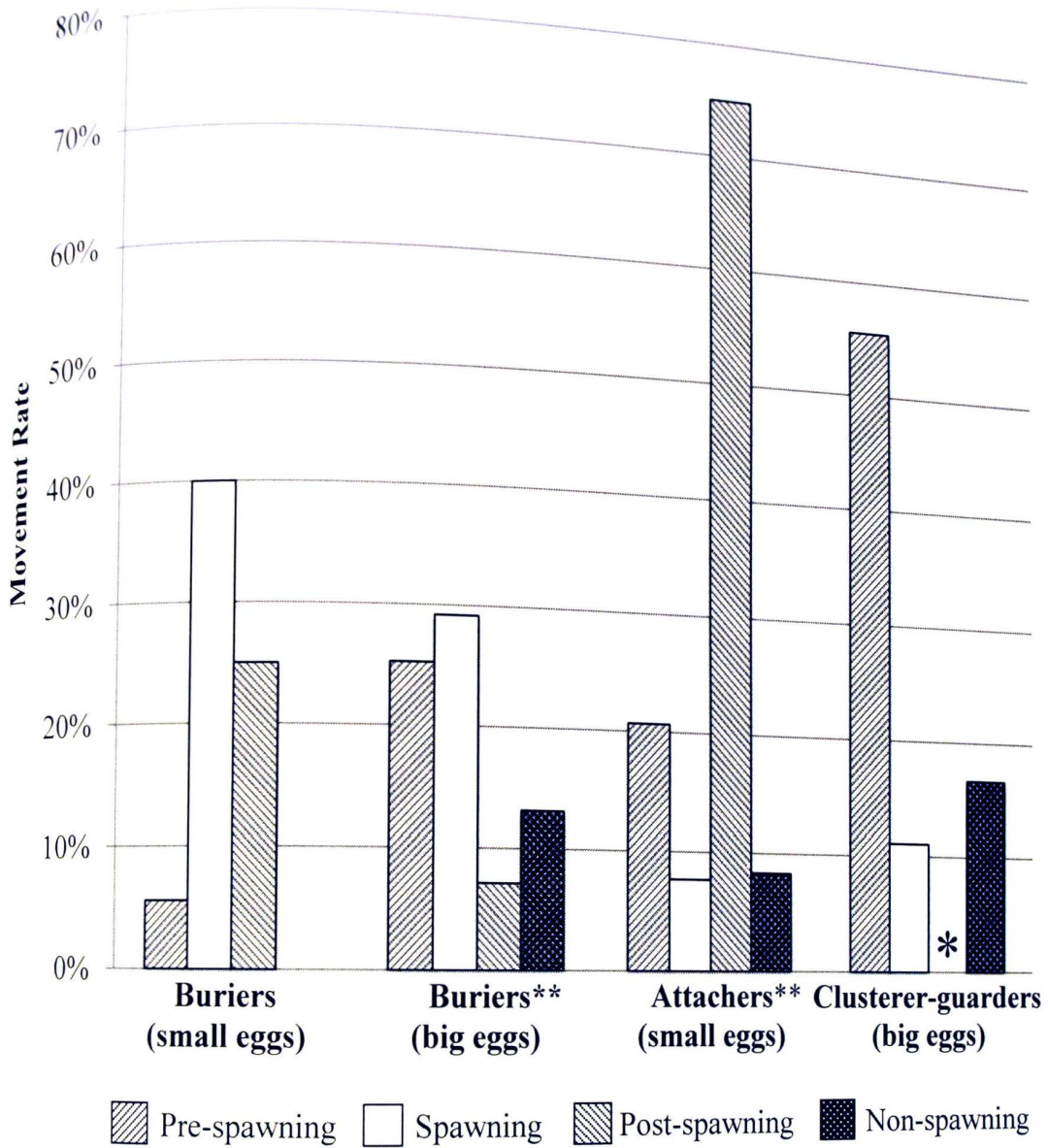
* No data
** $P < 0.05$ within life history category

Figure 14. Movement rates (% found in riffle other than that of release) within reproductive seasons grouped by life history categories of darters at Whiteoak Creek and Yellow Creek, Tennessee.
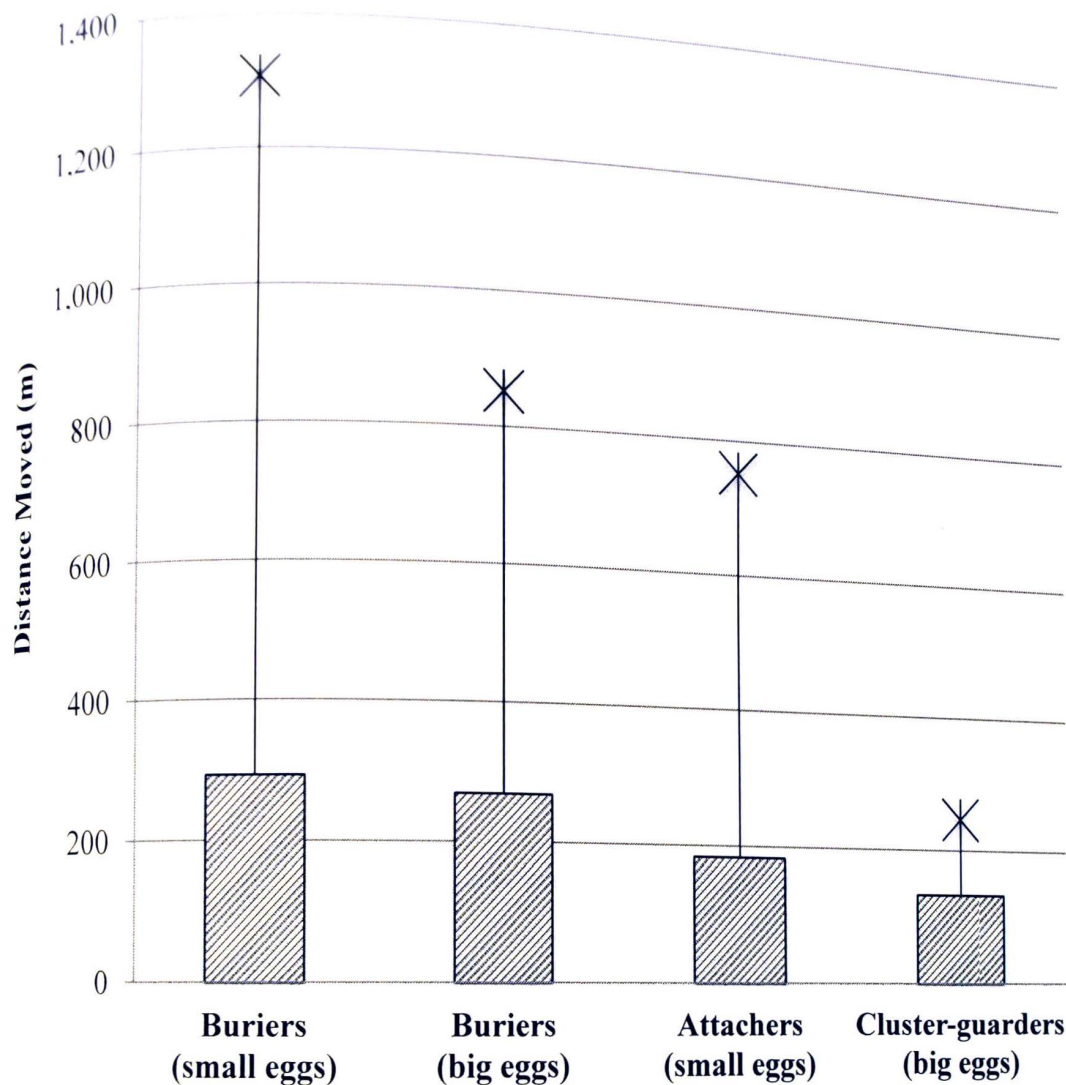
Figure 15. Mean distances moved (m; columns) within life history categories of darters at Whiteoak Creek and Yellow Creek, Tennessee. Asterisks and upbars indicate the 90% quantile for each category. Differences in means among the life history categories were significant ($P = 0.0012$). Life history categories are displayed in increasing order of reproductive investment to show the trend of decreasing distance moved with increased reproductive investment.
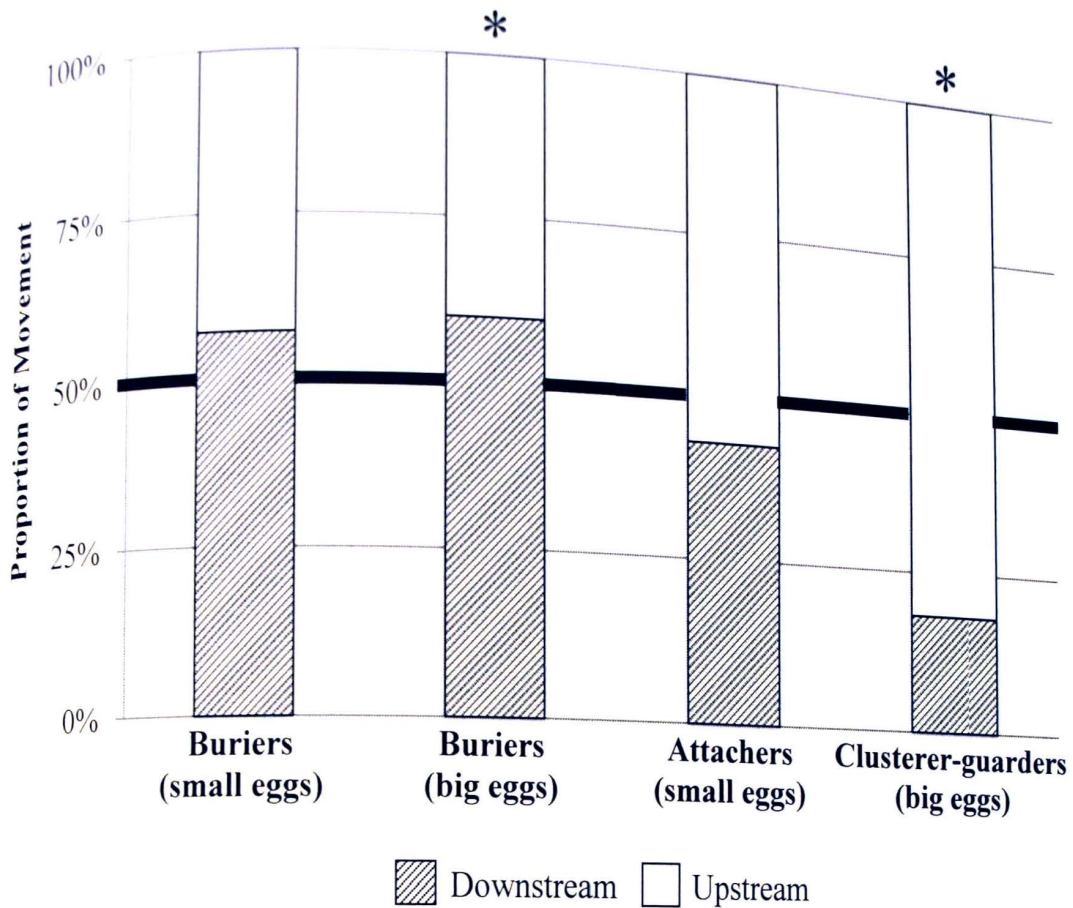
* Significant bias in individual ratio ($P < 0.05$)

Figure 16. Directional movement for each life history category of darters at Whiteoak Creek and Yellow Creek, Tennessee. The 50% gridline is bolded and is the point at which upstream and downstream movements were equal. Variation in the ratios among the life history categories was significant ($P = 0.0402$). Life history categories are displayed in increasing order of reproductive investment to show the relationship between directional bias and reproductive investment.
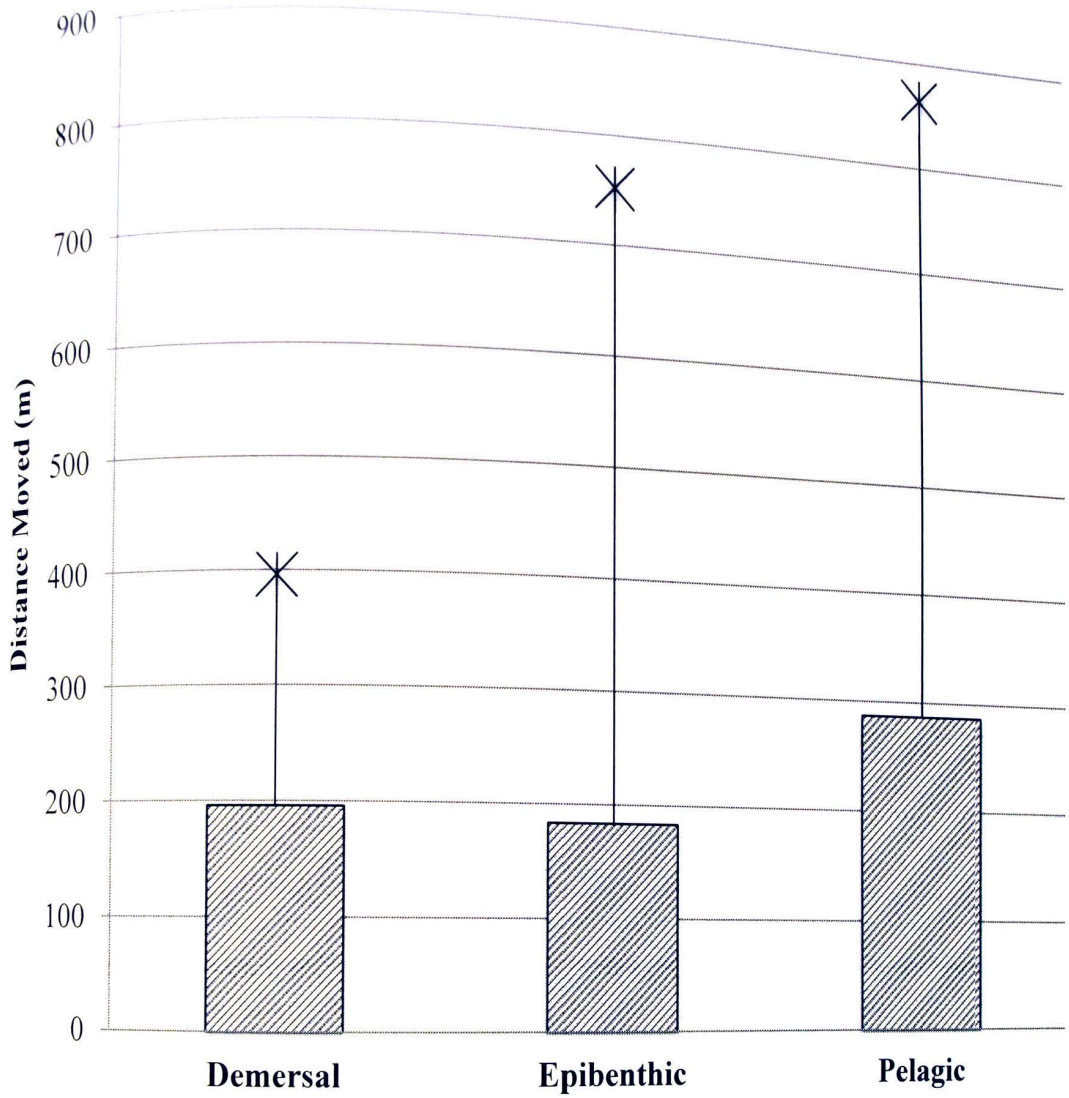
Figure 17. Mean distances moved (m; columns) within larval drift phases of darters at Whiteoak Creek and Yellow Creek, Tennessee. Asterisks and upbars indicate the 90% quantile for each phase. Differences in means among the larval drift phases were significant ($P = 0.0001$). Phases are displayed in increasing order of susceptibility to downstream drift as larvae to show the trend of increasing distance moved with increased susceptibility to downstream drift.
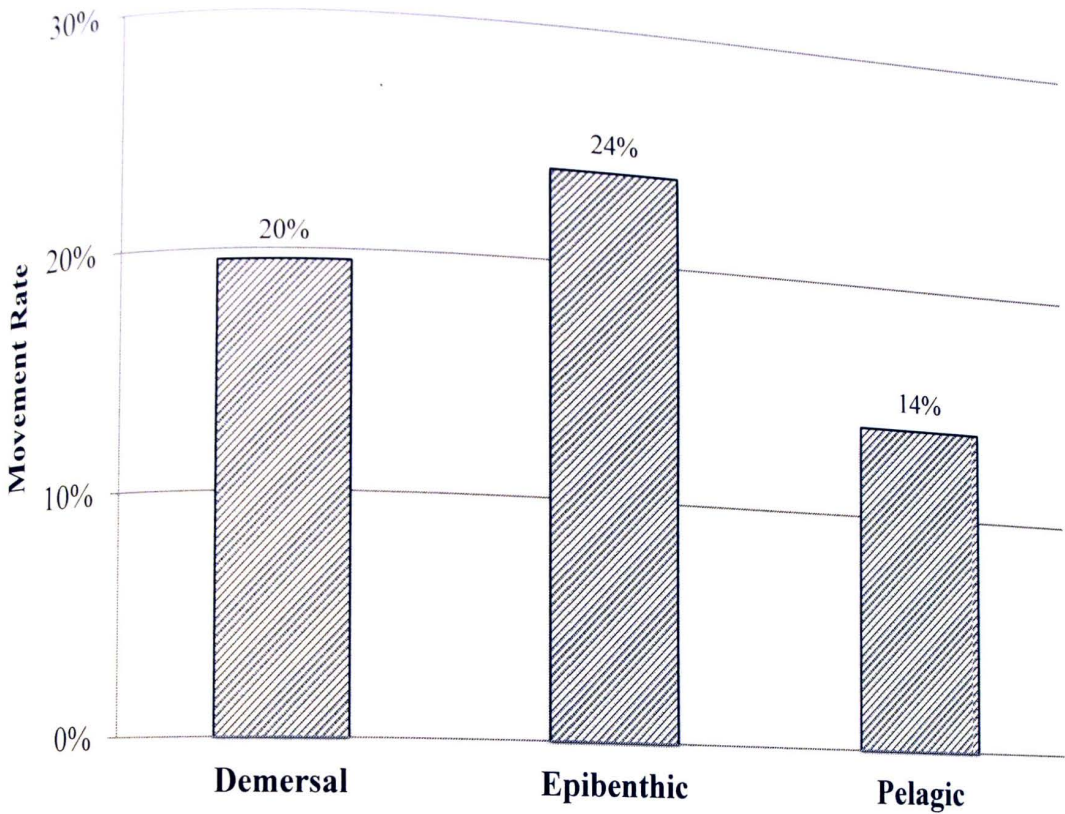
Figure 18. Movement rate (% found in riffle other than that of release) by larval drift phase of darters at Whiteoak Creek and Yellow Creek, Tennessee. Phases are displayed in increasing order of susceptibility to downstream drift as larvae to show the trend of decreasing movement rate with increased susceptibility to downstream drift. The differences among the three larval drift phases were significant ($P = 0.0273$).
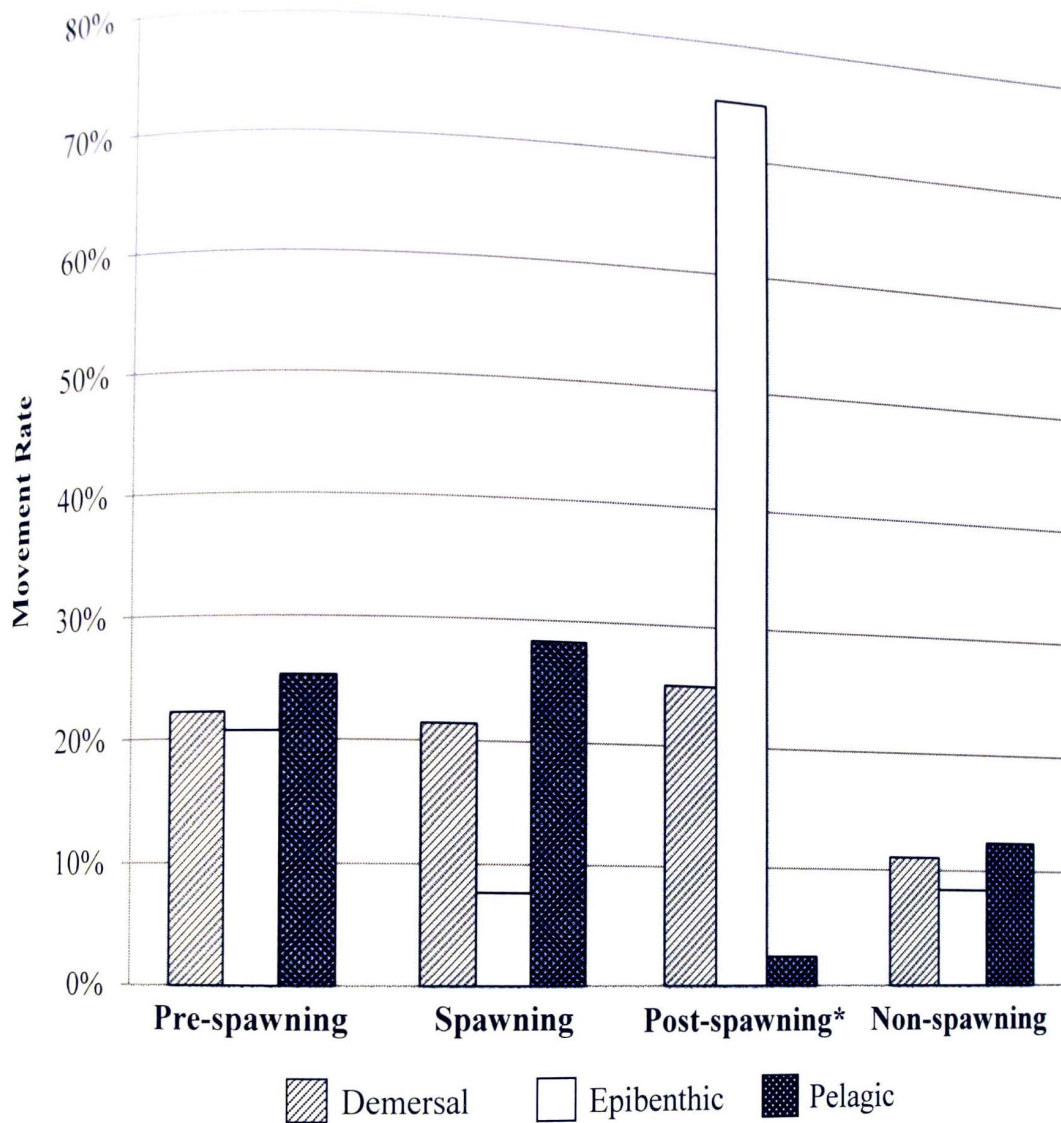
* $P < 0.05$ within reproductive season

Figure 19. Movement rates (% found in riffle other than that of release) within darter larval drift categories by reproductive seasons at Whiteoak Creek and Yellow Creek, Tennessee. Larval drift categories are displayed in increasing order of susceptibility to downstream drift as larvae to show the relationship between movement rate and larval drift within each season.
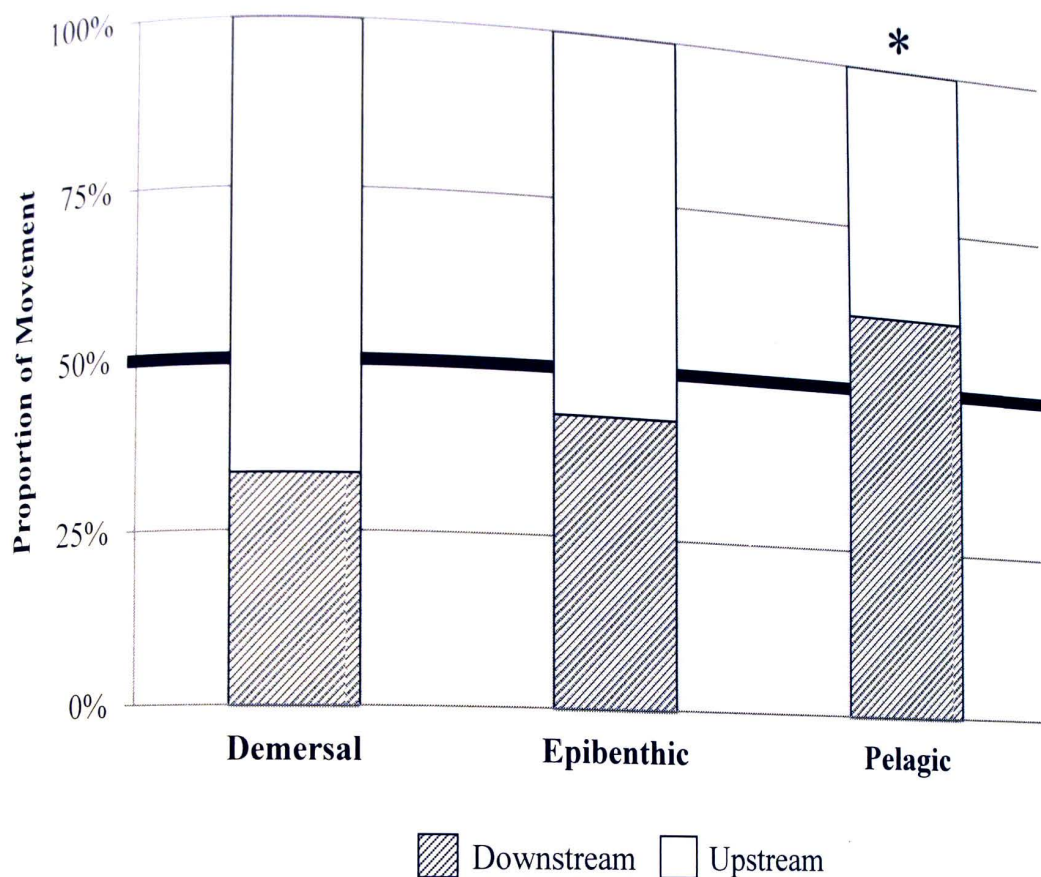
* Significant bias in individual ratio ($P < 0.05$)

Figure 20. Directional movement distributions for each larval drift phase of darters at Whiteoak Creek and Yellow Creek, Tennessee. The 50% gridline is bolded and is the point at which upstream and downstream movements were equal. Variation in the ratios among the larval drift categories was not significant ($P = 0.0503$). Larval drift categories are displayed in increasing order of susceptibility to downstream drift as larvae to show the relationship between directional bias and larval drift phase.

CHAPTER IV

Discussion

The movements of stream fishes have generally been found to be restricted, with few individuals making long distance dispersals or migrations (Gerking, 1953; Hill and Grossman, 1987; Smithson and Johnston, 1999; Petty and Grossman, 2004). This trend also applies to small, benthic fishes such as darters (reviewed in Schwalb et al., 2011). Of the few darter movement studies published, most darter movement studies have been restricted to single species, eliminating the opportunity to assess variation in movement associated with differences in life history strategies. Additionally, almost no seasonal movement studies have been conducted, and single seasons studies are almost exclusively conducted in the summer or fall, further limiting our knowledge of these highly imperiled fishes. This represents the first study on the seasonal movements of multiple darter species with various life history strategies.

Frequency of movement (16.6%) recorded in this study was higher than most previous studies of darters. The movement rate was even higher than expected when the sizes of the study sites are considered. Whiteoak Creek and especially Yellow Creek are larger streams than those used in most previous studies. Larger streams tend to have increased corridor lengths between preferred riffle habitats, which should decrease frequency of movement (Slack et al., 2004). Although not significant, Whiteoak Creek was composed of much shorter corridors and darters moved more frequently at this site than at Yellow Creek as predicted.

The overall higher rate of movement observed in this study may, in part, be due to the inclusion of multiple seasons. Ingersoll et al. (1984) performed one of the only

spring-based studies with darters and found a 22.7% movement rate, substantially higher than a similar fall-based study by Mundahl and Ingersoll (1983) that had a movement rate of 3.8%. Substantial increased movement in the pre-spawning and spawning seasons of this study coincide with these findings, and further highlight the importance of examining movement across all seasons. Furthermore, like in other multi-species darter studies (Reed. 1968: Roberts and Angermeier, 2007b), movement rates varied widely among species. demonstrating the significance of studying multiple species.

The low recapture rates in most movement studies (including this one) leaves a large portion of the movements (or non-movements) of a population unknown. This portion of the population is made up of an unknown number of fish that have 1) left the study site. 2) evaded capture within the study site, or 3) died. Roberts and Angermeier (2007b) contended that mortality rates and sampling efficiency accounted for a large portion of the non-recaptured fish in their study. While this study may have had reduced sampling efficiency due to larger stream sizes, recapture rates were also notably smaller. Supporting the idea of emigration, the detected maximum distance traveled by darters depends on the spatial extent of the study site (Schwalb et al., 2011). This type of inherent study bias has led many to caution the findings of limited movement in stream fishes (Funk, 1957; Gowan et al., 1994; Rodriguez, 2002). Study site lengths were larger than those of most previous studies. Therefore, it was not surprising that higher average and maximum distances were observed. Insight gained from studying streams of different sizes within this study further encourages caution. Of the individuals that moved at Yellow Creek. 22.3% moved distances greater than the extent of the entire study site at Whiteoak Creek. This finding supports the previous claims that spatial extent of the study

area can bias conclusions of distance moved. On the other hand, *Etheostoma blennius*, the species with the greatest movement frequency in this study (63%), was also the species with the highest recapture rate (35%), suggesting most darters may not have left the study site. Still, data presented from this study should be viewed as a minimum extent of movement for these fishes and not maximum extents. In addition to a bias from the spatial extent of the study area, by measuring distance traveled between the nearest points of two riffles, these data are inherently underestimates.

Male-biased movement of darters has been previously noted in pre-spawning (Winn, 1958) and spawning (Ingersoll et al., 1984) seasons. Data from this study show no difference in frequency of movement but males traveled significantly further than females during the pre-spawning season. In many species of darters, males become particularly territorial as the spawning season approaches, defending areas selected or prepared for spawning (Page, 1983). The increased distance traveled by males prior to spawning is likely in search of preferred spawning habitat. During the spawning season, as males are focused on defending territory rather than seeking preferred habitat, the difference between sexes was reduced and was not significant. Differences in movement between sexes were also not significant in post-spawning and non-spawning seasons.

Prior to spawning, larger darters moved more frequently than smaller ones. This bias has been observed in darters previously and is likely associated with increased fitness and decreased susceptibility to predation (Labbe and Fausch, 2000; Roberts and Angermeier, 2007b). Post-spawning, however, small individuals moved more frequently, indicating a possible shift in ecological pressures between seasons. Pre-spawning seasons for all darters in the study represented times of relatively high flow and therefore

increased riffle area. As extent of preferred habitat was greater, smaller darters were presumably able to more readily find adequate resources within their current riffle. Post-spawning, water levels fell and riffle areas shrank, leading to increased competition for fewer resources, resulting in smaller individuals moving more frequently to find adequate resources.

This conclusion is supported by the observation that movement rate increased with increasing congeneric density (CGD). The relationship was especially strong in the post-spawning season, the season in which smaller individuals moved more frequently than larger individuals. Increased movement in response to higher conspecific density has been previously observed in *Etheostoma podostemone* (Roberts and Angermeier, 2007b). Movement out of dense areas is expected as higher density increases competition for resources (food, mates, and cover). This response can also act as a predator avoidance tactic (predators often seek high densities of prey items; Hall, 1972). Petty and Grossman (2004) found that sculpin movement rates increased with conspecific density and were most strongly tied to the density of large adults. Further study of sculpins revealed that they used conspecific density as a broad cue for movement but that prey density directs fine-scale movements. More specifically, sculpins moved away from areas of higher conspecific densities on a reach-scale and into aggregations (areas of increased conspecific density) around food resources on a fine-scale (Lamphere, 2005). Such focused research on density has not been conducted with darters; however, similar findings may be expected due to ecological similarities between the taxa.

Riffle area stability (RAS) was expected to have a similar impact on darter movement as CGD. It was thought that as riffles shrank, availability of resources per fish

would decrease in the same way as if darter density increased, and would therefore lead
to increased movement. However, an increase in both movement frequency and mean
distance traveled was seen with increasing riffle size. This surprising finding, though, is
not contrary to the original hypothesis of increased movement with decreasing riffle area,
but to the assumption that as riffle size increased, darter density would decrease. Instead
as riffle size increased darter density also increased. This is presumably due to
immigration of darters into riffles either from outside the study area or from the corridors
within the sites.

Darters have been reported to make downstream migrations into deeper water
after spawning (Winn, 1958; May, 1969), potentially, from small tributaries into larger
streams. This timing corresponds with the period in which the relationships of CGD and
RAS with movement are strongest. The only tributaries within the study stretches,
however, are very small springs. Larger tributaries, more capable of contributing
substantial influxes of darters are distant enough (> 500 m) to require significant
migration of immigrants. Frequent movement of this magnitude has not been shown by
this study or previous studies for darters (Reed, 1968; Mundahl and Ingersoll, 1983;
Ingersoll et al., 1984; Roberts and Angermeier, 2007b). The other potential source of
immigration is the corridors. Many darters are known to move into adjacent pools or runs
at different points in the year (Etnier and Starnes, 1993). While snorkeling in the
corridors to assess predator density, darters were often encountered, in particular around
the edges of the corridors. As water levels increased, and riffle habitat became more
available, darters may have moved from the corridors into the riffles.

The presence of predators was expected to restrict the movement of darters across corridors. Roberts and Angermeier (2007b) found that the upper limit of distances traveled by darters was decreased by increased predator density in pools. Gilliam and Fraser (2001), however, observed increased movement in the presence of predators in a Trinidad killifish through experimental removal and introduction of predators into certain areas of their study stream. Darters in this study exhibited two different responses to increased predator density. The expected restriction on movement was seen in egg attachers, while all other darters displayed increased movement with increased predator density in the corridors. This increased movement could be a consequence of the tendency for greater predator density in the shorter corridors of the study area. The increase in frequency of movement would therefore be a result of the shorter distance to travel and not the higher predator density in these corridors.

Despite this possibility, egg attaching darters appear to be more sensitive to high predator density than the species from other life history categories. Throughout snorkeling efforts, when *Etheostoma flavum* and *E. occidentale* were observed in corridors, they were most frequently observed around logs and large rocks on the edge of pools. This habitat was also where predators were most frequently encountered. In one instance at Whiteoak Creek, three or four *E. flavum* were observed sitting on top of a large, fallen tree trunk in a pool of a corridor. Immediately underneath this tree were three large *Micropterus*. Other darter species, when observed in the corridors, were not in this habitat. Egg attaching darters' utilization of habitat such as logs and large rocks while in the corridors, which is the same place many predators are found, may be the cause for their increased sensitivity to predator density.

A negative relationship between mean distance traveled and average corridor depth (ACD) and a positive relationship to maximum corridor depth (MCD) was unexpected. This result, however, is likely due to study-site bias with respect to MCD. As a darter travels greater distances, it is more likely to traverse areas of greater depth. Thus, it is unlikely for an individual to travel long distances without crossing a deep portion of stream. For this reason, the positive relationship between MCD and distance traveled is interpreted as a lack of restriction on movement rather than a promoter of long distance movement. ACD on the other hand appeared to be a restricting factor on mean distance traveled. This result is not surprising for a group of fishes that typically prefer shallow benthic habitats (Page, 1983).

Movement rates of fishes have been shown to increase with higher flow rates (Hall, 1972; Albanese et al., 2004; Petty and Grossman, 2004). These higher flow rates typically occur during the spawning season, making it difficult to separate the two variables. Many fish utilize high flow events to access particular habitats needed for spawning, intrinsically connecting the two variables (Etnier and Starnes, 1993); but, this is not necessarily true for all species. The inclusion of multiple species with different spawning seasons in this study showed that increased movement rates across species are more specifically tied to spawning season than to increased flow. Buriers of small eggs (i.e., *Etheostoma caeruleum*) were the only darters that had their highest movement rate in the season with the highest flow (spring). Buriers of big eggs (i.e., *E. blennius* and *Nothonotus rufilineatus*) and attachers (i.e., *E. flavum* and *E. occidentale*) had their highest rate of movement in the season with the lowest flow (summer). With the exception of *N. rufilineatus* (because of their different spawning season), the non-

spawning season—which had the second highest rate of flow—was the only season that had consistently low movement across all life history groups.

Although movement rates were higher in seasons associated with spawning (pre-spawning, spawning, and post-spawning), rates varied among these seasons and across life history groups. Attachers (i.e., *E. flavum* and *E. occidentale*) and clusterer-guarders (i.e., *E. crossopterum*, *E. flabellare*, and *E. oophylax*) exhibited more frequent movement in the pre-spawning season. Frequency of movement in these categories was then reduced significantly during the spawning season. Buriers on the other hand show their greatest movement rate during the spawning season. Darters that bury their eggs typically do so in patches of gravel (Page, 1983). This substrate occurred commonly throughout the riffle habitat of each study site. Attachers and clusterer-guarders have higher spawning substrate specificity. Attachers included in this study use large rocks with small crevices and depressions in which eggs are laid one or two at a time (Keevin et al., 1989; Etnier and Starnes, 1993). Clusterer-guarders seek out large, flat slabs of rock under which they clean and prepare the nesting site (Lake, 1936; Page, 1974; Page and Burr, 1976; Page et al., 1982). Although not directly quantified, the frequency of these substrate types was much less common at the two study sites. Greater competition for fewer available sites leads to an increase in movement. Therefore, as sites are selected and prepared during the pre-spawning season, darters with higher spawning substrate specificity show greater frequency of movement. Less energy is contributed to pre-spawning movement by darters that bury eggs, as reproductive site availability is greater and competition therefore is reduced. During the spawning season, after reproductive territories have been established, darters with higher spawning substrate specificity move less frequently as they defend

these territories. Unlike attachers and clusterer-guarders, buriers have roaming territories during the spawning season (Winn, 1958). These roaming territories are likely a result of reduced spawning substrate specificity and explain their higher movement rates during the spawning season.

A predominant increase in the movement frequency of attachers occurred post-spawning. This may be associated with movement into deeper water after spawning that has been reported for other darter species (Winn, 1958). This was observed specifically for two fish in this study, *E. caeruleum* and *E. flabellare*. Unfortunately, and perhaps because of this movement into deeper water, no *E. flabellare* were recaptured during the post-spawning season. *Etheostoma caeruleum*, the representative of buriers of small eggs, did show its second highest movement rate during the post-spawning season.

Although higher frequency of movement was observed in darters with increased reproductive investment, the mean distance traveled was significantly shorter. Previous studies have shown reduced gene flow and greater population structure in species with small clutches and large eggs (Turner and Trexler, 1998; Faber and White, 2000). Turner and Trexler (1998) contend that reduced gene flow and genetic divergence among demes are evolutionary consequences of increased parental investment in species with small clutches and large eggs. The reduction in distance traveled with increasing reproductive investment in this study is consistent with these conclusions.

Stream fishes are thought to make upstream migrations as compensation for downstream drift as larvae (Hall, 1972; Slack et al., 2004). Upstream movement has been observed within seasons previously for darters (May, 1969; Mundahl and Ingersoll, 1983), and is particularly strong between years (Roberts and Angermeier, 2007b). The

shift in directional bias with increased reproductive investment was an interesting finding for which the ecological association is not fully understood. One possible explanation would be variation in larval drift phases. In general, darters that exhibit greater reproductive investment emerge from eggs as larger, more developed larvae (Turner, 2001). These larvae are demersal or epibenthic and exhibit limited downstream drift; smaller, less developed larvae are often pelagic and therefore more susceptible to downstream drift (Paine, 1984; Simon, 1994). Paine (1984) contended that species with pelagic drift intervals would undertake greater upstream spawning migrations as adults to compensate for downstream drift as larvae. Instead the opposite was observed in this study.

Some darter larvae, however, do not have drift phases that would be expected based on their egg size. For example, *E. caeruleum* exhibits relatively low reproductive investment as buriers of small eggs, yet its larvae are demersal (Simon and Wallus, 2006). To account for inconsistencies such as these, the effect of known larval drift phases on movement was examined directly. Darters with pelagic drift phases as larvae were observed to move greater distances over the course of the study as adults. However, even when examining the relationship between larval drift phases and movement directly, directional bias and movement frequency results were the opposite of what was expected. Darters with pelagic drift phases exhibited a statistically significant downstream movement bias and a decrease in movement frequency over the course of the study.

These findings are difficult to explain ecologically and are potentially an artifact of some unknown study bias. One possible study bias could be the location of the most preferred riffle habitat within the study site. Many darters prefer riffles with high

heterogeneity of substrate, which provides increased cover and food resources (Harding et al., 1998; Skyfield and Grossman, 2007). Furthermore, studies indicate that this increased habitat quality can influence the distribution, density, and movement of darters (Mundahl and Ingersoll, 1983). Although not directly quantified, the largest, most heterogenous riffles at both study sites were the riffles located furthest downstream. Thus, darters moving downstream were more likely to remain in these more preferred riffles than darters moving upstream into smaller riffles with more homogeneous substrates. Consequently, darters moving downstream may have been more likely to be detected than those moving in the upstream direction. The unintentional positioning of larger, more heterogeneous riffles within the study site therefore may have influenced the directional movement bias observed in this study. Further study regarding the influence of riffle habitat quality on darter movements would be beneficial.

Alternatively, significant upstream migration as adults may not be necessary. Slack et al. (2004) predicted source-sink populations in *Nothonotus rubrus* (*E. rubrum*) due to downstream larval drift, but their hypotheses were not supported. Variation in age structure of populations at their study site led them to conclude that downstream drift followed by upstream migration was not supported at large scales (> 1 km), but may be possible on smaller scales. Moreover, they predicted, based on drift studies of *Stizostedion vitreum* (by Franzin and Harbicht, 1992), that drift up to 300 m is probable in *N. rubrus*, but distances of 1-5 km are unlikely. These findings suggest that darters with pelagic drift phases may not require significant upstream migration to compensate for downstream drift. Finally, the movements of juvenile darters are unknown. Labbe and Fausch (2000) reported adults to be more mobile than juveniles but only darters > 25 mm

were marked, omitting a large portion of the juvenile age class. Petty and Grossman (2004) found juvenile sculpins to be more mobile than adults but did not report directional data. Furthermore, they found that juvenile sculpin that moved grew at a faster rate over the course of the study than those that did not. Adults displayed the inverse response. This presents an evolutionary advantage for juveniles to move, and may provide a compensatory mechanism for downstream drift as larvae.

Increased awareness of variation in fish movement patterns has many conservation implications. This study has provided insight into seasonal aspects of darter movements as well as correlations between life history characteristics and extent of movement. This information is critical for effective development of conservation practices. For example, Benton et al. (2008) showed restriction of fish movement across certain types of road crossing structures (i.e., box and tube culverts). Similar impacts have been demonstrated in both lab and field experiments of the federally threatened darter, *Percina pantherina* (Schaefer et al., 2003). Other sources of fragmentation can stem from degradation or loss of habitat. Slack et al. (2004) hypothesized increased isolation with increasing distance between riffle habitats, which is supported by data from this study. Darters found in larger streams, naturally consisting of greater distances between riffles, may be particularly susceptible to further habitat fragmentation. These impacts present the potential for fragmentation of species that are evolutionarily more susceptible to reduction in gene flow (e.g., darter species with high reproductive investment). Albanese et al. (2004) assert that the elimination of habitat favors ecological generalists because of increased stress induced through increased movement.

Through the examination of variation in movement with respect to life history characteristics, the ability to predict movements of species not studied is gained. In particular, this is useful for exploring the impacts of events such as habitat loss or fragmentation to imperiled or rare species for which a study of this nature would be difficult due to small populations and possible study-related mortalities. Caution is needed in the extrapolation of any data; thus, the following inferences are presented as hypothesized extensions of the results herein. With this understanding, predictions on the movements of several federally imperiled species can be made. As stated earlier, life history traits are largely conserved within darter subgenera (Page, 1983). Within *Catonotus* for example, all species produce small clutches of relatively large eggs that are clustered under flat rocks and guarded by males (Lake, 1936; Page, 1974; Page and Burr, 1976; Page et al., 1982). Five species within this subgenus (*E. chienense, E. lemniscatum, E. marmorpinnum, E. percnerum,* and *E. sitikuense*) are federally endangered ("U.S. Fish and Wildlife Service," 2012) and numerous others receive or are in need of state or federal protection (Jelks et al., 2008). The three species of *Catonotus* in this study (*E. crossopterum, E. flabellare,* and *E. oophylax*) together showed a significant reduction in distance traveled despite a higher occurrence of movement between riffles. Turner and Trexler (1998) and Faber and White (2000) proposed that these reduced movements have led to a reduction in gene flow and increased population structuring in *E. flabellare*. Species in this subgenus are potentially more susceptible to impacts that further fragment the riffle landscape and necessitate longer-distance movements to maintain gene flow. Moreover, increased fragmentation of habitat would impede the recolonization of extirpated populations.

Etheostoma chermocki and *E. scotti* are federally listed members of subgenus *Ulocentra* ("U.S. Fish and Wildlife Service," 2012). Although life histories of these species have not been directly studied, life history characteristics are strongly conserved within *Ulocentra* (Simon, 1994). Included members from this subgenus (*E. flavum* and *E. occidentale*) showed notable sensitivity to predator densities, with a significant reduction of movement through corridors with high predator densities. Therefore, caution should be taken regarding management and introduction or supplemental stocking of potential predator species within the ranges of these fishes.

Finally, four species within *Nothonotus* (*N. moorei*, *N. etowahae*, *N. wapiti*, and *N. rubrus*) are federally listed ("U.S. Fish and Wildlife Service," 2012). Species in this genus along with several imperiled *Percina* share the pelagic larval drift phase of *N. rufilineatus* (Slack et al., 2004; Simon and Wallus, 2006). *Nothonotus wapiti* has been shown to remain in the pelagic phase for up to 45 days (Rakes et al., 1999). Drift distance is inherently tied to a stream's flow rate. Alterations to flow rate due to impacts such as channelization or increased impervious surfaces within the watershed could lead to an increase in the downstream drift of the larvae with longer drift stages. Upstream migration of adults has been suggested as a compensatory mechanism (Hall, 1972; Slack et al., 2004) but this was not observed during any season of this study. Human-mediated increase in the downstream dispersal of larvae could therefore lead to genetic sinks downstream or the transport of larvae into unsuitable habitat.

CHAPTER V

Conclusions

The extent of movement of darters in this study was generally greater than previous studies with respect to both frequency of movement (16.6%) and average distance traveled (247.1 m). This, in part, may be due to the inclusion of multiple seasons, among which movement significantly varied. Most previous studies of darter movement have been conducted in the summer or fall, seasons that showed reduced movement in this study. Furthermore, the data herein suggest that increased movement rates across species are more specifically tied to spawning season than to increased flow.

Significant variation in the extent of movement was observed among the species studied, which demonstrates the importance of examining multiple species. Across all species, males traveled longer distances during the pre-spawning season. This provides empirical evidence to support previous observations of male-biased movement during this season (Winn, 1958).

Two corridor-specific factors had notable impacts on darter movement. At Yellow Creek, higher average corridor depth limited the distance darters traveled. This result is not surprising for a group of fishes that typically prefer shallow benthic habitats (Page, 1983). Darters that attach their eggs (i.e., *Etheostoma flavum* and *E. occidentale*) showed particular sensitivity to increased predator densities within corridors by having a significant reduction in movement rate through these portions of stream that was not seen in other species. This finding should provide caution to the management and introduction or supplemental stocking of potential predator species within the ranges of rare or

endangered fishes in this subgenus (*Ulocentra*), which all display very similar life histories.

Larger darters moved more frequently prior to spawning than smaller darters. A shift in ecological pressures may have occurred post-spawning, however, as the relationship between size and frequency of movement was reversed. Decreasing water levels reduced the extent of preferred habitat, presumably increasing competition for fewer resources which led to smaller, less competitive darters moving more frequently than larger ones. The finding of an increased rate of movement with increased congeneric density supports this conclusion of competition driven movement.

A positive relationship was observed between frequency of movement and reproductive investment. Moreover, the influence of reproductive investment varied by season. These trends are likely associated with variation in spawning substrate specificity, such that species with high specificity moved more frequently pre-spawning while locating and establishing spawning sites, and less frequently during the spawning season, when these sites were being defended. Species of darters with low substrate specificity showed higher movement in the spawning season as they have roaming territories rather than specific nest sites.

Distance traveled by darters decreased with increasing reproductive investment. This finding coincides with previous research that shows reduced gene flow in species with small clutches and large eggs (Turner and Trexler, 1998; Faber and White, 2000). Therefore, species with life history strategies incorporating high reproductive investment are potentially more susceptible to impacts that further fragment the riffle landscape.

Overall, an atypical, downstream directional bias was observed. This finding is contrary to the prediction of upstream migration of stream fishes as compensation for downstream drift as larvae (Hall, 1972). The unexpected directional bias may be due to the location of riffles containing greater habitat quality within the study site or support suggestions that substantial upstream migration of adults may not be necessary to compensate for downstream drift (Slack et al., 2004).

Although an inherent bias toward the detection of shorter movements may exist, this study provides a basis for the exploration of darter movement across spatial and temporal scales, taxa, and life history characteristics, which have important conservation implications for this highly imperiled group of fishes.

LITERATURE CITED

Albanese, B., P. L. Angermeier, and S. Dorai-Raj. 2004. Ecological correlates of fish movement in a network of Virginia streams. Canadian Journal of Fisheries and Aquatic Sciences 61:857-869.

Bart, H. L., Jr. and L. M. Page. 1992. The influence of size and phylogeny on life history variation in North American percids. Pp 553-572 *In*: R.L. Mayden (ed.) Systematics, historical ecology and North American freshwater fishes. Stanford University Press, Palo Alto, CA.

Benton, P. D., W. E. Ensign, and B. J. Freeman. 2008. The effect of road crossings on fish movements in small Etowah basin streams. Southeastern Naturalist 7:301-310.

Breen, M. J., C. R. Ruetz III, K. J. Thompson, and S. L. Kohler. 2009. Movements of mottled sculpins (*Cottus bairdii*) in a Michigan stream: how restricted are they? Canadian Journal of Fisheries and Aquatic Sciences 66:31-41.

Brown L. and J. F. Downhower. 1982. Summer movements of mottled sculpins, *Cottus bairdi* (Pisces: Cottidae). Copeia 1982:450-453.

Cooper, J. E. 1978. Eggs and Larvae of the Logperch, Percina caprodes (Rafinesque). American Midland Naturalist 99:257-269.

Detenbeck, N. E., P. W. DeVore, G. J. Niemi, and A. Lima. 1992. Recovery of temperate-stream fish communities from disturbance: a review of case studies and synthesis of theory. Environmental Management 16:33-53.

Etnier, D. A. and W. C. Starnes. 1993. The Fishes of Tennessee. The University of Tennessee Press, Knoxville, TN.

Faber, J. E. and M. W. White. 2000. Comparison of gene flow estimates between species of darters in different streams. Journal of Fish Biology 57:1465-1473.

Franzin. W. G. and S. M. Harbicht. 1992. Tests of drift samplers for estimating abundances of recently hatched walleye larvae in small rivers. North American Journal of Fisheries Management 12:396-405.

Freeman. M.C. 1995. Movements by two small fishes in a large stream. Copeia 1995:361-367.

Funk. J. L. 1957. Movement of stream fishes in Missouri. Transactions of the American Fisheries Society 85:39-57.

Gatz, A. J., Jr. and S. M. Adams. 1994. Patterns of movement of centrarchids in two warmwater streams in eastern Tennessee. Ecology of Freshwater Fish 3:35-48.

Gerking, S. D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology 34:347-365.

Gerking, S. D. 1959. The restricted movement of fish populations. Biological Reviews of the Cambridge Philosophical Society 34:221-242.

Gilliam, J. F. and D. F. Fraser. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology 82:258-273.

Goforth, R. R. and J. W. Foltz. 1998. Movements of the yellowfin shiner, *Notropis lutipinnis*. Ecology of Freshwater Fish 7:49-55.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626-2637.

Gowan, C. and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado

streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370-1381.

Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53:585-604.

Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. Journal of Fish Biology 24:415-426.

Harding, J. M., A. J. Burky, and C. M. Way. 1998. Habitat preferences of the rainbow darter, *Etheostoma caeruleum*, with regard to microhabitat velocity shelters. Copeia 1998:988-997.

Hill, J. and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. Copeia 1987:376-380.

Hoger, C. E. 1976. A biogeographic analysis of a Nebraska sand hills isolate of the lesser earless lizard (*Holbrookia maculate* Girard). Ph. D. dissertation. University of Nebraska, Lincoln, NE. 87 pp.

Hudy, M. and J. Shiflet. 2009. Movement and recolonization of Potomac sculpin in a Virginia stream. North American Journal of Fisheries Management 29:196-204.

Ingersoll, C. G., I. Hlohowskyj, and N. D. Mundahl. 1984. Movements and densities of the darters *Etheostoma flabellare*, *E. spectabile*, and *E. nigrum* during spring spawning. Journal of Freshwater Ecology 2:345-352.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Diaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L.

Warren, Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33:372-407.

Keevin, T. M., L. M. Page, and C. E. Johnston. 1989. The spawning behavior of the saffron darter (*Etheostoma flavum*). Transactions of the Kentucky Academy of Science 50:55-58.

Kuehne, R. A. and R. W. Barbour. 1983. The American Darters. University of Kentucky Press, Lexington, KY.

Labbe, T. R. and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774-1791.

Lake, C. T. 1936. The life history of the fan-tailed darter *Catonotus flabellaris flabellaris* (Rafinesque). American Midland Naturalist 17:816-830.

Lamphere, B. A. 2005. Movement and gene flow in an actively sedentary stream fish, the mottled sculpin (*Cottus bairdi*). Ph. D. dissertation, University of North Carolina, Chapel Hill, NC. 172 pp.

Lamphere, B. A. and M. J. Blum. 2012. Genetic estimates of population structure and dispersal in a benthic stream fish. Ecology of Freshwater Fish 21:75-86.

Lonzarich, D. G., M. L. Warren, Jr., and M. R. E. Lonzarich. 1998. Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. Canadian Journal of Fisheries and Aquatic Sciences 55:2141-2149.

May, B. 1969. Observations on the biology of the variegated darter, *Etheostoma variatum* (Kirtland). The Ohio Journal of Science 69:85-92.

Miller. M. P. 1997. RxC: a program for the analysis of contingency tables. http://www.marksgeneticsoftware.net/

Mundahl. N. D. and C. G. Ingersoll. 1983. Early autumn movements and densities of johnny (*Etheostoma nigrum*) and fantail (*E. flabellare*) darters in a southwestern Ohio stream. Ohio Journal of Science 83:103-108.

Natsumeda. T. 1998. Home range of the Japanese fluvial sculpin, *Cottus pollux*, in relation to nocturnal activity patterns. Environmental Biology of Fishes 53:295-301.

Natsumeda, T. 1999. Year-round local movements of the Japanese fluvial sculpin, *Cottus pollux* (large egg type), with special reference to the distribution of spawning nests. Ichthyological Research 46:43-48.

Page, L. M. 1974. The life history of the spottail darter, *Etheostoma squamiceps*, in Big Creek, Illinois. Illinois Natural History Survey Biology Notes 89:1-20.

Page. L. M. 1983. Handbook of Darters. TFH Publications, Neptune City, NJ.

Page. L. M. and B. M. Burr. 1976. The life history of the slabrock darter, *Etheostoma smithi*, in Ferguson Creek, Kentucky. Illinois Natural History Survey Biology Notes 99:1-12.

Page, L. M. and J. H. Knouft. 2000. Variation in egg-mimic size in the guardian darter, *Etheostoma oophylax* (Percidae). Copeia 2000:782-785.

Page. L. M., M. E. Retzer, and R. A. Stiles. 1982. Spawning behavior in seven species of darters (Pisces: Percidae). Brimleyana 8:135-143.

Page. L. M. and D. L. Swofford. 1984. Morphological correlates of ecological specialization in darters. Environmental Biology of Fishes 11:139-159.

Paine. M. D. 1984. Ecological and evolutionary consequences of early ontogenies of darters (Etheostomatini). Environmental Biology of Fishes 11:97-106.

Peterson. J. T. and P. B. Bayley. 1993. Colonization rates of fishes in experimentally defaunated warmwater streams. Transactions of the American Fisheries Society 122:199-207.

Petty. J. T. and G. D. Grossman. 2004. Restricted movement by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. Freshwater Biology 49:631-645.

Power. M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357-374.

Rakes, P. L., J. R. Shute, and P. W. Shute. 1999. Reproductive behavior, captive breeding, and restoration ecology of endangered fishes. Environmental Biology of Fishes 55:31-42.

Reed, R. J. 1968. Mark and recapture studies of eight species of darters (Pisces: Percidae) in three streams of northwestern Pennsylvania. Copeia 1968:172-175.

Roberts J. H. and P. L. Angermeier. 2004. A comparison of injectable fluorescent marks in two genera of darters: effects on survival and retention rates. North American Journal of Fisheries Management 24:1017–1024.

Roberts, J. H. and J. M. Kilpatrick. 2004. Predator feeding preferences for a benthic stream fish: effects of visible injected marks. Journal of Freshwater Ecology 19:531-538.

Roberts, J. H. and P. L. Angermeier. 2007a. Movement responses of stream fishes to introduced corridors of complex cover. American Fisheries Society 136:971-978.

Roberts, J. H. and P. L. Angermeier. 2007b. Spatiotemporal variability of stream habitat

and movement of three species of fish. Oecologia 151:417-430.

Roberts, J. H., A. E. Rosenberger, B. W. Albanese, and P. L. Angermeier. 2008. Movement patterns of endangered Roanoke logperch (*Percina rex*). Ecology of Freshwater Fish 17:374-381.

Rodriguez, M. A. 2002. Restricted movement in stream fishes: the paradigm is incomplete, not lost. Ecology 83:1-13.

Scalet, C.G. 1973. Stream movements and population density of the orangebelly darter, *Etheostoma radiosum cyanorum* (Osteichthyes: Percidae). The Southwestern Naturalist 17:381-387.

Schaefer, J. F., E. Marsh-Matthews, D. E. Spooner, K. B. Gido, and W. J. Matthews. 2003. Effects of barriers and thermal refugia on local movement of the threatened leopard darter, *Percina pantherina*. Environmental Biology of Fishes 66:391-400.

Schwalb, A. N., M. S. Poos, and J. D. Ackerman. 2011. Movement of logperch—the obligate host fish for endangered snuffbox mussels: implications for mussel dispersal. Aquatic Science 73:223-231.

Sheldon, A. L. and G. K. Meffe. 1995. Short-term recolonization by fishes of experimentally defaunated pools of a coastal plain stream. Copeia 1995:828-837.

Simon, T. P. 1994. Ontogeny and systematics of darters (Percidae) with discussion of ecological effects of larval morphology. Ph. D. Dissertation. University of Illinois, Chicago, IL. 672 pp.

Simon, T. P. and R. Wallus. 2006. Reproductive biology and early life history of fishes in the Ohio River drainage, Volume 4: Percidae – Perch, Pikeperch, and Darters. CRC Press, Boca Raton, FL.

Skyfield. J. P. and G. D. Grossman. 2007. Microhabitat use, movements and abundance of gilt darters (*Percina evides*) in southern Appalachian (USA) streams. Ecology of Freshwater Fish 17:219-230.

Slack. W. T., S. T. Ross, and J. A. Ewing, III. 2004. Ecology and population structure of the bayou darter, *Etheostoma rubrum*: disjunct riffle habitats and downstream transport of larvae. Environmental Biology of Fishes 71:151-164.

Smithson. E. B. and C. E. Johnston. 1999. Movement patterns of stream fishes in a Ouachita Highlands stream: an examination of the restricted movement paradigm. Transactions of the American Fisheries Society 128:847-853.

Turner, T. F. 2001. Comparative study of larval transport and gene flow in darters. Copeia 2001:766-774.

Turner, T. F. and J. C. Trexler. 1998. Ecological and historical association of gene flow in darters (Teleostei: Percidae). Evolution 52:1781-1801.

U.S. Fish and Wildlife Service Species Reports – Listed animals. Retrieved March 15, 2012, from http://ecos.fws.gov/tess_public/pub/listedAnimals.jsp

USGS Surface-Water Daily Data for the Nation. Retrieved March 15, 2012, from http://waterdata.usgs.gov/nwis/dv?

Walker, R. H. 2011. Movement patterns of southern redbelly dace, *Chrosomus erythrogaster*, in a headwater reach of an Ozark stream. Master's thesis. University of Central Arkansas, Conway, AR. 99 pp.

Waples, R. S. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 41:385-400.

Winn, H. W. 1958. Comparative reproductive behavior and ecology of fourteen species

of darters (Pisces-Percidae). Ecological Monographs 28:155-191.

APPENDIX A

List of Tests Completed

LIST OF TESTS COMPLETED

Tests are listed in the order in which they are referenced in text.

M:F = Males:Females. GOF = Goodness of Fit, DM = Distance Moved, MR = Movement Rate. TOI = Test of Independence, CL = Corridor Length, RS = Reproductive Seasons. D:U = Downstream:Upstream, RAS = Riffle Area Stability, ACD = Average Corridor Depth. MCD = Maximum Corridor Depth, ACW = Average Corridor Width, CGD = Congeneric Density, CPD = Corridor Predator Density, LHC = Life History Categories. and LD = Larval Drift phases.

Variables Examined	Test	n	Test Stat	P value
Marked M:F	Pearson's χ^2: GOF	10,136	$\chi^2 = 48.76$	< 0.0001*
Recaptured M:F	Pearson's χ^2: GOF	849	$\chi^2 = 0.27$	0.6067
DM between Sites	Mann-Whitney U	141	$\chi^2 = 60.11$	< 0.0001*
MR between Sites	Pearson's χ^2: TOI	849	$\chi^2 = 3.83$	0.0503
CL between Sites	Mann-Whitney U	25	$\chi^2 = 24.84$	< 0.0001*
MR among RS	Pearson's χ^2: TOI	573	$\chi^2 = 14.05$	0.0028*
DM among RS	Kruskal-Wallis	98	$\chi^2 = 4.32$	0.2289
Overall D:U	Pearson's χ^2: GOF	141	$\chi^2 = 0.86$	0.3543
Direction among RS	Pearson's χ^2: TOI	98	$\chi^2 = 2.43$	0.4883
Pre-spawning D:U	Pearson's χ^2: GOF	40	$\chi^2 = 0.40$	0.5271
Spawning D:U	Pearson's χ^2: GOF	18	$\chi^2 = 3.56$	0.0593
Post-spawning D:U	Pearson's χ^2: GOF	10	$\chi^2 = 0.40$	0.5271
Non-spawning D:U	Pearson's χ^2: GOF	30	$\chi^2 = 4.80$	0.0285*
DM by Direction	Mann-Whitney U	141	$\chi^2 = 1.61$	0.2045
DM between Sexes	Mann-Whitney U	141	$\chi^2 = 0.52$	0.4713
Pre-spawning	Mann-Whitney U	45	$\chi^2 = 4.45$	0.0348*
Spawning	Mann-Whitney U	22	$\chi^2 = 3.79$	0.0517
Post-spawning	Mann-Whitney U	24	$\chi^2 = 1.17$	0.2787
Non-spawning	Mann-Whitney U	50	$\chi^2 = 3.50$	0.0615
MR between Sexes	Pearson's χ^2: TOI	849	$\chi^2 = 0.26$	0.6125
Pre-spawning	Pearson's χ^2: TOI	167	$\chi^2 = 0.09$	0.7609
Spawning	Pearson's χ^2: TOI	75	$\chi^2 = 0.19$	0.6659
Post-spawning	Pearson's χ^2: TOI	92	$\chi^2 = 0.01$	0.9126

Variables Examined	Test	n	Test Stat	P value
Non-spawning	Pearson's χ^2: TOI	239	$\chi^2 = 0.22$	0.6367
Direction by Sex	Pearson's χ^2: TOI	141	$\chi^2 = 1.66$	0.1980
Female D:U	Pearson's χ^2: GOF	69	$\chi^2 = 2.45$	0.1176
Male D:U	Pearson's χ^2: GOF	72	$\chi^2 = 0.06$	0.8137
MR by Size	Logistic Regression	849	$\chi^2 = 0.16$	0.6851
Pre-spawning	Logistic Regression	167	$\chi^2 = 31.52$	< 0.0001*
Spawning	Logistic Regression	75	$\chi^2 = 0.99$	0.3191
Post-spawning	Logistic Regression	92	$\chi^2 = 6.73$	0.0095*
Non-spawning	Logistic Regression	239	$\chi^2 = 0.88$	0.3471
DM by Size	Linear Regression	141	$r^2 = 0.00$	0.6803
Pre-spawning	Linear Regression	40	$r^2 = 0.03$	0.2513
Spawning	Linear Regression	18	$r^2 = 0.07$	0.2919
Post-spawning	Linear Regression	10	$r^2 = 0.00$	0.9204
Non-spawning	Linear Regression	30	$r^2 = 0.04$	0.2862
Direction by Size	Logistic Regression	141	$\chi^2 = 0.45$	0.5041
DM by RAS	Linear Regression	98	$r^2 = 0.14$	0.0001*
MR by RAS	Logistic Regression	573	$\chi^2 = 2.95$	0.0861
Direction by RAS	Logistic Regression	98	$\chi^2 = 7.52$	0.0061*
MR by ACD	Logistic Regression	202	$\chi^2 = 1.17$	0.2797
MR by MCD	Logistic Regression	202	$\chi^2 = 0.24$	0.6266
MR by ACW	Logistic Regression	202	$\chi^2 = 3.57$	0.0588
DM by ACD: Yellow	Linear Regression	29	$r^2 = 0.15$	0.0393*
DM by MCD: Yellow	Linear Regression	29	$r^2 = 0.14$	0.0450*
DM by ACW: Yellow	Linear Regression	29	$r^2 = 0.10$	0.0872
DM by ACD: Whiteoak	Linear Regression	28	$r^2 = 0.03$	0.3425
DM by MCD: Whiteoak	Linear Regression	28	$r^2 = 0.00$	0.8666
DM by ACW: Whiteoak	Linear Regression	28	$r^2 = 0.01$	0.6115
MR by CGD	Logistic Regression	573	$\chi^2 = 8.84$	0.0030*
Pre-spawning	Logistic Regression	75	$\chi^2 = 0.21$	0.6506
Spawning	Logistic Regression	167	$\chi^2 = 0.32$	0.5714
Post-spawning	Logistic Regression	92	$\chi^2 = 19.33$	< 0.0001*

Variables Examined	Test	n	Test Stat	P value
Non-spawning	Logistic Regression	239	$\chi^2 = 0.03$	0.8525
Buriers/Small Eggs	Logistic Regression	30	$\chi^2 = 1.25$	0.2644
Buriers/Big Eggs	Logistic Regression	461	$\chi^2 = 6.77$	0.0093*
Attachers	Logistic Regression	58	$\chi^2 = 2.16$	0.1420
Clusterer-Guarders	Logistic Regression	24	$\chi^2 = 0.00$	0.9834
CGD between Sites	Mann-Whitney U	16	$\chi^2 = 29.21$	< 0.0001*
DM by CGD: Yellow	Linear Regression	44	$r^2 = 0.01$	0.4966
DM by CGD: Whiteoak	Linear Regression	54	$r^2 = 0.01$	0.5823
DM by CPD	Linear Regression	54	$r^2 = 0.01$	0.4085
MR by CPD	Logistic Regression	199	$\chi^2 = 1.92$	0.1658
Buriers/Small Eggs	Logistic Regression	9	$\chi^2 = 2.81$	0.0934
Buriers/Big Eggs	Logistic Regression	164	$\chi^2 = 5.55$	0.0185*
Attachers	Logistic Regression	17	$\chi^2 = 8.01$	0.0047*
Clusterer-Guarders	Logistic Regression	9	$\chi^2 = 1.52$	0.2177
MR among LHC	Pearson's χ^2: TOI	849	$\chi^2 = 6.931$	0.0741
Pre-spawning	Fisher's Exact Test	167		0.0365*
Spawning	Fisher's Exact Test	75		0.2426
Post-spawning	Fisher's Exact Test	92		0.0022*
Non-spawning	Fisher's Exact Test	239		0.8956
Buriers/Small Eggs	Fisher's Exact Test	30		0.1399
Buriers/Big Eggs	Pearson's χ^2: TOI	461	$\chi^2 = 19.19$	0.0002*
Attachers	Fisher's Exact Test	58		0.0334*
Cluster-guarders	Fisher's Exact Test	24		0.1366
DM among LHC	Kruskal-Wallis	141	$\chi^2 = 15.92$	0.0012*
Direction among LHC	Fisher's Exact Test	141		0.0402*
Buriers/Small Eggs D:U	Pearson's χ^2: GOF	7	$\chi^2 = 0.14$	0.7055
Buriers/Big Eggs D:U	Pearson's χ^2: GOF	102	$\chi^2 = 3.92$	0.0477*
Attachers D:U	Pearson's χ^2: GOF	21	$\chi^2 = 0.43$	0.5127
Clusterer-guarders D:U	Pearson's χ^2: GOF	11	$\chi^2 = 4.45$	0.0348*
DM among LD	Kruskal-Wallis	128	$\chi^2 = 17.70$	0.0001*
MR among LD	Pearson's χ^2: TOI	830	$\chi^2 = 7.20$	0.0273*

Variables Examined	Test	n	Test Stat	P value
Pre-spawning	Fisher's Exact Test	167		0.8943
Spawning	Fisher's Exact Test	73		0.3525
Post-spawning	Fisher's Exact Test	87		0.0002*
Non-spawning	Fisher's Exact Test	238		1.0000
Demersal	Fisher's Exact Test	54		0.8342
Epibenthic	Fisher's Exact Test	58		0.0334*
Pelagic	Pearson's χ^2: TOI	453	$\chi^2 = 25.49$	< 0.0001*
Direction among LD	Pearson's χ^2: TOI	129	$\chi^2 = 5.98$	0.0503
Demersal D:U	Pearson's χ^2: GOF	18	$\chi^2 = 2.00$	0.1573
Epibenthic D:U	Pearson's χ^2: GOF	21	$\chi^2 = 0.43$	0.5127
Pelagic D:U	Pearson's χ^2: GOF	90	$\chi^2 = 4.44$	0.0350*

Mark Stephen Hoger was born on 29 December 1983 in Orange, California and moved to Nebraska in 1989. He graduated from Seward High School in 2002. He then attended Truman State University in Missouri on academic scholarships. In May 2006, he graduated magna cum laude with a Bachelor of Science degree in Business Administration with a finance concentration and a minor in Statistical Methods.

On 28 March 2009, he married Emily Margaret Krogmann in Columbia, MO. Later that year, they moved to Tennessee to continue their education. Mark decided to change career paths and follow his life-long passion for biology. In 2010, after completing the necessary prerequisites, he began attending Austin Peay State University. He was awarded a research assistantship with the Center of Excellence for Field Biology under Dr. Rebecca Blanton Johansen. As part of his assistantship, he helped establish the ichthyology collection in the David H. Snyder Museum of Zoology. In addition to his assistantship, Mark received additional academic and research support from the Fred Stevenson Award (Federation of Fly Fishers—Southeastern Council), the Graduate Student Research and Creativity Grant (APSU), and the David H. Snyder Scholarship. He was awarded a Master of Science degree in Biology in May 2012 with a 4.0 GPA and given the Outstanding Graduate Student Award by the APSU Department of Biology.

Mark has presented his research at Southeastern Fishes Council (2011), Tennessee American Fisheries Society (2012), and as a guest speaker at Muhlenberg County (KY) High School's S.T.E.M. Program (2012). He placed third in the student oral competition at SFC. Following completion of his degree, he moved to Pennsylvania where he continues to pursue his passion for biology and conservation.