Factors Influencing Darter Dispersal Patterns in the Upper Roanoke River Watershed, Virginia

by

James H. Roberts

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APPROVED:

Dr. Paul L. Angermeier, Chair

Dr. Tammy J. Newcomb

Dr. C. Andrew Dolloff

Dr. Donald J. Orth, Department Head

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ABSTRACT

Effective delineation and management of stream fish populations requires a thorough knowledge of dispersal patterns, because these patterns affect a number of other demographic rates such as population growth, reproduction, survival, and gene flow. Previous studies of stream fish dispersal patterns have generally established species- and stream-specific home ranges and movement rates, but have largely failed to account for the environmental variables that may cause these parameters to vary. Many fishes occupy a variety of streams across a broad spectrum of ecological conditions, and movement rates (and thus population dynamics) may respond to these environmental gradients. Furthermore, enhanced understanding of the ecological features that induce or impede dispersal will help guide future management of stream channels for population connectivity.

To determine the instream features that influence the dispersal patterns of darters, I conducted a spatially intensive mark/recapture study of three darter species in the upper Roanoke River watershed. Logistic regression was used to relate observed inter-riffle movements to gradients in riffle and corridor attributes. During the first study period, habitat area loss and habitat spacing drove dispersal patterns. However, a model developed from these data transferred poorly to the second study period, in which density dependence was a more effective predictor of dispersal. Individual size did not seem to influence the probability of emigration, but did influence the distance traveled following emigration, particularly for the two more specialist species. This finding suggests a size-based dominance hierarchy for habitat selection and occupancy in darters. Predation threat had only a minor effect on the probability of traversing inhospitable corridors, but experimentally introduced structural cover significantly elevated dispersal rates through such corridors. Taken together, results of this study indicate that a complex array of ecological features interact to produce heterogeneity in dispersal rates across the stream landscape. Knowledge of these influences can be used to manage stream channels for dispersal permeability.

In addition to field studies, laboratory studies were undertaken to determine the efficacy of visible implant elastomer (VIE) and injectable photonic dye (IPD) for marking darters. No previous studies have rigorously evaluated these marks in darters, and comparisons of the two technologies in any taxa are few. Results of the laboratory study indicated that VIE is preferable to IPD for marking darters, particularly when mark longevity greater than 80 days is desired. Individuals marked with VIE exhibited higher survival and mark retention rates than did individuals marked with IPD. Additionally, VIE mark retention was more consistent across body locations. Retention of both marking technologies was biased by color. My study indicates that the results of tagging efficiency studies are not applicable across taxa, and that pilot studies are necessary prior to field use of marks in previously untested species.

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GENERAL INTRODUCTION

One of the greatest threats to the persistence of native species is the anthropogenic fragmentation of historically continuous populations. Large populations are divided into smaller sub-populations that may or may not exchange individuals over various temporal scales. Insularization of local populations poses several potential threats to the long-term viability of the species, including: 1) increased probability of local extinctions due to demographic and environmental stochasticity (Levins 1969), 2) loss of gene flow and genetic variability, with an accompanying risk of genetic erosion (Scudder 1989, Riddell 1993), 3) loss of large numbers of immigrants from reproductive source areas that sustain reproductive sinks (Sheldon 1987, Dennis et al. 1991, Rieman et al. 1993), 4) loss of overall range and outlying reaches that may contain refugia or other resources (Larimore et al. 1959, Cunjak 1988, Fausch and Young 1995, Matheney and Rabeni 1995), and 5) barriers to re-colonization after local extinctions have occurred (Sheldon 1987, Dennis et al. 1991, Rieman et al. 1993). In fragmented landscapes it is critical to salvage and/or enhance existing connectivity between sub-populations to increase the likelihood of species viability (Hanski and Gilpin 1991, Schlosser and Angermeier 1995).

Stream systems are naturally heterogenous landscapes composed of a mosaic of different habitat configurations that may be more or less suitable to a particular fish species (Frissell et al. 1986, Reeves et al. 1995). Some species evolved with a naturally small range, the extent of this range dictated by natural barriers, extreme habitat specialization, inter-specific competition, body size, or a combination of these factors. However, most species of stream fishes likely evolved within a larger natural range that exchanged individuals, even if only periodically (Jenkins and Burkhead 1994). Through dam construction, exotic predator introduction, and wholesale degradation of stream reaches, humans have since fragmented these ranges into disconnected regions that in modern times exchange individuals more rarely, if at all. The species most impacted by this fragmentation tend to be ecological specialists, whose modes of living are not supported in the human-impacted stream reaches between remaining "islands" of suitable habitat (Sheldon 1987, Winston et al. 1991, Angermeier 1995).

A clearer understanding of stream fish dispersal patterns is necessary to help set priorities for habitat remediation and to accurately discern relevant units of fish (e.g., populations, management units, evolutionarily significant units). Movement studies to date have focused primarily on game fishes such as salmonines (Gerking 1959; Gowan et al. 1994), even though non-game fishes are a more imperiled North American fauna, especially in the southeastern United States (Sheldon 1988, Angermeier 1995, Etnier 1997). Additionally, existing studies have determined species- and stream-specific movement rates, often failing to elucidate the ecological features that may cause these parameters to vary. The ranges of imperiled fishes may include streams that vary widely in terms of size, hydrology, and instream habitat features (see Jenkins and Burkhead 1994 for many examples), so an analysis of the connection between these variables and species' dispersal patterns seems in order.

Also hampering fish conservation efforts is the fact that scientists interested in the movements of small-bodied fishes typically cannot use radio telemetry due to the large size of the implanted transmitter. Despite the variety of other available marking techniques (i.e., those requiring specimen recapture), little consensus has been reached on which techniques can confidently be used in a given species, body location, and specimen size. In addition, key concerns such as slowed growth and elevated mortality resulting from marking have been given only cursory examination, and often are simply disregarded.

To further our understanding of the efficacy of marking small fishes and the interaction between instream features and stream fish dispersal patterns, I conducted laboratory and field studies, respectively, on regionally abundant representative species from the darter tribe. Darters were chosen because they are habitat specialists, and because little information is currently available on their marking. The laboratory study addressed two questions: 1) How do two mark technologies influence fish survival rates, and 2) What is the longevity of these marks? The field study addressed three questions: 1) How do instream features influence the dispersal patterns of darters, 2) How consistent are these influences between years, and 3) How does instream cover affect dispersal rates through inhospitable stream reaches?

CHAPTER 1. Evaluating injectable fluorescent marks for use in darters

INTRODUCTION

Despite the high conservation priority given to small-bodied native stream fishes in North America (Sheldon 1988; Angermeier 1995; Warren et al. 1997; Warren et al. 2000), development of methodologies for tracking individuals of these species have lagged behind the need for movement and population-size data. The practice of injecting visible liquid marks (e.g., paint, dye, and tattoo ink), a relatively simple and inexpensive method for identifying small-bodied fishes, has been in existence since the 1920's (McFarlane et al. 1990; Guy et al. 1996). However, recent research has shown that such marks may fade over time at varying rates, depending on mark type, color, location, and fish taxon (Hill and Grossman 1987b; Goforth and Foltz 1998; Albanese 2001). Injected marks are typically applied in a batch-specific fashion, although individual marks can be generated using different colors and body locations (Hill and Grossman 1987a; Johnston 2000; Skalski and Gilliam 2000). However, this methodology requires that mark retention be similar for different colors and body locations, an assumption that is seldom tested.

In the early 1990's, visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington) emerged as an alternative to liquid injected marks. The VIE compound comprises a colored polymer and a curing agent that, after being mixed and injected into subcutaneous tissue, solidifies into a pliable fluorescent sliver. Although VIE exhibits a short lifespan once mixed (i.e., 5 days in refrigeration; personal observation), it offers the benefits of reportedly high retention rates and low mortality effects in multiple fish taxa (Dewey and Zigler 1996; Haines and Modde 1996; Hale and Gray 1998).

Most adult darters (Percidae: *Etheostomatini*) are smaller than 100mm total length (TL), thus rendering the group a likely candidate for subcutaneous marking. However, darters exhibit several features, such as a benthic habit, variable coloration, and small scales, which could affect mark retention and readability. Recent investigators have used VIE successfully in darters (Labbe and Fausch 2000; J.R. Shute, unpublished data). Liquid injectable marks have also been used in darters (Freeman 1995; Warren and Pardew 1998), but mark performance has yet to be rigorously evaluated. Of particular interest is injectable photonic dye (IPD; New West Technology, Arcata, California), a relatively new liquid marking material that requires no mixing, and is specifically designed for marking aquatic organisms. Fish mortality rates from all types of subcutaneous marking appear low in the literature (Freeman and Grossman 1987b; Haines and Modde 1996; Johnston 2000), although data on darters is lacking (but see Labbe and Fausch 2000).

Because of the diversity of marking options currently available to researchers, I sought to rigorously evaluate two of the most promising marking technologies, VIE and IPD, on a group that has received little treatment in the tagging literature, the darters. The objectives of this study were to 1) determine the influence of VIE and IPD marks on fish survival, and 2) determine the influences of mark type, location, and color on mark retention. I applied marks to Roanoke darters *Percina roanoka* and riverweed darters *Etheostoma podostemone*, which are regionally abundant and represent the two most speciose genera of darters.

METHODS

Specimen collection

Fishes were captured from several locations in the North and South forks of the Roanoke River (Montgomery County, VA), between 11 and 26 June 2001, using a Smith-Root DC backpack electrofisher and a 5-mm-mesh seine. During collections, I retained all *P. roanoka* and *E. podostemone* individuals ≥40mm TL, and these were transported to the laboratory in Cheatham Hall on the Virginia Tech campus, Blacksburg, VA. At the lab, specimens were held in plastic bags in aquaria to acclimate to temperature changes.

Experiment design

Fishes were housed in two 636-L Living Streams (Frigid Units, Inc.), each containing a 1/3-horsepower chiller/re-circulator. Chiller temperatures were varied seasonally to correspond to the temperature of the Roanoke River (range 10-18º C). Chillers re-circulated water at a rate of 424L/min, ensuring equal distribution of temperature and water quality throughout the tanks. Additionally, I controlled the photoperiod and ambient temperature of the room containing the tanks, and varied these parameters according to season. Tank bottoms were covered with pea-size gravel and randomly distributed cobbles and hollow blocks to simulate instream cover conditions. Fishes were fed frozen bloodworms every 1-2 days. Water quality was checked daily for the first two weeks after fish introduction, and weekly for the duration of the experiment. I allowed specimens to acclimate to the tanks for a week before marking, and specimens were monitored daily for mortality or abnormal behaviors.

I randomly assigned individuals to the following treatments: Tank 1 – *P. roanoka* (32 VIE, 32 IPD, 30 control); Tank 2 – *E. podostemone* (28 VIE, 23 IPD, 25 control). Half of all marked specimens were randomly assigned to fluorescent yellow and the other half were assigned to fluorescent green. Furthermore, each treatment *P. roanoka* individual was randomly assigned to one of four marking locations: mid-ventral (MV), lower caudal peduncle (LCP), upper caudal peduncle (UCP), or mid-dorsal (MD). For *E. podostemone* I chose to maximize the replication of marks by applying marks to all four body locations on each individual (thus n=112 and 92 total marks for VIE and IPD, respectively, in *E. podostemone* versus n=32 total marks each for VIE and IPD in *P. roanoka*). Marks were applied to either the right (VIE) or left (IPD) of the individual's longitudinal midline.

During marking, I anesthetized specimens in MS-222 (Finquel). I injected 2-3-mm-long VIE marks subcutaneously using a 1-cc syringe equipped with a 29-gauge needle. For IPD marks, 0.1mL of dye was injected subcutaneously using the Pen-Ject™ tag applicator (New West Technologies, Inc.) equipped with a 30-gauge needle. To keep handling stress consistent across treatments, control individuals were handled for the same amount of time as marked individuals, and were pricked in one (*P. roanoka*) or four (*E. podostemone*) body locations with an empty 29-gauge needle. To differentiate control individuals from treatment individuals that had lost marks, I applied fin clips to the caudal fin of marked individuals (upper caudal for VIE versus lower caudal for IPD).

Marks were checked at 30, 80, 200, and 240 days post-marking. I chose to check marks at 30 and 80 days because these intervals correspond to the mark longevity required for a month-long or a seasonal field study, respectively. I chose 200 days to correspond with the length of two seasons, and intended to perform the final check at day 365. However, I terminated the experiment at day 240 due to high *P. roanoka* mortality levels (see Results). During each mark check, I anesthetized specimens in MS-222 and then recorded TL, the presence of marks, the presence of a fin clip, and the presence of any anomalies associated with marks. Fishes were inspected for fluorescent marks first using the naked eye and then with both a blue flashlight (VIE; Northwest Marine Technologies, Inc.) and an ultraviolet light (IPD; New West

Technology, Inc.). Tanks were inspected daily for mortality, and I recorded all of the above information for any dead individuals.

Data analysis

To test whether marks affected the probability of individual survival, I used logistic analysis (PROC GENMOD, SAS 2000) with survival (yes or no) as the response and mark type as the effect. Because comparisons across species were confounded with tank effects, and because results from the four check dates were not independent, I performed models on each species at each check date separately. I evaluated model significance using likelihood ratio (LR) χ^2 tests at $\alpha = 0.05$ (Stokes et. al 2000). Additionally, I designed *a priori* LR contrasts of VIE vs. control and IPD vs. control, and reported these tests when the effect of mark type was found significant by the overall LR test. I evaluated contrast significance using a Bonferroni-adjusted $\alpha = 0.025$ (for k=2 comparisons per model).

To test whether the probability of mark retention differed among treatments, I used logistic analysis with the retention of each mark (yes or no) as the response and mark type, mark location, and mark color as the effects. To provide interpretable statistical comparisons of retention among body locations, I converted each of the four body locations to one of two binary responses: ventral (MV, LCP) or dorsal (UCP, MD). This classification is biologically meaningful, because of the benthic habit of darters, and thus the likely increased abrasion and regeneration exhibited in ventral tissues. Individuals that died before a given check day were not included in the mark retention analysis for that day. In all mark retention models I first evaluated overall model significance, then significance of individual effects, using likelihood ratio (LR) χ^2 tests at $\alpha = 0.05$ (Stokes et. al 2000)

RESULTS

Individual survival

P. roanoka – Of the 94 Roanoke darters included in the experiment, 68 (72%) survived to day 240. Survival rate exhibited a gradual decline over time in control and VIE-marked specimens, whereas IPD-marked specimens exhibited much lower survival rates that declined more sharply over time (Figure 1.1). Logistic analysis indicated that mark type did not affect the probability of *P. roanoka* survival at day 80 ($\chi^2 = 5.83$, $p > 0.05$), but did significantly affect survival at days 30, 200, and 240 ($\chi^2 = 8.12$, $p < 0.05$; $\chi^2 = 12.87$, $p < 0.01$; and $\chi^2 = 12.37$, $p < 0.01$, respectively; Table 1.1). Contrasts revealed that IPD-marked individuals had significantly higher mortality than control individuals at days 200 and 240 ($\chi^2 = 6.05$, $p < 0.025$; and $\chi^2 = 6.26$, $p < 0.025$, respectively); no other contrasts were significant.

E. podostemone – Riverweed darters exhibited higher survival rates than did Roanoke darters, as 72 of the 76 original individuals (95%) survived to day 240 (Figure 1.1). Survival rate remained above 90% for all treatment groups for the duration of the experiment; control fish suffered no losses of individuals while the two marked groups lost only four individuals combined. Logistic models for days 30 and 80 failed to converge due to quasi-complete separation of the data, and could not be evaluated for significance. This condition occurs when the probability of a response (e.g., survival = yes) is very close to one, and was a consequence of low mortalities on those check days. At days 200 and 240 there was no significant effect of mark type on the probability of individual survival ($\chi^2 = 2.64$, $p > 0.2$; and $\chi^2 = 3.34$, $p > 0.1$; respectively; Table 1.1).

Mark retention

P. roanoka – Overall retention of VIE and IPD marks was 90% and 44%, respectively, in *P. roanoka* at day 240. The model failed to converge at day 30, and mark retention did not differ among treatments at day 80 ($\chi^2 = 10.04$, $p = 0.12$; Table 1.2). VIE marks had a significantly higher probability of retention than did IPD marks at days 200 and 240 ($\chi^2 = 15.06$, $p = 0.001$; and $\chi^2 = 19.36$, $p < 0.001$, respectively).

Mark retention varied in complex ways among body locations and between mark types and colors. Retention of VIE marks was similar among body locations, whereas retention of IPD marks was lower in dorsal body locations (UCP and MD; 25%) than in ventral locations (LCP and MV; 62%; Figure 1.2). The mark location factor was non-significant in all models; however, the interaction between mark type and mark location was significant at days 200 and 240 ($\chi^2 = 9.11$, $p < 0.01$; and $\chi^2 = 9.27$, $p < 0.01$, respectively; Table 1.3). Yellow IPD marks exhibited higher retention rates than did green IPD marks, whereas green VIE had a higher retention rate than yellow VIE (Figure 1.3). The mark type x mark color interaction was significant at day 240 ($\chi^2 = 4.81$, $p < 0.05$), but not at day 200. The mark color factor itself was non-significant in all models.

E. podostemone – On day 240, 79% of VIE marks and 83% of IPD marks remained in *E. podostemone*. Models failed to converge at days 30 and 80. Mark retention did not differ among treatments at days 200 or 240 ($\chi^2 = 1.54$, $p > 0.2$; and $\chi^2 = 0.59$, $p > 0.4$, respectively; Table 1.2).

Retention of marks was similar among body locations for both VIE and IPD (Figure 1.2). As was the case for *P. roanoka*, mark retention varied in subtle ways between mark types and colors. Although no *E. podostemone* models were significant, an interaction between mark type and mark color emerged. As with *P. roanoka*, green VIE marks were retained with greater probability than were yellow VIE marks, whereas the reverse was true for IPD marks (Figure 1.3).

DISCUSSION

Effects of marking on survival

Roanoke and riverweed darters marked with VIE suffered no short- or long-term reduction in survival compared to unmarked individuals. Survival rates declined gradually over time for both species. High survival rates following VIE application were observed in several previous studies in a range of fish taxa. Close and Jones (2002) observed no mortality in yearling rainbow trout *Oncorhynchus mykiss* that received VIE marks in translucent post-ocular tissues. Other investigators have used VIE and found <1% mortality in bull trout *Salvelinus confluentus* (Bonneau et al. 1995), bluegill *Lepomis macrochirus* (Dewey and Zigler 1996), Colorado pikeminnows *Ptychochelius lucius* (Haines and Modde 1996), and Arkansas darters *Etheostoma cragini* (Labbe and Fausch 2000) for studies 6-12 months in duration.

In the only published study I am aware of that contrasted VIE with IPD, Catalano et al. (2001) found survival rates of age-0 largemouth bass *Micropterus salmoides* marked in opercular tissues with VIE and IPD to be quite similar, at 77 and 78%, respectively. In my experiment, similarity or dissimilarity of survival rates between mark types depended upon the species marked. There was no short-term (≤80d) marking effect for either species. Over the long-term (200-240d), however, the probability of survival for IPD-marked *P. roanoka* was significantly reduced when compared to unmarked individuals, whereas there was no significant IPD effect on survival for *E. podostemone*.

Although there is little literature available on prior IPD use, other injectable liquid marks have shown mixed effects on mortality in previous applications. Hill and Grossman (1987b) found that acrylic paints applied with syringes to a variety of coolwater species had no measurable effects on growth or mortality. Haines and Modde (1996) found that Colorado pikeminnows tagged with tattoo ink experienced a higher mortality rate (10%) than did individuals tagged with VIE (<1%) or fin clips (0%). The investigators hypothesized that the tattoo needle used to apply the ink was too invasive, causing damage to the spinal column and internal organs of marked specimens. Goforth and Foltz (1998) marked yellowfin shiners *Notropis lutipinnis* with latex paint in both a laboratory and a field setting, and found that mortality was elevated only when marked individuals were <45mm standard length (SL), or when multiple marks per individual were applied. I found that multiple marks did not cause elevated mortality, as evidenced by the high survival rates of *E. podostemone*. I also saw no size-specific effect of marking on mortality rates, as the mean length of fishes that died in my experiment did not differ among marked and control groups (ANOVA: F = 0.26, p = 0.7765). Furthermore, I suspect that my technique for applying IPD marks was not as invasive as the tattoo needle used by Haines and Modde (1996), because mortality was not immediate, but rather declined gradually over time.

Because both marks used in my study are reportedly biocompatible, both were applied using similarly-sized needles, and both treatment groups were randomly assigned and subjected to the same anesthetic and handling procedures, I can offer three possible explanations for the differences in survival among marks and species that I found. First, whereas VIE cured and thus "sealed" the entry wound created by the needle, IPD did not, and may have increased the potential for secondary infection (although gross visual analysis never confirmed any such infection associated with wounds). Goforth and Foltz (1998) recognized tagging scars months after latex paint injection, whereas I have not encountered this phenomenon in any published application of or personal experience with VIE. Second, differences in swimming behavior between species may have affected mortality rates. Marking-related injuries to swimming muscles incurred during IPD application may have been irritated by the near-constant swimming behavior of *P. roanoka* in aquaria. Such injuries would have been less aggravated by the benthic, sedentary behavior of *E. podostemone* in aquaria. The swimming activity levels of *P. roanoka* in aquaria did not reflect its behaviors instream, where the species almost exclusively maintains contact with the substrate (personal observation). This artifact of the experimental environment may have exacerbated the effect of marking on fish survival. Finally, fin clip site (upper versus lower caudal fin) was confounded with mark type, and thus may have caused differential mortality rates between treatments, particularly for more active *P. roanoka*. However, previously published accounts of the effects of fin clipping on fish behavior and fitness have shown no deleterious impacts (Haines and Modde 1996; Conover and Sheehan 1999; Pratt and Fox 2002; Parsons et al. 2003).

Effects of mark type, location, and color on retention

For marking Roanoke darters, VIE emerged as a superior technology, as it was retained with high frequency in the short-term (≤80d), and with significantly greater probability than IPD over the long-term (200-240d). However, at 90 and 44%, respectively, both VIE and IPD retention rates fell within the range of other studies of injectable fluorescent marks: 27-100% in bluehead chubs *Nocomis leptocephalus* and torrent suckers *Thoburnia rhothoeca* (Albanese 2001), 29-33% in rainbow trout (Close and Jones 2002), 73% in coho salmon *Oncorhynchus* *kisutch* smolts (Bailey et al. 1998), 85-97% in Colorado pikeminnows (Haines and Modde 1996), and >99% in bluegill (Dewey and Zigler 1996). For marking riverweed darters, either marking technology appears appropriate, as both were retained at rates >96% in the short-term (≤80d), and >78% in the long-term (200-240d). Catalano et al. (2001) found that VIE and IPD performed similarly in age-0 largemouth bass, with overall retention rates of 84 and 67%, respectively. When classified by mark quality, however, the investigators found a significantly higher proportion of easily visible VIE marks than they did of easily visible IPD marks. Haines and Modde (1996) found that VIE and tattoo marks were retained with similar frequency in age-0 Colorado pikeminnows over a 21-day period (>97% for each), but with very different frequencies at the end of 142 days (85 and 26%, respectively).

Mark location appeared important to retention in some cases, but not in others. Both species retained VIE marks with similar frequencies across all body locations. Riverweed darters exhibited a similar pattern for IPD marks. In Roanoke darters, however, IPD marks were lost to differing degrees depending on where they were applied. Ventral marks were retained at a higher frequency than were dorsal marks, which is counter-intuitive for a benthic fish that would likely experience more abrasion and skin regeneration in ventral tissues. However, as previously noted, *P. roanoka* did not exhibit benthic behavior in aquaria. Hill and Grossman (1987b) and Goforth and Foltz (1998) found differential mark retention rates depending on application site, with better retention generally occurring in large, fleshy target areas, and lower retention in less fleshy areas and near major swimming muscles. Catalano et al. (2001) found variable retention of VIE and IPD across different fin locations, although anal fin marks performed best. Additionally, a given body location may be appropriate for marking one species, but not another. Albanese (2001) found that chin IPD marks performed well in torrent suckers (e.g., 92% retention at 83 days) but poorly in fallfish *Semotilus corporalis* (e.g., 10% retention at 65 days).

For both species, an interaction between mark type and mark color emerged. Green VIE was retained more frequently than was yellow VIE, whereas yellow IPD was retained more frequently than green IPD. Specimens were examined very thoroughly with blue and ultraviolet light, and because of the somewhat translucent musculature of the species used in this study, I do not feel that any marks went unseen. Because retention rates were not consistent within colors, differences in retention by color probably cannot be attributed to differences in mark readability, as was described in other studies (Close and Jones 2002; Goforth and Foltz 1998; Hill and Grossman 1987b). Rather, because differences in retention by color were consistent within types and across species, and the same individual applied all marks using the same equipment, differences are more likely attributable to variability in the chemical constituencies of the marks. Both marking materials are prepared by their respective manufacturers in batches, where the possibility for variance in viscosity, fluorescence, and biocompatibility emerges, and may confound the results of experiments in which multiple batches are used, as in this study. Only a rigorous examination of the quality of marks among versus within batches would determine whether batch effects are significant.

MANAGEMENT IMPLICATIONS

Overall, VIE appears to be the safest, most persistent mark for darters. Survival and retention rates were high in this and in many previous tests of VIE. Although IPD exhibits biases that may limit its long-term effectiveness in some species, it should still be considered as a convenient short-term mark. Future research should be devoted to comparative studies of these marking techniques in other taxa, in which IPD may be the preferable marking choice (Albanese 2001). Regardless of the mark material chosen, the possibility of variability in retention among locations and colors must be addressed. Finally, my findings highlight the difficulties of applying the results of marking studies across taxa. I therefore encourage the use of a pilot marking study to test all marking types, locations, and colors of interest, before beginning field use of subcutaneous marks in a new fish species.

Table 1.1. Results of logistic models for the effect of mark type on survival. Overall likelihood ratio (LR) test results are given for each model. Where models are significant, results of LR contrasts of each mark type versus control are also given. *E. podostemone* models for days 30 and 80 failed to converge (see text), and are not listed.

			Overall LR Test		LR Contrasts		
Species	Day	N	χ^2	Probability	Contrast	χ^2	Probability
P. roanoka	30	94	8.12	0.017	VIE = control	1.47	0.225
					IPD = control	2.92	0.088
	80	94	5.83	0.054			
	200	94	12.80	0.002	VIE = control	0.90	0.343
					IPD = control	6.05	0.014
	240	94	12.30	0.002	VIE = control	0.65	0.420
					IPD = control	6.26	0.012
E. podostemone	200	76	2.64	0.268			
	240	76	3.34	0.188			

Table 1.2. Results of logistic models for the effects of mark type, mark color, and body location on mark retention. Results of likelihood ratio (LR) tests for each model are given. Where models are significant, LR tests for each effect in the model are also given. Models failed to converge at day 30 for *P. roanoka* and at days 30 and 80 for *E. podostemone* (see text), and are not listed.

Species	Day	N	LR Test	χ^2	Probability
P. roanoka	80	59	Model	10.04	0.123
	200	57	Model	21.85	0.001
			Type	15.06	<0.001
			Color	1.23	0.267
			Location	3.06	0.080
			Type x Color	3.30	0.069
			Type x Location	9.11	0.003
			Color x Location	3.50	0.061
	240	54	Model	28.74	<0.001
			Type	19.36	<0.001
			Color	0.04	0.836
			Location	2.11	0.146
			Type x Color	4.81	0.028
			Type x Location	9.27	0.002
			Color x Location	1.90	0.169
E. podostemone	200	200	Model	4.49	0.611
	240	192	Model	6.66	0.354

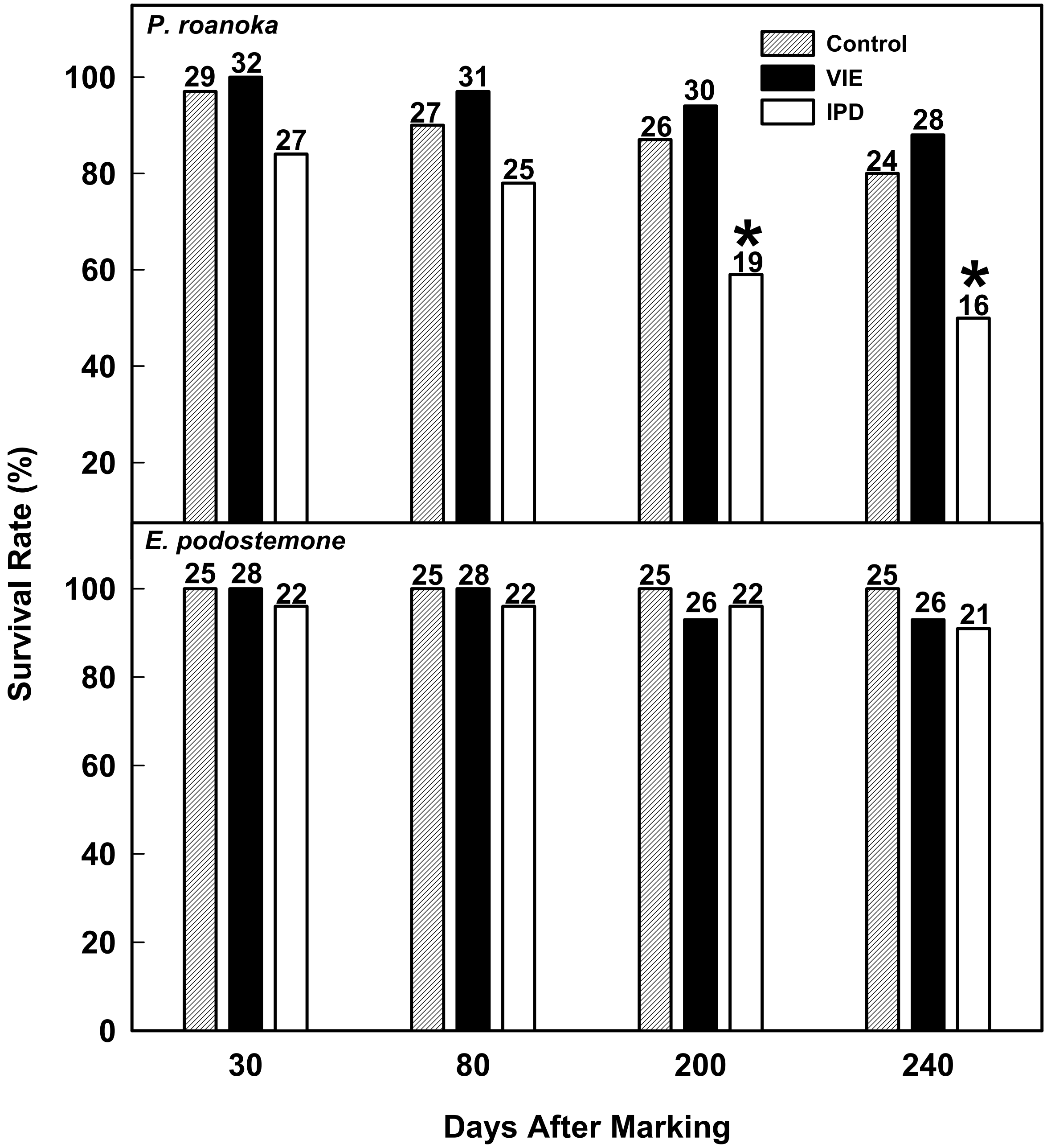

Figure 1.1. Survival rates of *P. roanoka* (top panel) and *E. podostemone* (bottom panel) for VIE and IPD treatments and the control group at 30, 80, 200, and 240 days post-marking. Values above bars indicate numbers of survivors remaining. Asterisks indicate significant differences from the control group at α = 0.05.

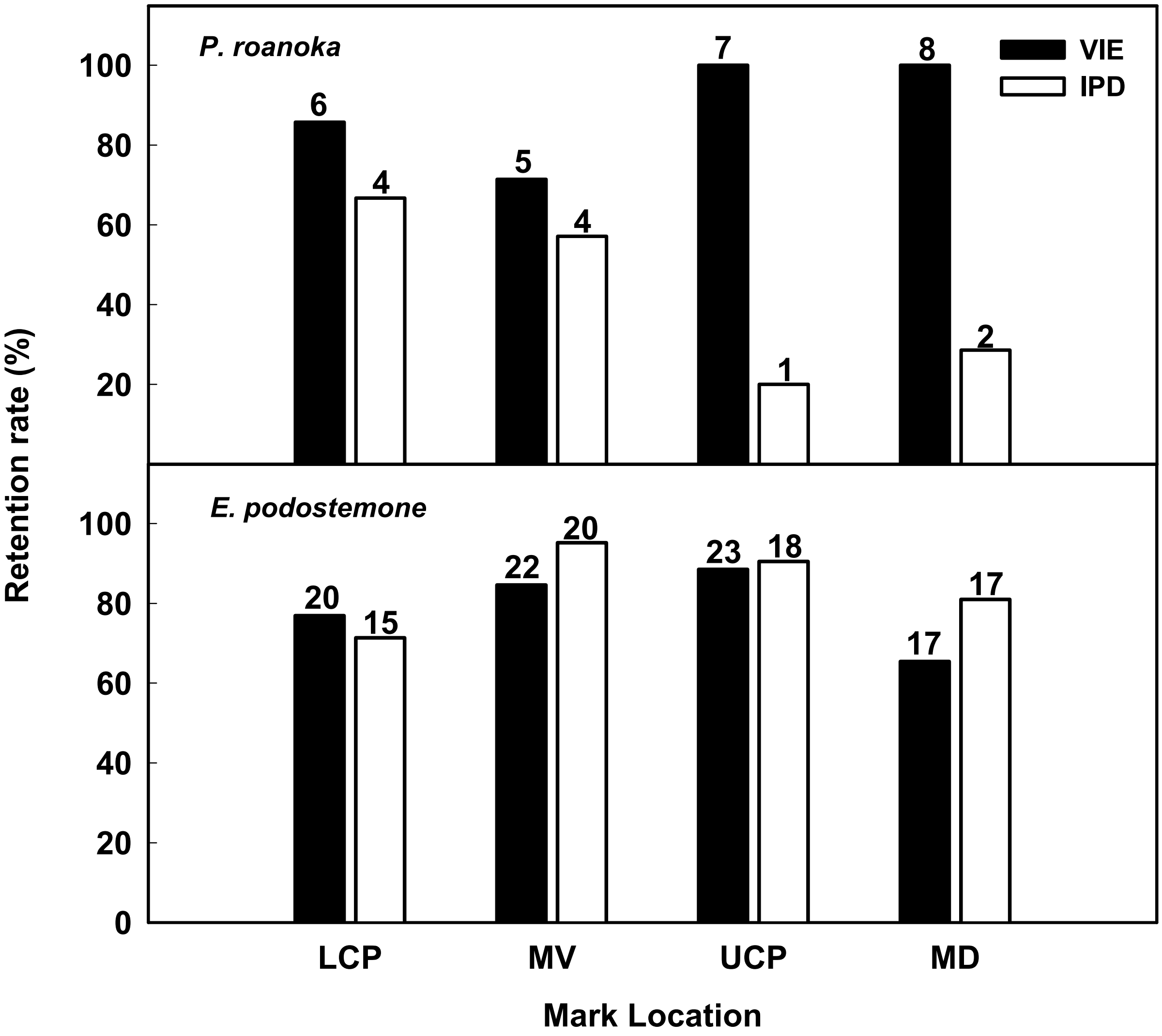

Figure 1.2. Retention rates of VIE and IPD marks at four body locations in *P. roanoka* (top panel) and *E. podostemone* (bottom panel) on day 240 of the experiment. Abbreviations are: lower caudal peduncle (LCP), mid-ventral (MV), upper caudal peduncle (UCP), and mid-dorsal (MD). Values above bars indicate numbers of marks remaining. The mark type x mark location interaction was significant for *P. roanoka* ($p<0.01$), but not for *E. podostemone*.

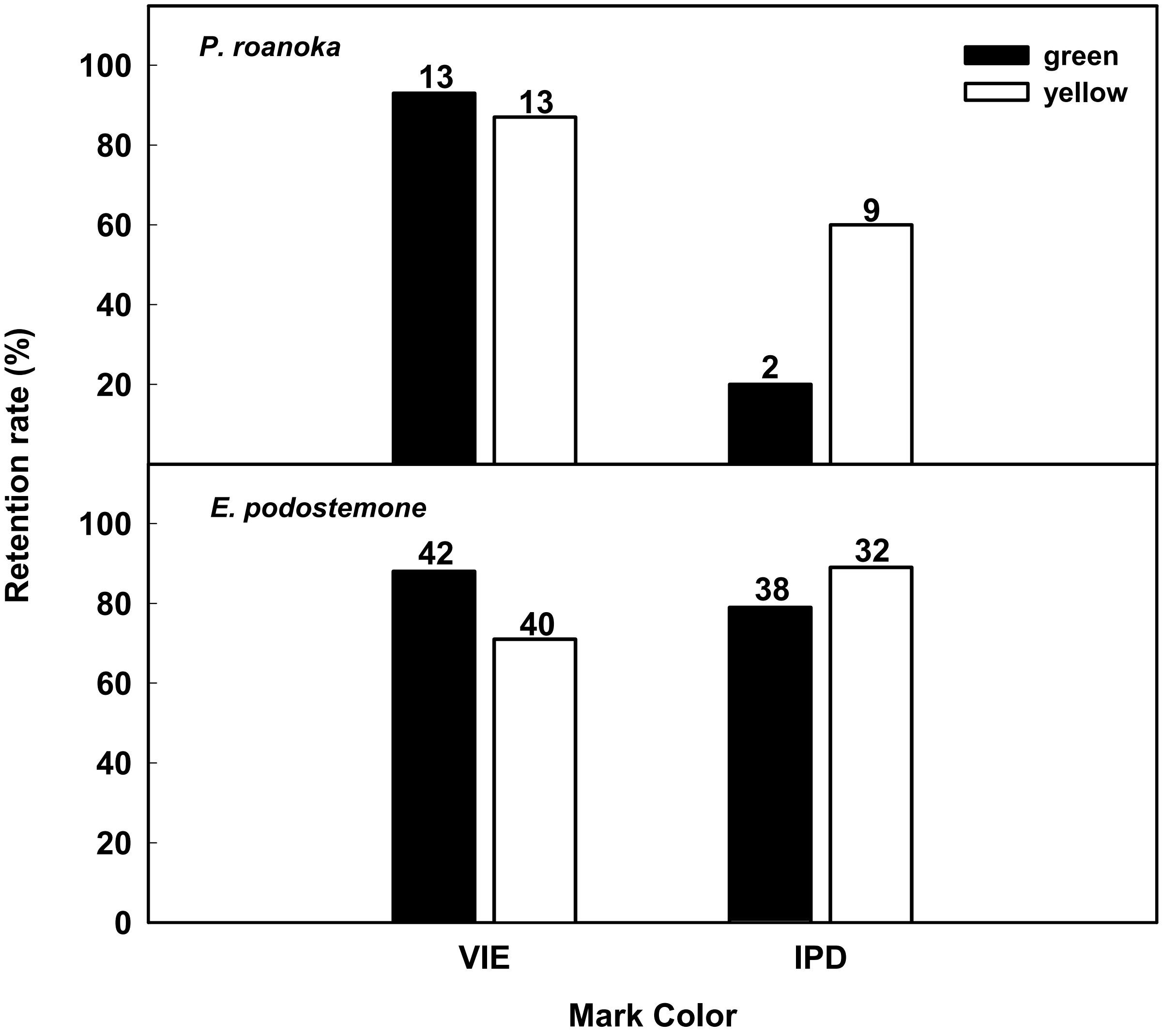

Figure 1.3. Retention rates of fluorescent green and yellow VIE and IPD marks in *P. roanoka* (top panel) and *E. podostemone* (bottom panel) on day 240 of the experiment. Values above bars indicate numbers of marks remaining. The mark type x mark color interaction was significant for *P. roanoka* ($p<0.05$), but not for *E. podostemone*.

CHAPTER 2. Factors influencing darter dispersal patterns in the upper Roanoke River watershed, Virginia

INTRODUCTION

Dispersal is a key ecological process for stream fishes. It allows individuals to evaluate the suitability of neighboring reaches and to re-colonize these areas after local extirpations. During various seasons, individuals may move into nearby or distant habitat patches to minimize metabolic requirements, escape environmental extremes, or maximize foraging or breeding opportunities (Schlosser and Toth 1984; Cunjak 1988; Dolloff et al. 1994; Schlosser 1995; Labbe and Fausch 2000). Tributaries may provide spawning habitat, as well as refugia from disturbances such as chemical spills, hydro-peaking dam release, or predation (Fraser et al. 1995; Fraser et al. 1999). Conversely, fishes may disperse from tributaries into mainstems in anticipation of extreme environmental conditions such as floods, droughts, and high and low temperatures, because of the greater buffering capacities of larger water bodies. The dynamic distribution of individuals throughout stream networks controls other demographic rates, including survival and reproduction (Hansson 1991). Knowledge of fish dispersal is therefore fundamental to understanding population ecology.

Abiotic barriers play a large role in shaping the dispersal patterns of stream fishes. Gradient and temperature barriers present longitudinal limits to the distribution of many species. Dams, waterfalls, and cascades create barriers to the upstream movement of some fishes (Martin-Smith and Laird 1998; Winston et al. 1991), or allow passage only during high-flow events (Adams et al. 2000). Schlosser (1995) found that dispersal of fishes from beaver ponds into adjacent lotic areas depended largely on stream stage; permeability of the dam end of the pond was realized only during high stage, but permeability was relatively constant at the upstream end of the pond, except during very low stage. The same study showed that during an entire summer of weir trapping, 33% of upstream movements occurred over 1 day, and that during the following summer, 48% of downstream movements occurred over 2 days. The effects of abiotic barriers on stream fish dispersal are relatively well understood, but other, less obvious ecological features also influence dispersal (Hansson 1991).

Recent studies have focused on the importance of habitat spacing in determining dispersal rates, particularly dispersal from source pools to destination pools (Goforth and Foltz 1998; Labbe and Fausch 2000). In Arkansas, Lonzarich et al. (2000) studied the movements of five species of pool-dwelling fishes and found that movement rates between pools separated by short riffles was three times higher than movement rates between pools separated by long riffles. In contrast, riffles were not barriers to pool dwelling blue shiners *Cyprinella caerulea* in Tennessee and Georgia; the species moved throughout an entire stream reach (Johnston 2000). In a Coastal Plain stream, Freeman (1995) found that the blackbanded darter *Percina nigrofasciata*, a habitat generalist, moved readily across adjacent mesohabitat boundaries. Individuals moved into pools as often as they moved into riffles (n = 6 and 5, respectively), and showed no directional or size bias in movement rates. The dispersal patterns of a habitat specialist species, on the other hand, would intuitively be constrained by the distance between suitable habitat patches (i.e., the length of the unsuitable transit corridor should be negatively related to the dispersal rate through it).

Structurally complex habitats are more capable than simple ones of providing the diverse resources needed by an organism over the course of its life (Dunning et al. 1992; Schlosser and Angermeier 1995). Gorman and Karr (1978) found that habitat complexity increased the spatial and temporal stability of fish communities, and these same data suggested that fishes emigrated less from complex stream reaches than from simpler reaches (Gorman 1986; O. Gorman, unpublished manuscript). Areas with greater habitat complexity (*sensu* Schlosser and Angermeier 1995) may exhibit lower dispersal rates because such areas are capable of satisfying the life history requirements of fishes more completely than can areas with simple habitat (e.g., Matheney and Rabeni 1995). Ensign (1995) found that *Percina roanoka* abundance in riffles of the upper Roanoke River watershed was positively related to the shallowness and substrate coarseness of adjacent pools. He postulated that such proximate pools provided quality foraging areas and reduced threat of predation for young darters. In complex stream reaches containing proximate complementary habitat units, individuals may be able to meet their life-history habitat requirements with minimal required movement. Such habitat complexity is most common in systems characterized by high gradient, low human impact, or both (Gorman 1986). Because gradient and human impacts are often inversely related, separating the effects of the two is difficult. As stream size increases and gradient decreases, mesohabitats become longer, are spaced further apart, and lose the proximity of complementary and supplementary resources (Frissell et al. 1986). Human impacts amplify natural shifts toward habitat homogeneity by removing riparian inputs that are important for pool formation, by increasing silt loads that widen the channel and make it shallower, and by removing sinuosity from the channel (Gorman and Karr 1978).

Predation may influence the dispersal rates of prey species. Shallow areas increase the vulnerability of all sizes of fishes to non-gape-limited terrestrial predators (Power 1987), whereas deep areas concentrate aquatic predators, increasing the vulnerability of small fishes to predation (Schlosser 1988). In a tropical setting, Gilliam and Fraser (2001) found that although predatory *Hoplias malabaricus* fragmented the distribution of *Rivulus hartii* into isolated refuge patches, predation threat actually increased the dispersal rate of the prey species through stream corridors, once prey individuals ventured into such corridors. Structural complexity, in the form of experimentally introduced cobble, further elevated movement through predator-containing corridors. In a temperate stream system, Labbe and Fausch (2000) found that the distribution of an introduced predator (*Esox lucius*) strongly affected the distribution, abundance, and population dynamics of a small-bodied prey species (*Etheostoma cragini*). Conceptually, then, predation may increase the probability of dispersal attempt, but should decrease the probability of dispersal success.

Competition for and variability in stream resources are additional factors that may drive dispersal patterns. The importance of deterministic versus stochastic processes in shaping stream fish population dynamics remains open for debate and varies among systems (Schlosser and Toth 1984; Strange et al. 1992; Taylor et al. 1996; Grossman et al. 1998). However, in most contexts stream resources (e.g., food, spawning habitat, refugia) probably become limiting during certain times of the year. Summer and winter have been proposed as the most metabolically taxing seasons for stream fishes (Cunjak 1988; Matheney and Rabeni 1995). Because most temperate fishes become quiescent and move little over the winter (Moore and Gregory 1988), summer resource flux is probably more important in controlling resource-acquisition-related dispersal dynamics (Schlosser and Toth 1984; Ensign 1990). Particularly, limitations to the volume of the stream, and thus loss of overall wetted habitat and concentration of individuals, may occur during the course of the summer as water levels decline (Ross et al. 1985). Decreased base flows have been observed in many streams following anthropogenic disturbances to the surrounding watershed. In this case both competitor density and habitat loss should be positively related to dispersal rates.

The Ideal Free Distribution (IFD) theory and its various derivatives (Fretwell and Lucas 1970; Fretwell 1972) predict that in a limited-resource environment individuals will distribute themselves among habitats to maximize the benefits of food and shelter resources and minimize the risk of being eaten. Experimental evidence supports the utility of the IFD model in predicting habitat selection by stream fishes (Fraser and Sise 1980; Tyler and Gilliam 1995; Grand and Dill 1997). Furthermore, the Ideal Despotic Distribution theory (Fretwell and Lucas 1970) predicts that as stream habitats shrink, sub-dominant fishes may leave or be forced out of their home patch in search of new resources (Winn 1958b; Gowan and Fausch 1996a; Hakoyama and Iguchi 2001). The efficiency of individual re-distribution relies upon the ability of individuals to assess adjacent habitat units for suitability, either through prior knowledge or through visitation. Inability to perceive differences in the quality of habitats causes deviation from the IFD model in the form of random individual distribution (Tyler and Clapp 1995; Hakoyama and Iguchi 1997). Mobile species may enjoy the freedom of frequent exploratory assessments, limited in number, extent, and duration only by physical impediments and predation risk (Gowan and Fausch 1996a). Sedentary species, on the other hand, must deal with the same limitations, but also must make less-informed occupancy choices based on a naturally low frequency of exploratory forays. Unless the stream offers clues about the quality of potential destination habitats (e.g., temperature or water quality information being swept downstream), less vagile individuals must rely on poorer information about adjacent areas. Therefore, it is probable that "departure rules" (i.e., factors influencing the probability of leaving a source habitat) are more accurate for predicting movement of sedentary species than are "destination rules" (i.e., factors influencing the probability of entering and remaining in a destination habitat), which appear to be more applicable to highly mobile species (Railsback et al. 1999; Belanger and Rodriguez 2002).

The darters (Percidae: *Etheostomatini*) are a highly diverse and threatened group of fishes endemic to North America (Warren et al. 1997; Warren et al. 2000). Many darter species are habitat specialists, and thus subject to population fragmentation from anthropogenic habitat modifications. Although their status as “charismatic microfauna” is growing among scientists, little is known regarding darter movement, largely because most darters are too small to mark using radio, PIT, or external tags (Guy et al. 1996), and because darters are often assumed to be sedentary (Lee and Ashton 1981). However the ability of these species to disperse among suitable areas and maintain outlying sub-populations has profound implications for species persistence.

In any given stream system, a complex interaction of ecological factors will shape the patterns of dispersal exhibited by darter individuals (Figure 2.1). Some factors affect the probability of a dispersal attempt, while others affect the probability of dispersal success. Factors that may influence the probability of a dispersal attempt from a source habitat include habitat complexity, competitor density, and habitat area flux at that source habitat. If we assume that darters are also capable of assessing adjacent transit corridors prior to making a dispersal decision, then individual size, corridor length, and predation risk in the corridor may influence the probability both of dispersal attempt and dispersal success. For example, if a species depends on riffles to complete most of its adult life, then the close proximity of sequential riffles (*sensu* the “stepping stones” of Johnston 2000) will make inter-riffle movements feasible over a short time-span. For a species that requires multiple habitat types to complete its life history (*sensu* Schlosser 1995), habitat complexity (in the form of complementation and supplementation) may dictate the suitability of a home riffle, and the necessity of moving from that riffle to another. If darters must move through unsuitable corridors to disperse between suitable patches, then increased predation levels in those corridors may color an individual's decision to disperse and increase its probability of being eaten in transit. Finally, an individual's size may determine a) whether it can effectively compete for resources or if it must disperse to acquire resources, b) the physical ability of the individual to traverse neighboring corridors (Adams et al. 2000), and c) the degree of importance of the predation threat in those corridors.

I synthesized the complex array of factors potentially shaping darter dispersal patterns into a working predictive model in order to better understand the magnitude and context-specificity of such effects. Based on the intuitively derived list of ecological factors mentioned above, I specifically addressed the following objectives:

1) Develop a model to predict emigration of individual darters from source riffles using mark/recapture and ecological data collected during summer 2001.

2) Assess the predictive power and transferability of my model using mark/recapture and ecological data collected during the summers of 2001 and 2002.

3) Assess whether enhancement of cover habitat increases darter transit rates through inhospitable corridors.

METHODS

Study system and site selection

The upper Roanoke River watershed (URRW) is a 1500-km^2 drainage basin in the Ridge and Valley and Blue Ridge physiographic provinces of Virginia (Figure 2.2). The watershed exhibits various land uses: 70% is forested, 16% is agricultural, and 11.5% is developed (Stancil 2000). The North Fork Roanoke River (the North Fork) drains primarily rural and agricultural lands in Roanoke and Montgomery counties, and joins the South Fork Roanoke River (the South

Fork), which has a steeper gradient and drains forested and agricultural portions of Floyd and Montgomery counties, in the village of Lafayette. From this confluence, the mainstem Roanoke River traverses rural and agricultural land before flowing through the cities of Salem and Roanoke. Below Roanoke, the river passes over Niagara Dam, at which point the fish assemblage changes dramatically (Jenkins and Burkhead 1994).

The URRW contains a diverse array of fishes and stream types. Fifty-nine species of fishes, including three that are endemic to the Roanoke River drainage, one that is of special concern in Virginia, and one that is federally listed as endangered, occur in the watershed. Streams in the URRW range from Blue Ridge freestone creeks >1000m in elevation (e.g., Big Laurel Creek) to mid-size streams winding through valley pastures (e.g., the North Fork) to a small river with floodplain backwaters in a heavily urban setting (the mainstem in Roanoke, VA). Because of the variety of stream types present in the URRW, as well as the existence of three abundant darter species, it was a good system in which to evaluate the influence of instream characteristics on darter dispersal patterns.

To achieve my objectives, I conducted a spatially intensive mark/recapture study in selected parts of the URRW. The three study species examined in this chapter prefer shallow mesohabitats; two are primarily riffle/run dwellers (*Etheostoma flabellare* and *E. podostemone*), and one is primarily a fast riffle dweller (*Percina roanoka*) (Vadas and Orth 2000). I therefore selected riffles as the focal units of study for dispersal patterns. In 2001, I selected three mark/recapture sites on the North Fork and three mark/recapture sites in the South Fork system, with varying positions in the stream network, to provide a wide gradient for each of the candidate ecological predictor variables (Figure 2.2). I chose marking sites that incorporated at least three distinct riffles (range 3-5) or were about 300m in length or greater (range 297-558m).

Whereas riffles within a site were sequential, sites were separated by at least 5 river kilometers (rkm). In 2002, I focused efforts on 2 of the 6 sites sampled in 2001, but expanded the length (range 679-693m) and number of marking riffles included (range 5-6) at each site. Mean stream width during the study period was 12m (range 6-22m). Stream flow during both sampling periods was below average (Figure 2.3).

Fish sampling

Fishes were marked between 5 June and 13 July 2001, and between 17 June and 3 July 2002. In both years, I initiated marking after completion of spawning to avoid any movement biases created by spawning migrations, which would have occurred in April and May, prior to the spawning season (Winn 1958b; Jenkins and Burkhead 1994). Riffle boundaries were delineated as the upstream and downstream ends of a discrete riffle, defined as a shallow channel unit with a straight to convex channel profile, total to partially submerged gravel/pebble/cobble substrate, velocity generally 20-50cm/s, and moderate surface turbulence (Arend 1999). In areas with high habitat complexity where riffles, runs, and pools blended into each other gradually, I visually estimated the boundaries of suitable darter habitat based on my judgment. Using a DC backpack electrofisher, the field crew (3 persons) shocked downstream into a stationary 5-mm-mesh seine, beginning at the bottom of the site and working net-sets upstream to the top of the site. While shocking into the net, the shocker disturbed the substrate by kicking, in an attempt to dislodge darters from substrate and cause them to drift into the net. In parts of riffles where I felt that the seine was inefficient for capturing darters (e.g., very shallow shoreline areas, low velocity areas, etc.), I used the electroshocker and hand-held dipnets to capture fishes. I conducted three passes at each riffle, and attempted to sample all of the riffle and capture all darters present on each pass.

Following each pass, all *P. roanoka*, *E. flabellare*, and *E. podostemone* captured were tallied, anesthetized using MS-222 (Finquel), and measured to the nearest mm total length (TL). All individuals >44mm TL were also given a riffle-specific VIE mark (Northwest Marine Technology, Inc., Shaw Island, WA) at one of 32 randomly assigned color x body location combinations. Darters were held until all members of a riffle were marked, then for an additional hour to monitor for mortality, and then were released at the center of the riffle of capture.

Recapture sessions occurred between 22 August and 3 October 2001, and between 14 and 30 August 2002. Sites were re-sampled in the order they were sampled during the marking session, and using methods identical to those used during marking. However, I expanded site boundaries to include at least one additional upstream and downstream riffle, making recapture sites substantially longer than marking sites (range 622-1,253m). Re-sampling greater lengths of stream homogenized the probability of detecting movements from riffles throughout the marking site, and increased the probability of detecting rare but potentially important movements of substantial distances (Gowan et al. 1994; Gowan and Fausch 1996a; Albanese et al., in press).

Because of the low recapture rates encountered during the 2001 recapture session (see Results), I followed the 2002 recapture session with a sampling bout for darters in corridors between mark/recapture riffles. Corridor sampling at the two 2002 sites occurred in one day immediately following riffle sampling, and was accomplished via one pass with a backpack electrofisher and hand-held dipnets. During all recapture samples, all darters >44mm TL were checked for marks in all body locations. All recaptured specimens were given a caudal fin clip, to ensure that no recaptures would be counted twice during a given recapture period.

I sampled corridors to estimate corridor predator density (see next section for calculation). To census predators, the field crew made one pass with a barge electrofisher, with one person towing the barge, two others spreading the electrodes from bank-to-bank, and all three personnel wielding long-handled dipnets. The predator census occurred at least two days after riffle fish sampling; I assumed that this waiting period allowed mobile predators to return to normal behaviors and locations. I used the species accounts of Jenkins and Burkhead (1994) to determine which species act as predators upon darters. The list of predators included *Ambloplites rupestris*, *Lepomis auritus*, *Micropterus dolomieu*, *Oncorhynchus mykiss*, and *M. salmoides* in order of decreasing relative abundance (Table 2.1). Only individuals of a size known to be piscivorous were included in the total predator catch.

Candidate ecological correlates

Following each marking and recapture sample, I made riffle habitat measurements at transects systematically placed perpendicular to stream flow. I measured wetted width at each transect, and quantified dominant substrate, depth, velocity, and silt embeddedness at several points along each transect. The number of transects and points per transect at a riffle varied with stream size, but the total number of points per riffle ranged from 40 to 60. Dominant substrate was described using a seven-category modified Wentworth scale. Velocity was measured at 0.6 x depth using a Marsh McBirney portable flowmeter. Silt embeddedness was quantified on a scale of one to five (Platts et al. 1983), with one being >75% embedded, three being 25-50% embedded, and five being <5% embedded. Depth, velocity, and substrate were categorized based on knowledge of darter biology (Table 2.2). Using point habitat measurements, I calculated a habitat complexity index similar to that of Angermeier and Schlosser (1989) to use as a potential ecological correlate. Points with embeddedness >50% were not used in the index, because I expected that such areas would not contribute to overall suitable darter habitat. Such points constituted <15% of the total number of points. From the remaining points, the diversity of unique combinations of depth, velocity, and substrate classes was used in the Shannon-Weiner equation to calculate a habitat complexity index (HCI) value for each marking riffle.

I used the average of stream widths across transects, multiplied by riffle length, to quantify riffle area. The proportional difference in riffle area between habitat sampling dates was recorded as a potential correlate variable, riffle area flux. Negative values for this parameter indicated loss of riffle area, whereas positive values indicated gain in area between sampling dates. Although measurements were only recorded at two points in time per summer, I reasoned that differences in flux among riffles would indicate differences in riffle morphology, and provide an index of riffles' vulnerability to over-summer drying, and thus their stability (Albanese 2001).

I used three-pass depletion data in program Microfish 3.0 (Van Deventer and Platts 1986) to estimate the total number of *P. roanoka*, *E. flabellare*, and *E. podostemone* >44mm TL (i.e., adults) that were present in each riffle during the marking session. This value divided by the sampled area of the riffle was used to calculate darter density, another dispersal correlate, for each riffle.

To characterize corridors, I quantified the length, area, and predator density of each inter-riffle habitat (e.g., pool, run-glide, etc.). Corridor length, a potential correlate, was calculated as the distance along the thalweg from top of one riffle to the bottom of the next. Predator density in a corridor (individuals/ha) was calculated as the total catch divided by corridor area (= corridor length x mean width) times 10,000.

To determine whether ecological conditions were similar between years, I used a two-tailed Student's t-test on the means of each of the five ecological variables for the seven riffle/corridor sequences that were sampled in both years. Riffle area flux was arcsine-square-root transformed prior to this analysis because of its proportional nature (Zar 1996). Differences between years were evaluated at α=0.05.

Corridor cover enhancement

In addition to examining the relationships between ecological variables and darter dispersal, I also sought to determine whether I could increase dispersal rates by increasing the number of complex cover items in inter-riffle corridors. Structurally complex corridors that provide refugia for darters could in theory increase the probability of dispersal attempts and successes. In 2002, I selected two corridors at each of the two sites to be structurally enhanced (n=4 modified corridors), and two corridors at each site to act as controls (n=4 control corridors). Cover availability was quantified using two of the cover categories of Newcomb et al. (1995), small velocity shelters (SVS's; 12.9-25.6cm at the widest point) and medium velocity shelters (MVS's; 25.7-51.2cm at the widest point). Prior to manipulation, I measured existing cover availability within each corridor by placing transects perpendicular to stream flow at 10-m intervals. I counted the number of SVS's and MVS's encountered within a 1-m-wide band along each transect (thus, by multiplying by ten, I could estimate the number of each type of shelter in the entire corridor). I calculated a cover index (C) for each corridor using the equation:

$$\mathbf{C = \frac{[SVS + (2 \times MVS)] \times 10}{Corridor\ Area}}$$

Where SVS equals the number of small velocity shelters and MVS equals the number of medium velocity shelters encountered in transects at a corridor. MVS was multiplied by two in the equation because I assumed *a priori* that an MVS would provide twice as much cover as an SVS. Student's t-tests revealed that modified and control corridors did not differ in length (t=0.169, p=0.871, df=6) or in existing cover index (t=1.875, p=0.110, df=6).

I chose 4-inch hollow concrete blocks (10-cm high x 19-cm wide x 29-cm long) as an appropriate material for enhancing corridor structure, because such blocks provided overhead cover for darters, could not be accessed by large-bodied predators, and were relatively inexpensive and transportable. I placed two longitudinal tracks of blocks along the entire length of each modified corridor (Figure 2.4). In the first track, blocks were spaced at 1-m intervals, and were alternately oriented either perpendicular or parallel to stream flow. The second track was placed adjacent to and 1m from the first, with blocks alternating orientations to those in the first track. Tracks were placed near the shoreline, except when doing so would allow falling summer water levels to expose the blocks, or when blocks would be in water >50cm deep. In these instances, tracks veered toward the center of the channel or the opposite shoreline. Each block was counted as one MVS, and so the total number of blocks added to a corridor was multiplied by two and added to the numerator of Equation 1 to calculate post-modification cover index. Pre- and post-modification C values were used to determine the degree to which corridor cover complexity was modified by my structural enhancements.

Data analysis

I define dispersal herein as recapture in a riffle other than the riffle of marking (hereafter recapture in a destination versus source riffle). This approach assumes no complex movements (i.e., multiple exploratory departure and/or return trips) between marking and recapture samples, and thus probably underestimates actual movement rates. Because the time lag between marking and recapture was similar across sites, I believe that biases due to my methodology are minor. Furthermore, complex movement data, though anecdotally valuable, would not have aided in satisfying my objectives, because straightforward dispersal analyses are not possible with such data. Although I recaptured in 2002 a small number of individuals that were marked in 2001 (Table 2.3), I did not include these observations in dispersal models, because I had no estimate of the retention rate of VIE in darters beyond 240d (see Chapter 1).

To determine whether my sampling efficiency was consistent across the wide spatial range of the 24 riffles I sampled in 2001, I conducted ANOVA with arcsine-square-root-transformed recapture rate as the dependent variable and riffle as the independent variable. To determine whether my sampling efficiency was consistent over time at the seven riffles I sampled in both years, I conducted a paired t-test on arcsine-square-root-transformed recapture rate for those riffles. Statistical significance in both tests was evaluated at $\alpha=0.05$.

Estimation of home range for these species was outside the goals of the study, and the methods used herein were not ideal for calculation of such due to design biases (Gowan and Fausch 1996a; Albanese et al., in press). However, because of the need for such information by conservationists, I did estimate summer home range for each species using the distances traveled by recaptured individuals. Because the precise points of departure and arrival of recaptured individuals were indeterminable from batch marks, home range for dispersers was calculated as the linear distance between midpoints of the source and destination riffles (Smithson and Johnston 1999). Fishes recaptured in their source riffle (i.e., non-dispersers) were attributed a home range equal to the length of the source riffle (Hill and Grossman 1987). Species summer home range was calculated as the arithmetic mean (with 95% confidence interval) of the home ranges of all recaptured individuals (Logan 1963). This method of home range estimation is likely biased downward by the assumption that no individuals left the study area, and biased upward by the assumption that all individuals explored the full extent of their source riffle, but represents the best available compromise. Only fishes that were recaptured in riffles were included in dispersal analyses, with one exception: fishes that had dispersed from a source riffle and traversed another riffle prior to recapture in a corridor were considered dispersers from the source to the traversed riffle.

Logistic Dispersal Models - I developed separate dispersal models for each darter species using 2001 mark/recapture and ecological data. Prior to inclusion of ecological variables into models, I constructed a Spearman correlation matrix of all potential regressors, examining the results for collinearity. No variables exhibited significant collinearity (i.e., $|\text{rho}| < 0.65$ in all cases), and so no candidate regressors were barred from subsequent analyses. For each species, I used logistic regression (PROC LOGISTIC, SAS 2000) to determine the influence of the candidate ecological variables on the probability of individual dispersal from source riffles. The full logistic model contained six regressor variables: habitat complexity index (HCI), individual total length (ITL), mean corridor length of the next upstream and downstream corridors (MCL), mean predator density of the next upstream and downstream corridors (MPD), source riffle area flux (RAF), and source riffle darter density (RDD). The binary response variable was individual dispersal (yes or no). Corridor length and predator density were averaged for the adjacent upstream and downstream corridors because an individual's decision to disperse upstream was not independent of its decision to disperse downstream. Global model significance was evaluated at $\alpha=0.05$ using a likelihood ratio χ^2 test, and if the model was significant, I proceeded as below.

To select the most parsimonious model, I applied backward elimination to the full model, with a probability-value cutoff of 0.1 for variable retention. Individual parameter estimates were evaluated for significance using likelihood ratio χ^2 tests. At each step, I removed the least significant variable, and proceeded until no further variables were above the cutoff. Generalized R^2 values, as well as Akaike's information criterion (AIC; smaller values indicate better model fit), were used to determine whether each step of variable reduction in the model caused a significant reduction in model fit or explanatory power (Stokes et al. 2000).

After selection of the most parsimonious model, the model was first validated using 2001 data. Each observation (i.e., recaptured individual with associated ecological information) was tested using the model, and I determined whether the model's prediction of dispersal or non-dispersal agreed with the actual behavior of the individual. Because all datasets were heavily biased toward non-dispersers, I changed the critical probability for predicted dispersal from its traditional level of 0.5 to a more liberal value of 0.06. I chose 0.06 because it corrected for the bias inherent in the data, as 6% of all recaptures were dispersers (Hosmer and Lemeshow 1989). Therefore, a model-predicted probability ≥ 0.06 was interpreted as a prediction of dispersal for that individual. Model sensitivity and specificity were evaluated as the proportion of correctly classified dispersers and non-dispersers, respectively. Following model validation, I tested the transferability of the model using 2002 mark/recapture and ecological data. Model transferability was assessed using sensitivity and specificity analyses, as above.

Corridor Cover Enhancement - Differences in dispersal rates through modified and control corridors were assessed using one-tailed Fisher's Exact Tests, for each direction (upstream vs. downstream) separately. Fisher's Exact Tests were used in lieu of χ^2 because exact methods are more robust in the presence of low cell counts (Stokes et al. 2000). The working hypothesis in each test was that the dispersal rate through modified corridors would be greater than the dispersal rate through control corridors. Dispersal rate was calculated for each experimental corridor as the number of individuals moving between the adjacent upstream and downstream riffles divided by the total number of individuals recaptured from those riffles (i.e., the number available for dispersal). I included only individuals from adjoining riffles in the analysis to avoid potential biases in recapturability created by a corridor's position within the mark/recapture site. In some cases, a given riffle was downstream of one experimental corridor and upstream of another. In such cases, when an individual moved across the upstream corridor, it was no longer available for movement across the downstream corridor, and vice versa (i.e., I was unable to detect both movements). I therefore subtracted the number of individuals that dispersed upstream from each riffle from the number available for downstream dispersal from that riffle, and vice versa.

RESULTS

Darter dispersal patterns

In 2001, I marked 4,575 darters among 24 riffles and recaptured 589 individuals, yielding an overall recapture rate of 13% (Table 2.4). In 2002, I marked 5,791 darters among 11 riffles and recaptured 955 individuals, yielding a recapture rate of 16%. Only 25 of the 2002 recaptures were in corridors, and these additional individuals increased the 2002 recapture rate by only 1%. Although there was a wide range of riffle-specific recapture rates (4-31%), rates did not differ significantly among sites in 2001 (F=2.43, df=23, p=0.0747), or between years for riffles sampled in both years (t=2.45, df=6, p=0.1097). Therefore, I concluded that my sampling efficiency was spatio-temporally consistent. No individuals with fin clips were recaptured, indicating that no fishes were captured twice within a given recapture period, and that each recaptured individual was unique. During both summers, recapture rates were highest for *P. roanoka*, lowest for *E. flabellare*, and intermediate for *E. podostemone* (Table 2.5). Because the majority of the recaptured (75%) and dispersed (70%) individuals captured during the two-year study were *E. flabellare*, many of the analyses that follow were restricted to that species.

Both years combined, 94% of riffle recaptures were within their source riffle, as only 97 individuals were captured in destination riffles. Of the 97 individuals that dispersed, 80 (82%) dispersed to a destination riffle adjacent to their source riffle. The remaining 17 dispersers crossed at least one riffle and two corridors between marking and recapture. One *P. roanoka* moved upstream across four riffles and five corridors during the 66 days between its marking and its recapture. The dispersal rates of all species increased between 2001 and 2002 (Table 2.4). Whereas in 2001 a large number of riffles (13) had no emigrants, in 2002 all riffles exhibited dispersal rates of at least 3% (Table 2.4). With riffles that were not sampled during the 2001 recapture session excluded, 38 individuals marked during summer 2001 were recaptured a year later, in summer 2002 (Table 2.3). Of these, a large proportion (34%) had dispersed to destination riffles.

During recapture events, marked *P. roanoka* and *E. podostemone* individuals were significantly larger than were unmarked ones (Figure 2.5). Marked and unmarked *E. flabellare* did not differ in length.

Mean summer home ranges were 65 ± 5m for *P. roanoka*, 65 ± 6m for *E. podostemone*, and 64 ± 2m for *E. flabellare*. However, these home range calculations were driven mostly by non-dispersers that were arbitrarily attributed individual home ranges equal to source riffle length, which averaged 46m overall.

Median dispersal distance of all fishes that dispersed was 127m (range 40-595m). Using *E. flabellare* as an example because of its large sample size, the frequency distribution of distances dispersed was leptokurtic and exhibited an upstream bias (Figure 2.6). Distance dispersed was significantly related to individual size (TL) for *P. roanoka* (p=0.0061), but not for *E. podostemone* or *E. flabellare* (p=0.2521 and p=0.2180, respectively; Figure 2.7). However, a negative relationship was evident for both *P. roanoka* and *E. podostemone*.

Whereas *E. flabellare* dispersers between 45 and 50mm TL were numerous, neither *P. roanoka* nor *E. podostemone* had dispersers within that length range (Figure 2.7). This lack of dispersers reflects a lack of recaptured individuals in that length range and not a lack of marked individuals; *P. roanoka* and *E. podostemone* individuals between 45 and 50mm TL contributed 23 and 17% of all marked individuals but only 2 and 1% of all recaptured individuals, respectively.

Logistic dispersal models

Candidate regressors used to construct logistic dispersal models often varied considerably among sites and between years (Table 2.6). Three variables were statistically similar between years: habitat complexity index (t=0.85, df=12, p=0.4108), mean corridor length (t=0.04, df=12, p=0.9657), and mean predator density (t=1.12, df=12, p=0.2851). Two variables, riffle area flux and riffle darter density, were significantly higher (i.e., more positive) in 2002 than in 2001 (t=3.12, df=11, p=0.0098; and t=2.60, df=12, p=0.0234; respectively).

The individual dispersal model for *E. podostemone* exhibited quasi-complete separation of the data, so model fit and explanatory power could not be assessed. This condition occurs when the probability of a response (e.g., dispersed = yes) is very close to zero. The full *P. roanoka* model explained 26.5% of the variance in individual dispersal, but was not significant ($\chi^2 = 8.41$, $p = 0.2097$, $df = 6$). All further results are from the *E. flabellare* individual dispersal model.

A likelihood ratio test revealed that the variance explained by the full (six regressor) logistic dispersal model for *E. flabellare* dispersal was significantly different from zero ($\chi^2 = 34.63$, $p < 0.0001$, $df = 6$). The model explained 29.5% of the variability in individual dispersal. Backward elimination procedures removed HCI and then ITL from the model, in neither case decreasing model fit (i.e., AIC decreased upon each removal), nor explanatory power (i.e., decrease in generalized $R^2 < 0.02$ in both cases). The reduced model was significant ($\chi^2 = 32.95$, $p < 0.0001$, $df = 4$), and explained 28.2% of the variance in individual dispersal using four regressor variables: MCL, MPD, RAF, and RDD. Of these parameters, MCL and RAF were highly significant, and had a large effect on the probability of individual dispersal (Figure 2.8). Both MPD and RDD approached significance, and all retained variables were negatively related to dispersal (Table 2.7).

For the 2001 data, the model correctly classified 10 of 18 dispersers, resulting in a model sensitivity of 56% (Table 2.8). The model also correctly classified 204 of 292 non-dispersers, resulting in a model specificity of 70%. However, the model transferred poorly to 2002 mark/recapture data, predicting that no fish would disperse and resulting in 0% and 100% sensitivity and specificity, respectively. In actuality, however, more *E. flabellare* dispersed in 2002 than in 2001 (50 versus 18).

To gain insight into which factors might have driven dispersal patterns during the summer of 2002, I constructed a new logistic dispersal model using 2002 data on the same six regressor variables, plus one new categorical variable, presence or absence of concrete blocks in adjacent corridors (BLK). Five of the variables, MPD, BLK, RAF, HCI, and ITL, did not meet the 0.1 p-value criteria to remain in the model, and were removed in that order. The remaining two-variable optimum model was significant (χ^2 =20.71, p<0.0001, n=789), but explained less variance (R^2 = 0.069 versus 0.282) and exhibited poorer fit (AIC = 357.9 versus 114.4) than did the 2001 model (Table 2.7). Of the two variables that remained in the 2002 model, RDD was highly significant, MCL approached significance, and both were positively related to dispersal. The 2002 model predicted 2002 dispersal better than did the 2001 model, correctly classifying 38 of 50 dispersers (76%), though only 312 of 739 non-dispersers (42%; Table 2.8).

Transit through corridors of varied complexity

The experimental addition of blocks affected both cover availability and darter dispersal patterns. A total of 938 blocks were added to the four modified corridors, causing C to become significantly higher in modified than in control corridors (one-tailed t=6.213, p=0.0004, df=6). Overall, 27 *E. flabellare* individuals moved upstream and 6 moved downstream through the eight focal corridors. Results of Fisher's Exact Test indicated that the proportion of *E. flabellare* individuals moving upstream did not differ between modified and control corridors (p=1.000, n=590). However, the proportion of individuals moving downstream was significantly greater through modified than through control corridors (p=0.0423, n=559). Very small sample sizes of the two other species precluded analysis of corridor enhancement effects on their dispersal rates.

DISCUSSION

The challenges of mark/recapture movement studies

The value of many mark/recapture studies has been questioned because of sampling design biases that underestimate movement rates and yield low recapture rates (reviewed in Gowan et al. 1994 and Gowan and Fausch 1996a). Because describing the extent of darter movement was outside the scope of this project, it was unnecessary for my study design to incorporate all of the safeguards proposed by Gowan and Fausch (1996a; e.g., weirs, extensive re-sampling, radio-telemetry, etc.). Of particular concern to me was low recapture rate, because conclusions drawn from a small sample of individuals may not represent the attributes of the entire population.

My overall recapture rate was low (ca. 15%). Cumulative recapture rates tend to increase with number of recapture events, but numbers of recaptures generally decline over time. Taking into account the time interval between marking and recapture (i.e., 60-80 days) and the one-recapture-period design of my study, my recapture rate is not aberrant compared to recapture rates documented in other studies of stream fishes: 8% for Arkansas darters *Etheostoma cragini* (Labbe and Fausch 2000; one-year study), 9% for a variety of warmwater species (Smithson and Johnston 1999; three-month study), 12% for central stonerollers *Campostoma anomalum* (Mundahl and Ingersoll 1989; 32-day study), 18% for blue shiners *Cyprinella caerulea* (Johnston 2000; 84-day study), 19% for rosyside dace *Clinostomus funduloides*, 28% for mottled sculpin *Cottus bairdi*, 33% for longnose dace *Rhinichthys cataractae* (Hill and Grossman 1987; 18-month study), and 38% for a variety of warmwater species (Skalski and Gilliam 2000; five-month study).

The question remains, what happened to the fish that I did not recapture? From three-pass depletion data, I calculated my average sampling efficiency in riffles to be 75%. Therefore, during recapture events, an average of 25% of the marked individuals present in a riffle could have gone undetected. Furthermore, I was able to estimate turnover rate, or the proportion of unmarked fish observed during recapture that was unaccounted for by the population estimate during marking. This rate estimates the proportion of the population that was mobile and evaded recapture by leaving the study area or by moving into corridors during riffle recapture sessions, and averaged 13%.

The remainder of the darters marked, 47%, may have been lost to mortality. Although information on stream fish mortality, much less darter mortality, is lacking, some evidence indicates that it may be high (Labbe and Fausch 2000). Because of the intense competition for resources caused by channel dewatering during the summer, it seems reasonable that a substantial portion of annual adult darter mortality takes place during that time.

Were the individuals that I recaptured representative of the population at-large? Some evidence supports the notion that stream fish populations are composed of both sedentary and mobile components, with the few individuals that are highly mobile being disproportionately important for re-colonization and population dispersal (Funk 1957; Gowan and Fausch 1996a). Because movement studies are biased towards over-sampling sedentary individuals and under-sampling mobile ones (Gowan et al. 1994), it is arguable whether recaptured fish ever accurately represent the population at-large. Conversely, if components are not fixed, and individuals switch between sedentary and mobile behaviors (Smithson and Johnston 1999), then a small sample of individuals may represent the full genotypic complement, if not the true movement distance distribution, of the larger population. It is unknown whether darter dispersal behavior is fixed or dynamic, so I could not infer how representative the individuals I recaptured were of the individuals I marked. In my study, physical attributes of dispersers (e.g., length) did not differ from those of non-dispersers, suggesting movement behavior plasticity. On the other hand, small marked individuals of two of the three species were significantly underrepresented during recapture events, suggesting either an ontogenetic shift in dispersal behavior, a genetic connection between size and mobility, or a cause-and-effect relationship between small size and the tendency to disperse.

Instream features influencing darter dispersal

A number of previous studies have addressed the question, “why do stream fishes move?” (Fraser and Sise 1980; Tyler and Gilliam 1995; Grand and Dill 1997; Lonzarich et al. 2000; Gilliam and Fraser 2001). Although rigorous, such studies have generally addressed only one or two potentially influential factors at a time, and often in a laboratory setting. All organisms, however, perceive their surroundings in a multivariate sense. I therefore sought to address the movement question in an uncontrolled system that allowed for substantial variability and interactivity in a suite of potential dispersal correlates. Moving away from the experimental design and toward the regression approach necessitated an extensive study area to find the broad spectrum of conditions I desired to model, but lent a realism to the experiment that could not have been duplicated within an artificial, controlled system.

I chose to model dispersal as a function of the characteristics of source and transit habitat unit characteristics, and not of destination unit characteristics. I made this decision because source and destination features were spatially auto-correlated within the larger study area, and were most likely heavily dependent on each other. In an attempt to avoid collinearity in dispersal models, I reasoned that source unit characteristics should more likely influence dispersal, because of a suspected general lack of darter vagility. Relatively sedentary species, by definition, make few exploratory visits to adjacent habitats, and therefore individuals of such species must make dispersal decisions based on limited knowledge of their surroundings. Thus, lacking comparative information about source and destination habitats, dispersal desiderata should be tied more to features of the source habitat (i.e., "departure rules"; Railsback et al. 1999; Belanger and Rodriguez 2002).

Despite my efforts to account for a wide variety of potential influences on dispersal, most of the variability in darter dispersal patterns that I observed was unexplained by ecological correlates. For two of the three species, ecological variables did not significantly relate to dispersal, and for a third only 28% of the variance was explained. One or both of two possibilities could account for my failure to fully predict dispersal: either I included the wrong or too few variables in my models, or darter dispersal is mostly random. I will address the first of these possibilities in greater detail later in this section. Regarding the second possibility, although previous investigators have related stream fish movement to numerous intrinsic and extrinsic factors (Winn 1958a; Schlosser and Toth 1984; Gorman 1986; Gowan and Fausch 1996a; Labbe and Fausch 2000; Lonzarich et al. 2000; Gilliam and Fraser 2001; Belanger and Rodriguez 2002; Gowan and Fausch 2002), a large amount of darter dispersal may be random. Some of the variability in dispersal may have been from "noise" created by individual-level phenotypic plasticity and response to environmental cues (Hansson 1991; Skalski and Gilliam 2000), or may have been guided largely by chance. Because mobile individuals are capable of assessing a wide range of potential habitats, ecological parameters should explain such individuals' dispersal patterns. Because sedentary individuals are more poorly informed about adjacent resources, however, a greater proportion of their dispersal may be random. Future investigators should determine whether the dispersal patterns of mobile (i.e., information-rich) fish are more explainable than those of sedentary (i.e., information-poor) fish.

Although I explained only a small portion of darter dispersal variability, what I did learn provides insight into the mechanisms that shape fish dispersal. During the summer of 2001, falling water levels attributable to a severe drought caused riffles of particular morphologies to dewater rapidly. These riffles typically had extensive shallow shoreline habitats that were highly suitable for darters but particularly vulnerable to drying (personal observation). Riffles that contained a broader range of depths offered refugia from falling water levels. Winn (1958a) found emigration of *E. flabellare* from shallow riffles as summer and fall water levels declined. Results of my 2001 logistic model provided strong evidence for this environmental control of dispersal, as riffle area flux was the most significant variable and contributed the greatest predictive ability to the model. However, the second-most influential variable in the model, mean length of the upstream and downstream corridors, placed constraints on the degree to which riffle area flux translated into dispersal. When corridors were short, a modest amount of habitat area loss caused elevated probabilities of dispersal, whereas when corridors were long, substantial area loss was required to induce dispersal. This condition suggests individuals' recognition of the disadvantages associated with longer transit distances, and that the risk associated with dispersal is weighed against the risk of remaining in habitat of declining suitability. Recognition of corridor length could come through previous attempts to cross it, or from visual or hydraulic cues. Conversely, corridor length may have been negatively related to dispersal success rate across corridors, with failing individuals returning to their source riffle.

Unfortunately, I was unable to separate influences on dispersal attempt from influences on dispersal success.

Biotic instream factors were less influential to darter dispersal in 2001. Although I had hypothesized that dispersal would be a positive function of darter density due to density-dependent resource limitations (Schlosser and Toth 1984; Ensign et al. 1990; Hansson 1991), dispersal was actually negatively related to darter density. The influences of riffle area flux and corridor length may have overridden any effects of conspecific competition in riffles. One would expect that riffle over-crowding would be the result of habitat area loss and the mechanism inducing emigration as riffles dewatered. However, riffle area flux and darter density were uncorrelated, suggesting that high darter densities in unstable riffles were maintained through high immigration rates (see "Comparisons among species" below).

Predator density in corridors influenced dispersal as expected, in a negative fashion. The presence of predators in deeper pool areas tends to drive smaller-bodied prey fishes from those pools (Labbe and Fausch 2000), and into shallower riffle areas (Power et al. 1985; Schlosser 1988; Gilliam et al. 1993). Laboratory feeding trials indicate that rock bass *Ambloplites rupestris* and smallmouth bass *Micropterus dolomieu*, two of the most abundant predator fishes in my study reaches, are highly effective predators of *E. flabellare* (Angermeier 1992; Roberts and Kilpatrick, unpublished data). High densities of these predators could have decreased the probability of dispersal attempt, dispersal success, or both.

I hypothesized that riffles exhibiting complex habitat (i.e., diverse combinations of depth, velocity, and substrate) would also exhibit low emigration rates, because such riffles would be capable of satisfying more of a species' life-history needs than could simple riffles (Dunning et al. 1992; Schlosser and Angermeier 1995). Gorman (1986), for example, found a lower emigration rate from a complex wooded stream reach than from simpler, channelized reaches. I found no effect of habitat complexity on dispersal rate, suggesting that darters based their decision to stay or to disperse not on the diversity of habitat configurations present, but on the amount or proportion of habitat that was suitable at that time. Although stream fishes utilize a range of habitats during their lifetime and even over the course of each year (Schlosser 1995), the timeframe of my study was perhaps too short to capture a range in life-history habitat requirements. Unfortunately, I was unable to add a measure of habitat suitability to models, because such an index would have been highly collinear with the habitat complexity index. Matching the spatio-temporal scale at which I measured habitat complexity to the scale over which darters make ontogenetic and seasonal habitat choices may have improved the predictive power of that variable. Indeed, multi-scale predictive models often perform better than single-scale models (Ensign 1995; Leftwich et al. 1997).

For *E. flabellare*, size was neither related to the probability of dispersal nor the distance dispersed following dispersal. Although I was unable to model the probability of dispersal for *P. roanoka* or *E. podostemone*, both species exhibited a negative size to distance dispersed relationship. Skalski and Gilliam (2000) noted a positive relationship between movement probability and size for creek chubs *Semotilus atromaculatus* and a negative relationship between size and distance moved for redbreast sunfish *Lepomis auritus*, indicating that larger fish were more likely to move, but that smaller fish actually moved farther. Similarly, Gowan and Fausch (1996a) found that trout exhibiting extensive movements were in poorer condition than were those that moved little, presumably because such individuals were forced to disperse in search of suitable resources. Gowan and Fausch (2002) linked movement behavior to competition with their finding that smaller trout were forced into sub-optimal habitats by more dominant large trout, and this same phenomenon has been recorded for a number of darter species (Winn 1958b). Although in my study the connection between size and the likelihood of leaving a riffle was undocumented, perhaps size did affect how far individuals had to travel to find acceptable habitat once they did leave. This hypothesis is corroborated by the finding that small-bodied individuals of two of the three species were underrepresented during recapture events. Smaller fishes either exhibited lower survival rates or higher turnover rates post-marking than did larger fishes. Because Chapter 1 indicates that small fishes do not exhibit disproportionately high marking-related mortality, the latter explanation is more probable. Smaller marked individuals may have been more likely to disperse beyond the boundaries of the study area and be replaced in riffles by unmarked immigrants that dispersed into the study area.

My four-variable logistic dispersal model left 72% of the variability in individual fantail darter dispersal unexplained. This variability may be accountable for by other variables I did not measure, such as the amount and flux of food resources in riffles (Ensign 1990), the presence of shallow shoreline refugia in corridors (Gilliam and Fraser 2001), or by hydrologic events like spates and scours. The first two of these factors were either too time consuming (food resources) or too complex (morphometry of shorelines) to quantify during the span of my study. Flow events were potentially the most influential factors on dispersal that I did not measure. Multiple studies have attributed pulses of movement to elevated hydrologic stage (Hill and Grossman 1987; Schlosser 1995; Gowan and Fausch 1996a). Without continuous sampling methods (e.g., weirs or radio-telemetry), however, I was unable to document whether movements that occurred between marking and recapture happened gradually, or whether they occurred over a short time span, as Schlosser (1995) found. Because no floods occurred during the course of this study, I assume that no displacement of individuals occurred. Furthermore, any elevated flows would have occurred across all sites, thus reducing their effect on dispersal variability.

The logistic model had fair predictive power, as it correctly classified 69% of 2001 fantail darter recaptures, including 56% of the dispersers. However, its transferability was weak. Although it correctly classified 94% of 2002 observations, none of the dispersers were correctly classified. Poor transferability of a predictive model suggests that key limiting factors either are not included in the model or that they differ among datasets (Leftwich et al. 1997). The latter problem is compounded by the fact that darters probably disperse across a wide range of environmental conditions, thus seemingly requiring an ecological variable to be at the extreme of its range to cause an obvious increase or decrease in dispersal. Because they are anomalous, these extreme conditions are not likely to be spatio-temporally consistent. In my study, the limiting factors differed among datasets because of differential environmental conditions experienced during the two study summers. Riffle area flux, so important to 2001 dispersal because of its putative control of habitat availability, was not as prominent during the summer of 2002. As a result, riffle area flux performed poorly as a predictor of dispersal in 2002, and other variables (e.g., darter density) were more significant.

The negative relationship between darter density and dispersal probability in 2002 is evidence for the density-dependent mechanism of resource partitioning and individual displacement I had hypothesized. Corridor length also approached significance, but strangely was positively related to the probability of dispersal. Perhaps the degree to which corridor length constrains movement is highly dependent on the influences of other ecological features (e.g., degree of channel dewatering).

The role of structural cover in aiding dispersal

Shoreline structural complexity can make unsuitable stream corridors more suitable for inhabitance or through-travel by providing hiding and resting areas that are safe from predators (Matheney and Rabeni 1995; Fraser et al. 1999; Gilliam and Fraser 2001). I hypothesized that poor open-water swimming performance would make darters particularly vulnerable to predation in deep, low-velocity corridors, and that they would benefit from increased overhead cover in such areas. Furthermore, I reasoned that introduced complexity would effectively shorten corridors by providing stepping stones of habitat between source and destination riffles.

Introduction of hollow blocks provided no apparent advantage to individuals moving upstream, as darters moved through corridors with tracks of added blocks no more often than they moved through un-modified corridors. However, blocks did elevate the proportion of fantail darters moving downstream through corridors. The reasons for this difference are unclear. Given that predator density had only a minor influence on dispersal in the 2001 model, and no appreciable effect in 2002, refuge effects probably cannot explain elevated dispersal rates through enhanced corridors. Stream fishes are known to move more often between suitable habitats that are spaced closely together than between those spaced farther apart (Lonzarich et al. 2000; this study). Perhaps, rather than acting as refugia from predators, blocks simply provided suitable stepping-stones of resting habitat during dispersal events, thus shortening the perceived length of the corridor. Tracks of blocks also may have artifactually attracted and funneled individuals between source and destination riffles as darters investigated the introduced, unexploited cover items.

Although downstream movement is intuitively less energetically costly than upstream movement (Lonzarich et al. 2000), fantail darters exhibited a bias toward upstream movement in my study. Perhaps the factors that inhibit downstream dispersal under ordinary circumstances were overridden by the addition of blocks in this objective. The number of blocks added to corridors was guided by financial and logistical considerations, but it is possible that with the addition of enough blocks, upstream dispersal would have increased as well.

Comparisons among species

Perhaps the most unfortunate consequence of the low recapture rates I experienced was the lack of sample size necessary to model the dispersal of *P. roanoka* and *E. podostemone*. At first glance, these species seem physically and ecologically similar enough to make generalizations across species justifiable. All three species utilize similar riffle habitats, grow to a similar size, and probably are vulnerable to the same predators. The *P. roanoka* dispersal model, though not significant, explained approximately the same amount of variability in dispersal as did the *E. flabellare* model. However, I could not assume that the same variables were important across species, because environmental changes may produce very different responses from apparently similar species. Schlosser and Toth (1984) found that rainbow darters *E. caeruleum* responded to low summer and fall stream-flows by shifting to deeper microhabitats, while *E. flabellare*, by virtue of a flexible body morphology that allowed access to small crevices in the substrate, were less responsive. Furthermore, this ability to persist in shallow habitats during low flows enabled *E. flabellare* to avoid the predation risk associated with movement into deeper areas, and thus seemed to make *E. flabellare* populations more temporally stable than were populations of *E. caeruleum*.

Three of my findings seem to contradict those of Schlosser and Toth (1984), although they do support the notion that species respond differently to environmental changes. First, recapture rates in my study were higher for *P. roanoka* and *E. podostemone*, two species with limited flexibility and relatively large scales, than for *E. flabellare*, a flexible species supposedly highly adapted to shallow water. If sampling efficiency is high and consistent, recapture rate should be inversely related to turnover rate (Gowan et al. 1994; Gowan and Fausch 1996a), and, given Schlosser and Toth's (1984) findings, should have been higher for *E. flabellare*. Second, I found that riffle drying was significantly related to *E. flabellare* emigration during a dry summer (2001), despite Schlosser and Toth's (1984) finding that *E. flabellare* could persist in drying riffles. Third, although their study would have predicted higher dispersal rates of *P. roanoka* and *E. podostemone* during a dryer summer than during a wetter summer, I found the opposite; dispersal rates of both species were higher in 2002 than in 2001.

In addressing contrasts one and two above, habitat-use patterns of fantail darters may explain differences in the studies' findings. Relative to the other species, *E. flabellare* is a habitat generalist (personal observation), and could often be seen in the margins of my study corridors. The ability to occupy a variety of habitats may have conferred upon the species the ability to move freely through the stream and evade recapture, thus lowering recapture rates. However, even during times of high emigration and turnover, I continually found high densities of *E. flabellare* in riffles, most being unmarked. Therefore, in the absence of marking and recapture, I would have perceived *E. flabellare* populations as stable, as did Schlosser and Toth (1984). If their study had incorporated marking of individuals, they might have detected high turnover rates, as I did, and might have reached different conclusions about the temporal stability of *E. flabellare* populations.

Regarding the third contrast, in a univariate sense dispersal of *P. roanoka* and *E. podostemone* did not seem to follow Schlosser and Toth's (1984) patterns. However, when a multivariate explanation is invoked, these disagreements may be reconciled. Emigration rates should have been higher during low flow in summer 2001, but dispersal was actually more common during summer 2002. However, the low-flow conditions of 2001 may have forced individuals out of riffles and into predator-laden corridors, thus increasing mortality but failing to produce a measurable dispersal response (i.e., emigrants only contributed to dispersal rate when they *succeeded* in inter-riffle dispersal). Elevated stream stage in 2002, though not contributing to increased emigration from riffles, may have produced unmeasured benefits for dispersing individuals (e.g., inundated shoreline refugia) and a corresponding increase in detected dispersal rate. These complexities underscore the necessity of understanding correlates both of dispersal attempt and dispersal success.

The three species examined in this study appeared to differ in their size-mediated dispersal responses to instream conditions. Fantail darters of all sizes dispersed, and distance dispersed was at most weakly related to individual size. Riverweed and particularly Roanoke darters, on the other hand, dispersed greater distances at smaller sizes, and below 50mm seemed to disperse out of the study area altogether. Prior studies have shown the mobile component of a population to comprise smaller individuals (Skalski and Gilliam 2000), larger individuals (Tyus and McAda 1984; Skalski and Gilliam 2000), or individuals of all sizes (Smithson and Johnston 1999). The high dispersal rates of small *P. roanoka* and *E. podostemone* in my study may be explained by one of two darter life-history patterns: either the two species do the majority of their lifetime dispersal while they are small, or the dominance hierarchy I have previously discussed forced small individuals to look for alternative suitable habitats. If the latter possibility is correct, it makes sense that the size-distance relationship existed for these two species and not for *E. flabellare*. Whereas the former two species are habitat specialists and would have needed to roam until precise habitat configurations were found, the latter is a relative habitat generalist and would have had access to a greater range of nearby habitat configurations. For example, Freeman (1995) found that generalist blackbanded darters of all sizes moved throughout a mesohabitat sequence including gravel riffle, boulder riffle, and pool. Although small *P. roanoka* and *E. podostemone* may have exhibited considerable exploratory behavior and turnover, high overall recapture rates of the two species suggest high site fidelity of larger individuals.

Stream fish dispersal modeling – advances and impediments

Relative to our understanding of other biological and ecological processes in stream fishes, our understanding of dispersal dynamics is weak. This is largely due to logistical difficulties in obtaining unbiased fish location and movement information (reviewed in Gowan et al. 1994). Despite such difficulties, ecological studies have linked stream fish movement to a host of environmental factors including predation threat (Fraser et al. 1995; Gilliam and Fraser 2001), habitat loss (Winn 1958a; Schlosser and Toth 1984), individual size (Skalski and Gilliam 2000), individual fitness (Gowan and Fausch 1996a; Skalski and Gilliam 2000), habitat complexity (Gorman 1986), habitat spacing (Lonzarich et al. 2000), competition (Gowan and Fausch 2002), elevated discharge (Schlosser 1995), suitable habitat acquisition (Fraser and Sise 1980; Gowan and Fausch 2002), and transit corridor refugia (Gilliam and Fraser 2001). Current efforts to individually model stream fish movement based on habitat suitability, predation risk, and optimal foraging theory seem promising (Railsback et al. 1999). However, based on my findings I see five complications that, unless they are more thoroughly researched, will continue to cloud our understanding of why stream fishes move.

First, life history information is lacking for many native stream fishes, including ways in which size-based hierarchies affect competition and habitat selection, and how mobility and home range change over species' lifetimes. I could not, for example, determine whether extensive movements made by small *P. roanoka* and *E. podostemone* in my study were due to innate life-history traits of the species or in response to environmental conditions.

Second, model accuracy depends upon good measures of habitat suitability, which may be spatio-temporally variable. Fishes may select habitats based on immediate energetic gain, temporal stability (Gorman and Karr 1978), proximity to complementary or supplementary resources (Ensign 1995; Schlosser and Angermeier 1995), or a combination of these, and the interactions of these features will be complex to model.

Third, the interaction of dispersal attempt and dispersal success probabilities may make it difficult to forecast even the direction of a dispersal response. For example, Gilliam and Fraser (2001) found that predation threat increased the probability of dispersal attempt, but dispersal threat should also decrease the probability of dispersal success. Similarly, although sub-dominance may force an individual out of a source habitat (Fausch and White 1986) and increase its probability of dispersal attempt, the same lack of size or fitness will make that individual less capable of dispersal (Adams et al. 2000) and decrease its probability of dispersal success.

Fourth, scientists must determine the relative values of departure and destination rules in predicting fish movement among habitat patches. Current individual-based models of salmonid movement focus on the interplay of departure and destination rules in determining habitat patch selection (Clark and Rose 1997; Van Winkle et al. 1998; Railsback et al. 1999). In other words, such models require knowledge of the quality of departure and destination habitats to predict habitat choice, and thus potentially require a substantial amount of field data. Based on empirical observations of emigration and immigration rates, Belanger and Rodriguez (2002) argued that destination rules more accurately predict habitat selection for highly mobile brook charr *Salvelinus fontinalis*. Based on this logic, I assume that the inverse should be true and that departure rules should more accurately predict habitat selection for sedentary species. The crux of this argument is that fishes are capable of deciding only among the habitats that are known to them, and that the more mobile an individual is, the greater an area it will be able to assess quickly and accurately (Railsback et al. 1999). To my knowledge, no one has compared the relationship between mobility and the predictive power of departure versus destination rules across taxa. Knowing the more valuable set of rules could reduce field data collection and increase the accuracy of dispersal models, but will require a better understanding of the relative mobility of non-salmonid stream fishes.

Finally, because of the leptokurtic shape of many stream fish movement distributions (Gowan and Fausch 1996a; Skalski and Gilliam 2000), modelers must deal with two components of a stream fish population (mobile versus sedentary) that may respond differently to environmental conditions. Skalski and Gilliam (2000) derived two formulas to predict movement distances for individual bluehead chubs, one for “fast fish” and one for “slow fish”, that when combined produced the population-level leptokurtosis in movement distances that the authors observed during empirical studies. The authors did not include the influences of outside factors (e.g., size, growth, predation hazard) in the model, but indicated that incorporation of such features would make dispersal models robust over longer time scales. Related to the third complication above, factors that influence dispersal success intuitively should be similar across mobile and sedentary components but factors that influence dispersal attempt may not be. This will be particularly prevalent if the distinction between the two components is sharp; the mobile group may attempt to move regardless of ecological conditions, whereas the sedentary group may *not* attempt to move regardless of conditions. In such a situation, instream features (i.e., departure and destination rules) will be poor predictors of dispersal, and dispersal patterns may be difficult to forecast.

MANAGEMENT IMPLICATIONS

A note should be made regarding the mobility of darters in my study. A number of investigators have indicated that small-bodied stream fishes exhibit small home ranges (Hill and Grossman 1987; Mundahl and Ingersoll 1989; Goforth and Foltz 1998; Smithson and Johnston 1999; Johnston 2000). Gowan et al. (1994) were the first to systematically expose the biases inherent in many mark/recapture movement studies that result in higher capture probabilities of non-movers than of movers. Gowan and Fausch (1996a) and Skalski and Gilliam (2000), examining brook trout and chubs, respectively, found that when study design biases were corrected, fishes did indeed regularly range beyond the limits of typical study areas. Despite these advancements, the extensive sampling required to generate accurate movement distance distributions is an ongoing impediment to conducting rigorous movement studies of other taxa.

Published mark/recapture movement studies of darters are few, and my study was not designed to calculate the spatial extent of darter movement. The movement distances that I recorded (40-595m) were similar to those recorded by Freeman (1995) for blackbanded darters (43-420m). The over-summer dispersal rates of the three darters examined in my study, 3-8%, are indicative of sedentary species. However, my finding of a 34% inter-annual dispersal rate reveals that mobility is defined by the temporal scale of interest. Seasonal (i.e., over-summer) dispersal was a useful time-step for examining the influence of instream features on individual dispersal. For a manager interested in critical habitat designation or remediation, however, dispersal over an annual time-step may be more relevant. If so, it seems that small-scale (i.e., tens of meters) management activities designed to benefit "local" populations would be inconsequential to species such as the darters in this study, as protected or enhanced areas may represent a trivial portion of the exploitable range of the species (i.e., hundreds of meters; Gowan and Fausch 1996b). Because home range is often a positive function of time frame (Freeman 1995; Johnston 2000), managers should define a relevant temporal scale of interest before attempting to determine the spatial range of a population. Moreover, for management activities to benefit stream fish populations, accessibility of protected or enhanced areas to outlying individuals must be ensured (Gowan and Fausch 1996b).

The goal of this study was to determine the instream features that induce or impede fish dispersal. Such information could be incorporated into models that predict fish responses to instream changes, such as population viability analyses (Boyce 1992), instream flow incremental methodologies (Bovee 1982), and indexes of biotic integrity (Karr et al. 1986). Although darters were selected as the focal taxonomic group because of their habitat-use characteristics, the information obtained in this study should be more broadly applicable to the management of stream channels for entire assemblages of fishes. Going even one step further, because fish dispersal patterns affect the population dynamics of other organisms (e.g., unionid mussels; Neves et al. 1997), management of streams for dispersal permeability takes on ecosystem-level importance.

I determined that reduction in summer stream flow elevated dispersal by concentrating competing individuals into shrinking habitat units and forcing them to seek alternative habitats. Inflated dispersal can be viewed in a negative light, because it is physiologically demanding and increases an individual's vulnerability to stress and predation. Over-summer channel dewatering is a natural process, but is exacerbated by a number of anthropogenic activities. Water withdrawals and increases in impervious surfaces within a watershed both act to decrease groundwater levels and stream base-flow, particularly during the summer (Poff et al. 1997), a critical time period for the growth and survival of stream fishes (Cunjak et al. 1988; Ensign 1990). However, these patterns may be less crucial to other species that do not congregate on riffles during the summer and fall, or to darters during other seasons in which deeper habitats are occupied. Future research efforts should seek connections between stream flow and dispersal patterns for a variety of fish guilds (e.g., benthic riffle-dwellers, pool cover dwellers, open-water swimmers; Vadas and Orth 2000) over a range of hydrologic conditions and during different times of the year (e.g., during spawning or over-wintering).

I also found that dispersal was aided by the proximity of suitable habitat units and by the presence of instream cover. Channelization, sediment inputs, riparian deforestation, and snag removal all act to homogenize stream reaches, increasing the distance between habitat units and decreasing the cover complexity of the stream channel (Frissell et al. 1986). These actions may thereby reduce the probability of successful dispersal between suitable habitat patches. The importance of habitat spacing should be greater in large than in small streams, because natural geomorphic processes related to channel gradient and form tend to produce greater distances between channel units (e.g., riffles) in larger streams (Frissell et al. 1986). Anthropogenic disturbances may also decrease habitat diversity and stability. Whereas headwaters are temporally unstable environments with fish assemblages that are likely adapted to this instability (Horwitz 1978; Grossman et al. 1998), mainstem assemblages have not historically been subjected to as much environmental instability, and probably are not as well adapted to it. In larger streams fishes may thus have a more difficult time redistributing among distant habitats following habitat-restructuring events (e.g., flash floods, hydroelectric discharges, channelizations).

Many anthropogenic modifications to the landscape seem to increase the necessity, while increasing the difficulty, of dispersal. By increasing the difficulty of dispersal, human activities may actually enhance the evolutionary fitness of sedentary species or sedentary members of populations, because of such fishes' "safe" lifestyle. If the riskier strategy of dispersal is selected against, even greater insularization of local populations may be expected.

I must caution against extrapolating my findings beyond the temporal scale of my study. During other seasons and during higher-flow periods dispersal may be governed by an entirely different set of factors, or it may be much less restricted. However, because summer is a critical, potentially limiting season for fishes, it was an instructive time to observe the importance of preserving natural aspects of the stream (e.g., stream flows, riparian inputs, channel complexity). To maintain population connectivity and resource accessibility for stream fishes, managers should strive to maintain adequate stream flow and preserve or enhance the complexity of instream habitat.

Table 2.1 – Abundance and density per corridor of predators used to calculate corridor predator density, averaged across corridors. Number of individuals is abbreviated “ind”.

	Average Abundance (ind)		Average Density (ind/ha)	
Species	2001	2002	2001	2002
O. mykiss	0	1	5	4
M. dolomieu	4	4	50	32
M. salmoides	0	0	1	0
A. rupestris	8	13	94	88
L. auritus	8	5	58	30
Predator total	20	19	207	129

Table 2.2 – Ranges for classes of continuous and categorical habitat variables used to calculate habitat complexity indices.

Habitat variable	Class 1	Class 2	Class 3	Class 4	Class 5
Dominant substrate	silt	sand	gravel	cobble/boulder	bedrock
Depth (cm)	>25	10-25	<10		
Velocity (cm/s)	>25	10-25	1-9	0	
Silt embeddedness (%)	<25	25-50	>50		

Table 2.3 – Numbers of individuals marked during summer 2001 and recaptured during summer 2002. Corrected figures exclude recaptures from riffles that were not sampled during 2001 recapture events, in order to standardize recapture effort between the two years.

Species	Number Recaptured	Number Dispersed	% Dispersed Recaptures	Corrected Number Recaptured	Corrected Number Dispersed	Corrected % Dispersed Recaptures
P. roanoka	6	0	0%	6	0	0%
E. podostemone	4	2	50%	3	1	33%
E. flabellare	30	13	43%	29	12	41%
Total	40	15	38%	38	13	34%

Table 2.4 – Summary of combined results from marking and recapture of *Percina roanoka*, *Etheostoma podostemone*, and *E. flabellare* during the summers of 2001 and 2002 in the upper Roanoke River watershed. Numbers dispersed are the numbers of fish that moved from, not to, the associated source riffle.

Site name (number)	Riffle	Number marked		Number recaptured (% of marked)		Number dispersed (% of recaptured)	
		2001	2002	2001	2002	2001	2002
Sowder	SO1	-	649	-	140 (22)	-	8 (6)
Hollow (1)	SO2	423	657	61 (14)	65 (10)	0 (0)	10 (15)
	SO3	431	386	35 (8)	65 (17)	12 (34)	11 (17)
	SO4	283	411	29 (10)	67 (16)	0 (0)	3 (4)
	SO5	432	792	32 (7)	127 (16)	0 (0)	11 (9)
	SO6	-	645	-	153 (24)	-	5 (3)
Wickham	WI1	-	276	-	38 (14)	-	1 (3)
Farm (2)	WI2	-	311	-	60 (19)	-	6 (10)
	WI3	380	813	51 (13)	118 (15)	1 (2)	7 (6)
	WI4	216	551	35 (16)	95 (17)	1 (3)	3 (3)
	WI5	91	300	7 (8)	27 (9)	1 (14)	4 (15)
Bower	BO1	163	-	51 (31)	-	0 (0)	-
Farm (3)	BO2	308	-	58 (19)	-	3 (5)	-
	BO3	128	-	20 (16)	-	0 (0)	-
Sutphin	SU1	241	-	35 (15)	-	0 (0)	-
Farm (4)	SU2	75	-	13 (17)	-	2 (15)	-
	SU3	125	-	18 (14)	-	0 (0)	-
	SU4	78	-	4 (5)	-	0 (0)	-
	SU5	45	-	5 (11)	-	0 (0)	-
Bottom	BT1	39	-	5 (13)	-	2 (40)	-
Creek (5)	BT2	45	-	5 (11)	-	0 (0)	-
	BT3	234	-	32 (14)	-	2 (6)	-
	BT4	238	-	28 (12)	-	0 (0)	-
Sisson	SI1	97	-	5 (5)	-	1 (20)	-
Farm (6)	SI2	46	-	2 (4)	-	0 (0)	-
	SI3	93	-	12 (13)	-	2 (17)	-
	SI4	130	-	23 (18)	-	1 (4)	-
	SI5	234	-	23 (10)	-	0 (0)	-
	Total	4,575	5,791	589 (13)	955 (16)	28 (5)	69 (7)

Table 2.5 – Summary of results, by species, for marking and recapture of *Percina roanoka*, *Etheostoma podostemone*, and *E. flabellare* during the summers of 2001 and 2002 in the upper Roanoke River watershed.

	Number marked		Number recaptured (% of marked)		Number dispersed (% of recaptured)	
Species	2001	2002	2001	2002	2001	2002
P. roanoka	504	359	124 (25)	108 (30)	4 (3)	9 (8)
E. podostemone	512	292	101 (20)	58 (20)	6 (6)	4 (7)
E. flabellare	3,559	5,140	364 (10)	789 (15)	18 (5)	56 (7)
Total	4,575	5,791	589 (13)	955 (16)	28 (5)	69 (7)

Table 2.6 – Summary of potential ecological correlates measured during the summers of 2001 and 2002 in the upper Roanoke River watershed. Abbreviations include habitat complexity index (HCI) and numbers of individuals (ind).

Site name		HCI		Mean corridor length (m)		Mean predator density (ind/ha)		Riffle area flux (%)		Riffle darter density	
(number)	Riffle	2001	2002	2001	2002	2001	2002	2001	2002	2001	2002
Sowder	SO1	-	1.0	-	117	-	139.4	-	18	-	1.29
Hollow (1)	SO2	1.1	1.1	93	101	285.3	98.1	[a]	14	0.80	1.82
	SO3	0.9	1.1	72	77	307.6	184.9	-49	10	1.16	2.13
	SO4	1.1	1.1	62	60	279.6	211.9	-6	18	1.13	1.39
	SO5	1.2	1.1	74	59	229.4	184.2	-3	-7	1.02	1.83
	SO6	-	1.0	-	47	-	216.1	-	-3	-	0.88
Wickham	WI1	-	1.0	-	38	-	43.9	-	1	-	1.11
Farm (2)	WI2	-	1.2	-	106	-	83.7	-	-4	-	1.34
	WI3	1.0	1.1	74	117	31.6	73.6	0	2	0.52	1.04
	WI4	0.9	1.0	109	109	57.7	37.0	-6	3	0.44	1.34
	WI5	1.1	1.2	144	102	83.8	77.4	-13	-1	0.09	0.43
Bower	BO1	0.5	-	244	-	85.8	-	-13	-	0.26	-
Farm (3)	BO2	0.4	-	176	-	72.9	-	-23	-	0.18	-
	BO3	0.5	-	109	-	60.0	-	-1	-	0.39	-
Sutphin	SU1	0.7	-	71	-	121.7	-	-1	-	1.05	-
Farm (4)	SU2	0.5	-	46	-	120.8	-	3	-	0.68	-
	SU3	0.4	-	22	-	218.1	-	-5	-	1.17	-
	SU4	0.6	-	37	-	403.8	-	0	-	0.55	-
	SU5	0.4	-	52	-	491.3	-	-1	-	0.76	-
Bottom	BT1	1.1	-	14	-	207.1	-	-16	-	0.16	-
Creek (5)	BT2	1.2	-	34	-	230.4	-	1	-	0.14	-
	BT3	1.2	-	49	-	234.2	-	-16	-	0.41	-
	BT4	1.0	-	43	-	214.8	-	-14	-	0.38	-
Sisson	SI1	0.5	-	117	-	133.8	-	-4	-	0.14	-
Farm (6)	SI2	0.6	-	80	-	143.3	-	-11	-	0.12	-
	SI3	0.6	-	28	-	103.9	-	-6	-	0.38	-
	SI4	0.8	-	26	-	88.6	-	-1	-	0.62	-
	SI5	0.6	-	38	-	122.4	-	-4	-	0.58	-

[a] Riffle area flux was unobtainable for riffle SO2 during 2001 because it was impounded between habitat samples by a beaver dam.

Table 2.7 – Summary of optimum logistic regression models to estimate the probability of individual *Etheostoma flabellare* dispersal from source riffles in the upper Roanoke River watershed during the summers of 2001 and 2002. Parameter estimates are maximum likelihood estimates (SAS 2000), and model and variable significance is based on maximum likelihood chi-square (Stokes et al. 2000). The threshold probability level for variable retention was 0.1. Abbreviations include Akaike's information criterion (AIC), numbers of individuals (ind), mean corridor length (MCL), mean predator density (MPD), riffle area flux (RAF), and riffle darter density (RDD).

Variable	Parameter estimate	Standard error	Chi-square statistic	df	Probability
2001 model (χ^2 = 32.95, df = 4, p < 0.0001, R^2 = 0.28, AIC = 114.45)					
Intercept	0.6384	1.7171	0.14	1	0.7101
MCL (m)	-0.0310	0.0126	9.98	1	0.0016
MPD (ind/ha)	-0.0134	0.0091	2.91	1	0.0882
RAF (%)	-15.5206	5.3576	26.55	1	<0.0001
RDD (ind/ha)	-0.0002	0.0001	3.51	1	0.0611
2002 model (χ^2 = 20.71, df = 2, p < 0.0001, R^2 = 0.07, AIC = 357.93)					
Intercept	-6.2485	1.0478	35.56	1	<0.0001
MCL (m)	0.0112	0.0065	3.20	1	0.0738
RDD (ind/ha)	0.0002	<0.0001	19.77	1	<0.0001

Table 2.8 – Classification tables for logistic regression models to estimate the probability of individual *Etheostoma flabellare* dispersal from source riffles in the upper Roanoke River watershed. Classifications are based on a critical value of 0.06, the overall proportion of dispersers (Hosmer and Lemeshow 1989).

Model and observation	Number observed	Number predicted		Correct
		Dispersers	Non-dispersers	
Summer 2001 mark/recapture dataset				
2001				
Dispersers	18	10	8	56%
Non-dispersers	292	88	204	70%
Total	310	98	212	69%
Summer 2002 mark/recapture dataset				
2001				
Dispersers	50	0	50	0%
Non-dispersers	739	0	739	100%
Total	789	0	789	94%
2002				
Dispersers	50	38	12	76%
Non-dispersers	739	427	312	42%
Total	789	465	324	44%

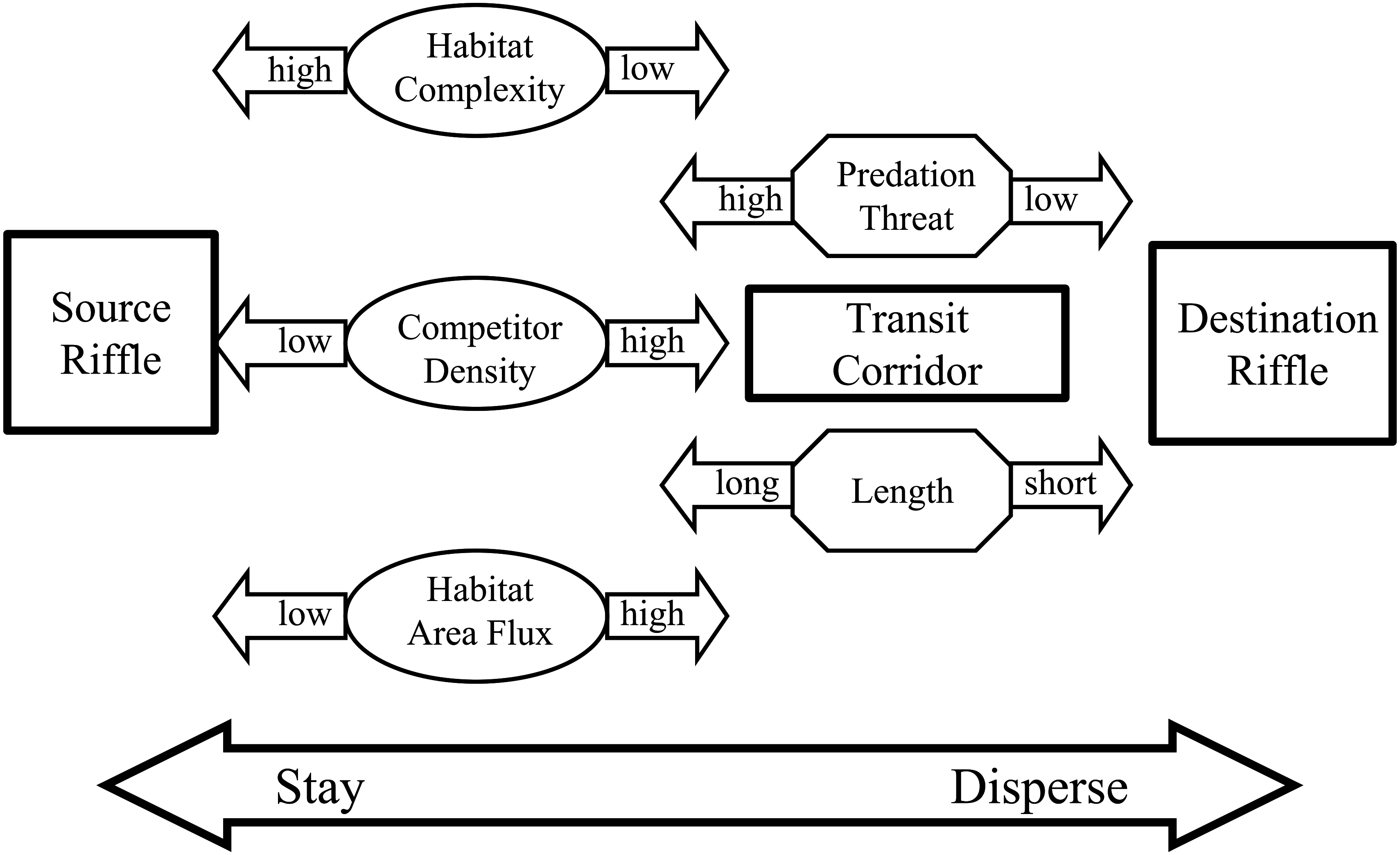

Figure 2.1 – A conceptual representation of the array of ecological factors potentially influencing an individual's decision to stay in a source riffle or to disperse to an adjacent destination riffle. Before and during dispersal, individuals encounter numerous source riffle attributes (ovals) and transit corridor attributes (octagons) that either encourage (right-pointing arrows) or discourage (left-pointing arrows) dispersal. The destination riffle in this sequence then becomes the source riffle in the next sequence, and the decision process is repeated.

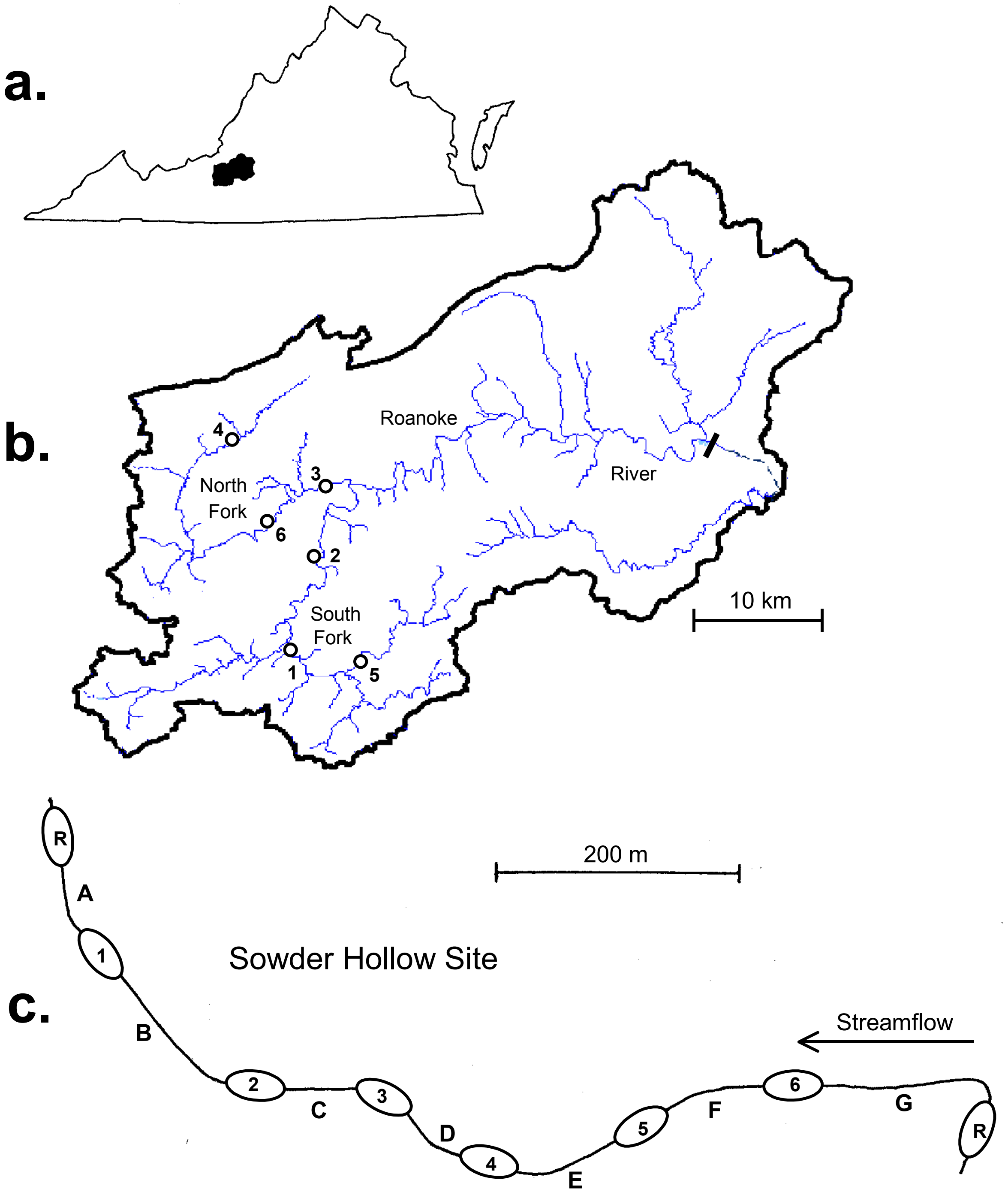

Figure 2.2 – **a.** Location of the upper Roanoke River watershed (shaded) in Virginia, USA. **b.** The upper Roanoke River watershed, with mark/recapture sites delineated by numbered circles. Niagara dam is indicated by a black bar. **c.** An example mark/recapture site, Sowder Hollow (site number 1), with mark/recapture riffles indicated by numbered ovals, and recapture-only riffles indicated by ovals labeled "R". Corridors are indicated by capital letters. Site length is to scale, but riffle and corridor lengths are not.

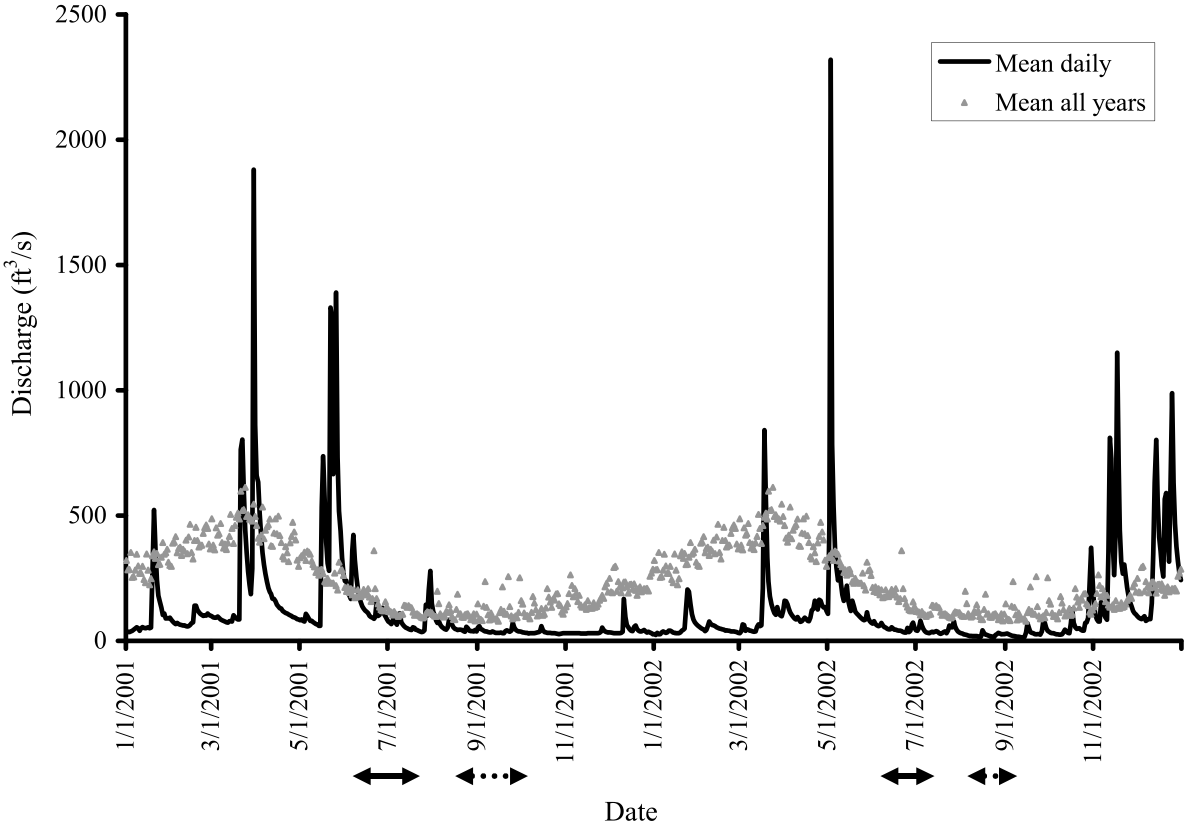

Figure 2.3. – Hydrograph from the Lafayette gauging station at the confluence of the north and south forks of the Roanoke River (USGS #02054500) during the period from 1 January 2001 to 31 December 2002. The plotted line indicates mean daily streamflow and triangles indicate the mean streamflow over 58 years of record for each day. Solid and dashed arrows indicate timing of marking and recapture periods, respectively.

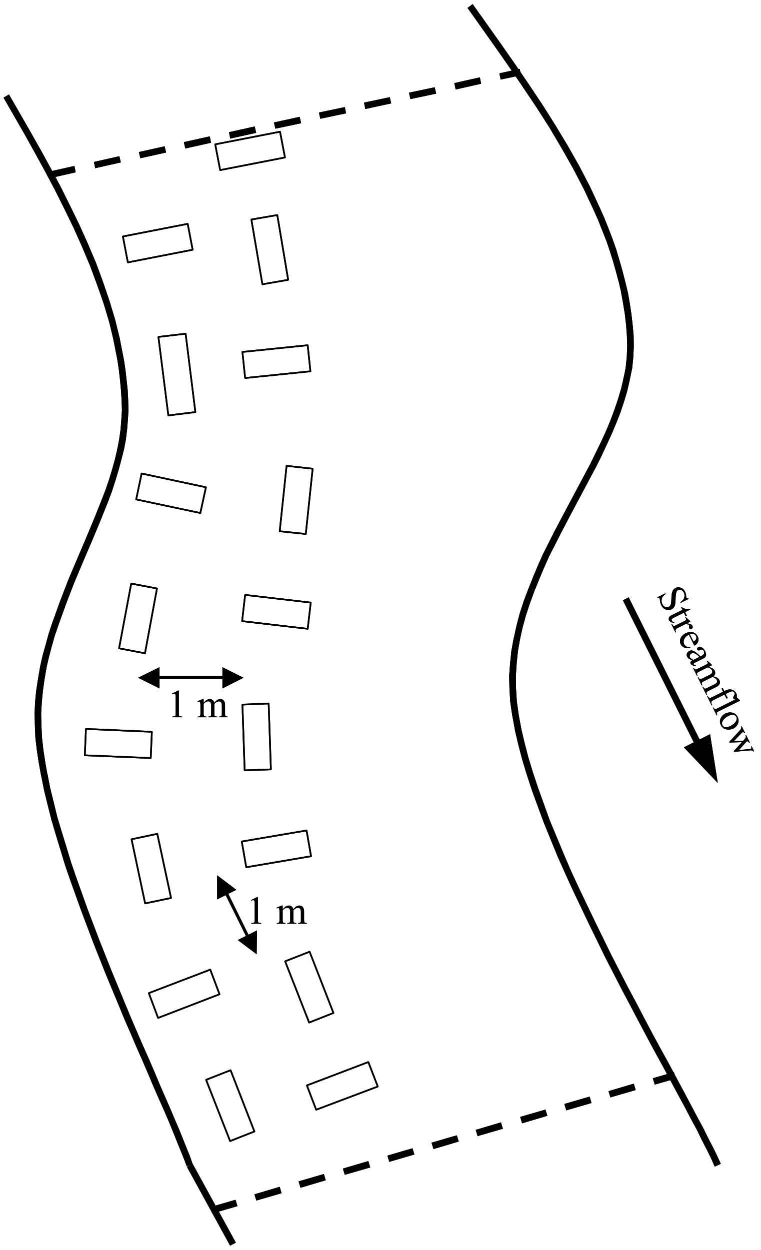

Figure 2.4 – Diagram showing the arrangement of blocks for Objective 3, in a hypothetical corridor. Blocks are indicated by rectangles, and dashed lines indicate the upstream and downstream boundaries of the corridor. Blocks were always oriented with openings parallel to the plane of the streambed, but longitudinal orientation was alternated as shown. Block and stream sizes are not to scale.

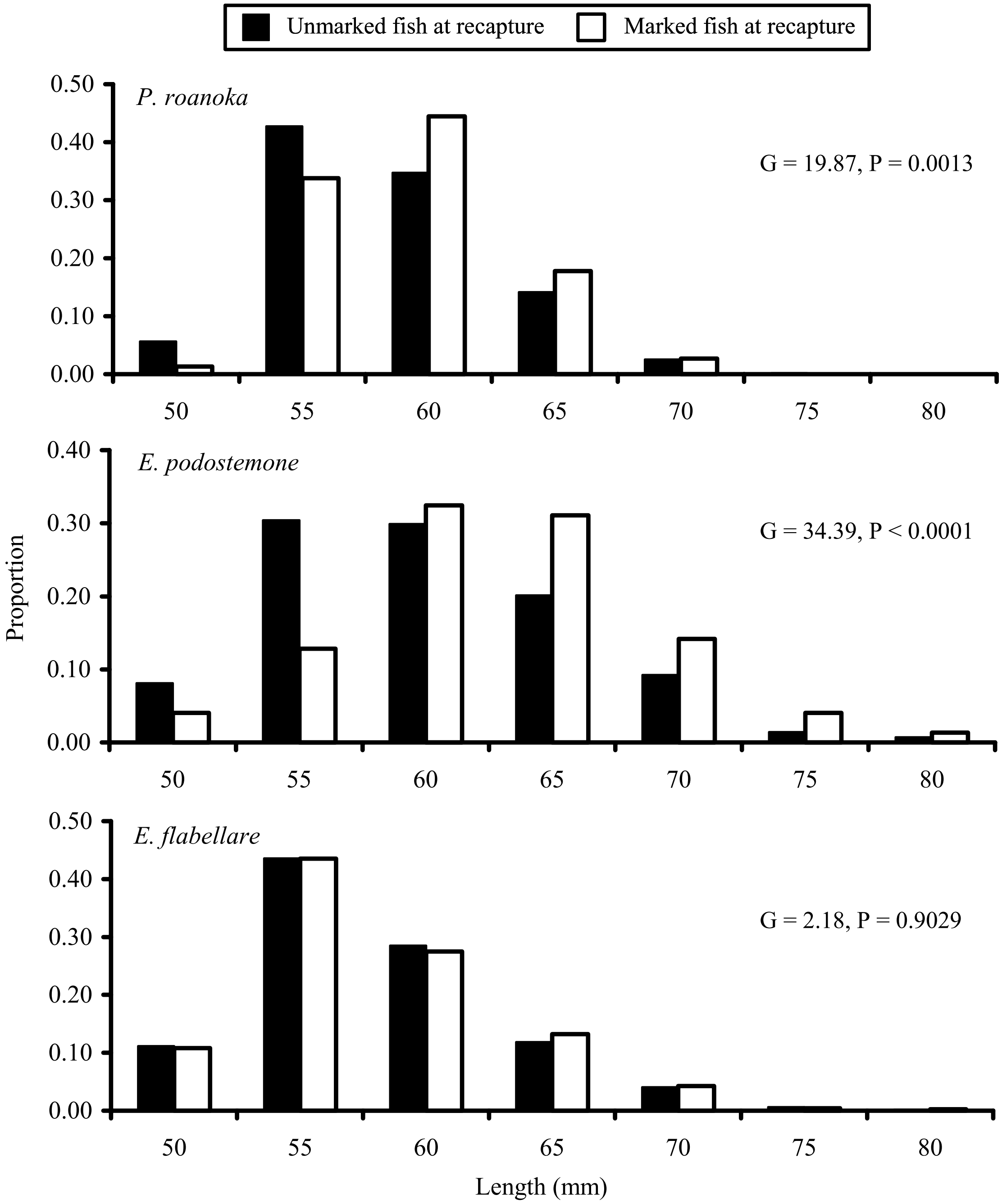

Figure 2.5 – Frequency histograms of the proportions of *Percina roanoka* (top panel), *Etheostoma podostemone* (middle panel), and *E. flabellare* (bottom panel) of each length class captured during recapture events with and without marks, for 2001 and 2002 combined. To account for potential growth between marking and recapture, only individuals >49mm are included. Results of G-tests for homogeneity of distributions are shown. Significance indicates a length bias of marked recaptures relative to the population at-large.

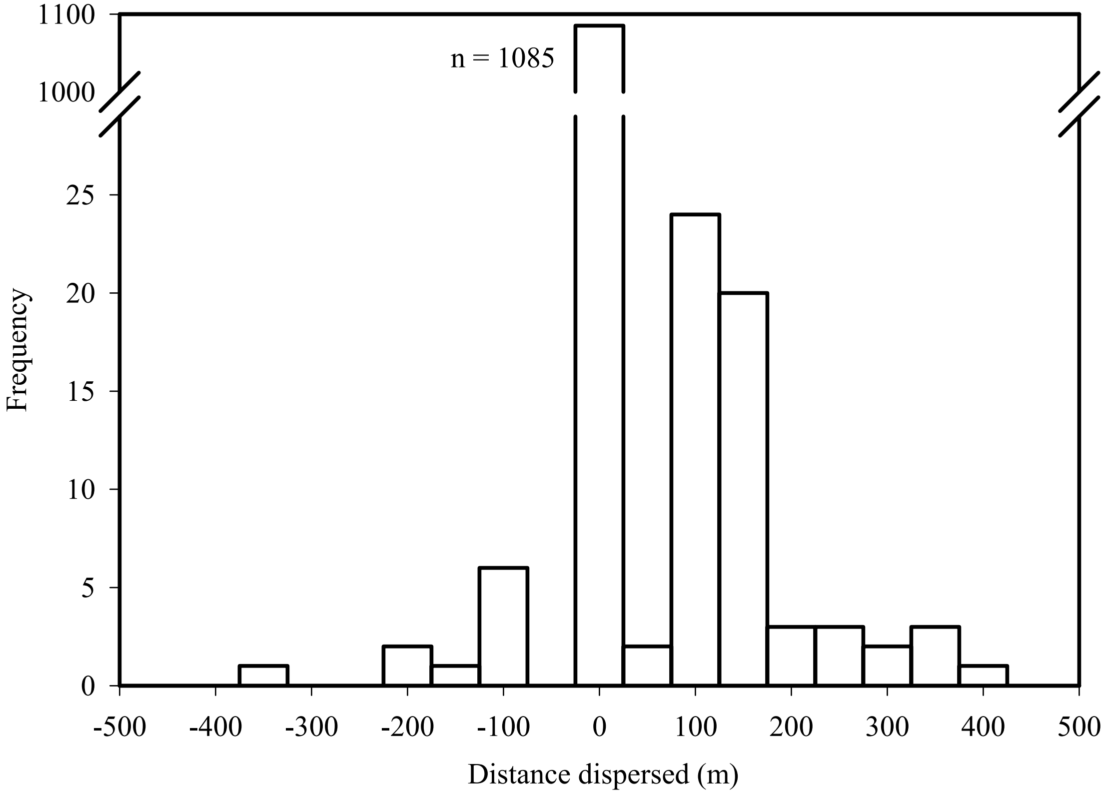

Figure 2.6 – Frequency of distances dispersed by recaptured *Etheostoma flabellare* individuals, for 2001 and 2002 combined. Note the break in the Y-axis. Upstream and downstream movement distances are arbitrarily coded as positive and negative, respectively.

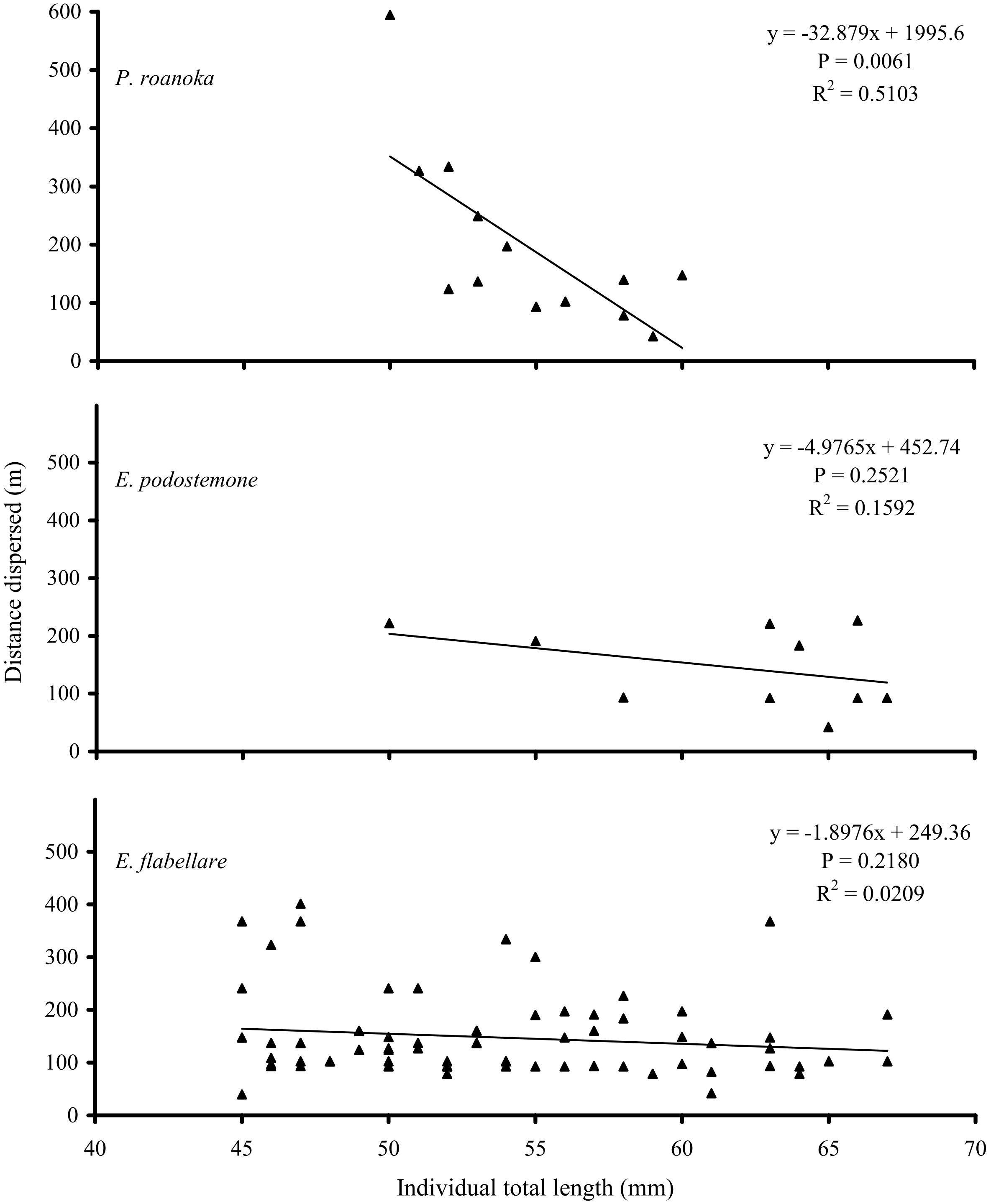

Figure 2.7 – Relationship between total length and distance dispersed for all recaptured *Percina roanoka* (top panel), *Etheostoma podostemone* (middle panel), and *E. flabellare* (bottom panel) individuals that dispersed, for 2001 and 2002 combined.

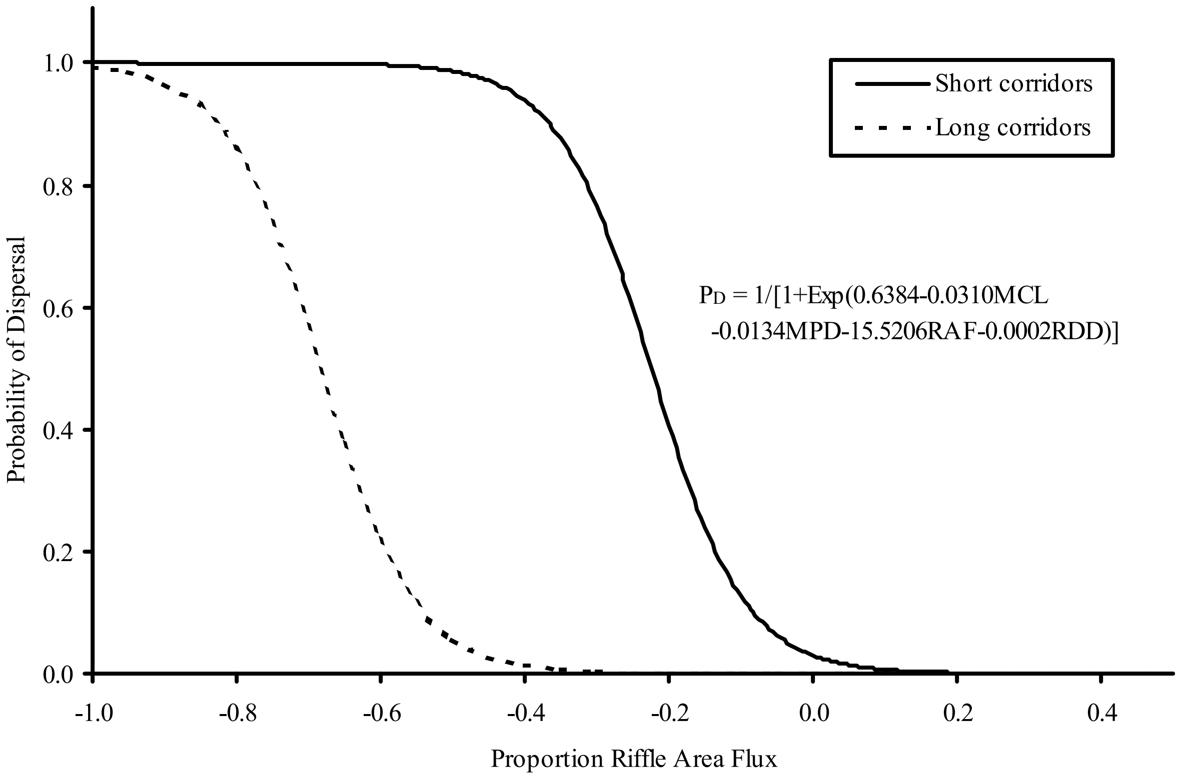

Figure 2.8 – Logistic regression curves for the probability of individual *Etheostoma flabellare* dispersal as a function of riffle area flux (RAF) at two levels of mean corridor length (MCL), for summer 2001. “Short corridors” represents the relationship when MCL is held constant in the model at its minimum value recorded during 2001, whereas “long corridors” represents the relationship when MCL is held constant at the maximum value recorded. Other parameters in the model (MPD and RDD) were held constant at their mean recorded values.

GENERAL CONCLUSIONS

I undertook this Thesis to answer a general question that intrigued me and that might provide us with other answers relevant to stream fish ecology, “Why do fishes move?” Of course, fishes cannot simply move wherever they want through the streamscape, so a related question emerged, “What constrains fish movement?” I reasoned that the balance between those forces inducing dispersal and those acting to impede it creates heterogeneous mobility and home ranges across various spatial and temporal scales. Darters seemed good candidates for testing my theory, because in the upper Roanoke they could be relegated to discrete suitable habitats (riffles) between which movement through unsuitable habitats (corridors) was required, and because I suspected them to exhibit constrained movement. I painstakingly attempted to document the patterns of dispersal exhibited by these fishes and to relate these to an intuitively derived list of ecological features that they experienced during dispersal.

First, the bad news. I was plagued by low recapture rates, as is often the case during mark/recapture studies of stream fishes. Although site-specific recapture rates ranged as high as 31%, on the whole 85% of marked individuals were never seen again. With sampling efficiency factored out, I was forced to attribute the remaining 60% of lost fishes to mortality or emigration from the study site. Mortality rates for darters living 3+ years are unknown, but evidence from Labbe and Fausch (2000) indicates that summer darter mortality may be high. Furthermore, although turnover rates were not explored in great detail, they seemed suspiciously high, particularly for small individuals, and they increased over time. Although I documented over-summer mobility in only 6% of recaptured individuals, inter-annual dispersal rate was 34%. The notion that the mobility of small-bodied stream fishes is limited (e.g., Hill and Grossman 1987a) remains a tenuous position that may be debunked some day by a study incorporating all of the proper design attributes (Gowan and Fausch 1996a).

Another weakness of my study was the low predictive power of my dispersal models. Even the best model, that for fantail darters in summer 2001, explained only 28% of the variance in dispersal probability. Additional potentially influential factors that I failed to account for included food variability and corridor morphometry, but developing suitability metrics to account for these variables for the three species of interest would have been a thesis in itself. The underwater world, as it is perceived by the fish, is so complex that modeling its influence on movement choices is as yet an imperfect science. I suspect that the timing and duration of flow events may regulate much of stream fish dispersal patterns (Schlosser 1995), but the difficulty of fish sampling instream during high flows makes this position hard to test. Additionally, an unknown but potentially great proportion of dispersal variability may be due to chance. Despite their impracticality, I believe that future studies of stream fish movement should incorporate weirs, because these devices enable researchers to correlate movement rates with hydraulic conditions, and allow the calculation of site escapement rates. Better yet, perhaps someday we will have very small radio transmitters suitable for use in small-bodied fishes, that will give real-time estimates of fish position, shrink the spatial grain of mobility measurement, and allow for the detection of complex and long-distance movements.

The good news is that I did determine several instream features that played a significant role in fantail darters' probability of dispersal. Fishes were prone to leave riffles that dewatered during summer drought, and also emigrated when competitor density became high. Presumably, individuals gauged that competition for resources was becoming too great, and sought greener pastures in adjacent riffle areas. This decision to leave seemed to be weighed against the distance to the next riffle, however, because corridor length was negatively related to dispersal probability. However, it was difficult to separate recognition of risk from failed attempts at dispersal in my analyses. The observed ranges and modeled effects of most variables were inconsistent over time, and only at the extreme ends of their ranges did most variables produce measurable variability in dispersal.

Interestingly, individual size did not predict dispersal for fantail darters, and size did not relate to distance traveled by dispersers of the species. Though low sample size kept me from modeling dispersal probability for Roanoke and riverweed darters, size was negatively related to distance traveled for those two species. Alternative life-history explanations for small fish moving farther include 1) the majority of species dispersal is accomplished by young individuals, and 2) small individuals were forced out of optimal riffle habitats and had to roam extensively to find other suitable, unoccupied habitats. These possibilities are untested for darters, but were supported by observed high turnover rates for small individuals and high recapture rates for large individuals of those two species. Other than studies of larval drift, dispersal over ontogeny is an untouched topic for most stream fishes, and may give clues to the mechanisms of habitat selection and population regulation.

Because corridor length seemed to dictate dispersal probability, a logical experiment followed that attempted to shorten the length of corridors, as perceived by the fish, and cause dispersal rates through shortened corridors to increase. Introduction of overhead cover via concrete block addition did seem to aid the transit of fantail darters moving downstream, but not those moving upstream, although sample sizes were very low. Logistical constraints dictated the number of blocks added to the stream, and it is possible that with the addition of enough blocks, upstream dispersal would have noticeably increased.

The final aspect of my thesis was a laboratory experiment to determine the influence of injected marks on darter survival rates, and the influences of mark type, location, and color on mark retention rates. Neither VIE nor IPD had been rigorously tested and contrasted in darters. Evidence from my study supported my expectations; VIE performed well in darters, with high survival and mark retention rates. Although IPD performed fairly well in the short-term, over the long-term Roanoke darters marked with IPD exhibited elevated mortality and decreased mark retention. This may have been due to the somewhat unnatural behavior of Roanoke darters in my experimental tank. Also, some strange type x location and type x color interactions emerged that were difficult to explain but serve as warnings that retention may not be consistent across body locations or across batches of marking material. My results affirm what scientists should already suspect, that pilot marking studies are required prior to using marks in the field.

Though the topics presented in the two chapters of this Thesis seem disparate, when combined they do offer a suite of new findings on a relatively understudied group, the darters. I have established guidelines for marking darters, and given suggestions for the best ways to document the movements of darters and other stream fishes in the field. I have supported by empirical data four theoretically-supported ecological features that guide dispersal rates, habitat loss, habitat spacing, competitor density, and structural complexity, and done so for the first time in a multivariate analysis. These features may be expected to operate over small spatio-temporal scales, such as those found in my study. To give a more complete picture of dispersal, particularly as it relates to populations instead of individuals, larger-scale population structure and dynamics analyses should be undertaken that engage the disciplines of biology, behavioral ecology, landscape ecology, and population genetics.

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VITA

James Henry Roberts III was born on Groundhog's Day in 1978 in Athens, Georgia. His loving parents were and are Jim and Dale Roberts. Most of his formative years were spent alternately making jokes, picking on his little brother Justin, and being a Georgia Bulldog.

During his freshman year at UGA, he began dating Tonja Bolin, and soon thereafter decided that he wanted to marry her. She agreed to this. In July of 1997, Jamie and Tonja brought a baby girl into the world, Holly Rebecca Roberts. Back at school, Jamie decided that he wanted to work in the outdoors and transferred into the Fisheries and Aquaculture program. He had two notable mentors there: Dr. Bob Reinert taught him that professors can be down-to-earth, kind-hearted people, and Dr. Gary Grossman hired Jamie to work at the Coweeta Hydrologic Lab in Otto, NC, and thus introduced him to the fascinating world of native stream fishes. Bob Ratajczak helped Jamie maintain relative sanity as he completed his Senior Thesis on dace reproduction.

In 2000 Jamie went to the Department of Fisheries and Wildlife at Virginia Tech for his Master's. Working for his advisor Dr. Paul Angermeier on a stream fish movement project served to deepen Jamie's respect for aquatic biota, and gave him a thirst for doing research. In September of 2002, Jamie and Tonja brought forth another baby girl, Riley Rose Roberts. In October of 2002 Jamie took a job supervising a monitoring project for endangered Roanoke logperch *Percina rex* in the Roanoke River.

Jamie plans to pursue his Doctorate in fisheries science at Virginia Tech, examining the genetic structure of logperch populations in Virginia. He hopes to use this information to more effectively manage the logperch, and to enhance our understanding of stream fish population structure and dynamics.